PHYSIOLOGICAL PROCESSES ASSOCIATED WITH GENETIC PROGRESS IN YIELD POTENTIAL OF WHEAT (*Triticum aestivum* L.)

BY

KHALED A BOULGASEM AISAWI

B. Sc. Agricultural Sciences
M. Sc. Crop Sciences

Thesis submitted to the University of Nottingham for the degree of Doctor of Philosophy

University of Nottingham

School of Biosciences

Sutton Bonington Campus

Leicestershire, LE12 5RD

December 2011

DEDICATION

This PhD thesis is dedicated to my wife (Amal), my daughter (Maha), and my sons (Muhammad-Boulgasem) and (Alhasan).

ACKNOWLEDGEMENTS

I would like to express my sincere thanks and gratitude to my supervisors, Dr John Foulkes, Prof Matthew Reynolds and Dr Sean Mayes for their guidance and support throughout this study.

My deepest appreciation also goes to Dr Erik Murchie for the voluble knowledge obtained from his courses.

Many thanks go to Araceli Torres, Eugenio Perez, Israel Peraza and other person who were involved in the field experiments in Cd. Obregon, Mexico, and to John Alcock, Matthew Tovey for the help in setting up the experiments in the field experiments in the experimental station in Sutton Bonington Campus, University of Nottingham.

Special thanks to Jayalath De Silva, Julian Pietragalla, Brianne Apodaca, Marta Da Silva, Jim Craigon, Sue Golds, Emma Hooley and Fiona Wilkinson for their support and help.

My profound gratitude to Abraham Valdez Lopez and his wife Malena and their family for the hospitality during the field experiments in Mexico.

This work has been made possible by funding from the Libyan government and CIMMYT.

Last but not least, I would like to thank my wife (Amal), my father, mother, brothers and sisters for their love, encouragement and support.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPRIVIATIONS

United Nation	UN
Carbon dioxide	CO_2
Centro Internacional de Mejoramiento de Maiez Y Trigo	CIMMYT
International Center for Agricultural Research in the Dry Areas	ICARDA
Tons per hectare	$t\ ha^{-1}$
Kilogram per hectare per year	$kg\ ha^{-1}\ yr^{-1}$
Mega hectare	M ha
Megaton	M t
Squared metre	m^{-2}
Canopy temperature depression	CTD
Normalized Difference Vegetation Index	NDVI
Radiation use efficiency	RUE
Harvest index	HI
Canopy temperature	CT
Degrees Celsius	°C
Northwest	NW
Tiller inhibition gene	Tin gene
Doubled haploid	DH
Near-isogenic lines	NILs
Dry matter	DM
Above ground dry matter	AGDM
Growth stage Onset stem extension	GS
First generation	F_1
2,4-dichlorophenoxy acetic acid	2, 4-D
Micromole per square metre per second	$\mu mol\ m^{-2}\ s^{-1}$
Photosynthetically active radiation	PAR
Milligram per litre	mg/l
Radiation interception	RI
Ear partitioning index at anthesis	EPI
Ear fertility index	EFI

Green area index	GAI
Crop growth rate	CGR
photosynthetically active radiation above the canopy	I_0
PAR below the *i* layer of leaves	I*i*
Green area index	L
Extinction coefficient of the canopy	*k*
Gram per square metre per day	$g\ m^{-2}\ d^{-1}$
Net photosynthetic rate	A_n
Net assimilation rate	NAR
Ribulose 1-5 bisphosphate	RuBP
Water soluble carbohydrate	WSC
Milligram per Degree Celsius	$mg\ °C^{-1}$
Mega gram per hectare	$Mg\ ha^{-1}$
Centimetre	cm
Kilogram nitrogen per hectare	$kg\ N\ ha^{-1}$
Millilitre per hectare	$ml\ ha^{-1}$
Litre per hectare	$l\ ha^{-1}$
Fresh weight	FW
Thousand grain weight	TGW
Near infrared	NIR
Air temperature	T_a
Canopy temperature	T_c
Analysis of variance	ANOVA
Least significant differences analysis	LSD
Long term mean	LTM
Mega joule per square metre	$MJ\ m^{-2}$
Millimetre	mm
Probability	*P*
Standard error of differences of means	S.E.D
Coefficient of variation	C.V
Degrees of freedom	d.f
Non significant	n.s
Physiological maturity	PM

Cultivar	cv
Fractional interception of photosynthetically active radiation	$FPAR_{INT}$
Gram per mega joule	$g\ MJ^{-1}$
Microgram per Degrees Celsius per day	$\mu g\ ^{\circ}C\ d^{-1}$
Grain weight	GW
Seed rate	SR
Quantitative trait loci	QTL

ABSTRACT

Wheat (*Triticum* aestivum L.) is the most widely grown of any crop and provides one-fifth of the total calories of the world's population. Since the 1960s, increases in productivity have been achieved as a result of wide-scale adoption of Green Revolution technologies. However, in spite of growing demand, the challenges of increasing production to feed an estimated world population of 9 billion in 2050 are still considerable. Due to the increased demand, it is estimated that food production must be increased by about 50% by the year of 2050. Improving wheat productivity through developing cultivars with high yield potential and with high adaptability to specific environments is the key objective in the wheat breeding programs worldwide to fill the gap between the production and the demand. The overall aims of the present study were to: (i) investigate the physiological basis of yield potential progress from 1966 to 2009 in spring bread wheats released at the International Center for Maize and Wheat Improvement (CIMMYT) in the irrigated high potential environment of NW Mexico, (ii) investigate the physiological basis of effects of the tiller inhibition *Tin1A* gene on ear-fertility traits and yield potential and interactions with plant density in NW Mexico and UK environments in lines of a doubled-haploid (DH) population segregating for *Tin1A/non-Tin1A* alleles and (iii) identify breeding targets for new cultivars with higher yield potential.

Four experiments were conducted in NW Mexico at the CIMMYT research station at Ciudad Obregon. Two of these experiments studied a set of 12 historic CIMMYT spring wheat cultivars released from 1966 to 2009 in 2008/9 and 2009/10. The other two experiments examined selected lines from a doubled-haploid (DH) population derived from a cross between CIMMYT spring wheat L14 and UK winter wheat Rialto contrasting for the presence/absence of the *Tin1A* allele for tiller inhibition and their interaction with seed rate in 2008/9 and 2009/10. In addition, two other field experiments were conducted in the UK, one in 2008/09 at KWS-UK Ltd in Thriplow, Hertfordshire and one in 2009/10 at the University of Nottingham Farm, Sutton Bonington campus, Leicestershire. The plant material for both of these experiments was selected lines from the CIMMYT spring wheat advanced line L14 (+*Tin1A* allele) x UK winter wheat Rialto (-*Tin1A* allele) DH population and the Rialto parent. In the experiment at

Thriplow in 2008/09 the DH lines were examined at one seed rate and in the experiment at Sutton Bonington in 2009/10 at two seed rates.

At the CIMMYT site in 2008/9 and 2009/10, a randomized complete block design was implemented with four replications for the experiments examining the CIMMYT wheat historic releases and a split-plot randomised complete block design with three replications was implemented for the experiments examining the +/- *Tin1A* DH lines, with three seed densities (50, 150 and 450 seeds per square metre); seed rates were randomized on main plots and eight genotypes randomized on sub-plots. At the UK site, in the KWS experiment, 24 DH lines (12 +*Tin1A* allele) and (12 -*Tin1A* allele) from the L14 x Rialto population were used. There was only one seed rate (300 seeds m^{-2}) and a completely randomised design in three replicates was implemented. The same 24 DH lines were examined in the experiment at the SB site, at two seed rates (40 and 320 seeds m^{-2}) in a split-plot randomised complete block design in three replicates. Seed rate was randomized on main plots and DH lines were randomized on sub-plots. In all experiments examining the DH lines of the L14 x Rialto population, lines were selected in pairs so that the two groups of +*Tin1A* and –*Tin1A* lines were approximately balanced for flowering time and plant height, i.e. every +*Tin1A* line has a non-*Tin1A* pair with similar height and flowering date.

Plots were sampled for destructive measurements of dry weight and DM partitioning and ear-fertility traits at four stages in the historic experiments at (GS31, GS39, GS61+7d and at maturity) and at two stages in the DH population experiments (GS61+7d and at maturity). The water soluble carbohydrate (WSC) content of the stems plus attached leaf sheaths was also measured at GS61+7d and at maturity. In the historic experiments, at GS 61+14 days, a degraining treatment was implemented by removing all spikelets from one side of the ear (i.e. ca. 50% of the spikletes) in the historics experiment. Non-destructive measurements were taken for stomatal conductance, canopy temperature, fractional photosynthetically active radiation (PAR) interception and normalized difference vegetative index at various dates both pre- and post-anthesis in the historic experiments.

In the experiments examining the set of 12 historic CIMMYT spring wheat releases, results showed that from 1966 to 2009 the linear rate of genetic gain in

yield potential was 32 kg ha^{-1} yr^{-1} (0.59 % yr^{-1}) (r = 0.76, P = 0.01). Yield progress was primarily associated with harvest index (percentage above-ground DM as grain DM) in the period from 1966 until about 1990 increasing from 43% to 49%, but deceased with year of release thereafter A non-linear genetic gain in AGDM was evident over the 43-yr period with AGDM increasing from about 1990 from which point it increased rapidly to 2009. There was no association between genetic progress in grain yield and grain number per m^2 in this set of cultivars; a small increase in ears per m^2 was counteracted by a decrease in grains per ear. However, grain weight tracked the improvement in yield potential over the 43-year period with a linear increase of 0.23 mg yr^{-1}.

No change was found in rachis length with plant breeding; however, number of fertile spikelets per ear decreased since about 1990 and was associated with the decrease in grains per ear. There were statistically significant differences in above-ground DM production at all growth stages and a tendency to produce more biomass during the GS31 to GS61+7d phase with year of release. No differences amongst cultivars were found in the amount of radiation intercepted by the whole canopy from GS31 to GS61+7 days. Although not conclusive, since Bacanora was an exception to the trend and radiation-use efficiency (above-ground biomass per unit PAR interception; RUE), there was a tendency for RUE to increase with year of release which was consistent with a positive association with crop growth rate (above-ground DM per m^2 per day; CGR) and the trend for an increase in biomass accumulation during the stem-elongation phase with plant breeding. Although there was a trend for an increase in biomass accumulation from GS31-GS61+7d this was counteracted by a decrease in ear DM partitioning so that ear DM per m^2 at GS61+7d and grains per m^2 did not change with plant breeding.

Results showed that the improvement in the individual grain weight from 1966 to 2009 in this set of cultivars was associated with improvements in the grain filling rate from 1966 to ca. 1990 and in the duration of grain filling from ca. 1992 to 2009. Averaging across years, there was a significant positive association between post-flowering canopy-temperature depression and grain yield. Fractional PAR interception by the canopy layers of the ear, flag leaf and the penultimate leaf was increased with year of release since about 1990. This

increase in the fractional interception of PAR correlated significantly with the grain weight and grain yield amongst the 12 cultivars.

Grain growth of the cultivars in this historic set was generally sink limited rather than source limited. There was no change in source-sink balance as indicted by grain growth responses to the degraining treatment with year of release. The percentage increase in grain weight in the manipulated ears ranged amongst cultivars from 0.5 to 13.2%, but differences between cultivars in the response to degraining were not statistically significant and the responses were not correlated with year of release. The results also indicated that potential grain weight has increased with plant breeding over the 43-year period, since the final grain weight of the grains in the degrained ears increased linearly with year of release. Overall the contribution of stem WSC to grain DM growth in the current study was relatively low (4 - 18%) which is consistent with the hypothesis that under the high radiation, irrigated environment in Northwest Mexico, yields of modern cultivars are more likely to be sink than source limited.

Results of *Tin1A* experiments showed that under the UK environment, *Tin1A* lines produced more grain yield than non-*Tin1A* lines under high seed densities. The main yield component explaining this was grains per m^2. *Tin1A* lines had a longer rachis, a wider ear, and more total and fertile spikelets per ear than non-*Tin1A lines*. Non-*Tin1A* lines produced more ears per plant than *Tin1A* lines under low seed density; however, both groups of lines had similar values of ears per plant under high seed density. Non-*Tin1A* lines produced heavier grains than *Tin1A* lines either under high or low seed density, and individual grain weight was not affected by the increase of seed density.

Under the Mexican environment, there was a slight increase in the yield of non-*Tin1A* compared to *Tin1A* lines, but only at low seed density. This increase was attributed mainly to heavier individual grains in non-*Tin1A* than *Tin1A* lines. Although *Tin1A* lines produced fewer ears m^{-2} than non-*Tin1A* lines (-13.4, -12.5 and -11.3%, under seed densities of 50, 150 and 450 seed m^{-2}, respectively), *Tin1A* lines produced more grains m^{-2} at all seed densities and this resulted from a longer rachis, more total and fertile spikelets per ear and thus more grains per ear. There was a reduction in the grain yield in non-*Tin1A* lines with increasing seed density. However, *Tin1A* lines continued to increase grain yield with increasing seed density, so that the two groups of lines yielded similarly at high

plant density. This result therefore supported the hypothesis that *Tin1A* lines yield relatively better under high seed density than non-*Tin1A* lines and may have a higher economic optimum seed density. Overall, in contrast to in the UK experiments, it seemed that under the high temperature and radiation environment in NW Mexico, possessing the *Tin1A* allele may not be an advantage compared to the non-T*in1A* allele even under high seed rates.

Overall, several target traits were identified for future improvement of yield potential in CIMMYT plant breeding and worldwide in the present study. Genetic progress in grain yield potential in the CIMMYT spring wheat program from 1966 to 2009 of 37 kg ha^{-2} yr^{-1} was positively associated with above-ground biomass and grain weight. The amount of radiation intercepted during the stem-elongation phase did not change with breeding; however, there was an apparent tendency for RUE to be increased with year of release. Potential grain weight also tracked increases in final grain weight. Therefore target traits as selection criteria in wheat breeding programs for yield potential should include a combination of traits favouring enhanced RUE during the stem elongation and potential grain weight. In addition, in winter wheat in the UK restricted tillering with the introduction of the *Tin1A* allele offers scope to increase grains m^{-2} and grain yield, associated with more fertile spikelets per ear and grains per ear, in wheat crops with established plant densities in the range ca. 150 - 200 plant m^{-2}.

CHAPTER 1 INTRODUCTION

1.1 WHEAT PRODUCTION AND WORLD DEMAND

The global human population was 3.1 billion in 1970, and this was more than doubled to 6.8 billion in 2010 (http://www.ers.usda.gov/Data/Macroeconomics/), and is predicted to reach 9.1 billion in 2050,

(http://www.un.org/apps/news/story.asp?NewsID=13451&Cr=population&Cr1.

The UN similarly forecasts that the world population will reach 9.4 billion by 2050. The world must therefore develop the capacity to feed 10 billion within the next 40 to 50 years. The majority of people worldwide consume wheat as the first or second source for their daily requirement of calories (Fig. 1.1).The increase in wheat production has to come from greater yields on existing cropland; but also without proportionate increases in the use of water or fertilizer, and within the context of climate change (Hirel *et al.*, 2007; Catavelli *et al.*, 2008). Climate has changed during the last decades, with an increase in the atmospheric CO_2 level and temperature, and a decline in rainfall in many areas with increases in others and a decrease in the solar radiation reaching the earth's surface (Asseng *et al.*, 2009).

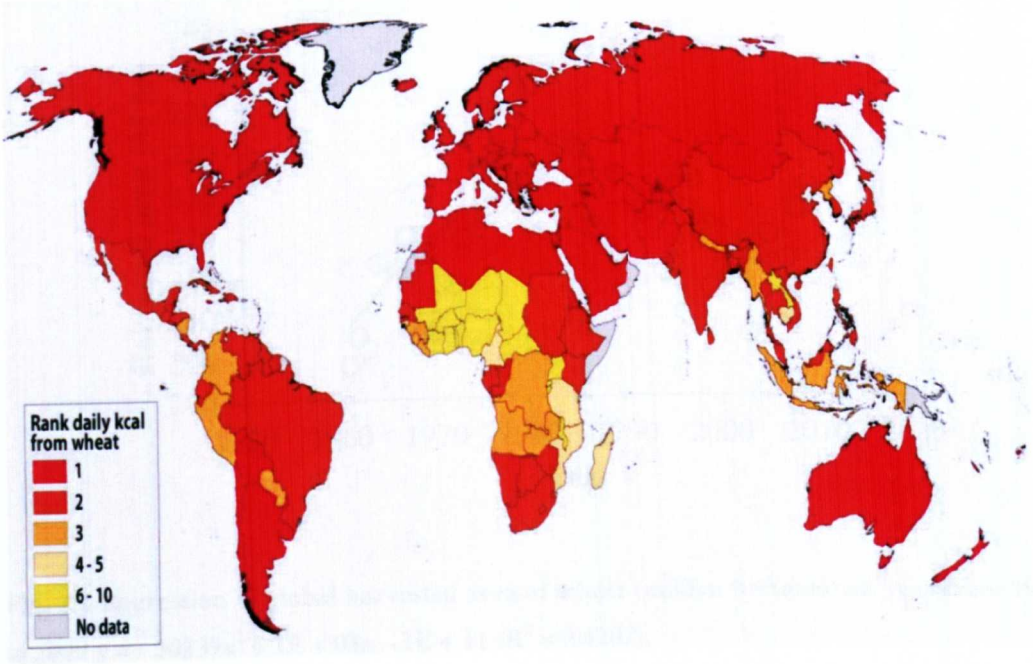


Fig. 1.1 Relative rank of wheat as a food crop worldwide according to daily kilo calories in human diets.

Source: WHEAT-Global Alliance for Improving Food Security and the Livelihoods of the Resource-poor in the Developing World. Proposal submitted by CIMMYT and ICARDA to the CIGIAR Consortium Board.

Though there has been a reduction in the harvested area of wheat since about 1980 (Fig. 1.2), wheat production worldwide has increased steadily from 222 Mt in 1961 to 686 Mt in 2009, with a linear progress of about 8.8 Mt per year (Fig. 1.3). In addition, average yield has increased from 1.09 t ha^{-1} in 1961 to 3.04 t ha^{-1} in 2009 with a linear progress of 40.5 kg ha^{-1} yr^{-1} (Fig 1.4) (FAOSTAT, 2009). About half of this progress has been attributed to the genetic contribution from plant breeding while the other half has been attributed to the improvement in the agronomic practices (Bell *et al.*, 1995; Austin *et al.*, 1989).

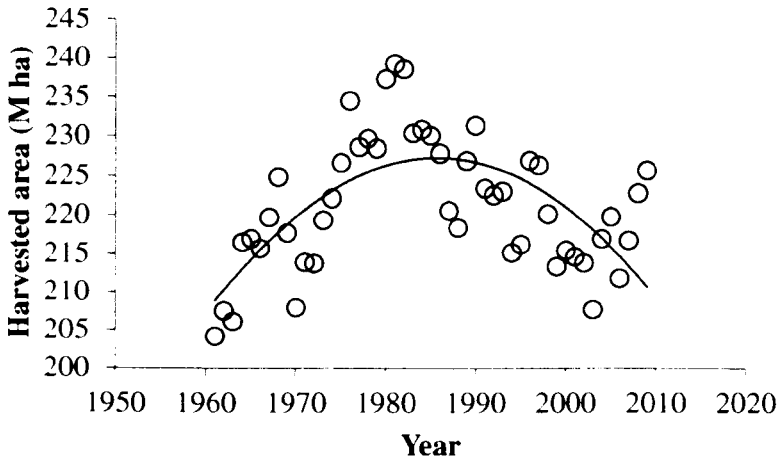


Fig. 1.2 Regression of global harvested area of wheat (million hectares) on year from 1961 to 2009 y = - 30239x^2 + 1E + 08x – 1E + 11 (R^2 = 0.4207).

Source: (FAOSTAT, 2009).

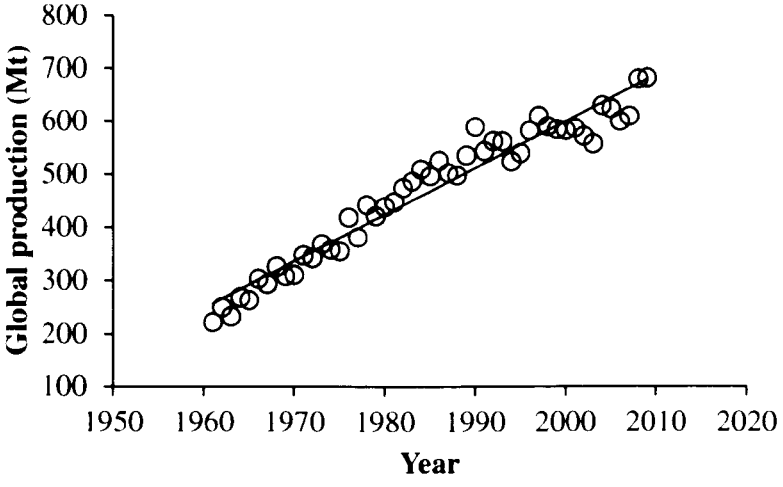


Fig 1.3 Regression of global production of wheat on the year from 1961 to 2009 y = 8.8492x – 17095 (R^2 = 0.9456).

Source: (FAOSTAT, 2009).

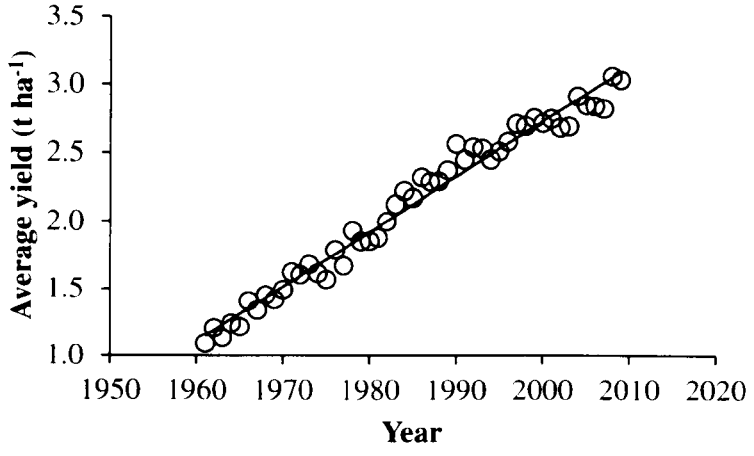


Fig. 1.4 Regression of average global yield of wheat on the year from 1961 to 2009 y = 0.0405x – 78.266 (R^2 = 0.9767).

Source: (FAOSTAT, 2009).

According to Calderini and Slafer (1998), there was no systematic progress in wheat yield during the first two to five decades of the last century from a study of 21 countries and the steady increase of wheat yield potential has started from the beginning of the second half of the last century. The increase in the global production of wheat is correlated mainly with the improvement of the average yield per hectare ($r = 0.99$, $P < 0.001$) (Fig. 1.5).

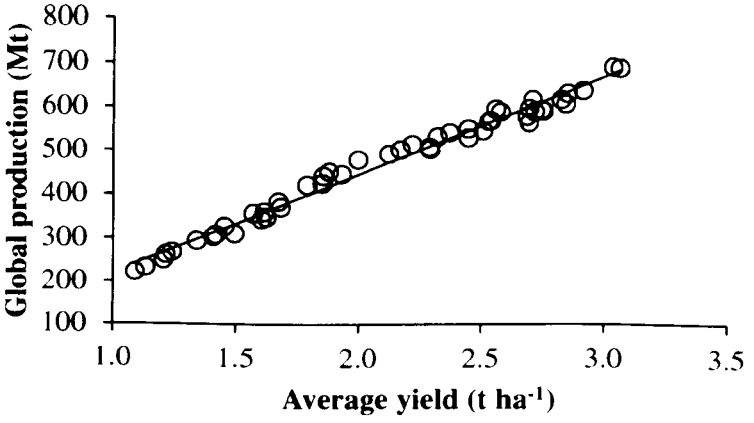


Fig. 1.5 Regression of global production of wheat on average yield: y = 220.24x + 2.488 (R^2 = 0.9835).

Source: (FAOSTAT, 2009).

There was a positive relationship between the global production of wheat and the harvested area only from 1961 to 1982 (Fig. 1.6); from 1983 till 2009 there was no correlation between the global production and the area harvested (Fig. 1.7).

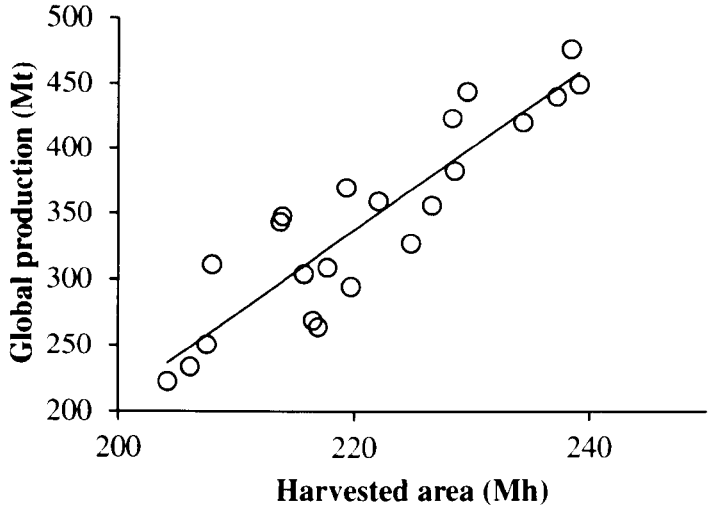


Fig. 1.6 Regression of global production of wheat on harvested area from 1961 to 1982: y = 6E – 06x – 1063.9 (R^2 = 0.8116).

Source: (FAOSTAT, 2009).

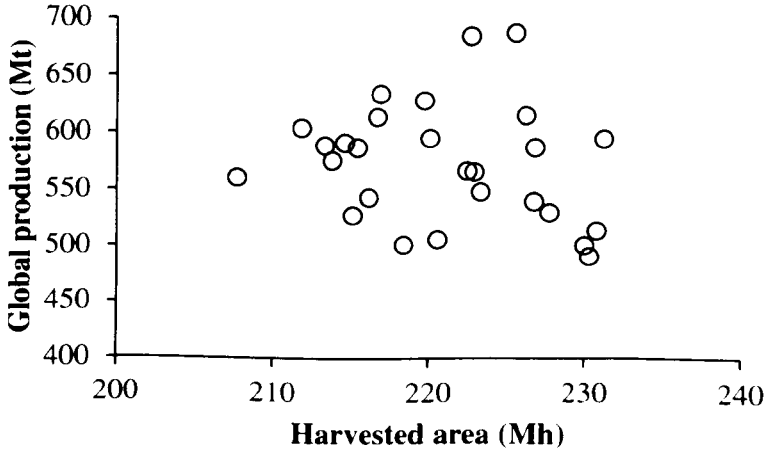


Fig 1.7 Regression of global production of wheat on harvested area from 1983 to 2009

Source: (FAOSTAT, 2009).

1.2 BREEDING AND WHEAT GERMPLASM IMPROVEMENT

Wheat is one of the oldest cultivated crops and the first evolutionary steps started approximately 10,000 years ago (Evans *et al.*, 1975). The common hexaploid wheat was derived from three different diploid donor species (Zohary *et al.*, 1969). These diploid donors involved: *Triticum urartu* which contributed with genome A, *Aegilops speltoides* which contributed with genome B and *Triticum tauschii* which contributed with genome D (Gill and Friebe, 2002). Hexaploid bread wheat cultivars are classified by: (i) length of growing season, e.g. winter wheat (with vernalization requirements vs. Spring wheat (with no vernalization requirements). (ii) end-use quality, e.g. high vs low gluten content and/or hard vs soft grain texture and (iii) grain colour (red or white).

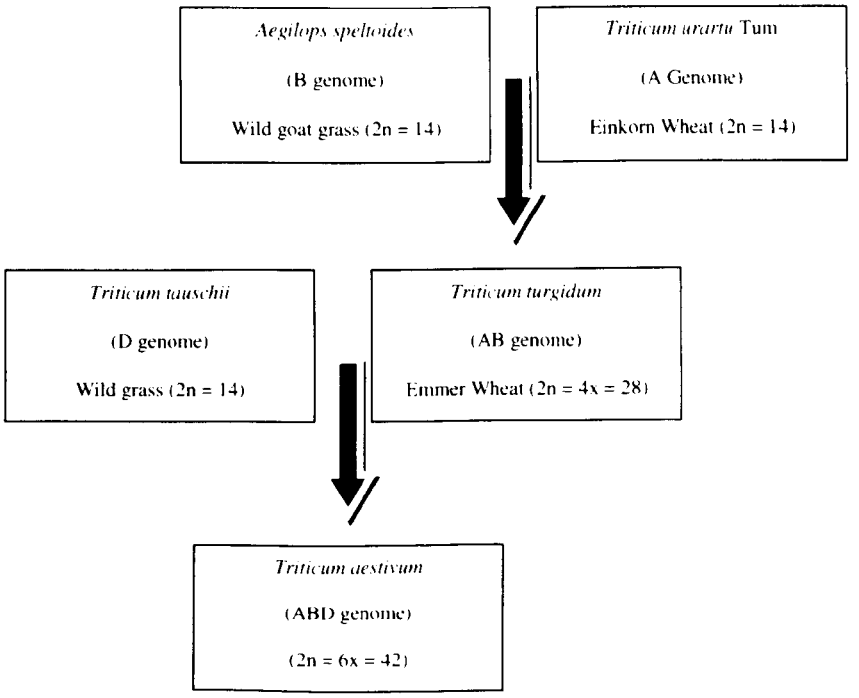


Fig. 1.8 Phylogeny of polyploidy wheats

Source: Adapted from Gill and Friebe, (2002).

Due to the continuity in the growth of the world population by a rate of 1.4% or about eighty million per year, it was estimated that food production must be increased by about 50% by the year of 2025 (Khush, 2001). The International Center for Maize and Wheat Improvement (CIMMYT) is one of the most important worldwide organisations for wheat breeding in the public sector that plays a major role in improving bread and durum wheat yields in developing countries in improving wheat productivity through developing cultivars with higher yield potential, resistant and/or tolerant to biotic and abiotic stresses and with high adaptability to specific environments. The key objective in the wheat breeding program in CIMMYT is to fill the gap between the production and the demand in developing countries (Singh and Trethowan, 2007). The wheat breeding programme at CIMMYT historically can be divided to three major phases: 1) Bilateral phase from 1944 to 1960 just within Mexico (USA and Mexico), 2) Green Revolution phase from 1961 to 1976 at an international level and 3) from 1977 to present at the global level (Rajaram, 1994).

Improvement of yield potential of wheat due to the Green Revolution was a result of the introduction of the high-yielding cultivars released from about 1961 and 1971 (Briggs, 2009). The introduction of the semi-dwarfing genes in the new cultivars with increased yield potential and lodging resistance was one of the main reasons for the Green Revolution. These genes (*Rht-B1b*, formerly *Rht1*, and *Rht-D1b*, formely *Rht2*) were introduced from the Japanese source of Norin 10 which is the origin of the semi-dwarfing genes of > 70% of the cultivated wheat globally (Hedden, 2003). The cultivated area with these modern varieties of wheat increased sharply from 12 million ha in 1970 to 50 million ha in 1990 with 70% of the area in the developing countries excluding China (Reynolds and Borlaug, 2006). In addition, there were other ways of improvement such as 1BL/1RS translocation from rye to wheat. However, it was concluded that the 1BL/1RS translocation is associated with reduced bread-making quality in some iso-genic wheat lines grown in different environments (Lelley *et al.*, 2004). Furthermore, Peake *et al.* (2011) reported that possessing the 1BL/1RS translocation caused a lower yield than the lines without the 1BL/1RS when grown under low yielding environments and this negative effect was mainly due to a decrease in the grains m^{-2}.

The yield progress has been clearer in the developing than in the developed countries since the Green Revolution; however, the rate of yield progress during the last decades has apparently slowed in the developing countries (Heisey, 2002). This slowing down in yield gains is associated partly with some agronomic aspects linked with the use of the new varieties in the developing countries including the education level of farmers and the availability of credit (Dixon *et al.*, 2006).

It was concluded by Wouw *et al.* (2009) that there was a reduction in the genetic diversity due to the use of the modern cultivars instead of the landraces due to modern plant breeding, however, after a complete replacement this reduction stopped. This trend was also mentioned by Reif *et al.* (2005), who reported that the genetic diversity of wheat has decreased from 1950 to 1989 and then increased again in the period from 1990 to 1997. The term of 'genetic erosion' was first applied by Jack Harlan (Smale *et al.*, 2002). The main factor contributing to the genetic erosion was the replacement of the landraces or local cultivars with the modern cultivars (Ceccarelli *et al.*, 1992). Smale *et al.* (2002) reported that though almost 77% of the spring bread wheat cultivars cultivated in the developing countries are CIMMYT-related wheats, there is no evidence that the genetic diversity of wheat germplasm in these countries has decreased. In addition, Huang *et al.* (2007) reported that modern plant breeding has not changed the genetic diversity in a study of 511 cultivars of winter wheat of Central and Northern Europe.

1.3 APPLYING PHYSIOLOGICAL STRATEGIES IN WHEAT BREEDING

To date improvement of yield potential has been mainly empirically based on yield *per se* (Evans, 1993). However, yield has a relatively low heritability and this approach may not be the most efficient as there is a high genotype x environment interaction (Jackson *et al.*, 1996; Slafer, 2005). There is therefore a strong case that understanding of traits at the physiological level may help to identify indirect selection criteria that could be applied to accelerate breeding

progress. Such an integrated approach may complement empirical breeding and hasten progress (Araus *et al.*, 2002; Reynolds & Borlaug, 2007).

Understanding the physiological processes determining yield is essential for breeders to design strategies for yield potential improvement. It is very difficult to understand and improve functions of plant organs by studying them from the gene level upwards towards the physiological trait; however, studying a trait from the physiological level to the gene level may be a more effective way to improve such a yield-enhancing trait (Fischer, 2011).

The role of physiologists in breeding programmes includes their participation in determining and defining targeted environments, identifying and testing the important traits affecting yield potential in these environments, and identifying and measuring the interaction amongst all traits correlated directly and indirectly with enhanced yield potential (Andradi *et al.*, 2009).

Improving the understanding of the physiological basis of genetic progress in yield has become more important in the last decades for several reasons; for example: 1) the rate of genetic gain in yield potential resulting from plant breeding has apparently slowed down recently in some countries; and 2) the improvement in the field-based sensors used in the high-throughput phenotyping of leaf and canopy physiological traits means they are now more reliable and accurate (Fischer, 2007; Reynolds *et al.*, 2007). Examples of important physiological tools which could be used as selection criteria are canopy temperature depression (difference between ambient temperature and canopy temperature; CTD) using an infra-red thermometer indicative of photosynthetic capacity and spectral reflectance indices using spectral radiometers indicative of canopy size and biomass (Reynolds *et al.*, 1999; Babar *et al.*, 2006). Also, it was concluded that using canopy reflectance information such as: NDVI, is a valuable way to estimate the RUE and HI (Li *et al.*, 2011).

There is a significant negative relationship between canopy temperature (CT) and canopy photosynthesis and grain yield amongst wheat genotypes (Reynolds *et al.*, 1994b; Reynolds *et al.*, 1997). Bilge *et al.* (2008) found canopy temperature depression of durum wheat was higher than bread wheat in Turkey, and it correlated positively with yield and its components in both species.

Fischer *et al.* (1998) found, in a series of spring wheat cultivars released from 1962 to 1988 in NW Mexico, that canopy temperature decreased with year of release by about 0.6 °C. In addition, Ayeneh *et al.* (2002) reported that there were no interactions between grain yield and CTD of different organs of spring wheat (spike, flag leaf, penultimate and whole canopy). Thus, using CTD to measure crop temperature depression during grain-filling period is safe and reliable. Reynolds *et al.* (2000) reported a positive correlation between stomatal conductance and grain yield in 16 spring wheat varieties in NW Mexico. Under a high solar radiation environment, modern cultivars had better carbon exchange rate than the older cultivars in spring wheat released from 1968 to 1986 (Blum, 1990). Genotypes with higher values of CTD usually have high values of stomatal conductance (Pinter *et al.*, 1990; Amani *et al.*, 1996; Fischer *et al.*, 1998). In general, physiological strategies should complement traditional selection for yield in yield traits, to improve the efficiency of wheat breeding. Reynolds *et al.* (2011) suggested that yield potential could potentially be increase by 50% by application of physiology to improve RUE and this would be achieved through processes including the introduction of C4 like traits, improving the vertical distribution of light interception, and improving the ear and the whole canopy photosynthesis.

1.4 THE OVERALL AIMS OF THE STUDY

The overall aims of this thesis are to:

1. Quantify the genetic gains in yield potential progress during the period from 1966 to 2009 in spring bread wheats released at CIMMYT in the irrigated high radiation environment of NW Mexico through the field analysis of a set of historic cultivars.

2. Quantify the changes in physiological traits at harvest associated with the genetic yield progress, such as grains m^{-2}, grain weight, harvest index (HI) and harvest biomass.

3. Identify the physiological basis of these changes in yield potential and harvest parameters with years of release through detailed analysis of the growth and

development through the season of the set of historic cultivars in field experiments.

4. Quantify whether the tiller inhibition *Tin1A* gene is associated with high expression of ear fertility traits and yield potential under rainfed UK environments and the high radiation, irrigated environment of NW Mexico in doubled-haploid (DH) lines segregating for *Tin1A*/non-*Tin1A* alleles.

5. Investigate the physiological basis of effects of the *Tin1A* gene on ear-fertility traits and yield potential in doubled haploid (DH) lines segregating for *Tin1A/non-Tin1A* alleles on responses of yield and underlying traits to plant density.

CHAPTER 2 LITERATURE REVIEW

2.1 GENETIC GAINS IN GRAIN YIELD POTENTIAL

Yield potential has been defined as the yield of a cultivar grown under environmental conditions to which it is adapted and with the optimal agronomic conditions, resulting in absence of lodging, and biotic and abiotic stresses (Evans, 1993). When a cultivar grows under unfavourable conditions but is constrained by the presence of one or more of the yield-limiting factors, this equates to the farm yield or the actual yield. The difference between the potential and the actual yield is called the exploitable yield gap (Fischer and Edmeades, 2010).

Many studies worldwide demonstrate genetic gains in yield in both spring and winter wheats. Several studies examining yield progress in sets of historic wheat cultivars have been carried out in spring wheat. Sayre *et al.* (1997) reported that genetic progress of yield potential in NW Mexico for eight cultivars released from 1962 to 1988 was 67 kg ha^{-1} yr^{-1}. Underdahl *et al.* (2008) reported linear progress in yield with year of release in 33 genotypes released from 1968 to 2006 of 30.4 kg^{-1} ha^{-1} yr^{-1} (1.3% yr^{-1}), in North Dakota, USA, and Perry and D'Antuono (1989) observed a rate of increase of 5.8 kg ha^{-1} (0.57% yr^{-1}) in Australia for 28 cultivars released from 1860 to 1989. Moreover, Siddique *et al.* (1989) comparing ten genotypes released from the 1860s to 1986 in Australia observed that the most recent cultivars had a grain yield increase of 63% compared to the oldest ones released in the 1860s. Waddington *et al.* (1986) in NW Mexico observed genetic progress for seven cultivars of 59 kg ha^{-1} (1.1 %) yr^{-1} from 1950 to 1982. Royo *et al.* (2007) found the genetic gain in yield of durum wheat from years before 1930 until 2000 was ca. 20 kg ha^{-1} yr^{-1} in Italy and Spain.

Similar studies on sets of historic cultivars have been carried out in winter wheats worldwide. In the UK, Austin *et al.* (1980a) found that the cultivar 'Hobbit' released in 1977 outyielded the cultivar 'Little Joss' released in 1908 by about 40%. The genetic progress in grain yield in the UK was assessed again by Austin *et al.* (1989) who found that the most advanced cultivar 'Slejpner'

released in 1986 produced 80% more grain yield than the oldest cultivar 'Squarehead Master' released in 1830. Zhou *et al.* (2007) found genetic gains of grain yield ranged from 32.1 to 72.1 kg ha^{-1} yr^{-1} in Northern China for 47 cultivars released from 1960 to 2000 and Brancourt-Hulmel *et al.* (2003) showed that yield progress in France was 49 kg ha^{-1} yr^{-1} in 14 cultivars released from 1946 to 1992. Berzonsky and Lafever (1993) reported an increase in the yield of winter wheat of 15.5 kg ha^{-1} yr^{-1} for 24 cultivars released from 1871 to 1987 in Ohio, USA. In the UK, Sherman *et al.* (2005) following on the earlier studies referred to above reported a linear genetic gain in grain yield of 120 kg ha^{-1} (1.2 %) yr^{-1} for eight cultivars introduced from 1972 to 1995. A study of 14 genotypes in the USA reported a range of grain yield in the Great Plains from 2.72 t ha^{-1} for Turkey (released in 1873) to 4.99 t ha^{-1} for the experimental line released in the 1990s with a genetic gain of 0.44% yr^{-1} (Donmez *et al.*, 2001). A linear increase of 16.2 kg ha^{-1} yr^{-1} in grain yield of 35 hard red winter wheat released from 1874 till 1987 was observed in Kansas (Cox *et al.*, 1988).

As well as in wheat, yield potential of barley has also increased in the last decades. For example, Abeledo *et al.* (2003) found that rate of grain yield improvement in Argentina of nine cultivars released from 1944 to 1998 was 41 kg ha^{-1} yr^{-1} and Boukerrou and Rasmassun (1990) reported genetic progress of 15.7 kg ha^{-1} yr^{-1} in 42 cultivars released from 1920 till 1984 in the USA. Yield potential progress may be beginning to slow or even plateau in some countries. Graybosch and Peterson (2010) suggested that there had been no statistically significant change in grain yield in the Great Plains of North America since 1983. Also, Peltonen-Sainio *et al.* (2009) reported that Finnish wheat yield production has levelled off since ca. 1995. In addition, in Turkey comparing spring durum wheat genotypes released from 1974 to 1997 with a cultivar released in 1933 yield progress was reported during the 1970s and 1980s compared to the control cultivar but no further progress was found during the 1990s (Barutcular *et al.*, 2006).

2.2 THE PHYSIOLOGICAL BASIS OF GENETIC PROGRESS IN YIELD POTENTIAL

Studying the physiological basis of the yield progress for cultivars released in different eras during the period before and after the Green Revolution is important in order to understand how breeding progress has occurred and hence to inform on future strategies for raising yield potential.

The presence of the semi-dwarfing genes in near-isogenic lines (NILs) led to a reduction in the plant height of ca. 20% with either *Rht-B1b (formerly Rht1)* or *Rht-D1b (formerly Rht2)* and of 45% with *Rht-B1b* + *Rht-D1b* compared to the tall *(rht)* control (Fischer and Stockman, 1986). An alteration in the dry matter partitioning allowed more assimilates to be allocated to the ear of the wheat plant at anthesis. Allan (1983) reported that harvest index (percentage of above-ground DM as grain; HI) was 41.4, 38.0 and 31.6% for lines containing semi-dwarfing genes *Rht-B1b* and *Rht-D1b*, one of the semi-dwarfing genes and tall lines, respectively. Plant height of NILs containing either the *Rht-B1b* or *Rht-D1b* genes or a combination of both was reduced by 24 and 52%, respectively, compared to their recurrent parent "Burt" (Allan, 1986). Possessing *Rht-B1b* and *Rht-D1b* provided greater advantages in yield in taller and older near-isogenic genetic backgrounds than new ones (Chapman *et al.*, 2007). Blake *et al.* (2009) reported that segregation in *Rht-D1* alleles in the F_2 generation of five crosses of spring wheat caused large variation in grain yield and grain protein concentration (67% and 42%, respectively). Borrell *et al.* (1991) observed that producing more grains m^{-2} in NILs of spring wheat was due to an increase in grains per ear for the lines possessing *Rht-B1b* and in the ears per plant for lines with *Rht-D1b* compared to the tall (rht) control. Some studies showed that lines possessing the *Rht-B1b* gene performed better than those with the *Rht-D1b* gene under fully irrigated environments, e.g. (Butler *et al.*, 2005). However, Mathews *et al.* (2006) found that the relative performance of the semi-dwarf lines and tall lines was the same under stressed and non-stressed environments. Na *et al.* (2009) in China concluded that lines with the *Rht-B1b* and/or *Rht-D1b* genes were less suitable under water stress environments than those carrying the *Rht8* gene which had a smaller effect on the coleoptile length. This was in agreement with

Ellis *et al.* (2004) and Botwright *et al.* (2001), who reported that lines with *Rht8* or *rht* had the same coleoptile length and that this was longer than coleoptiles in *Rht-D1b* lines.

The main effect of the introduction of the semi-dwarfing genes was the increase in HI. Austin (1980b) predicted that a maximum theoretical HI of 62% could be achieved by a 50% decrease in the stem and leaf sheath DM and increasing chaff DM *pro rata* with grain yield while maintaining the AGDM at harvest. However, a more recent study carried out by Shearman *et al.* (2005) demonstrated that AGDM at harvest had increased in UK winter wheat cultivars since ca. 1990 and the ratio of chaff to grains decreased during the period from 1980 to 1995, hence the theoretical upper limit of HI could be as high as 64% (Foulkes *et al.*, 2011).

In spring wheat, many studies have investigated the physiological traits associated with yield gains in the last decades. The majority of these studies suggest that the main physiological component explaining yield potential progress during the second half of the last century was higher HI, in turn, associated with more grains per unit land area. Sayre *et al.* (1997) found that grain yield progress in NW Mexico from 1962 to 1988 was positively correlated with grains per unit area and HI, but not with above-ground biomass or grain weight (or days to anthesis, ears m^{-2} or grains per ear). Perry and D'Antuono (1989) observed that HI as well as grains ear^{-1} and grains m^{-2} were the main components associated with yield progress in Australia from 1860 till 1989. Ortiz-Monasterio *et al.* (1997) reported that the genetic progress in grain yield in spring wheat cultivars released in CIMMYT from 1950 to 1985 was associated with an improvement in HI rather than AGDM. Waddington *et al.* (1986) in NW Mexico similarly attributed the genetic gains in yield potential to grains m^{-2}, in turn, associated with more grains ear^{-1}. Acreche *et al.* (2008a) observed in eight spring wheat cultivars released from 1940 to 1998 that grain yield increased significantly from 1940 until 1970s related to improvement in HI and grains m^{-2}, whereas biomass and grain weight did not change during this period. Abbate *et al.* (1998), however, reported yield progress of Argentine spring wheat cultivars during the 1980s and early 1990s was due to more grains m^{-2}, and this was mainly due to improvement in the grains to ear dry weight ratio (at anthesis)

rather than increased assimilate partitioning of crop dry matter to the ear. All of the above studies did not find any genetic progress in the grain weight.

In winter wheat, results from many studies showed that the yield progress was also associated with greater HI mainly due to the introduction of the semi-dwarfing genes. These studies include those of Austin *et al.* (1980a) and Austin *et al.* (1989), who observed gains of UK winter wheat yield from 1908 to 1985 were mainly associated with HI. Brancourt-Hulmel *et al.* (2003) explained that the most important factor associated with grain yield progress in France during the second half of the last century was decreased plant height, hence more grains m^{-2} and higher HI. Zhou *et al.* (2007) found that the main reason for the genetic gain for winter wheat yield potential in China was more grains per ear and HI contributed by the semi-dwarfing genes and the *1B/1R* translocation. Siddique *et al.* (1989) also observed genetic yield progress in Australia was mainly due to an increase in HI. Donmez *et al.* (2001) reported grains m^{-2} was associated with genetic progress in yield in the Great Plains in hard red winter wheat. Finally, Acuna *et al.* (2011) suggested higher grains per ear as an important trait increasing yield potential in the high-rainfall zone in Southern Australia.

The majority of the above studies therefore concluded grain number per unit area was an important component determining yield progress. However, some researchers have argued that grain number is itself a consequence of the amount of resource accumulation (carbon and nitrogen), which also influences grain growth, rather than directly a yield determinant (Sinclair and Jamieson, 2006). Association between the accumulation of nitrogen and the number of grains was mentioned also by Demotes-Mainard *et al.* (1999), who reported in winter wheat cultivar 'Soissons' in France a strong positive relationship between nitrogen content of ears at the beginning of the rapid ear-growth phase and the number of grains per ear. Moreover, Peltonen (1992) suggested that applying nitrogen fertilizer at the double ridge stage comparing to other timing led to a higher number of the grains per spike. A reply to the review by Sinclair and Jamieson (2006) was made by Fischer (2008), who argued that grain number is related to assimilate accumulation pre-anthesis; and that grain yield in modern cultivars grown under potential conditions is usually limited by post-anthesis grain sink size and genetic progress of post-anthesis assimilate has been a consequence of

increasing number of grains per unit area by breeding. This view has also been supported by several other recent reviews on yield potential progress in wheat (Reynolds *et al.*, 2009; 2011; Foulkes *et al.*, 2009).

HI was the main target for wheat breeding programs in the 1960s and 1970s. Nevertheless, since the 1990s it may be that an upper limit for HI (e.g. 62% proposed by Austin *et al.* (1980a) is being approached in some countries, and the main way to increase the yield potential in the future may be through enhancing biomass whilst maintaining the HI (Foulkes *et al.*, 2007). Indeed, Austin (1999) suggested that in the long term genetic gain in wheat yield potential would be achieved by increasing the above-ground biomass via improving the efficiency of photosynthetic processes. Increases in biomass rather than HI have already been found in some cases to be an alternative mechanism raising yield in favourable environments in recent years. For example, Waddington *et al.* (1986) indicated that, from 1950 to 1982, after 1970 HI for modern CIMMYT cultivars was lower than the old ones, whereas above-ground biomass was increased. Moreover, Shearman *et al.* (2005) showed that an increase in HI from 1972 to the late 1980s and above-ground biomass after ca. 1983 were associated with genetic gains in yield potential of UK winter wheat from 1972-1995. They attributed the increase in above-ground biomass at harvest in the most recent cultivars in part to an increase in radiation-use efficiency (above-ground biomass/radiation interception; RUE) in the pre-anthesis phase during stem elongation (GS31 - GS61). However, Calderini *et al.* (1997) in contrast reported in Argentine wheats released from 1920 till 1990 a tendency to produce less biomass with year of release. Nevertheless, no decrease was found in biomass accumulation in the period from GS31 to GS61 with breeding. An increase of the harvest AGDM was attributed to the *1BL/1RS* wheat-rye translocation in wheat cultivars released in the 1980s and 1990s in several countries (Villareal *et al.*, 1998; Foulkes *et al.*, 2007; Zhou *et al.*, 2007).

In the studies cited above, individual grain weight was almost always reported not to increase with year of release. Since grain weight is one of the two principal yield components and has more environmental stability than grain number per unit area (Cossani *et al.*, 2011), genetic progress in grain weight is therefore an important future strategy to improve yield. More recently, some

studies including cultivars released since about 1990 indicated changes in grain weight were contributing to genetic progress in grain yield in spring wheat, e.g. Underdahl *et al.* (2008) who found grain weight was associated with yield progress of hard red spring wheat cultivars from 1968 to 2006 in the Great Plains. In winter wheat, a few studies also partly explained the genetic gains in yield by heavier individual grain weight, such as Cox *et al.* (1988), who attributed the progress in winter wheat yield potential in Kansas from 1874 to 1987 to heavier grains, in turn, associated with a decrease in days to heading and plant height.

There are several other physiological changes reported to be associated with genetic yield progress. For example, Royo *et al.* (2007) found that earlier heading and a longer grain-filling period were correlated with yield progress in tall cultivars; but not in the semi-dwarf cultivars in their study. Significant genetic changes in yield through time in UK winter wheat germplasm were attributed to improved RUE in the pre-anthesis period as mentioned above and hence more water soluble carbohydrates and ear biomass at anthesis (Shearman *et al.*, 2005). In addition, Fischer *et al.* (1998) reported genetic gains in the maximum photosynthetic rate of the flag leaf by 23% in the period from 1962 to 1988 in spring wheat in Mexico. On the other hand, Acreche *et al.* (2009) reported no changes in the intercepted radiation and RUE in bread wheat released from 1950 to 2006 in the Mediterranean area of Spain during the pre-anthesis phase; though the two oldest cultivars had lower RUE than modern cultivars. Calderini *et al.* (1997) similarly did not find any changes in biomass and RUE in Argentine wheats released during the period from 1920 to 1992, but did observe increases in radiation interception due to the differences in length of developmental phases associated with yield progress.

A detailed review of the physiological traits associated with yield progress in barley, rice and maize is beyond the scope of the current literature review, but fortunately recent reviews are available (e.g. Foulkes *et al.*, 2009). In barley, there is some evidence for biomass increases associated with grain in yield potential. Briefly, Abeledo *et al.* (2003) reported yield potential progress from 1944 to 1998 was associated with grains m^{-2} and biomass at maturity, but not with HI or plant height. Boukerrou and Rasmassun (1990) attributed progress in

yield potential from 1920 to 1984 in spring barley to both above-ground biomass and grain weight; and Abeledo *et al.* (2003) found in 2-rowed malting barley cultivars greater radiation interception was the main reason for an increase in biomass at heading with year of release.

2.3 DOUBLED-HAPLOID TECHNIQUE

Improving wheat yield potential is the most important objective in worldwide wheat breeding programs. There are several germplasm development methods used to obtain this target.

Producing new genotypes by conventional breeding using the pedigree method typically takes from 7 to 9 years where an out-crossing between selected parents is made by hand and then seeds of F_1 plants are grown as spaced plants. The initial selection process occurs from the F_2 to till F_5 generation and then from F_6 generation till F_{9}., preliminary and multi-location yield trails are conducted (as plants are selfed in each generation) to evaluate and compare the new selected lines with local cultivars (Poelham and Sleper, 1995). Even when modifying this method, e.g. by incorporating single seed descent to accelerate intermediate generations, it may require 4 to 5 years to generate homozygous lines (Brim, 1966).

One of the most important methods used currently to minimize the time required to reach homozygosity is the doubled-haploid (DH) technique, which is used to produce homozygous plants from F_1 plants within one generation. Doubled-haploid lines are produced by two main methods: i) anther culture and ii) the wheat × maize pollination method. The use of the anther culture method in wheat is restricted due to the high rate of albino plants produced which are not able to survive (Maluszynski *et al.*, 2003). The wheat × maize pollination technique is used widely and consists of the following steps: Firstly, *Hybridisation* between two wheat genotypes to produce the F_1 generation. Secondly, *Emasculation*, which is done for F_1 plants from 1 to 3 days before anthesis by removing anthers from the florets and then covering the ears with glassine bags. Thirdly, *Pollination*: the emasculated florets are pollinated with fresh maize pollens and then covered again with glassine bags. Fourthly: *Hormonal applications*: after 24 hours from pollination, the uppermost internode of the pollinated tillers is

injected with 2,4-D (2,4-dichlorophenoxy acetic acid), also small drops of 2,4-D are added to the pollinated florets. The reason behind this procedure is that the endosperm is inadequate to stimulate the embryo growth. Fifthly: *Embryo rescue*: This is conducted by separating embryos from their caryopses and then growing in a culture media under a controlled environment until they generate haploid plants which are treated with colchicine to double their chromosome number (Verma *et al.*, 1999; Campbell *et al.*, 2000). The final result is a large number of homozygous plants differing from each other genetically which are produced in a short period of approximately 18 months comprising the doubled-haploid population.

The generation of new germplasm segregating for target traits is the first step in wheat breeding programs. The second step is the evaluation of these genetic materials in specific environments and studying their interaction with the environmental factors. Many studies showed significant variation in the combining ability between wheat and the maize pollinator even among maize genotypes (Karanja *et al.*, 2002; Verma *et al.*, 1999). In addition, Bitsch *et al.* (1998) reported that large embryo size is one of the factors leading to better germination compared to smaller embryos and this could be obtained from higher auxin concentration and delayed embryo rescue. Light intensity also affects the success of the wheat × maize cross. Campbell *et al.* (2001) reported that two light intensities of (250 and 750 μmol m^{-2} s^{-1}, PAR) led to a 65 and 22% of cross success percentage, respectively. Thus, careful evaluation for this combining ability could be useful to increase the efficiency to regenerate haploid plants. One of the main disadvantageous of the wheat × maize pollination technique is the high cost of the hormonal treatment, though Brazauskas *et al.* (2005) reported that the variation in 2,4-D concentration within the range (20-100 mg/l) had no significant effects on the efficiency of this technique.

2.4 PHYSIOLOGICAL DETERMINANTS OF GRAINS M^{-2}

A physiological model of the determination of grains m^{-2} is:

Grains m^{-2} = RI x RUE x EPI x EFI **Equation 2.1**

Where RI is the radiation interception from emergence to anthesis (GS61), RUE is the radiation-use efficiency (above-ground DM / radiation interception), EPI is the ear partitioning index at anthesis (ear DM/AGDM) and EFI is the ear fertility index (grains per gram ear DM at anthesis). The following review of physiological processes determining grains m^{-2} will broadly address these physiological components (radiation capture, radiation conversion, DM partitioning and the grains to ear DM ratio), as well as phenology, tiller production and floret fertility underlying these components.

2.4.1 Phenology: Tiller production and mortality, floret production and mortality

Because development is a complex process, it is very important to find a standard way to describe this development. The most widely used scale for describing development of cereals is the scale designed by (Zadocs *et al.*, 1974). Table 2.1 shows the 10 main growth stages labelled from 0 to 9.

Table 2.1 Zadoks decimal growth stages (Z0.0 to Z9.9)

Main stage	Description	Sub-stage	Main stage	Description	Sub-stage
0	Germination	**0.0 – 0.9**	**5**	Heading	**5.0 – 5.9**
1	Main stem leaf production	**1.0 – 1.9**	**6**	Anthesis	**6.0 – 6.9**
2	Tiller production	**2.0 – 2.9**	**7**	Grain milk stage	**7.0 – 7.9**
3	Main stem node production (stem elongation)	**3.0 – 3.9**	**8**	Grain dough stage	**8.0 – 8.9**
4	Booting	**4.0 – 4.9**	**9**	Ripening	**9.0 – 9.9**

Source: Adapted from Rawson and Gonzales 2000

Tiller production starts at growth stage 20 and ends at growth stage 29 according to Zadoks' scale (Zadoks *et al.*, 1974). The process of tiller production starts when the tiller bud primordia are initiated at the apex of the shoot after germination and then tillers are produced from these buds in the leaf axils on the main stem (Evans *et al.*, 1975; Kirby and Appleyard, 1984).

Many tillers usually abort before producing fertile ears in a process called tiller mortality; and wheat cultivars differ from each other in tiller survival (Hucl and Baker, 1989; Sharma, 1995). This tiller death typically starts from the onset of the stem-elongation phase due to the increase in competition for assimilates from the stem (Satorre and Slafer, 1999). This was demonstrated in winter wheat by Shanahan *et al.* (1985), who reported genetic variation in grains m^{-2} and grain yield was associated with shoot survival rather than the maximum number of shoots produced. Tillers which emerge later are more likely to be aborted (Davidson and Chevalier, 1990). Elhani *et al.* (2007) reported that under irrigated conditions the main shoot contributed to grain yield more than tillers (68 and 32% respectively), in durum wheat. Evans (1975) suggested some advantages of tillers which do not produce any ears according to their contribution of assimilate to the main shoot and the fertile tillers, especially under abiotic environmental stresses.

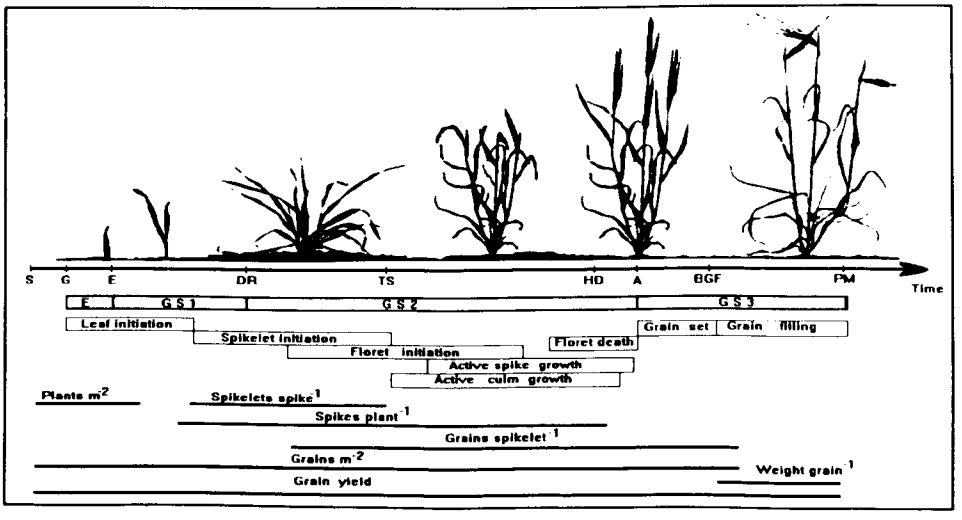


Fig. 2.1 Schematic diagram of wheat growth and development stages, periods of initiation or growth of specific organs and periods of different components of grain yield

Source: Adapted from Slafer and Rawson (1994)

Tiller removal resulted in an 86% increase in grain yield of the main shoot compared to the control treatment in wheat in Australia under water stress due to increases in both spikelets per ear and grains per spikelet. Berry *et al.* (2003) found a negative relation between non-surviving shoots and grain yield in UK winter wheat cultivars under favourable conditions due to the competition between these tillers and developing ears in surviving shoots for assimilates. The competition amongst shoots for assimilate during floret development is reported to be the main driver affecting grain number (Kemp and Whingwiri, 1980).

Wheat genotypes differ from each other in their tillering ability. There is a major recessive gene restricting tillering, the *Tin1A* 'Tiller inhibition gene', located on chromosome 1AS and linked to the hairy glumes trait (Richards, 1988). Moreover, there is evidence that spring wheat genotypes possessing the *Tin1A* gene produce more grains per ear through producing a longer rachis with more spikelets per ear and a higher ear partitioning index at anthesis (Gaju *et al.*, 2009). Effects of the *Tin1A* gene on grain yield and underlying physiological traits have been reported previously in Mexico (Gaju, 2007) and Australia (Duggan *et al.*, 2005), but not in the UK.

An agronomic evaluation of the tiller inhibition gene in four near-isogenic lines of spring wheat (Bodallin ± *Tin1A*, Banks ± *Tin1A*, Kite ± *Tin1A* and Osprey ± *Tin1A*) under terminal drought conditions in Australia was done by Duggan *et al.* (2005), who found that *Tin1A* decreased fertile ears per m^2 by 11%, but increased grains per spike by 9%, grain weight by 2% and harvest index by 2%. Moreover, the grain yield of *Tin1A* lines was 0.2 t ha^{-1} more than freely tillering lines under a high seed rate of 300 seeds m^{-2}, but no differences were observed under a low seeding rate of 150 seeds m^{-2}. Similar results were found by Mitchell *et al.* (2006) in Australia for two freely tillering cultivars (Banks and Kite) and their near-isogenic lines (+ *Tin1A* gene), whereby *Tin1A* lines produced heavier grain weights than the free-tillering lines especially under drought stress. Motzo *et al.* (2004) who examined the progeny of bread wheat genotypes Kite and Janz containing the *Tin1A* gene crossed with the durum wheat (*T. turgidum* subsp. *durum*) cultivars Simeto and Valbelice, found that the positive relationship between the presence of the *Tin1A* gene and grains per ear was associated with higher spikelet fertility. Lines with *Tin1A* partitioned more DM to ears at

anthesis and stored more water soluble carbohydrate in stems than the check lines (Duggan *et al.*, 2005b). Also some studies showed that there is a linkage between the presence of the *Tin1A* gene and the stunting under long days and low temperatures (Duggan *et al.*, 2002).The number of tillers per plant also depends on the environmental factors such as the availability of nitrogen during the tiller production and survival phase . For example, Abeledo *et al.* (2004) found that in 2-rowed barley cultivars released from 1944 to 1998, tillers per plant increased with the increase of nitrogen availability and this response was stronger in modern cultivars than the old ones.

In general, under optimum conditions, the yield potential of genotypes is sink limited rather than source limited (Borras *et al.*, 2004). The grain sink size is the storage capacity of the grains for assimilates, whereas the source size is the photosynthetic capacity of the crop to fill the grains. Therefore, during the pre-anthesis period it is very important to improve ear fertility traits; and this requires genotypes with more fertile florets per unit land area associated with more fertile spikelets per ear and/or fertile florets per spikelet (Foulkes *et al.*, 2011). Floret initiation in the spikelet starts at the double-ridge stage and continues until the appearance of the flag-leaf ligule; and then from the booting stage to anthesis many of these florets abort (Satorre and Slafer, 1999). The number of fertile spikelets per ear is not usually affected by environmental factors after the formation of the terminal spikelet. However, the number of fertile florets per spikelet usually decreases (Evans, 1975). According to Kirby (1988) a decrease of fertile florets per spikelet from 10 to 4 was due to competition between the stem and ear for assimilate. The availability of assimilates to the rapidly growing ear is therefore a key factor affecting the number of grains per ear. Acreche *et al.* (2009) reported the effect of shading at different stages pre-anthesis on the number of grains in a comparison between old and new wheat genotypes in Spain. They found that the old cultivar had fewer grains per spikelet and spikelets per spike (45 and 15%, respectively) than the modern cultivar and shading decreased only the number of grains per spikelet. Also, Bindrabal *et al.* (1998) found that biomass accumulation during the period from booting to anthesis explained 80% of the variation of the grains m^{-2} in spring wheat cultivars in NW Mexico. This is consistent with Cossani *et*

al. (2009) who reported that ear DM growth during the period between 20 days pre-anthesis to 10 days post-anthesis explained the differences in grains m^{-2}, with a $r^2 = 0.84$ for the French bread wheat cultivar (Soisson) released in 1988. In addition, Borras *et al.* (2009) suggested that modifying the pre-anthesis period by decreasing the duration of the pre-GS31 phase whilst maintaining anthesis date and increasing the duration of the stem-elongation phase may increase grains per m^2 by increasing grains per ear without any negative effects on ears per m^2. Bancal *et al.* (2009) suggested that the proportion of florets that set a grain for a floret position within the spikelet was positively associated with the ratio of ovary width to that of the most advanced floret at the onset of floret death, thus emphasizing the role of partitioning in grain set: only florets able to divert assimilate survived after the onset of floret death and eventually set a grain.

Environmental factors, mainly temperature, affect grain yield through modifying the duration of these key development phases in the pre-anthesis period determining grain number. For example under tropical condition in Sudan, it was suggested that the highest yield was obtained when plants flowered during the coolest time of the year due to a manipulation in sowing date (Ishag and Ageeb, 1991).

Gibson and Paulsen (1999) reported a decrease in grain yield and grains per m^2 of hard red winter wheat by 78 and 63%, respectively, when plants were exposed to 35 °C compared to 20 °C ten days after sowing. In addition, Ferris *et al.* (1998) found that grain yield of spring wheat was reduced by 350 g m^{-2} by an increase in temperature of 10°C at flowering time and this decrease resulted from a decrease in grains per ear. Fischer and Maurer (1976) reported from an analysis of several field experiments a 4% decrease in grain yield for each 1 °C increase in temperature and this decrease was related mainly to a decrease in ears per m^2 and grains per spikelet in spring wheat.

The main feature of the 'Green Revolution' was the introduction of the semi-dwarfing genes which decreased the plant height by ca. 20% and decreased stem DM partitioning and thus made more assimilates available for ear growth. This was demonstrated by many studies, e.g. Brooking and Kirby (1981) who

reported similar number of florets were initiated in two F_4 lines homozygous for *Rht-D1b* and their tall parents, but more assimilates were available for ear growth in the semi-dwarf lines resulting in more grains per spikelet. Alvaro *et al.* (2008a) reported a comparison between old and modern Italian and Spanish cultivars and suggested that genetic gains in grains per ear in the Spanish cultivars was due to enhanced spikelet fertility associated with the introduction of the *Rht-D1b* gene. This is in agreement with findings of Miralles *et al.* (1998) examining bread wheat near-isogenic lines in Argentina that the presence of *Rht-B1b* or *Rht-D1b* genes led to more distal fertile florets per spikelet. In addition, genetic improvements in fertile florets per ear are reported associated with more spikelets per spike. For example, Gaju *et al.* (2009) reported that the *Tin1A* gene increased the fertile florets and spikelets per ear resulting from an extension of the phase of spikelet primordia production.

2.4.2 Radiation capture

The number of ears per unit land area influences the green area index during stem elongation. Increasing the green area index (ratio of the area of one side of the canopy area projected areas of leaf lamina, stem-and-leaf-sheath and ear) to the ground area; GAI) results in interception of more solar radiation leading to a higher crop growth rate (above-ground DM per m^2 per day; CGR). The light interception increases up to the point when all the incident radiation is intercepted by the canopy, at which point increasing the green area of the upper leaf lamina will only shade the lower leaf lamina, thus decreasing the CGR (Gardner *et al.*, 1985). The light attenuation within the canopy is determined mainly by the canopy architecture relating to the leaf inclination and the morphology of the ear (with or without awns). Both the quantity and the quality of the intercepted radiation are changed as the radiation is transmitted through the canopy layers. This vertical attenuation of the radiation in the canopy is explained by Beer's law of absorption:

$$I_i/I_o = e^{-kL} \qquad \textbf{Equation 2.2}$$

Where I_o is the PAR (photosynthetically active radiation, 400-700 nm; PAR) above the canopy, I_i is the PAR below the *i* layer of leaves, L is the green area

index of the canopy to the *i* layer of leaves, and *k* is the extinction coefficient of the canopy (Gardner *et al.*, 1985).

Consequently, GAI and leaf inclination affect the amount of radiation transmitted through the canopy (Gardner *et al.*, 1985), and reducing the extinction coefficient (more vertical leaf attitude) would optimize the distribution of the intercepted radiation within the canopy, hence, radiation use efficiency through reducing light saturation of the upper leaves (Araus *et al.*, 1993). This negative relationship between RUE and k was described by Green (1989). Although delaying canopy senescence may play an important role to increase assimilates via current photosynthesis during the grain-filling period under abiotic stress, this is not usually an advantage when grain growth is sink limited under optimal conditions in wheat or maize (Borras *et al.*, 2004).

2.4.3 Radiation use-efficiency

Radiation-use efficiency (RUE) is defined as the amount of DM produced per unit PAR intercepted by the canopy (Stockle and Kemanian, 2009). Crop growth rate of 20 g m^{-2} d^{-1} is considered a typical value for C3 plants (Gardner *et al.*, 1985). However, Loomis and Williams (1963) estimated the maximum theoretical crop growth rate for wheat to be 71 g m^{-2} d^{-1}. Fischer *et al.* (1998) reported no change in the CGR with year of release amongst eight cultivars introduced from 1962 to 1988 in CIMMYT spring wheat in NW Mexico.

Canopy architecture plays a major role in the activity of photosynthesis processes. The main advantages of more vertical leaves compared to the horizontal ones are that they allow more light to penetrate to lower levels of the canopy and also more light is reflected to the canopy rather than to the atmosphere; and as a result canopy photosynthesis is optimised (Stoskopf, 1981 and Duncan, 1971). As described above, it was concluded that the erect canopies are more efficient in RUE attributed to reduced light saturation of the upper leaves (Araus *et al.*, 1993). Also, it was reported that area of the flag leaf is negatively correlated with the rate of photosynthesis (Evans and Dunstone, 1970). In addition, Murchie *et al.*, (2002) reported no association between the rate of grain filling rate and the light-saturated photosynthesis per unit leaf area in six cultivars in rice. Reynolds *et al.* (2000) observed that there was a strong

relationship between net photosynthetic rate (A_n) and yield under warm, irrigated environments in 16 wheat cultivars.

Photosynthesis activity increases linearly during leaf expansion and then photosynthesis declines after the leaf reaches its full size (Hay and Walker, 1989). Leaf age plays a major role in the photosynthesis rate. The photosynthesis process is affected negatively by senescence which is accelerated under nutrient-limited conditions (Gardner *et al.*, 1985). Senescence also has a negative effect on the net assimilation rate (the rate of photosynthesis minus respiration losses; NAR) because although both photosynthesis and respiration is reduced in older leaves, reduction in photosynthesis rate is proportionally higher than the reduction in respiration rate (Milthorpe and Moorby, 1979; Stoskopf, 1981). In addition, Shearman *et al.* (2005) reported that higher flag-leaf specific dry weight (DM per unit leaf area) was positively associated with genetic progress in pre-anthesis RUE in UK winter wheat.

At the metabolic level, Austin (1999) suggested a priority to achieve genetic progress in RUE to be the modification of the CO_2 fixation enzyme Rubisco (ribulose 1-5 bisphosphate carboxylase oxgenase) by increasing its carboxylase activity and decreasing its oxygenase activity. Reynolds *et al.* (2009) suggested another promising way to increase RUE is to improve photosynthetic efficiency through improving Rubisco's catalytic activity which may theoretically increase the yield by 50% or more. Parry *et al.* (2007) and Parry *et al.* (2011) postulated several avenues to improve Rubisco's activity, e.g. increasing the amount of Rubisco protein in the chloroplast, improving Rubisco's catalytic rate, maintaining Rubisco activity, faster regeneration of RuBP (ribulose bisphosphate) , increasing the CO_2 concentration at Rubisco's catalytic site and decreasing the lost energy due to photorespiration. Several authors have concluded that if the carbon concentration mechanisms in the C4 plants were introduced into the C3 plant wheat, a quantum step in yield gains could be expected (Reynolds *et al.*, 2009 and Parry *et al.*, 2011).

2.4.4 Optimizing DM partitioning and ear fertility index

Dry matter partitioning is the allocation of assimilate which is produced by green tissues amongst plant components for growth and storage processes (Gardner *et al.*, 1985). Many studies indicated that the proportion of assimilates partitioned to the ear pre-anthesis was positively correlated amongst genotypes with the grain number per m^2, e.g. Slafer *et al.* (1990) reported genetic progress in grain yield in Argentina through HI was due to the improvement of pre-anthesis biomass partitioned to the ears. Many investigators also found that as less assimilate is partitioned to stems, HI increased. For example, Austin *et al.* (1980) reported decreased stem dry weight was the main reason for the increase of HI in UK cultivars increased from 1908 to 1978 and he argued that a further increase in HI (to 60%) could be achieved by decreasing stem-and-leaf sheath partitioning at harvest to 20% whilst maintaining the above-ground biomass. Similarly, Alvaro *et al.* (2008b) found in an experiment conducted in Spain for several Italian and Spanish cultivars divided into old (released before 1930), intermediate (released from 1950 to 1985) and modern (released from 1988 to 2000) cultivars, that the partitioning of the pre-anthesis assimilate to the ear at anthesis was increased with breeding. On the other hand, Abbate *et al.* (1998) reported that in the Argentinean cultivars released between 1984 and 1994 the yield improvement was related to the increase of the ear fertility index rather than ear partitioning index at anthesis. Bancal (2008) investigating the relationship between floret fertility and rates of stem and spike growth pre-anthesis for six French winter wheats (chosen for their differences in ear to stem ratio) concluded that even though ear:stem competition decreased floret survival, it was only loosely correlated to grain number. However, in a recent review of the determinants of floret fertility in wheat the onset of floret death was shown to be associated with the timing of accelerated ear growth at around the onset of stem elongation in six independent experiments in wheat (Gonzalez *et al.*, 2011). Changes in flag-leaf and lamina DM partitioning with plant breeding have been less important for increasing grains per m^2 than those in the ear: stem ratio (Austin *et al.*, 1989; Fischer *et al.*, 1998; Foulkes *et al.*, 2005). Fischer *et al.* (1998) reported that there was no change in the flag-leaf area or specific leaf dry weight from 1962 to 1988 in spring wheat. Nonetheless, in the UK, there was a

decrease in the flag leaf green area and an increase on flag leaf specific dry weight.

It was reported that the percentage contribution of stem water soluble carbohydrate (WSC) to the grain yield was at least 21% in spring wheat in Australia (Borrell *et al.*, 1989). This trait was positively associated with grain yield under both irrigated and drought conditions amongst six cultivars in UK winter wheat (Foulkes *et al.*, 2007b). Dreccer *et al.* (2009) suggested that an increase in the grain weight in high stem WSC lines may compensate for low grains per unit area. Furthermore, Dreccer *et al.* (2009) found that lines with high amounts of stem WSC yielded the same or higher than lines with low WSC amounts, i.e. due to lower grains m^{-2} but heavier grains. Shearman *et al.* (2005) reported WSC content in stems and leaf sheaths shortly after anthesis increased by 4.6 g m^{-2} yr^{-1} in the UK winter wheat from 1972 to 1995 and was positively correlated with grain yield. Moreover, Foulkes *et al.* (2007) suggested that the recent increase in biomass in UK winter wheat cultivars was partly associated with an increase in the stem WSC. Genetic variation in stem WSC amount in the range 220 – 300 g m^{-2} was observed by Foulkes *et al.* (2002) amongst six winter wheat cultivars grown in the UK. Genetic variation in the percentage of WSC in the stem at anthesis is reported from 5-43% in wheat (Reynolds *et al.*, 2007; Ehdaie *et al.*, 2006; Foulkes *et al.*, 1998). Also, in a study investigating 22 wheat genotypes in Australia, it was proposed that there were significant differences in the percentage stem WSC at anthesis (from 11.2 to 21.3%) among those genotypes and this variation was associated with a large broad-sense heritability (H = 0.90) (Ruuska *et al.*, 2006). Differences may arise because of differences in carbon availability or the available capacity for carbon reserve storage being different between genotypes.

Borrell *et al.* (1993) found in a comparison between near-isogenic lines of cultivar 'Triple Dirk' possessing the *Rht-B1b* or *Rht-D1b* gene reduced the percentage of WSC in the stems by 35 and 39%, respectively, compared to the tall control and this was a result of the reduction in the plant height by 21%. However, stem WSC generally makes a higher percentage contribution to yield under unfavourable conditions where heat and water stress are present during grain filling (Blum *et al.*, 1994). Nevertheless, Davidson and Chevalier (1992)

reported that more stem WSC was accumulated and remobilized from spring wheat stems grown under irrigated than under non-irrigated conditions in the USA. This result was supported by Ehdaie *et al.* (2008) who reported in spring wheat that the contribution of stem WSC to the grain yield under irrigation in California ranged from 19.1 to 53.6%. Ehdaie *et al.* (2006) found a strong positive correlation (r = from 0.89 to 0.99) between pre-anthesis stem WSC content and the utilized amount of WSC, indicating cultivars which accumulate more WSC pre-anthesis seem able to mobilize this storage as efficiently as cultivars with lower stem WSC accumulation. A larger amount of water soluble carbohydrate is mobilized during grain-filling from the second internode rather than the first one (the peduncle) (Cruz-Aguado *et al.*, 2000).

Foulkes *et al.* (2009) suggested that selecting for lower stem WSC DM partitioning at anthesis may not result in increased ear DM at anthesis under Northwest Europe conditions, since stem WSC accumulation in the peduncle mainly occurs after sink demand of the ear and structural stem carbohydrate has been satisfied. A more beneficial strategy for increasing ear partitioning index was suggested to be decreasing structural stem DM partitioning at anthesis which may compete more strongly with ear growth.

2.5 DETERMINANTS OF GRAIN WEIGHT

2.5.1 Determinants of potential grain weight

The individual grain weight has high values of heritability (Welsh, 1981). Bhatt (1972) found that this high heritability improved the efficiency of selection for high grain weight. Furthermore, Sun *et al.* (1972) indicated that the broad sense heritability for grain weight ranged from 51 to 85%.

The final number of the endosperm cells which are formed at the end of the cellularization phase is a key factor determining both the potential grain weight and the DM accumulation in the grain (Brocklehurst, 1977; Foulkes *et al.*, 2011). At the end of the cellularization phase, the grain contains the maximum volume of water and this volume appears to be closely correlated with the final size of the grain (Flafer *et al.*, 2009).

Martinez-Carrasco *et al.*, (1988) reported that halving the ears at several dates after anthesis led to increase in the number and size of the A type of the starch granules in three cultivars of winter wheat and the earlier the treatment after anthesis the higher the effect. Some workers suggest that potential grain weight is not only affected by high temperature during the post-anthesis phase but also during the pre-anthesis phase. These negative effects of high temperature during pre-anthesis on grain weight were due to reducing the carpel size (Calderini *et al.*, 1999a; Calderini *et al.*, 1999b; Calderini *et al.*, 2001). In addition, Calderini and Reynolds (2000) reported that a de-graining treatment applied pre-anthesis (at heading) had a larger effect on the grain weight than a post-anthesis treatment and this was due to a positive effect on the carpel size of the de-graining treatment pre-anthesis. However, increasing temperature (28 °C day, 20°C night) during the period of grain growth accelerated the rate of cell division and the dry matter accumulation but also shortened this period which resulted in similar cell number and final cell size compared to control treatment (23 °C day, 15°C night) (Nicolas *et al.*, 1984). Radley (1976) also suggested that the maximum grain size correlated negatively to the increase of the temperature and this effect was positively related to a significant increase in the gibberellins. Foulkes *et al.* (2011) suggested that improving our understanding of the factors such as temperature affecting grain size and weight especially of the maternal tissues would be a key factor to increase grain weight potential.

Jones et *al.* (1985) found a strong correlation between the number of endosperm cells and the number of starch granules and final grain weight of wheat and maize (r = 0.76 and 0.85, respectively). Similar results were obtained in six lines of wheat Gleadow *et al.*, (1982). Moreover, Lizana *et al.* (2010) reported that grain length was the trait most strongly correlated genetically to final grain weight (r^2 = 0.98) and the duration of the first third of grain filling is more related to potential grain weight. Not all the initiated endosperm cells survive until the end of cell division phase. Gao *et al.* (1992) found that final number of endosperm cells depends on the number of lost cells during this phase.

2.5.2 Determinants of final grain weight

The final grain weight is determined by the rate and the duration of grain filling. Many studies have been conducted to investigate the factors affecting both these processes. Temperature is the main environmental factor affecting the rate and the duration of grain filling. The stay-green trait may be an important trait in future years for increasing grain weight. In barley grown under temperate conditions in the UK, variation of grain weight of cv. Pearl amongst six sites was associated more with rate than the duration of grain growth (Bingham *et al.*, 2007).

Many studies were carried out to examine the effect of temperature on the final grain weight. Jones *et al.* (1985) reported a reduction of 49 and 78% in grain weight and a reduction in starch granules of 70 and 97% in starch granules compared with field temperature when plants were exposed to 15 and 30°C, respectively. This was in agreement with Commuri and Jones (2001). The negative effect of increasing temperature on the final grain weight was reported to be due to a decrease in the B-type granules of starch rather than the A-type granules (Bhullar and Jenner, 1985).

Generally, duration of grain filling decreases and the rate of grain filling increases as the temperature increases (Calderini *et al.*,1999). However, Wardlaw, (1994) reported that the increase in the grain filling rate does not compensate the reduction in the period of grain filling and the result is a reduction in the grain weight. Reduction in grain weight due to increasing temperature was reported by many researchers. For example, Asana and Williams (1965) in Australia found a reduction of 16% in grain weight when temperature increased from 25 to 31°C, but increased temperature from 9 to 12°C at night did not affect grain weight. Tashiro and Wardlaw (1989) reported reduction in grain weight of the Australian wheat cultivar Banks by 5% for every 1°C increase in temperature from 17.7 to 32.7°C. Yin *et al.* (2009) assessed the effect of increasing temperature on winter wheat at two temperatures (20/15 and 25/20 °C for day/night) from anthesis till maturity in a glasshouse experiment in the Netherlands. They found that increasing the temperature by 5 °C decreased the duration of grain filling by more than 30% and at the same time increased the

grain filling rate by 20%. In addition, Wiegand and Cuellar (1981) reported a shortening of 3.1 days in the grain-filling period and a reduction in rate of grain growth of 2.8 mg $°C^{-1}$ in both winter and spring wheats in field experiments in Texas. Moreover, Ugarte *et al.* (2007) reported in a field experiment in Argentina grain weight decreased up to 23% when plants were exposed to a temperature 5.5C° higher than the air temperature from booting to anthesis.

It was reported by Wardlaw *et al.* (1980) that altering either the sink or the source did not prevent the negative effect of increasing temperature on grain size which indicate that this effect is related to the grain itself.

With regard to genetic variation in grain weight, under heat and/or water stress high grain filling rate seems to be the more important of the two determinants (Bruckner and Frohberg, 1987). These authors reported that, extension of the period of grain filling does not seem to be a breeding strategy to increase individual grain weight under heat and water stress conditions. In durum wheat, Motzo *et al.* (2010) suggested that the variation in the individual grain weight was related mainly to the differences in the grain filling rate. However, it was suggested that due to the weak relation between the rate of grain filling and the grain weight, genetic improvement in the selection of higher grain-filling rate would not be a priority (Frederick and Bauer, 1999). In favourable conditions where water and the heat stresses are absent, genotypes which have a longer grain filling duration seem to be more effective than those with shorter grain filling duration (Evans *et al.*, 1975; Austin, 1982)

Many studies have reported the inverse relationship between grains per ear and grain weight. e.g. Bremner and Rawson (1978) found negative relation between grain weight and its distance from the ear rachis. Wiersma *et al.* (2001) found that, after eight cycles of recurrent selection for grain weight in spring wheat, grains per ear decreased in proportion to the increase in grain weight. Aggarwal *et al.* (1986) observed that competition among grains started when grain number increased above 11,000 grains m^{-2} in a study of 17 cultivars of *Triticum aestivum*, *T. Durum* and triticale. However, the usual negative relationship between the number of grains and the individual grain weight, e.g. with the introduction of the semi-dwarf genes, is mainly due to the increase of the number of grains formed at distal positions of lower potential grain weight and

consequently lowering the average of all grains (Acreche and Slafer, 2006; Miralles and Slafer, 1995).

It was suggested that to break the negative relationship between grain number and weight it is necessary to the increase the grains m^{-2} and the availability of assimilates simultaneously to avoid increased competition during the grain growth (Slafer *et al.*, 1996). In addition, Gaju *et al.* (2009) reported that producing a less compact ear in CIMMYT spring wheat advanced lines (increased rachis length per spikelets) led to more ear photosynthesis per spikelet and hence a larger potential and final grain weight compared to a check cultivar Bacanora with conventional ear phenotype.

As described above in section 2.2, individual grain weight was usually reported not to increase with year of release in investigations examining historic sets of cultivars, e.g. (Loss *et al.*, 1989). More recently, some other studies with cultivars released since about 1990 indicated that grain weight was also an important avenue for the yield progress in spring wheat, e.g. Underdahl *et al.* (2008) who found grain weight was associated with yield progress of hard red spring wheat cultivars from 1968 to 2006 in the Great Plains. In winter wheat, a few previous studies also explained genetic gains in yield by an increase the grain weight, e.g. Cox *et al.* (1988) who attributed yield progress in Kansas from 1874 to 1987 to heavier grain weight and a decrease in days to heading and plant height.

2.6 Source-sink relationships

A source organ produces sugars which are translocated to a sink organ where these sugars are utilized (Gardner *et al.*, 1985). In other words, the organ is defined as a source or a sink according to the direction of the assimilates, and sometimes the same organ such as young leaves may start as sink organs when they are not able to produce enough sugars to meet their requirements and then become source organs when they have the ability to produce sugar through photosynthesis in excess of requirement (Hay and Walker, 1989).

Many studies suggest that grain growth of wheat cultivars is more likely to be sink limited rather than source limited under optimal conditions. For example,

Zhang *et al.*, (2010) reported that under the high-rainfall regions of south-western Australia spring wheat are more likely to be sink limited rather than limited by assimilate availability. Borras *et al.* (2004) concluded in a review of 18 studies with different types of source-sink manipulation treatments that grain growth of wheat under favourable conditions was almost always sink limited, as the availability of the assimilates during the grain filling period were usually at a saturation level. Snyder *et al.* (1993) reported no change in grain mass in soft red winter wheat in response to a sink manipulation treatment where 25% of spikelets were removed at four days post-anthesis. Cartelle *et al.* (2006) reported that, under Mediterranean conditions in Spain, grain yield in both old and modern varieties was mainly sink limited. Miralles and Slafer (1995) observed that in *Rht* isogenic lines of spring wheat increasing the source-sink ratio by removing all spikelets from one side of the ear seven days after anthesis did not increase the individual grain weight in semi-dwarf and standard height cultivars, but resulted in a slight increase in the dwarf cultivars. Slafer and Savin (1994) reported that altering the source-sink ratio by removing all spikelets from one side of the ear 10 days after anthesis did not affect the grain weight at apical, central or basal positions in the ear, and grain yield in the studied cultivars was either sink or co-limited by source and sink. Walpole and Morgan (1974) describe the source-sink co-limitation when the rate of assimilate supply was sufficient for the grain growth during the first period 'twenty days' after anthesis followed by the phase till the physiological maturity when grain growth was limited by the assimilate supply. Indeed, Aggarwal *et al.* (1990) found that grain growth was not affected after removal of the flag leaf post-anthesis and suggested that breeding for smaller flag leaves would be useful to allow more assimilates to be allocated to ears at anthesis. In addition, Ahmadi *et al.* (2009) reported that defoliation of all leaves at booting and anthesis did not reduce either the number of grains or grain weight in winter wheat cv. Godes in Iran. In general, these investigations tended to show that grain yield potential was limited under optimal conditions by the grain sink size, defined as the capacity of the grain to store assimilates, rather than grain source size defined as the photosynthetic capacity of the crop to supply assimilate to the grains during grain filling. It was reported by Jenner and Rathjen (1975, 1978) that the decline in the starch accumulation was not due to a decrease in the assimilate supply but

rather to factors operating within the grain itself leading to a fall in the capacity of the grains to synthesize starch.

A small number of studies, however, are not in agreement with this conclusion, e.g. shading plants early after anthesis led to a reduction in the grain size; also halving the grain number in the ear after anthesis resulted in an increase in the grain weight in the spring wheat cultivar 'Kleiber' (Martinez-Carrasco and Throne, 1979). Kurk *et al.* (1997) reported that modern cultivars were more likely to be source limited than an older one based on responses to defoliation of the flag leaf during the post-anthesis period in cultivars released from 1920 to 1990. Acreche and Slafer (2009) reported that, in bread wheat genotypes released from 1940 to 2005 in Spain, when modifying the source/sink balance by removing all the upper-half of the spike grain weight was not changed in the old cultivars and increased in the newest cultivars. They concluded that modern genotypes have a co-limitation of grain growth by source and sink rather than source limitation. Moreover, Koshkin and Tararin (1989) concluded in a study on spring wheat cultivars in Russia released from 1950 to 1980 that grain yield was source limited for the modern cultivars, since the difference between the actual and potential yield of the ear was higher in the modern cultivars. Cruz-Aguado *et al.* (1999) also suggested that, under tropical conditions, grain yield of spring wheat was source limited. Ma *et al.* (1995) found that in the red winter wheat in USA the increase of grain weight in the ear of main shoot and tillers after 50% removal of the spikelets at anthesis ranged from 9 to 23% and 11 to 26%, respectively. In addition, in a study of the effect of source-sink modification on a historical set of durum wheat cultivars, Alvaro *et al.* (2008) showed that the basal part of the ear was most affected by the source-sink manipulation and modern genotypes were generally source-limited. Decreasing the number of spikelets per spike through source/sink manipulation treatments does not therefore lead to an increase the final grain weight in all cases, and there are some indications that more modern cultivars may be in closer source/sink balance than their predecessors. In general, increasing source size pre-anthesis is important for increasing ear DM at anthesis and consequently grain m^{-2}. Higher grains m^{-2} may also increase grain growth post-anthesis through increasing post-anthesis RUE in response to increased grain sink strength.

Cruz-Aguado *et al.* (1999) found that, under tropical conditions, final grain weight in spring wheat decreased when all spikelets were removed except the four central spikelets due to feedback inhibition of photosynthesis. Furthermore, Ma *et al.* (1996) reported that no differences were found in the final grain weight between 50 and 75% of spikelets removal treatments and the amount of WSC in stems of the 75% spikelets removal treatment was higher than a 100% spikelets removal treatment but less than with a 50 and 25% spikelets removal treatment. Limitation in sink capacity was concluded to be in part the reason for a reduction in RUE during the second half of grain-filling in barley in the UK (Bingham *et al.*, 2007). Some studies have indicated that increasing post-anthesis photosynthetic capacity was associated with genetic progress of the yield, e.g. Fischer *et al.* (1998) who reported that improvement in some leaf traits (stomatal conductance and canopy temperature depression) measured in both pre- and post-anthesis phases indicative of photosynthetic activity was correlated with genetic gains in yield potential in spring wheat in NW Mexico from 1962 to 1988. This likely reflected that post-anthesis source-type traits increased in response to an increased sink strength post-anthesis associated with genetic progress in grains m^{-2}. These authors also reported that there was no significant effect of other leaf traits such as flag leaf area on grain yield progress.

2.7 Interaction of plant density and ear fertility traits

It is well known that the optimum plant density varies according to plant traits such as tillering ability and lodging resistance (Gardner *et al.*, 1985). Faris and De Pauw (1980) found that optimum seed rate ranged between 300 and 675 seeds m^{-2} for spring wheat cultivars in North-western Canada and suggested that tests of optimum seed density should be done before release of cultivars.

It was concluded that increasing plant density caused a decrease in fertile tillers $plant^{-1}$, spikelets ear^{-1}, grains ear^{-1}, and at the same time increasing the sterile spikelets ear^{-1} and these effects increased sharply towards the apex and the base of the ear^{-1} in the semi-dwarf high yielding wheat cultivar 'Sonalika' (Mishra and Mohapatra., 1987).

Thinning treatments in spring wheat between 50 and 100 days after sowing resulted in a slight increase in spikelets per spike; however, grains per spike and individual grain weight were decreased significantly (Fischer and Laing, 1976). Moreover, decreasing seeding rate as low as 16 kg ha^{-1} led to an increase in the proportion of the secondary tillers; however, it also resulted in a decrease in the plant population by 63.3% and grain yield 0.8 Mg ha^{-1} in winter wheat genotypes in the Great Plains (Geleta *et al.*, 2002).

Generally, plant density is inversely related with grains per ear, as interplant competition is increased and consequently less assimilates from photosynthesis are available for ear growth (Darwinkel, 1978). However, genotypes may differ from each other in their response to inter-plant competition. Otteson *et al.* (2007) reported responses of four spring wheat cultivars in the USA to two seed rates (290 and 420 seeds m^{-2}); three cultivars did not respond to seed rate whereas the fourth produced more grains m^{-2} at the lower seed density since plants were less tolerant to increasing inter-plant competition. The advantage in this case would be a saving in costs of seed during sowing. Das and Yaduraju (2011) found that leaving 20% rows unsown caused a 8-17% increase in grain yield compared to 0% rows unsown. Chen *et al.* (2008) observed that increased yield obtained by narrow row spacing cannot be achieved by increasing seed rate in wide row spacing in hard red spring wheat in Montana, USA.

Reynolds *et al.* (1994) reported that low yield potential lines were more responsive to decreasing the inter-plant competition than high yield potential lines. They suggested that high yield potential lines have better adaptation to increased inter-plant competition at high plant densities. Increasing plant density is usually positively correlated with above-ground biomass and grain yield, but this may not mean a change in HI. Sharma and Smith (1987) in their study of the effect of two seed rates (67.2 and 16.8 kg ha^{-1}) on ten winter wheat genotypes noted that changing the plant density did not have any significant effect on HI. However, increasing seed rate above the economic optimum seed rate will not give more profit. Otteson *et al.* (2008) found that increasing the seed density from 290 to 420 seeds per square metre increased ears m^{-2}, but decreased the other yield components significantly. Yu *et al.* (1988) indicated in two experiments on winter wheat in China and USA that grains per ear decreased

from 51 to 28 as plant density increased from 18 and 229 plants m^{-2}, respectively, due to higher floret abortion rate with increasing plant density. Similar results were reported by other authors (Done and Whittington, 1980; Carr *et al.*, 2003; Lloveras *et al.*, 2004 and Geleta *et al.*, 2002). Grain yield was not increased when seed density increased from 100 to 160 seeds m^{-2} in winter wheat in Iran (Memmat and Taki, 2001).

Whaley *et al.* (2000) reported that increasing the plant population density from 20 to 640 plants m^{-2} in UK winter wheat resulted in a decrease in the number of grains per ear from 48 to 32 and that was associated with a decrease in RUE and an increase in the light extinction coefficient and they found that grain yield was not affected in the range 80-320 plants m^{-2}. Fischer *et al.* (1976) in spring wheat in Mexico found that grain yield and most yield components were not affected in the range of 10 to 45 cm row spacing or 80 to 200 plants m^{-2}. Also, no significant differences in grain yield m^{-2} were reported between plant densities of 83 and 416 plants m^{-2}; since plants under low plant density produced 8.13 g $plant^{-1}$ compared to 1.67 g $plant^{-1}$ of high plant density (Stephen et al., 2005). Therefore, increasing the number of tillers per plant under low plant densities may sometimes compensate fully for the decrease in the plants m^{-2}. Thus, using genotypes possessing tiller inhibition *Tin1A* gene with high grains per ear in plant breeding programmes may increase the economic optimum seed rate compared to conventional cultivars (see chapter 7 in which this hypothesis is examined in the present study)

2.8 OBJECTIVES AND HYPOTHESIS

2.8.1 The objectives of this study were to:

1. Quantify changes in grains m^{-2}, grain weight, HI and harvest biomass associated with yield progress for a set of 12 representative CIMMYT spring wheat cultivars released from 1966 to 2009 in field experiments in high radiation, irrigated conditions in NW Mexico.
2. Identify the physiological basis of these changes by examining the developmental rates, green area production, radiation capture, radiation-use

efficiency (RUE) , partitioning of dry matter and leaf activity traits of the 12 historic cultivars through the season.

3. Quantify the changes of the source/sink balance of the twelve representative CIMMYT spring wheat cultivars released from 1966 to 2009.

4. Quantify effects of the tiller inhibition *Tin1A* gene on ear-fertility traits and grain yield in field experiments under rainfed UK environments and the high radiation, irrigated environment of NW Mexico by comparison across groups of +/- *Tin1A* doubled-haploid lines balanced for flowering time and plant height, and investigate the physiological basis of effects of the *Tin1A* gene.

5. Quantify responses of ear fertility traits and grain yield in DH lines segregating for the *Tin1A* gene to plant density and investigate the physiological basis of these responses to plant density under rainfed UK environments and the high radiation, irrigated environment of NW Mexico.

6. Identify physiological traits and trade-offs and synergies between traits for raising yield potential and improve understanding of the physiological mechanisms determining the traits to facilitate the deployment of yield-enhancing traits in plant breeding programs in Mexico, the UK and worldwide.

2.8.2 The specific hypotheses to be tested in this study are:

1. Grain yield potential has increased linearly with year of introduction in spring wheat cultivars released by CIMMYT in the period from 1966 to 2009.

2. There is a positive association between this genetic increase of grain yield and each of grains m^{-2} and HI, but genetic progress of HI with year of release is non-linear and is beginning to plateau with plant breeding.

3. Genetic gains in grains m^{-2} have been associated with increases in both number of ears m^{-2} and grains ear^{-1} from 1966 to 2009.

4. Genetic gains in CIMMYT spring wheat cultivars from 1966 to 2009 in grains ear^{-1} have been positively associated with rachis length and fertile spikelets per ear.

5. Individual grain weight has not changed with plant breeding in the CIMMYT program in NW Mexico from 1966 to 2009.

6. Genetic progress in above-ground biomass in CIMMYT spring wheat cultivars from 1966 to 2009 has been non-linear with year of release with gains in biomass beginning to contribute to genetic gains in grain yield coinciding with the plateau in HI.

7. Plant height has not changed with plant breeding in CIMMYT spring wheat cultivars over the period 1966 to 2009 since each cultivar introduced during this period contained a semi-dwarf gene (either *Rht-B1b* or *Rht-D1b*).

8. Genetic progress in grains m^{-2} has been positively associated with dry matter partitioning to the ear at anthesis (GS61) and in turn with ear DM per unit ground surface area at anthesis.

9. The proportion of above-ground DM partitioned to structural stem at GS61 is more closely correlated with changes in HI through CIMMYT wheat plant breeding than leaf DM partitioning or stem WSC DM partitioning.

10. There is a negative relationship between the percentage of DM partitioned to ears and to stems at GS61 amongst the set of historic CIMMYT cultivars released from 1966 to 2009.

11. Radiation interception by the canopy and RUE in the pre-anthesis phase have not changed with plant breeding from 1966 to 2009 in the CIMMYT program.

12. Canopy temperature and stomatal conductance in the pre-anthesis phase have not changed with plant breeding from 1966 to 2009 in the CIMMYT program.

13. There has been no change in the stem WSC accumulation at GS61+7 days and the amount of stem WSC remobilization to the grains with plant breeding from 1966 to 2009 in the CIMMYT program.

14. Grain growth of modern CIMMYT spring wheat releases is sink-limited as indicated by response of grain growth to degraining (removing 50% spikletes from the ear) at GS61+14 days.

15. The *Tin1A* gene reduces ears per m^2 at harvest but increases rachis length, spikelets per ear and grains per ear and hence grains per m^2 in wheat grown under UK rainfed conditions and high radiation, irrigated conditions in NW Mexico when gown at commercial plant density.

16. The *Tin1A* gene increases grain yield in wheat grown under UK rainfed conditions and high radiation, irrigated conditions in NW Mexico when grown at commercial plant density.

17. Lines with the *Tin1A* allele produce relatively fewer ears per m^2 than non-*Tin1A* lines under low plant density than under high plant density, so the economic optimum plant density for *Tin1A* lines is higher than for non *Tin1A* lines.

CHAPTER 3 MATERIALS AND METHODS

This chapter describes the materials and methods used in the field experiments carried out in Mexico and the UK.

Four experiments were conducted in NW Mexico at the CIMMYT research station at Ciudad Obregon. Two of these experiments studied a set of twelve historic CIMMYT spring wheat cultivars released from 1966 to 2009 in 2008/9 and 2009/10. The other two experiments examined selected lines from a doubled-haploid (DH) population derived from a cross between CIMMYT spring wheat advanced line L14 and UK winter wheat Rialto contrasting for the presence/absence of the *Tin1A* allele for tiller inhibition and their interaction with seed rate in 2008/9 and 2009/10.

Two field experiments were conducted in the UK, one in 2008/09 at KWS-UK Ltd in Thriplow, Hertfordshire and one in 2009/10 at the University of Nottingham Farm, Sutton Bonington campus, Leicestershire. The plant material for both these experiments was selected lines from the CIMMYT L14 x Rialto wheat DH population contrasting for the presence/absence of the *Tin1A* allele and the Rialto parent. In the experiment at Thriplow in 2008/09 the DH lines were examined at one seed rate, and in the experiment at Sutton Bonington in 2009/10 at two rates.

3.1 EXPERIMENTAL FIELD SITES

3.1.1 CIMMYT, Ciudad Obregon site

Experiments were conducted at the CIMMYT experimental station near Cd. Obregon, NW Mexico (20° 27′ N, 54° 109′ W, 38 m above sea level). The site is a temperate high radiation environment and the experiments were carried out under full irrigation (Reynolds *et al*, 2007). The soil type is coarse sandy clay, mixed montmorillonitic typic calciorthid, low in organic matter (<1%) and slightly alkaline (pH 7.7) (Limon-Ortega *et al.*, 2002).

3.1.2 The UK sites

Two experiments were carried out during the seasons of 2008/9 and 2009/10 as follows: The first one was conducted at KWS-UK Ltd Thriplow, Hertfordshire (52° 06′ N, 0° 06′ E), 66 m above sea level in 2008/09. The second experiment was conducted at University of Nottingham Farm, Sutton Bonington, Leicestershire (52° 50′ N, 1° 15′ W), 80 m above sea level in 2009/10. At Sutton Bonington the soil type was a medium stony loam to 80 cm over Kyper marl clay with good drainage (Dunnington Heath Series). At KWS the soil type was a sandy clay loam.

3.2 EXPERIMENTAL TREATMENTS AND DESIGN

3.2.1 CIMMYT wheat historic releases experiments

In each of the experiments in 2008/09 and 2009/10, 12 cultivars released from 1966 to 2009 were examined (Table 3.1). A randomized complete block design was implemented with four replications. Each plot consisted of two beds, each of which was 4 m long and 0.8 m wide with two rows 30 cm apart per bed.

3.2.2 CIMMYT L14 x Rialto DH population (*Tin1A*) experiments

3.2.2.1 Experiments at CIMMYT Cd. Obregon

A split plot randomised complete block design with three replications was implemented in 2008/9 and 2009/10, with three seed densities (50, 150 and 450 seeds per square metre); seed rates were randomized on main plots and eight genotypes randomized on sub-plots. The eight genotypes were eight DH lines (4 +*Tin1A* allele) and (4 -*Tin1A* allele) from the DH population derived from the cross between the UK winter wheat cultivar Rialto and the CIMMYT spring wheat large-ear phenotype line (L14) (Table 3.2). Lines were selected according to previous data to be balanced for flowering date and crop height across the +*Tin1A* and –*Tin1A* groups. Sub-plot size was 2 m × 0.80 m, with 2 rows 30 cm apart per sub-plot.

Plate 3.1 The experiment site at CIMMYT experimental station in Cd. Obregon in north-west Mexico for wheat historic releases in 2008/9.

Plate 3.2 The experiment site at CIMMYT experimental station in Cd. Obregon in north-west Mexico for L14 x Rialto DH population (*Tin1A*) in 2009/10.

3.2.2.2 Experiment at KWS UK Ltd Thriplow, Hertfordshire UK 2008/9

Twenty four DH lines (12 +*Tin1A* allele) and (12 -*Tin1A* allele) from the L14 x Rialto population were used. The groups of lines were selected as far as possible to have similar plant height and flowering time, according to previous data. Lines were selected in pairs, e.g. every +*Tin1A* line has a non-*Tin1A* pair with similar height and flowering time (Table 3.3). In this experiment, there was only one seed rate (300 seeds m^{-2}). A completely randomised design in three replicates was implemented. Plot size was 1 x 6 m with 8 rows 12 cm apart per plot.

3.2.2.3 Experiment at Sutton Bonington, Leicestershire UK 2009/10

In this experiment the same 24 DH lines as examined in the experiment at Thriplow (Table 3.3) were examined, at two seed rates (40 and 320 seeds m^{-2}) in a split plot design in three replicates. Seed rate was randomized on main plots and DH lines were randomized on sub-plots. Sub-plot size was 12 × 1.625 m, with 12 rows 13 cm apart per sub-plot.

Table 3.1 Information on the year of release, pedigree, the presence of Norin 10 semi-dwarfing genes and the *1BL/1RS* translocation for 12 CIMMYT spring wheat cultivars released from 1966 to 2009

Specific name	Year of release	Pedigree	Norin 10 semi-dwarfing genes	Presence of *1BL/1RS* translocation
Siete Cerros	1966	PENJAMO T 62/GABO 55	*Rht-B1b*	No
Pavon	1976	VICAM S 71//CIANO F 67/SIETE CERROS T66/3/KALYANSONA/BLUEBIRD	*Rht-D1b*	No
Seri	1982	KAVKAZ/BUHO//KALYANSONA/BLUEBID	*Rht-B1b*	Yes
Bacanora	1988	JUPATECO F 73/BLUEJAY//URES T 81	*Rht-B1b*	Yes
Attila (PBW 343)	1990	NORDDEPREZ/VG9144//KALYANSONA/BLUEBIRD/3/YACO/4/VEERY #5	*Rht-B1b*	Yes
Baviacora	1992	BOBWHITE/NACOZARI F 76//VEERY/3/BLUEJAY/COCORAQUE F 75	*Rht-B1b*	Mixed
Tarachi	2000	SERI M 82/RAYON F 89	*Rht-B1b*	No
Tacupeto	2001	BABAX*2/9/KENTANA/BAGE//FRONTANA/URQUIZA O GRAL. URQUIZA/3/BONZA/4/TORIM F 73/5/ALDAN/6/SERI M 82/7/YECORA F 70/8/OPATA M 85	*Rht-B1b*	No
Roelfs	2007	TACUPETO F2001*2/KUKUNA	*Rht-B1b*	No
Navojoa	2007	ATTILA/PASTOR	*Rht-B1b*	No
Becard	2009	WEEBILL1*2/KIRITATI	*Rht-B1b*	No
Croc_1/Ae Squarrosa (205)//Borl95/3/Prl/Sara/Tsi/Vee#5/4/Fret2	2009	CROC_1/AE.SQUARROSA (205)//BORLAUG M 95/3/PARULA/ICTA SARA 82//TESIA F 79/VEERY #5/4/FRET2	Information not available	Information not available

Table 3.2 The DH lines of the L14 x Rialto population examined in the experiments in 2008/09 and 2009/10 at C. Obregon.

Line pairs	Line name	*Tin1A* allele	Flowering date*	Height (cm)*
Pair 1	L14/Rialto-1	Yes	14 Mar	69.9
	L14/Rialto-87	No	13 Mar	65.8
Pair 2	L14/Rialto-61	Yes	4 Mar	88.2
	L14/Rialto-93	No	10 Mar	92.9
Pair 3	L14/Rialto-90	Yes	13 Mar	86.8
	L14/Rialto-51	No	10 Mar	89.8
Pair 4	L14/Rialto-124	Yes	14 Mar	66.0
	L14/Rialto-36	No	11 Mar	65.1

*Lines selected according to previous data (Gaju, 2007) to be balanced for flowering date and crop height across +*Tin1A* and –*Tin1A* groups.

Table 3.3 The 24 DH lines of the L14 x Rialto population examined in 2008/09 and 2009/10 at KWS Thriplow, Hertfordshire and University of Nottingham Farm, Sutton Bonington, UK, respectively.

Line pairs	Lines name	*Tin1A* allele	Flowering date*	Height (cm)*
Pair 1	L14/Rialto-110	Yes	22 May	92.1
	L14/Rialto-34	No	23 May	92.7
Pair 2	L14/Rialto-65	Yes	17 June	85.6
	L14/Rialto-114	No	19 June	86.5
Pair 3	L14/Rialto-48	Yes	25 May	69.1
	L14/Rialto-59	No	25 May	69.3
Pair 4	L14/Rialto-78	Yes	31 May	79.9
	L14/Rialto-60	No	28 May	80.8
Pair 5	L14/Rialto-61	Yes	17 May	96.0
	L14/Rialto-93	No	17 May	90.1
Pair 6	L14/Rialto-1	Yes	22 Jun	64.0
	L14/Rialto-101	No	22 Jun	63.6
Pair 7	L14/Rialto-30	Yes	13 Jun	75.1
	L14/Rialto-129	No	13 Jun	76.8
Pair 8	L14/Rialto-24	Yes	15 Jun	63.3
	L14/Rialto-9	No	15 Jun	61.3
Pair 9	L14/Rialto-90	Yes	13 Jun	85.5
	L14/Rialto-86	No	13 Jun	84.3
Pair 10	L14/Rialto-124	Yes	22 May	80.8
	L14/Rialto-4	No	22 May	81.9
Pair 11	L14/Rialto-25	Yes	23 Jun	66.5
	L14/Rialto-2	No	24 Jun	64.3
Pair 12	L14/Rialto-112	Yes	15 Jun	74.1
	L14/Rialto-47	No	13 Jun	72.3

*These data were obtained from 2005/06 and 2006/07 experiments at Sutton Bonington on the same population (Foulkes unpublished).

3.3 Plot management

3.3.1 CIMMYT wheat historic releases experiments

The sowing date was 18 November 2008 (and emergence on 28 November) in 2008/09. In 2009/10, the sowing date was on 3 December 2009 (emergence on 13 of Dec). Wheat was the previous crop at both seasons.

In each year, plots were irrigated using a gravity-based system four to six times during the crop cycle at 3- to 4-week intervals. During 2008/09, irrigation was applied four times (at 19 Dec, 15 Jan, 13 Feb and 7 Mar) and during 2009/10 also four times (at 13 Jan, 20 Feb, 3 Mar and 31 Mar). The fertilizer application regime was the same in both seasons. The first application of nitrogen (N) (50 kg N ha^{-1}) was applied as urea during land preparation followed by 40 kg ha^{-1} of phosphorous (P) as triple super phosphate at sowing. The second application of nitrogen (50 kg N ha^{-1}) as urea was added at the time of first irrigation.

Herbicides were applied in each season as follows: Buctril (1300 ml ha^{-1}) and Estrane (750 ml ha^{-1}) for broad leaves weeds and Axial (500 ml ha^{-1}) for narrow leaves weeds. In each season, a fungicide application of folicur (500 ml ha^{-1}) was applied four times. Insecticides applied were applied in each season as follows: Aflix (1 l ha^{-1}) and Lorsban (1400 ml ha^{-1}). Details of application dates are given in Appendix II

3.3.2. CIMMYT L14 x Rialto DH population (*Tin1A*) experiments

3.3.2.1. Experiments at CIMMYT C. Obregon

In each year, irrigation was applied using a gravity-based system as described above in 3.3.1. The sowing dates and the management of the experiments was also as described above for historic experiments in 2008/09 and 2009/10 in 3.3.1.

3.3.2.2. Experiment at Thriplow, Hertfordshire UK 2008/9

The field was drilled on 28th October 2008. Fertilizer applications were Multisulph 20 kg ha^{-1} and nitrogen fertilizer as Nitram in two doses 80 and 145 kg N ha^{-1} respectively. Fungicides were applied at four growth stages as: Bravo (1 l ha^{-1}), Tracker (0.5 l ha^{-1}), Flexity (0.25 ha^{-1}) and Mirage (1 ha^{-1}) at GS 26-30; Tracker (1.5 ha^{-1}), Bravo (1 l ha^{-1}) and Talius (0.15 l ha^{-1}) at GS 30-31; Opus (0.75 l ha^{-1}), Comet (0.75 l ha^{-1}) and Bravo (1 l ha^{-1}) at GS 39-45; Fandango (1.25 l ha^{-1}) at GS 51-61. Details of application dates are given in Appendix II. The previus crop was oil seed rape.

3.3.2.3. Experiment at Sutton Bonington, Leicestershire UK 2009/10

The previous crop was winter oats. The field was ploughed on 16 September, harrowed on 16 October and drilled on 23 October 2009. Manganese Jett (1.0 l ha^{-1}) was applied during early tillering. Nitrogen fertilizer was applied as ammonium nitrate prill in three doses: 40 kg N ha^{-1} (with 13.3 kg S ha^{-1} as SO_3^{1}; 80 kg N ha^{-1} and 60 kg N ha^{-1}. Applied in March, a GS31 and GS33 respectively.

Herbicides were applied as: Picona SC (3.0 l ha^{-1}) on 12th Nov 2009, Hatra (1.2 l ha^{-1}) and Biopower (1 l ha^{-1}) on 28th April 2010. Fungicides were applied as: Alto Elite (0.75 l ha^{-1}) on 08th April 2010, Proline (0.65 l ha^{-1}), Amistar Opti (0.75 l ha^{-1}) on 28th April 2010, Folicur (0.25 l ha^{-1}), Corbel (0.5 l ha^{-1}) and Justice (0.15 l ha^{-1}) on 09th July 2010. Insecticides applied were applied as: Permasect C (0.25 l ha^{-1}) on 12th Nov 2009, Aphox (0.25 kg ha^{-1}) on 09th July 2010. The plant growth regulators applied were Chlormequat (1.5 and 0.75 ha^{-1}) on 08th April 2010 and Moddus (0.2 l ha^{-1}) on 28th April 2010.

3.4. Crop measurements

3.4.1. CIMMYT historic cultivars experiments

3.4.1.1. Plant establishment and crop development

In each year, plants were counted in each plot at GS31 (Tottman *et al.*, 1987) in a 0.5 x 0.8 m quadrat area. Developmental stages were assessed every 2-3

days according to decimal codes of Zadoks *et al.* (1974) and updated by Tottman *et al.* (1987). Date of a stage was recorded when ≥ 50% of shoots in the plot were at that stage. The following stages were recorded: GS31 (first detectable node), GS39 (flag leaf ligule just visible), GS61 (beginning of anthesis) and physiological maturity (GS89; when the spike and the flag leaf were completely senesced).

3.4.1.2 Crop growth analysis

In each experiment, at GS31, GS39 and GS61, plants were sampled on the actual date of reaching the developmental stages and therefore different cultivars were sampled on different calendar dates. At each stage, plants were sampled in an area of 0.4 m^2 (0.5 m plot length by two adjacent rows (0.8 m), avoiding the plot area 0.5 m from the ends of the plots. Plants were cut at ground level.

3.4.1.2.1 GS31

In each experiment in each plot, the number of fertile (newest leaf is green and shows no signs of dying back from the tip) and infertile (no green material or newest expanding leaf has begun to turn yellow at the tip) shoots was counted in the plant material sampled from the 0.5 x 0.8 m area and their dry weight recorded separately after drying for 48 hours at 85 °C.

3.4.1.2.2 GS39

Samples were only taken at GS39 in 2009/10. In each plot a 50% sub-sample of the plant material sampled was taken by fresh weight (FW) and used for the growth analysis. The dry weight of the infertile shoots was recorded after drying at 85°C for 48 h. A further 50% sub-sub-sample of the fertile shots by FW was randomly selected and this material separated into: i) green lamina, ii) non-green stem plus attached leaf sheath and iii) green stems plus attached leaf sheath, and the dry weight of each fraction recorded after drying at 85°C for 48h. The dry weight of the other 50% remainder sub-sub-sample of the fertile shoots was also recorded after drying at 85°C for 48h. There was no dead lamina at GS39.

3.4.1.2.3 GS61

In both years, the growth analysis was carried out as described for GS39 above, except that:

(i) Fertile shoots were defined as those which either had a visible ear or were clearly booting and infertile shoots as those without a visible ear or no visible signs of booting.

(ii) From the fertile shoot sub-sample 15 shoots were randomly selected as a sub-sub-sample and separated into five components (a) ear, b) flag-leaf green lamina, c) remaining green lamina, d) remaining non-green lamina and e) stem plus attached leaf sheath.

(iii) Additional ear traits (rachis length, ear width (at widest point), awns length, and total and fertile number of spikelets per ear) were recorded on the 15 fertile-shoot sample

(iv) The water soluble carbohydrate (WSC) content of the stems plus attached leaf sheaths was measured for the 15 fertile-shoot sample. The WSC analysis was determined by near-infrared spectroscopy in 2009; however, colorimetry based on the anthrone reagent (Yemm & Willis, 1954) was used in 2010. In both seasons, 15 fertile shoots were sampled at GS61 + 7 days and again at maturity. After drying the shoots at 85°C for 48 hours, stems plus leaf sheath were separated from lamina and spikes. Then, the stems plus leaf sheaths were ground to a very fine powder and put in small bottles. Samples were sent to the plant analysis laboratory in CIMMYT for chemical analysis of %WSC.

3.4.1.2.4 Harvest GS 92

In each year at harvest (growth stage 92), 100 ear-bearing shoots were sampled randomly per plot. Samples were put in an oven to dry at 85°C for 48 hours. After drying the following measurements were taken: above-ground dry matter (AGDM) was measured by weighing the whole sample. Then the samples were threshed and the grains cleaned and oven-dried at 85°C for 48 hours and weighed. Thousand-grain weight was determined from a dried sample of 200 grains from each plot from the combine grain samples (see 3.4.1.5 below). All

other components, i.e., harvest index, number of ears per square metre, grains per square metre, and grains per ear were computed from the data obtained as described above as follows:

$$1 - \text{Grain yield } m^{-2} = \frac{Plot\ grain\ weight \times \frac{DW\ grain\ sub\ sample}{FW\ grain\ sub\ sample} + DW\ grain\ of\ 100\ ears}{Combined\ area\ m^{-2}}$$

$$2 - \text{Ears } m^{-2} = \frac{(Combined\ grain\ yield\ (g) \times number\ of\ subsample\ ears)}{Grain\ yield\ of\ subsample\ ears\ (g)}$$

$$3 - \text{Thousand grain weight (TGW)} = \frac{(Grain\ weight\ of\ 200\ grains\ (g) \times 1000)}{200}$$

$$4 - \text{Grains } m^{-2} = \frac{(Combined\ grain\ yield\ (g) \times 1000)}{TGW\ (g)}$$

$$5 - \text{Grains ear}^{-1} = \frac{Number\ of\ grains\ m^{-2}}{Number\ of\ ears\ m^{-2}}$$

$$6 - \text{AGDM } m^{-2} = \frac{(Number\ of\ ears\ m^{-2} \times AGDM\ of\ 100\ culms)}{100}$$

$$7 - \text{Harvest index (HI)} = \frac{Grain\ yield\ m^{-2}}{AGDM\ g\ m^{-2}}$$

$$8 - \text{Ears DM } m^{-2} = \frac{(Number\ of\ ears\ m^{-2} \times DM\ of\ 100\ ears)}{100}$$

$$9 - \%\ \text{of ears DM } m^{-2} = \frac{(Ears\ DM\ m^{-2} \times 100)}{AGDM\ g\ m^{-2}}$$

$$10 - \text{Lamina DM } m^{-2} = \frac{(Number\ of\ ears\ m^{-2} \times lamina\ DM\ of\ 100\ culms)}{100}$$

$$11 - \%\ \text{of lamina DM } m^{-2} = \frac{(Lamina\ DM\ m^{-2} \times 100)}{AGDM\ g\ m^{-2}}$$

$$12 - \text{Stems DM } m^{-2} = \frac{(Number\ of\ ears\ m^{-2} \times stems\ DW\ of\ 100\ culms)}{100}$$

$$13 - \%\ \text{of stems DM } m^{-2} = \frac{(Stems\ DW\ m^{-2} \times 100)}{AGDM\ g\ m^{-2}}$$

3.4.1.3 Plant height

Plant height was measured in the field for 12 randomly selected fertile shoots per plot in 2008/09 and 10 fertile shoots per plot in 2009/10. Measurements were taken from the ground level to the tip of the ear during approximately the middle of the grain filling period.

3.4.1.4 Combine grain yield

Combine yield was obtained by machine harvest from an area of 5.6 m^2 in 2009 and 5.2 m^2 in 2010. Moisture content was measured from a sub-sample from the combined harvest and grain yield expressed at 100% DM.

3.4.1.5 Relative greenness and SPAD and Canopy Spectral Reflectance

3.4.1.5.1 Relative greenness (SPAD)

Figure 3.1 The hand-held meter (model SPAD 502, Minolta, Spectrum Technologies Inc., Plainfield, IL)

SPAD values were measured once pre-anthesis at GS39 in both seasons. For SPAD readings and other remote-sensing leaf activity traits all readings were taken on the same calendar date for genotypes at respective readings. Post-anthesis SPAD was measured once in 2009 (12 March) and 2010 (6 April), around 4 weeks after anthesis using a hand-held meter (model SPAD 502, Minolta, Spectrum Technologies Inc., Plainfield, IL) as an indicator of the chlorophyll content. Three measurements were made at different positions (basal, middle and apical) on each of ten randomly selected flag leaves per plot.

3.4.1.5.2 Normalized Difference Vegetation Index (NDVI)

In each year, NDVI was determined using the Green Seeker Hand-Held model (505 Optical Sensor, *NTech*, Industries Inc) The equipment sensor was held about 50 cm above the canopy. Pre-anthesis measurements were taken on 4, 10, 15 and 29 December in the 2008/09 season and on 18 Dec, 28 Dec, 05 Jan, 11 Jan, 22 Jan and 6 Feb in 2009/10 season. Post-anthesis measurements were taken only on 26 Mar in 2008/09 season and on 24 Mar, 5 Apr, 15 Apr and 19 Apr in 2009/10 season.

Figure 3.2 the Green Seeker Hand-Held model (505 Optical Sensor, *NTech*, Industries Inc)

This instrument measures the amount of near infrared (NIR) and red light reflected by the canopy. Plants absorb red light for photosynthesis and reflect NIR. Thus, a higher NDVI value is obtained when the plant absorbs more red light relative to NIR light, and is associated with larger green canopy area. NDVI was calculated as:

NDVI = (reflected NIR – reflected red) / (reflected NIR + reflected red). **Equation 3.1**

NDVI values range from -1 to +1.

3.4.1.6 Leaf Activity Traits

3.4.1.6.1 Stomatal conductance

In both years, stomatal conductance was measured using the Decagon SC-1 Leaf Porometer (Decagon Devices, Inc., Pullman, Washington) every week from the beginning of February till the end of March. Stomatal conductance is usually measured as an average of the adaxial (the upper surface of the leaf) and the abaxial (the lower surface of the leaf) surfaces (Fischer *et al.*, 1998); and, because Lu (1989) found that under favourable conditions, stomatal resistance of the adaxial was higher than the stomatal resistance of the abaxial, measurements must be done for the same surface for all treatments or as an average of both surfaces. In the current experiment, the measurement was taken on the middle of the adaxial surface of the flag leaf which was fully

exposed to the sunlight. The process was repeated for four leaves per plot and for four replications of around midday (from 11:00 am to 15:00 pm) on clear, sunny days. Each measurement took about 30 seconds. Readings of the instrument are shown in units of mmol m^{-2} s^{-1}.

Figure 3.3 the Decagon SC-1 Leaf Porometer (Decagon Devices, Inc., Pullman, Washington)

3.4.1.6.2. Canopy temperature

Figure 3.4 hand-held (Sixth Sense LT300) infrared thermometer, (Total Temperature Instrumentation, Inc).

In both years, canopy temperature was determined by using a hand-held (Sixth Sense LT300) infrared thermometer, (Total Temperature Instrumentation, Inc). In each plot, readings were taken at an angle approximately 30° to the horizontal approximately 0.5 m above the canopy. Measurements were made approximately weekly from the beginning of February (flag leaf emergence) until the end of March (mid grain filling) in the early after-noon during cloudless periods. On each occasion two readings per plot were carried out. Air temperature was measured at the same time as the canopy temperature and canopy temperature depression was calculated as :

$$CTD = T_a - T_c$$

Equation 3.2

Where T_a is the air temperature and T_c is the canopy temperature.

3.4.2 CIMMYT L14 x Rialto DH population (*Tin1A*) experiments

3.4.2.1 Experiments at CIMMYT C. Obregon

3.4.2.1.1 Crop growth analysis at GS61 and harvest

During the 2008/09 season at GS61 the sample size was 10 randomly selected fertile shoots from each plot and during the 2009/10 season was 20 randomly selected fertile shoots per plot. Samples avoided plot areas 0.5 m from the ends of the plots. Shoots were divided to four categories (ears, flag leaf lamina,

remaining lamina and stems plus attached leaf sheaths). These parts were separately oven-dried for 48 hours at 85 °C and weighed. Ear traits (rachis length, total number of spikelets and fertile number of spikelets per ear) were measured for 10 ears in 2009 and for 12 ears in 2010. Measurements of plant establishment and anthesis date and crop height were as described for the CIMMYT historic cultivars experiments. Harvest growth analysis was as described for the CIMMYT historic cultivars experiments in 3.4.1.2.4 except the sample size which was 50 ear-bearing shoots.

Combine grain yield was measured as described in 3.4.1.5 except that the combined area per plot was 1.6 m^2, and yields were adjusted by adding in the grain weights from the 50 ear-bearing shoot samples.

3.4.2.2 Growth analysis in experiment at KWS UK Ltd Thriplow 2008/9

All measurements were carried out at harvest. At harvest approximately 100 ear-bearing shoots were sampled randomly by pulling up from the soil in each plot avoiding outer rows and plot areas 0.5 m from the ends of plots. Roots were cut off at ground level and the fresh weight was recorded. A sub-sample (approximately 50 shoots by fresh weight) was taken and the exact number of fertile shoots and infertile shoots recorded. The dry weight of the ears of the sub-sample was recorded after drying for 48 h at 80°C. The fresh weight of the straw of the sub-sample was recorded and approximately 25% (by FW) was taken as a sub-sub-sample and the dry weight recorded. Ten fertile shoots were selected randomly from the remaining material of the original sample. Plant height was recorded for 5 of the 10 fertile shoots and ear traits (rachis length, ear width (at the widest point), and total and fertile spikelets per ear) were measured on all 10 fertile shoots. These shoots were then separated into: i) ears, ii) lamina and iii) stems plus leaf sheath and the dry weight recorded after drying for 48 h at 80°C. The dry-weighted ears from the 25% sub-sample were threshed and the grains weighed again. Chaff dry weight was calculated from difference between the ear and grain dry weights. 200 grains were counted by a seed counter (Contador Seed Counter, Hoffman Manufacturing, Inc, USA) and weighed. The combine yield was recorded on each plot and yields were adjusted by adding in the grain weights from the grab samples. Combine yield

was measured as described for CIMMYT historic experiments, except that the combined area was 5 m^2.

3.4.2.3 Experiment at Sutton Bonington, Leicestershire UK 2009/10

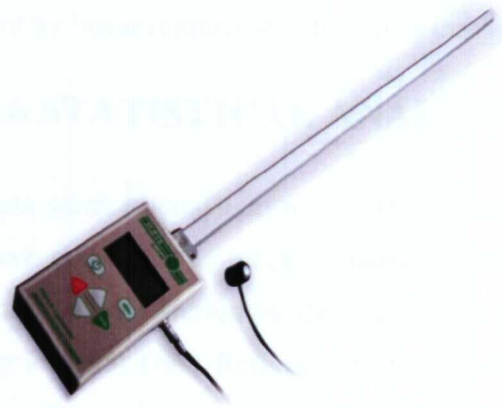
All measurements were carried out at harvest. Two to three days prior to harvest, approximately 100 ear-bearing shoots from each sub-plot were sampled by pulling up plants. The roots were removed, and fertile and infertile shoots (defined as above) were counted and their fresh weight recorded separately. For 10 randomly selected fertile shoots, plant height, peduncle length, rachis length, and total and fertile spikelets per ear were measured. Ears were removed from all fertile shoots in the original sample and then threshed and the chaff and grain weighed and recorded separately after drying at 80°C for 48 h. For a 50% sub-sample of the straw by FW, the straw was divided into two components (leaf lamina and stems plus leaf sheaths), which were weighed separately after drying at 80°C for 48 h. 200 grains were counted and weighed after drying at 80°C for 48 h. AGDM, grain yield, ears m^{-2}, grains per ear, grains m^{-2}, TGW, HI, stem and leaf sheath DM per m^2 and lamina DM per m^2 were calculated from the combine yield data and the data obtained as described above in 3.4.1.2.4.. Combine yield was measured as described for CIMMYT historic experiments, except that the combined area per sub-plot was 9.5 m^2.

3.5 Environmental measurements

3.5.1 Meteorological data

In each experiment, data on solar radiation, rainfall, and maximum and minimum air temperatures were recorded on a daily basis by an automatic weather station located within at least 1 km of the experimental sites.

3.5.2 Fractional interception of photosynthetically active radiation (PAR)



The fraction of PAR (400-700 nm) intercepted was measured only in 2009/10 in the historic experiments at Cd. Obregon. Measurements in each plot were taken at GS31, GS39, GS61+7d and mid grain filling by using a hand-held LP-80 Ceptometer (Decagon Devices, Inc., Pullman, Washington, USA). Two readings per plot were carried out, and the ceptometer was placed between the two rows.

Figure 3.5 The hand-held LP-80 Ceptometer, (Decagon Devices, Inc., Pullman, Washington, USA)

At GS31, readings were taken above the canopy, below the canopy at ground level and inversely about 5 cm above the canopy. At GS39 measurements were taken above the canopy, below the flag leaves (at the flag-leaf ligule), below the canopy at ground level and inversely above the canopy. At GS61+ 7d and during the grain filling period measurements were taken above the canopy, below the ears at the ear collar, below the flag leaves (at the flag-leaf ligule), half way between the flag leaf ligule and the ground level, below the canopy and inversely above the canopy.

Radiation-use efficiency (RUE) was calculated over the period from GS31 to GS61+7d as the ratio of the cumulative AGDM for sequential samplings to

cumulative PAR interception. Values of daily fractional PAR interception were obtained by interpolation between readings at GS31, GS39, GS61+7d; these were applied to the daily incident solar radiation to calculate the daily radiation interception, assuming PAR was equal to 0.5 solar radiation (Monteith, 1972). Values for RUE from GS31 to GS61+7d were calculated individually for each plot by linear regression fitting lines through the origin.

3.6 STATISTICAL ANALYSIS

Data were entered into excel 2007 spreadsheets, and then relevant variables were converted to metre squared. Correlation analysis was done in Excel. Data was transferred to the GENSTAT program (Thirteenth Edition Lawes Agricultural Trust, Rothamsted Experimental Station; 2010) to analyse the data according to analysis of variance (ANOVA) and regression analysis.

Standard analysis of variance (ANOVA) procedures were used to calculate treatment means, standard errors and significant differences between treatments. Linear regression analysis was used to determine relationships and correlations between crop and plant variables. Examples of GENSTAT outputs are given in Appendix IV. The significance of the treatment effects was determined by ANOVA where the variation due to the main effects and their interactions were compared with the residual variation within the treatments between replicates (blocks). A probability value of 0.05 or less ($P < 0.05$) was taken to be significant, although consistent values between 0.05 and 0.10 may receive comment in the text. Means were compared by using the least significant differences analysis (LSD) at probability of 0.05 and 0.01. Where the effect of cultivar was statistically significant, regression analyses (linear and non-linear) to test the responses of the cultivars to year of release was done. For ANOVAs across years, Bartlett's test (P 0.05) was used to test for the homogeneity of variances, and years were regarded as random effects. The mean square for the year effect was tested against an error mean square representing the variation between blocks. The mean square of the cultivar and year effects was tested against an error B mean square representing residual variation. Treatment means were compared using the LSD of the means of Fisher, calculated from standard errors of the difference of the means using

appropriate degrees of freedom, when the ANOVA indicated significant differences.

In the KWS and SB experiments, ANOVA for randomized complete block design and a split plot design were used to analyse differences among all lines in general. In addition, differences between the *Tin1A* and the non *Tin1A* groups was tested by using the ANOVA contrasts.

CHAPTER 4 EFFECTS OF BREEDING ON YIELD AND YIELD COMPONENTS

4.1 INTRODUCTION

This chapter describes the effect of plant breeding on grain yield, biomass, harvest index and yield components in the period from 1966 to 2009 in CIMMYT wheat cultivars. Experiments were conducted in the seasons of 2008/09 and 2009/10 at CIMMYT experimental station near Cd. Obregon, NW Mexico. Twelve spring wheat (*Triticum aestivum* L.) cultivars released at CIMMYT in the period from 1966 to 2009 were used in the study. This period includes the period of the green and post-green revolution phases (1961-1976 and 1977 – present, respectively) (Rajaram and Hettel, 1994). Eleven of the cultivars in the present study were semi-dwarfs and possessed the Norin 10 dwarfing gene *Rht1* except for cultivar Pavon (1976) which possessed the *Rht2* gene. The *1BL/1RS* translocation was present in four cultivars: Seri (1982), Bacanora (1988), Attila (1990) and Baviacora (1992). (Note, one line had not been tested for the *rht* and *1BL/1RS* translocation). A randomized complete block design was implemented with four replications. Each plot consisted of two beds, each of which was 4 m long and 0.8 m wide with two rows per bed. Plant establishment, developmental rate, height, yield and yield components were measured, analysed and will be described in this chapter.

The specific hypotheses tested in this chapter were:

1. Grain yield potential has increased linearly in spring wheat cultivars released in CIMMYT in the period from 1966 to 2009.
2. There is a positive correlation between grain yield and HI, with the increases in HI contributing to genetic gains in yield most strongly in the first half of the period from 1966 to 2009.
3. Grain yield is positively related to grains m^{-2} amongst the 12 historic CIMMYT spring wheat cultivars.

4. Genetic gains in grains m^{-2} have been positively associated with both number of ear m^{-2} and grains ear^{-1} since 1966.
5. Genetic gains in grains ear^{-1} were positively associated with rachis length and fertile spikelets per ear.
6. Above-ground biomass and individual grain weight have not changed with year of release during the period from 1966 to 2009.
7. Plant height has not changed with year of release within the twelve semi-dwarf cultivars from 1966 to 2009

4.2 MATERIALS AND METHODS

In each of the experiments in 2008/09 and 2009/10, 12 cultivars released from 1966 to 2009 were examined. A randomized complete block design was implemented with four replications. Each plot consisted of two beds, each of which was 4 m long and 0.8 m wide with two rows 30 cm apart per bed.

Plants were counted in each plot at GS31 (Tottman *et al.*, 1987) in a 0.5 × 0.8 m quadrat area. At harvest (growth stage 92), 100 ear-bearing shoots were sampled randomly per plot. Samples were put in an oven to dry at 85°C for 48 hours. After drying, the following measurements were taken: above-ground dry matter (AGDM) was measured by weighing the whole sample. Then the samples were threshed and the grains cleaned and oven-dried at 85°C for 48 hours and weighed. Thousand-grain weight was determined from a dried sample of 200 grains from each plot from the combine grain samples. All other components, i.e., harvest index, number of ears per square metre, grains per square metre, and grains per ear were computed from the data and the combine grain yield.

Plant height was measured in the field for 12 randomly selected fertile shoots per plot in 2008/09 and 10 fertile shoots per plot in 2009/10. Measurements were taken from the ground level to the tip of the ear during approximately the middle of the grain filling period.

Combine yield was obtained by machine harvest from an area of 5.6 m^2 in 2009 and 5.2 m^2 in 2010. Moisture content was measured from a subsample from the combined grain and grain yield expressed at 100% DM.

4.3 RESULTS

4.3.1 Environmental conditions

The weather in the experiments during January to April is very important as this period encompasses onset of stem extension to physiological maturity when yield is determined especially during February and March. The season 2008/09 was slightly warmer than the following season and the long-term mean in the months of January and March. Both years also had higher radiation receipts than the long-term mean.

Table 4.1 Temperature, humidity, solar radiation, rainfall and the long-term mean (LTM, from 1987 to 2010) in CIMMYT agricultural station in Obregon, Mexico during the period of 2008-2010.

Month	Temperature °C						LTM
	2008/09			2009/10			
	Mean	Max	Min	Mean	Max	Min	
Nov	**21.1**	29.5	14.5	**20.5**	29.9	12.9	20.2
Dec	**17.1**	25.5	10.4	**15.2**	23.9	8.0	15.4
Jan	**15.6**	25.0	8.5	**15.3**	24.8	7.6	15.0
Feb	**15.2**	25.6	7.3	**15.4**	24.3	8.0	15.7
Mar	**17.8**	26.9	10.0	**17.0**	27.1	8.4	17.0
Apr	**20.2**	30.6	10.8	**19.7**	29.1	10.9	20.3
Month	Relative Humidity %						LTM
	2008/09			2009/10			
	Mean	Max	Min	Mean	Max	Min	
Nov	**66.0**	88.8	33.8	**62.2**	85.9	30.2	60.4
Dec	**68.9**	89.7	39.3	**65.7**	88.6	33.7	64.5
Jan	**69.7**	92.3	34.4	**67.1**	90.4	32.4	67.7
Feb	**70.1**	92.9	32.2	**71.6**	92.8	36.8	71.3
Mar	**70.5**	92.6	37.8	**65.2**	90.4	29.3	66.8
Apr	**55.4**	86.6	23.1	**62.4**	89.2	27.5	56.7
Month	Solar radiation MJ m^{-2}						LTM
	2008/09			2009/10			
Nov		494.5			487.1		488.9
Dec		431.6			451.3		445.5
Jan		464.0			474.1		464.5
Feb		541.9			556.2		520.6
Mar		702.2			752.3		718.9
Apr		783.6			791.1		773.6
Total		3418			3512		3412
Month	Rainfall mm						LTM
	2008/09			2009/10			
Nov		**1.2**			**3.0**		7.1
Dec		**0.0**			**1.2**		8.6
Jan		**1.2**			**18.8**		7.6
Feb		**0.0**			**8.6**		7.9
Mar		**1.8**			**0.0**		1.4
Apr		**0.0**			**0.0**		0.8

4.3.2 Plant establishment

Plant establishment was slightly higher in 2008/09 compared to 2009/10 (P = 0.001; Table 4.2). There were significant differences amongst the genotypes in 2009 (P = 0.001), but not in 2010 (P = 0.390). Overall there were small differences in plants m^{-2} between the cultivars (P = 0.001). There were no significant differences amongst 11 of the 12 cultivars in the range 173 – 202 plants m^{-2}, but Bacanora had slightly lower establishment at 139 plants m^{-2}. There was no correlation between year of release and plant establishment or interaction between year and cultivar (P = 0.311).

Table 4.2 Number of plants m^{-2} for 12 CIMMYT spring wheat cultivars differing in year of release in 2008/09 and 2009/10.

Cultivar (Year of release)	Plants m^{-2}		
	08/09	09/10	Mean
Siete Cerros (1966)	203.1	142.5	172.8
Pavon (1976)	207.2	163.8	185.5
Seri (1982)	187.2	166.3	176.7
Bacanora (1988)	145.9	132.5	139.2
Attila (1990)	188.4	177.5	183.0
Baviacora (1992)	227.8	176.9	202.3
Tarachi (2000)	198.8	166.3	182.5
Tacupeto (2001)	207.8	185.0	196.4
Roelfes (2007)	185.0	164.4	174.7
Navojoa (2007)	236.3	162.5	199.4
Becard (2009)	203.8	155.0	179.4
Line 1 (2009)	203.4	159.4	181.4
Mean	199.6	162.7	181.1
S.E.D (df) (Years)			6.71(6)
(Cultivars)	16.54 (33)	19.64 (33)	12.84(66)
(Interaction)			18.52(70.04)
Prob. (Years)			0.001**
(Cultivars)	0.001***	$0.390^{n.s}$	0.001**
(Interaction)			$0.311^{n.s}$
C.V %	11.70	17.10	14.20
Correlation with (Year of release)	n.s	n.s	n.s
(Grain yield)	n.s	n.s	n.s

* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

4.3.3 Developmental rate

The experiment was sown later in the 2009/10 season. The emergence date was 28 November in 2008/09, and 13 December in 2009/10. In general, averaging across the seasons, there were no associations between year of release and the date of GS31, flowering (GS61) and physiological maturity. The range between cultivars for these stages was relatively small: at 8, 10 and 7 days, respectively. However, the duration of the grain filling period from GS61 to physiological maturity (PM) tended to increase with year of release especially after ca. 1990.

4.3.4 Plant height

Results showed differences amongst the cultivars in both years ($P < 0.001$; Table 4.4). In addition, there were differences in the plant height between the years ($P = 0.026$). Plants were taller in 2009, perhaps because of the earlier sowing resulting in more shoots per square metre and increased competition for light and also stem extension occurring under less bright conditions. There was an interaction between cultivar and year ($P = 0.002$). The most recent cultivars tended to be relatively taller in 2009 except for Line 1. However, differences between years for cultivars released before 2000 were much smaller. There was a non-linear increase in the plant height with year of release ($P < 0.05$), with height increasing from ca.1990. Averaging over seasons, plant height ranged from 91.6 cm for Bacanora (1988) to 114.3 cm for Roelfes (2007).

Table 4.3 Dates of growth stages 31, 61 and physiological maturity (PM) and days for phases between stages for 12 CIMMYT spring wheat cultivars in 2008/09 and 2009/10.

Cultivar	GS 31(onset stem extension)			GS 61(flowering)			PM(physiological maturity)		
(Year of release)	08/09	09/10	Mean	08/09	09/10	Mean	08/09	09/10	Mean
Siete Cerros (1966)	26-Dec	25-Jan	10-Jan	06-Feb	01-Mar	17-Feb	03-Apr	15-Apr	09-Apr
Pavon (1976)	28-Dec	27-Jan	12-Jan	10-Feb	09-Mar	23-Feb	07-Apr	20-Apr	13-Apr
Seri (1982)	27-Dec	28-Jan	12-Jan	12-Feb	09-Mar	24-Feb	05-Apr	18-Apr	11-Apr
Bacanora (1988)	02-Jan	02-Feb	17-Jan	16-Feb	05-Mar	24-Feb	05-Apr	15-Apr	10-Apr
Attila (1990)	26-Dec	27-Jan	11-Jan	16-Feb	10-Mar	27-Feb	06-Apr	16-Apr	11-Apr
Baviacora (1992)	29-Dec	27-Jan	12-Jan	16-Feb	05-Mar	24-Feb	08-Apr	24-Apr	16-Apr
Tarachi (2000)	29-Dec	29-Jan	13-Jan	12-Feb	07-Mar	23-Feb	08-Apr	17-Apr	12-Apr
Tacupeto (2001)	30-Dec	24-Jan	11-Jan	16-Feb	05-Mar	24-Feb	10-Apr	18-Apr	14-Apr
Roelfes (2007)	26-Dec	25-Jan	10-Jan	10-Feb	03-Mar	20-Feb	04-Apr	20-Apr	12-Apr
Navojoa (2007)	28-Dec	24-Jan	10-Jan	16-Feb	07-Mar	25-Feb	10-Apr	22-Apr	16-Apr
Becard (2009)	02-Jan	28-Jan	15-Jan	10-Feb	01-Mar	19-Feb	12-Apr	17-Apr	14-Apr
Line 1 (2009)	26-Dec	23-Jan	09-Jan	06-Feb	03-Mar	18-Feb	12-Apr	17-Apr	14-Apr
Cultivar	**Days from emergence to GS31**			**Days from GS31 to GS61**			**Days from GS61 to PM**		
(Year of release)	**08/09**	**09/10**	**Mean**	**08/09**	**09/10**	**Mean**	**08/09**	**09/10**	**Mean**
Siete Cerros (1966)	29	44	36.5	42	36	39	57	45	51
Pavon (1976)	31	46	38.5	44	42	43	57	42	49.5
Seri (1982)	30	47	38.5	47	41	44	53	40	46.5
Bacanora (1988)	36	52	44	45	32	38.5	49	41	45
Attila (1990)	29	46	37.5	52	43	47.5	50	37	43.5
Baviacora (1992)	32	46	39	49	38	43.5	52	50	51
Tarachi (2000)	32	48	40	45	38	41.5	56	41	48.5
Tacupeto (2001)	33	43	38	48	41	44.5	54	44	49
Roelfes (2007)	29	44	36.5	46	38	42	54	48	51
Navojoa (2007)	31	43	37	50	43	46.5	54	46	50
Becard (2009)	36	47	41.5	39	33	36	62	47	54.5
Line 1 (2009)	29	42	35.5	42	40	41	66	45	55.5
Mean (days)	31.4	45.7	38.5	45.8	38.8	42.3	55.3	43.8	49.6

Table 4.4 Plant height for 12 CIMMYT spring wheat cultivars in 2009 and 2010.

Cultivar (Year of release)	Plant height (cm)		
	08/09	09/10	Mean
Siete Cerros (1966)	95.6	97.9	96.8
Pavon (1976)	103.6	102.5	103.1
Seri (1982)	91.9	91.9	91.9
Bacanora (1988)	93.2	90.0	91.6
Attila (1990)	103.5	101.9	102.7
Baviacora (1992)	106.4	104.4	105.4
Tarachi (2000)	101.1	102.0	101.6
Tacupeto (2001)	104.7	98.4	101.6
Roelfes (2007)	117.1	111.6	114.3
Navojoa (2007)	110.5	103.5	107.0
Becard (2009)	106.3	98.7	102.5
Line 1 (2009)	104.8	103.7	104.2
Mean	103.2	100.5	101.9
S.E.D (df) (Years)			0.65(3)
(Cultivars)	1.29 (11)	1.67(22)	1.16(33)
(Interaction)			1.73(34)
Prob. (Years)			0.026*
(Cultivars)	< 0.001***	< 0.001***	< 0.001***
(Interaction)			0.002**
C.V %	1.2	2.0	1.80
Correlation with (Year of release)	0.67*	n.s	0.58*
(Grain yield)	n.s	n.s	n.s

* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

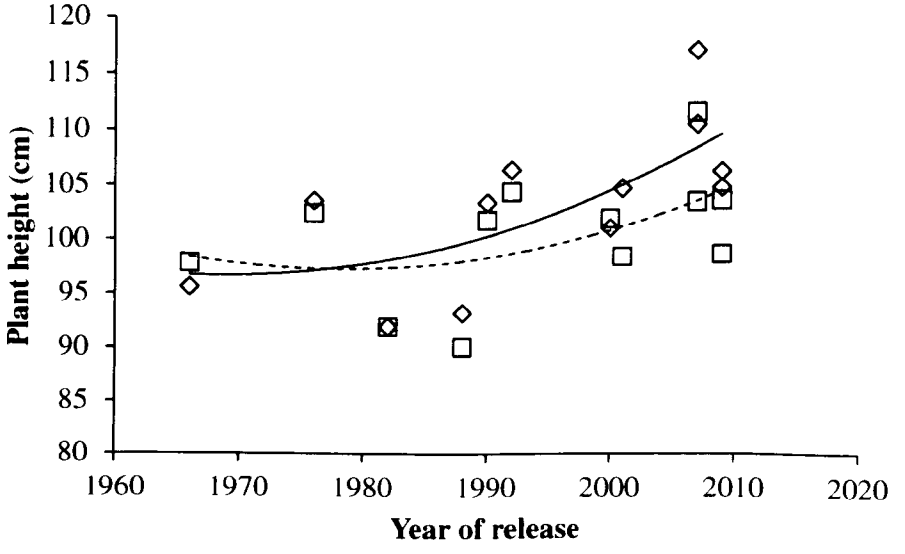


Figure 4.1 Regression of year of release on plant height for 2009 (__◇__) y= 0.0079x² – 31.192x + 30799 (R^2 = 0.4838; *P* = 0.05), and 2010 (---□---) y= 0.0079x² – 30.178x + 29947 (R^2 = 0.2479; *P* = 0.28) for 12 CIMMYT spring wheat cultivars.

4.3.5 Grain yield

There were differences in grain yield amongst the cultivars in both years ($P < 0.001$), but no effect of year ($P = 0.350$), or for the year × cultivar interaction ($P = 0.265$; Table 4.6). Grain yield increased from 1966 to 2009 from 630.4 g m^{-2} to 791.3 g m^{-2}. No significant differences were found between Becard (2009), the highest yielding entry and Baviacora (1992), Navojoa (2007) and Line 1 (2009); and no significant differences were found between Pavon (1976) the lowest yielding entry, and Siete ceros (1966) and Seri (1982). However, overall there was a linear increase in grain yield with year of release of 2.91 g m^{-2} yr^{-1} ($R^2 = 0.52$) and 3.42 g m^{-2} yr^{-1} ($R^2 = 0.58$) for 2009 and 2010, respectively. Although the linear regression explained the data better than non-linear functions, Baviacora (1992) produced almost the same grain yield as the highest yielding cultivar Becard (2009). No statistically significant relationships were found between either plant height or anthesis date and grain yield amongst the cultivars.

Table 4.6 Grain yield (100% DM) for 12 CIMMYT spring wheat cultivars in 2009 and 2010.

Cultivar (Year of release)	Grain Yield (g m^{-2})		
	2009	2010	Mean
Siete Cerros (1966)	654.1	606.7	630.4
Pavon (1976)	654.5	601.4	628.0
Seri (1982)	639.9	646.7	643.3
Bacanora (1988)	741.7	742.4	742.1
Attila (1990)	731.8	739.0	735.4
Baviacora (1992)	766.5	783.5	775.0
Tarachi (2000)	674.6	675.0	674.8
Tacupeto (2001)	707.5	699.7	703.6
Roelfes (2007)	726.1	735.8	730.9
Navojoa (2007)	764.2	762.8	763.5
Becard (2009)	820.5	762.0	791.3
Line 1 (2009)	774.6	763.2	768.9
Mean	721.3	709.9	715.6
S.E.D (df) (Years)			11.36(6)
(Cultivars)	17.92(33)	27.72(33)	16.50(66)
(Interaction)			25.07(60.26)
Prob. (Years)			$0.35^{n.s}$
(Cultivars)	<0.001***	<0.001***	<0.001***
(Interaction)			$0.265^{n.s}$
C.V %	3.50	5.50	4.60
Correlation with (Year of release)	0.72**	0.76**	0.76**
(Grain yield)	1.00	1.00	1.00

* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

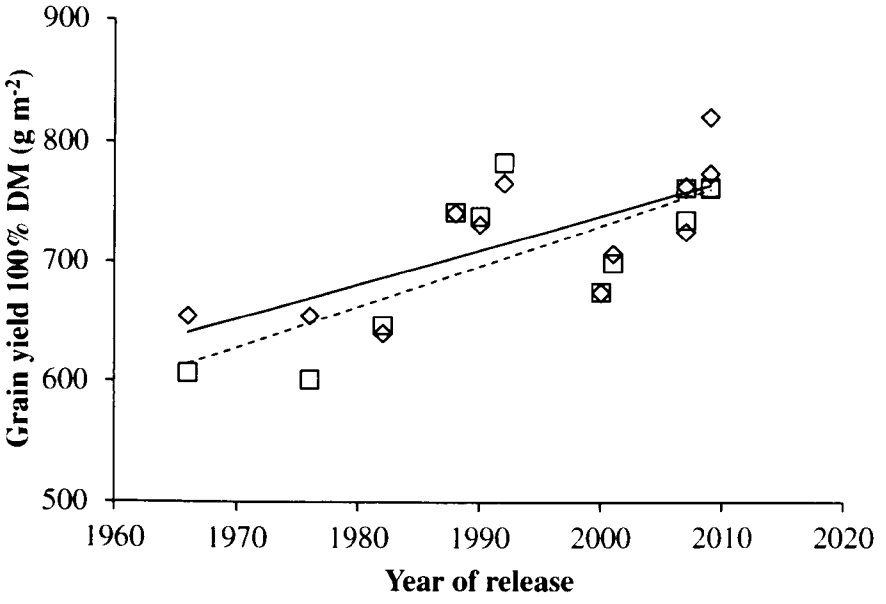


Figure 4.2 Regression of year of release on grain yield for 2009 (__◇__) y=2.9051x - 5071.1 (R^2 = 0.52; P = 0.034), and 2010 (---□---) y=3.4236x - 6116.6 (R^2 = 0.5799; P = 0.012) for 12 CIMMYT spring wheat cultivars.

4.3.6 Above-ground DM and harvest index

Averaging across cultivars, above-ground DM was greater in 2009 (1639.3 g m^{-2}) than 2010 (1538.4 g m^{-2}). There was no significant interaction between year and cultivar (P = 0.565). Results in 2009 indicated that AGDM initially did not increase with year of release during the period from 1966 to 1982, but then increased from about 1982 until 2009 (Table 4.7). In 2010, the regression analysis showed a linear increase in biomass across the whole period. Overall, pooling the data from both years, there was a linear increase in biomass (R^2 = 0.59). A quadratic regression fitted the data for year of release versus HI and indicated that HI increased only from 1966 until about 1982. Results showed that HI then actually decreased with year of release since about 1990. However, the increase in biomass after 1990 was proportionally greater than the decrease in HI and consequently grain yield continued to increase from ca. 1990 to 2009. There was a positive correlation between AGDM and both year of release and grain yield (r = 0.77, P < 0.01) and (r = 0.90, P < 0.01), respectively. No statistically significant correlation was found between HI and either year of release or grain yield (Table 4.7).

Table 4.7 Above-ground dry matter (AGDM) and harvest index for 12 CIMMYT spring wheat cultivars in 2009 and 2010.

Cultivar (Year of release)	Above ground dry matter (gm^{-2})			Harvest index (%)		
	2009	2010	Mean	2009	2010	Mean
Siete Cerros (1966)	1527.0	1387.9	1457.4	46.5	55.4	43.3
Pavon (1976)	1510.9	1343.5	1427.2	38.9	53.1	44.0
Seri (1982)	1348.5	1302.0	1325.2	48.6	56.8	48.6
Bacanora (1988)	1628.6	1542.7	1585.6	46.1	58.1	46.8
Attila (1990)	1669.7	1574.9	1622.3	36.9	44.1	45.4
Baviacora (1992)	1678.7	1661.7	1670.2	45.3	59.8	46.4
Tarachi (2000)	1496.3	1468.1	1482.2	41.2	49.3	45.5
Tacupeto (2001)	1652.6	1556.2	1604.4	41.9	44.6	43.9
Roelfes (2007)	1682.4	1685.3	1683.8	43.7	49.8	43.4
Navojoa (2007)	1832.5	1654.9	1743.7	39.8	46.9	43.9
Becard (2009)	1784.8	1589.0	1686.9	41.6	46.9	47.0
Line 1 (2009)	1859.5	1694.2	1776.9	32.6	44.3	43.3
Mean	1639.3	1538.4	1588.8	41.9	50.7	45.1
S.E.D (df) (Years)			33.26(6)			0.005(6)
(Cultivars)	74.06(33)	71.60(33)	51.51(66)	0.015(33)	0.011(33)	0.009(66)
(Interaction)			77.26(63.38)			0.014(67.89)
Prob. (Years)			0.023*			0.008**
(Cultivars)	<0.001***	<0.001***	<0.001***	0.006**	<0.001***	<0.001***
(Interaction)			$0.565^{n.s}$			$0.674^{n.s}$
C.V %	6.40	6.60	6.50	4.80	3.50	4.1
Correlation with (Year of release)	0.72**	0.78**	0.77**	n.s	n.s	n.s
(Grain yield)	0.89**	0.91**	0.90**	n.s	n.s	n.s

* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

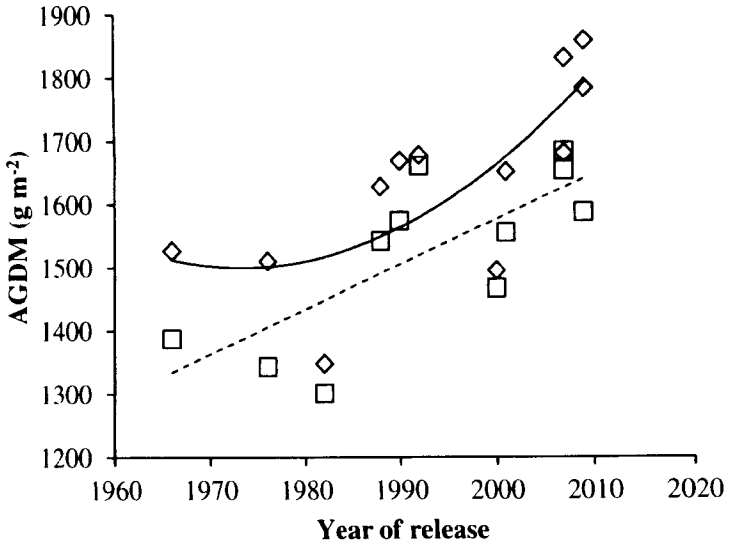


Figure 4.3 Regression of year of release on AGDM for 2009 (__◇__) y= 0.2299x^2 – 907.24x + 896649 (R^2 = 0.5918; *P* = 0.018), and 2010 (---□---) y= 7.1405x - 12704 (R^2 = 0.5668; *P* = 0.003) for 12 CIMMYT spring wheat cultivars.

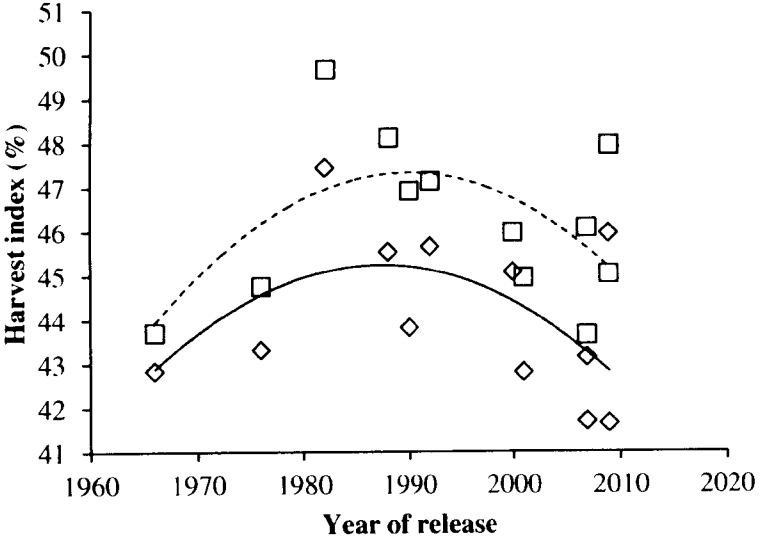


Figure 4.4 Regression of year of release on HI for 2009 (__◇__) y= -5E–05x^2 + 0.2052x–203.41 (R^2 = 0.3015; *P* = 0.313), and 2010 (---□---) y= -6E-05x^2 + 0.235x – 233.3 (R^2 = 0.3318; *P* = 0.074) for 12 CIMMYT spring wheat cultivars.

4.3.7 Yield components

Results showed a significant effect of cultivar and for the interaction with year for grains m^{-2} (Table 4.8). Thus, some cultivars produced relatively more grains m^{-2} in 2009 than in 2010. Averaging over of the two years, Bacanora (1988) produced most grains m^{-2} (21,175) and Seri (1982) the fewest (15,490). The correlation analysis showed no significant relationship between grains m^{-2} and either grain yield or year of release for either year or for the 2-year mean. Figure 4.5 indicates that there was no systematic improvement in the grains m^{-2} during the period from 1966 till 2009, although there were differences between individual cultivars, e.g. Bacanora (1988) vs Seri (1982). No statistically significant correlations were found between grains m^{-2} and either plant height or anthesis date.

In general, the majority of the cultivars produced more ears m^{-2} in 2009 (421) than in 2010 (348). Ears m^{-2} in 2009 ranged from 313 for cv Seri (1982) to 537 for Line 1 (2009); and in 2010 from 285 for cv Seri (1982) to 398 for Line 1 (2009). Analysis of variance indicated that the interaction between year and cultivar was significant ($P < 0.001$). Although most of the cultivars produced more ears in 2009, there were no statistically significant differences between the two seasons in ears m^{-2} for some cultivars. Regression analysis (Fig 4.6) showed no change in ears m^{-2} with year of release from 1966 to 2009. In addition, the correlation between this trait and the grain yield amongst cultivars was not statistically significant.

More grains per ear were produced in 2010 (50.7) than 2009 (41.9) ($P < 0.001$). The higher ears m^{-2} in 2009 was associated with fewer grains ear^{-1} in this season. The genetic range in grains ear^{-1} was 32.6 (Line 1, 2009) to 48.6 (Seri, 1982) and from 44.1 (Attila, 1990) to 59.8 (Baviacora, 1992) in 2009 and 2010, respectively. There was no systematic change in grains ear^{-1} with year of release in 2009. However, in 2010 there was a slight decrease in grains ear^{-1} with plant breeding which was associated with a trend for more ears per unit area ($P = 0.01$ Fig. 4.7). Averaging across years, there was linear decrease in grains per ear with year of release of 0.2 grains ear^{-1} yr^{-1} ($P < 0.05$; Table 4.8). Though grains ear^{-1} was higher in 2010 than 2009, there were no differences in

grain yield between the seasons, since there were fewer ears m^{-2} in 2010. Fewer grains per ear in 2009 was likely associated with an increase of the inter-shoot competition (Table 4.8; Fig. 4.8).

Table 4.8 Grains m^{-2}, ears m^{-2} and ears $spike^{-1}$ for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2008/09 and 2009/10.

	Grains m^{-2}			Ears m^{-2}			Grains ear^{-1}		
Cultivar (Year of release)	**2009**	**2010**	**Mean**	**2009**	**2010**	**Mean**	**2009**	**2010**	**Mean**
Siete Cerros (1966)	19272.4	18267.0	18769.7	406.3	331.2	368.8	46.5	55.4	50.9
Pavon (1976)	18038.2	16857.6	17447.9	467.9	319.7	393.8	38.9	53.1	46.0
Seri (1982)	14801.3	16177.9	15489.6	312.9	284.9	298.9	48.6	56.8	52.7
Bacanora (1988)	21739.3	20611.1	21175.2	465.5	355.7	410.6	46.1	58.1	52.1
Attila (1990)	16023.7	17324.0	16673.8	441.9	393.1	417.5	36.9	44.1	40.5
Baviacora (1992)	16036.5	18048.4	17042.5	367.7	302.6	335.2	45.3	59.8	52.6
Tarachi (2000)	16403.9	16348.3	16376.1	401.4	332.2	366.8	41.2	49.3	45.2
Tacupeto (2001)	17084.7	16828.1	16956.4	411.4	377.9	394.7	41.9	44.6	43.3
Roelfes (2007)	15652.1	16663.4	16157.8	361.1	335.1	348.1	43.7	49.8	46.7
Navojoa (2007)	17640.3	18056.0	17848.2	444.4	385.0	414.7	39.8	46.9	43.3
Becard (2009)	18117.9	16850.8	17484.3	435.6	360.0	397.8	41.6	46.9	44.3
Line 1 (2009)	17265.1	17612.1	17438.6	536.6	398.2	467.4	32.6	44.3	38.4
Mean	17339.6	17470.4	17405.0	421.1	348.0	384.5	41.9	50.7	46.3
S.E.D (df) (Years)			319.98(6)			4.97(6)			0.46(6)
(Cultivars)	493.04(33)	756.77(33)	451.61(66)	20.11(33)	17.70(33)	13.40(66)	2.02(33)	2.48(33)	1.60(66)
(Interaction)			690.14(58.69)			18.81(71.83)			2.21(70.51)
Prob. (Years)			$0.697^{n.s}$			<0.001***			<0.001***
(Cultivars)	<0.001***	<0.001***	<0.001***	<0.001***	<0.001***	<0.001***	<0.001***	<0.001***	<0.001***
(Interaction)			0.002**			<0.001***			0.01**
C.V %	4.00	6.10	5.20	6.80	7.20	7.00	6.80	6.90	6.90
Correlation with (Year of release)	n.s	n.s	n.s	n.s	n.s	n.s	n.s	-0.62*	-0.58*
(Grain yield)	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s

* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

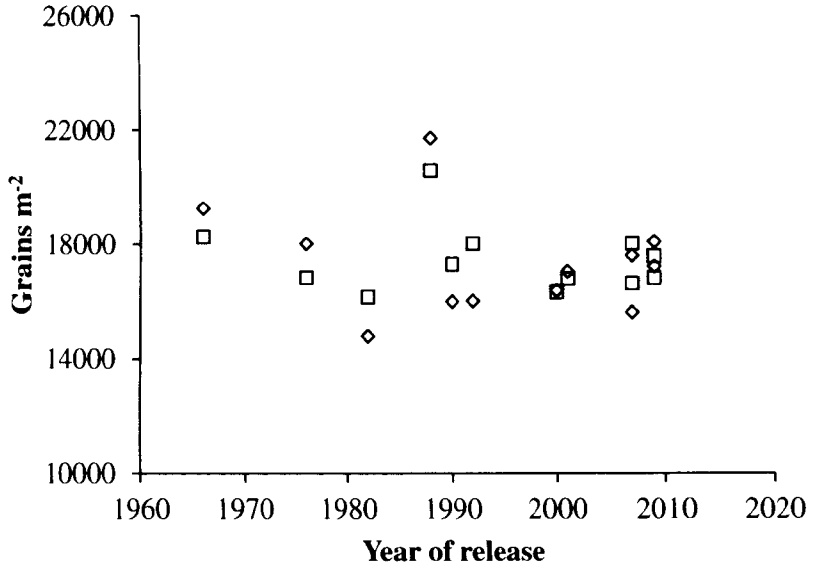


Figure 4.5 Regression of year of release on grains m^{-2} for 2009 (__◇__) $y = 2.2584x^2 - 9020x + 9E+06$ ($R^2 = 0.107$; $P = 0.601$), and 2010 (---□---) $y = 0.4531x^2 + 1786.6x - 2E+06$ ($R^2 = 0.0428$; $P = 821$) for 12 CIMMYT spring wheat cultivars.

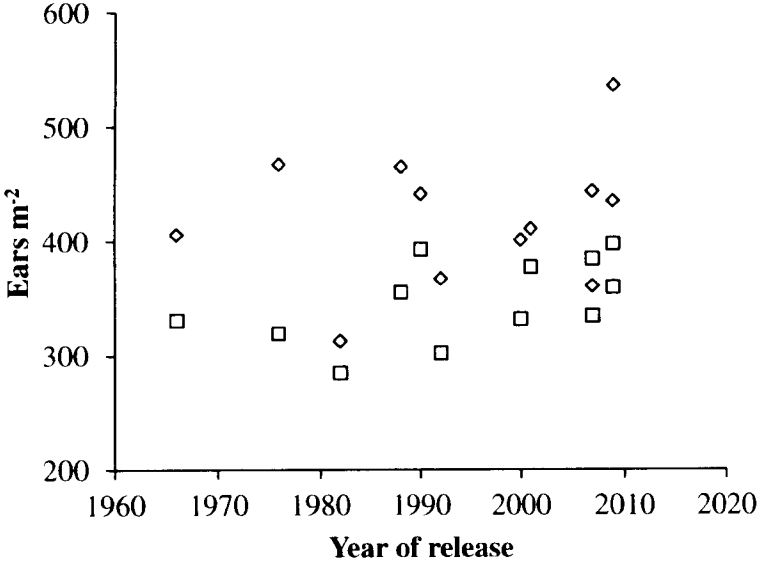


Figure 4.6 Regression of year of release on ears m^{-2} for 2009 (__◇__) $y = 0.076x^2 - 301.49x + 299490$ ($R^2 = 0.1002$; $P = 0.622$), and 2010 (---□---) $y = 0.0355x^2 - 139.73x + 138007$ ($R^2 = 0.3072$; $P = 0.192$) for 12 CIMMYT spring wheat cultivars.

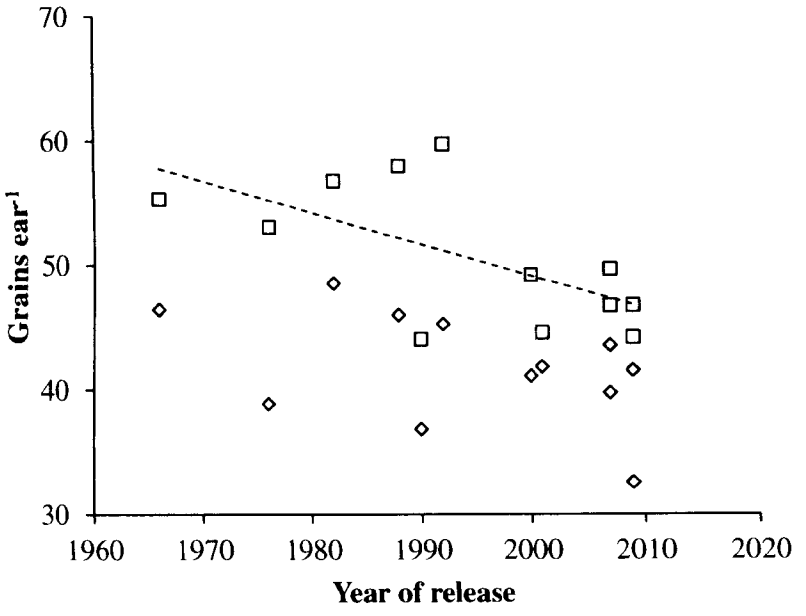


Figure 4.7 Regression of year of release on grains ear^{-1} for 2009 (__◇__) y= -0.0034x2 + 13.506x - 13249 (R^2 = 0.2278; *P* = 0.313), and 2010 (---□---) y=-0.0071x2 + 28.149x - 27702 (R^2 = 0.4419; *P* = 0.074) for 12 CIMMYT spring wheat cultivars.

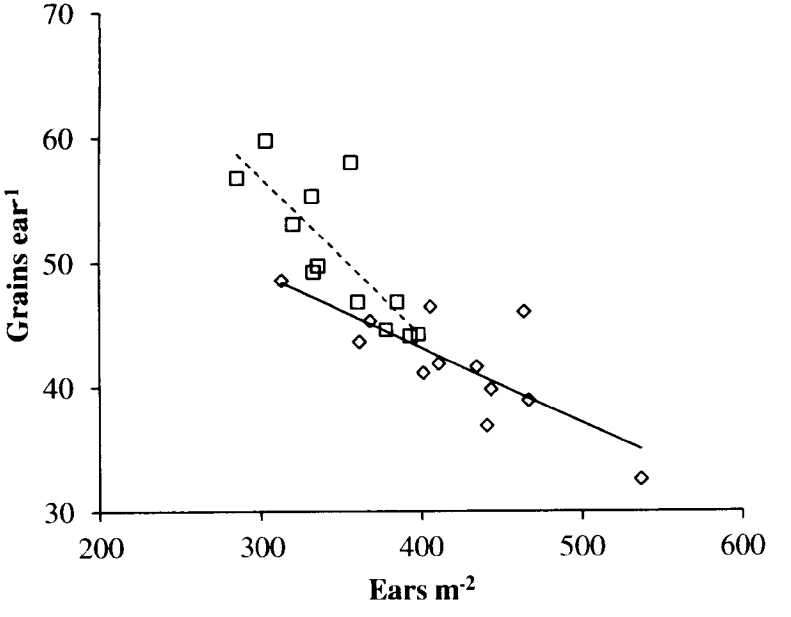


Figure 4.8 Regression of ears m^{-2} on grains ear^{-1} for 2009 (__◇__) y= 0.0599x + 67.149 (R^2 = 0.6034; *P* = 0.003), and 2010 (---□---) y=0.1266x + 94.806 (R^2 = 0.6568; *P* = 0.001) for 12 CIMMYT spring wheat cultivars.

Yield progress was associated with grain weight improvement rather than grain number per unit area. Grains were heavier in 2009 (41.7) than in 2010 (40.8) mg but this was not statistically significant ($P = 0.115$). Grain weight ranged from 33.9 mg for the oldest cultivar (Siete Cerros, 1966) to 45.4 mg for one of the most recent cultivars (Roelfes, 2007). Grain weight was positively correlated with both year of release and grain yield ($r = 0.79$, $P < 0.01$) and ($r = 0.69$, $P < 0.05$), respectively.

Genetic progress in grain weight was most apparent up to about 1990. Since there were no systematic changes during the period of 1966 to 2009 in both ears m^{-2} and grains per ear, individual grain weight was the principal numerical yield component explaining the genetic progress in the yield amongst the cultivars. This result is consistent with the positive relationship between the yield progress and the AGDM.

There was a linear increase in the individual grain weight from 1966 till 2009 ($P = 0.01$) in 2009 and ($P < 0.001$) in 2010 (Fig. 4.9). This improvement in grain weight was most evident during the period from 1966 (Siete Cerros) to 1992 after which the rate of increase slowed down to 2009.

Table 4.9 Thousand grain weight for 12 CIMMYT spring wheat cultivars in 2009 and 2010

Cultivar (Year of release)	TGW 100% DM (g)		
	2009	2010	Mean
Siete Cerros (1966)	34.7	33.2	33.9
Pavon (1976)	36.1	35.7	35.9
Seri (1982)	42.2	40.0	41.1
Bacanora (1988)	34.6	36.0	35.3
Attila (1990)	44.9	42.7	43.8
Baviacora (1992)	46.3	43.4	44.9
Tarachi (2000)	40.9	41.3	41.1
Tacupeto (2001)	41.1	42.1	41.6
Roelfes (2007)	46.6	44.2	45.4
Navojoa (2007)	43.3	42.3	42.8
Becard (2009)	45.3	45.2	45.3
Line 1 (2009)	44.3	43.3	43.8
Mean	41.7	40.8	41.2
S.E.D (df) (Years)			0.493(6)
(Cultivars)	0.748(33)	1.412(33)	0.799(66)
(Interaction)			1.189(65.25)
Prob. (Years)			$0.115^{n.s}$
(Cultivars)	<0.001***	<0.001***	<0.001***
(Interaction)			$0.153^{n.s}$
C.V %	2.50	4.90	3.9
Correlation with (Year of release)	0.71**	0.87**	0.79**
(Grain yield)	n.s	0.75**	0.69*

* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

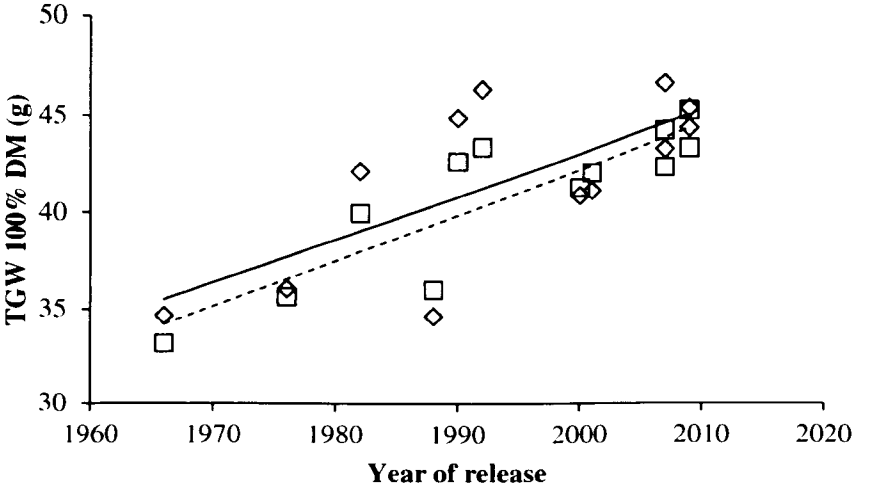


Figure 4.9 Regression of year of release on grain weight for 2009 (__◇__) y = 0.2212x – 399.35 (R^2 = 0.5073; *P* = 0.01), and 2010 (---□---) y = 0.2347x – 427.25 (R^2 = 0.751; *P* < 0.001) for 12 CIMMYT spring wheat cultivars.

4.4 DISCUSSION

4.4.1 Physiological basis of genetic progress in grain yield

Results of this study showed a linear genetic progress in grain yield under irrigated conditions from 1966 to 2009 in the northwest of Mexico. The rate of progress was 32 kg ha^{-2} yr^{-1} (r = 0.76, P < 0.01, Tables 4.6, 4.11 and Figure 4.2) or 0.6% p.a. This was less than the genetic progress reported in some other studies conducted on CIMMYT wheat cultivars. Waddington *et al.* (1986) and Sayre *et al.*, (1997), at the same site, found genetic gains in grain yield of 59 from 1950 to 1982 and 67 kg ha^{-1} yr^{-1} from 1962 to 1988, respectively. However, genetic gain in grain yield was relatively similar to these studies during the corresponding periods from 1966 to 1988 (58 kg ha^{-1} yr^{-1}; Figure 4.11). The grain yield progress was not statistically significant for the sub-set of cultivars introduced from 1992 to 2009 when analyzed alone, although there was still a tendency for an increase with year of release. The situation here is relatively better than the result showed by Graybosch *et al.* (2010) who reported no genetic progress in grain yield in the Great Plains of the USA since 1983. In the present study, in the period from 1966 till about 1988, HI primarily contributed to genetic yield progress rather than biomass (Fig. 4.4). However, from 1988 till 2009, the yield progress is primarily attributed to the increase in the above-ground dry matter (Fig. 4.3), with HI actually decreasing. Figure 4.12 shows a comparison between the results of the current study and the study of Sayre *et al.* (1997) for the five common cultivars.

4.4.1.1 Effects of plant breeding on grains m^{-2}

The majority of previous studies on the genetic gain in grain yield worldwide showed that yield increase was mainly associated with the progress in the number of grains per unit land area (Sayre *et al.*, 1997; Perry and D'Antuono., 1989; Waddington *et al.*, 1986 and Abbate *et al.*, 1998) rather than individual grain weight. Nonetheless, in the present study, the relationship between grain number and year of release was not significant. Nevertheless, if a comparison is made between results in the present study and previous CIMMYT studies with some common cultivars (Waddington *et al.*, 1986 and Sayre *et al.*, 1997),

similar effects are apparent. In the study of Waddington *et al.* (1986) two cultivars were common with the present study (Siete Cerros, 1966 and Seri, 1982), whereas in the study of Sayre *et al.* (1997) five cultivars were common (Siete Cerros, 1966; Seri, 1982; Bacanora, 1988; Attila, 1990 and Baviacora, 1992). No differences were found in grains m^{-2} between Siete Cerros (1966) and Seri (1982) in the study of Waddington *et al.*, (1986). In the study of Sayre *et al.* (1997), Attila (1990) and Baviacora (1992) produced only 90.1 and 92.8 % respectively, of the grains m^{-2} which Bacanora (1988) produced. Figure 4.13 shows a comparison between the current study and the study of Sayre *et al.* (1997) in grains m^{-2} for the five common cultivars. For both sets of cultivars, there was no change with year of release for grains m^{-2} but a significant increase in grain weight with year of release (Fig. 4.14).

The reduction in the plant height with the introduction of the semi-dwarfing genes played an important role to improve the ear partitioning index at anthesis and decrease the competition between the growth of ear and stem during the pre-anthesis phase (Fischer, 1987). In the studies of Waddington *et al.* (1996) and Sayre *et al.* (1997), the groups of cultivars studied contained older tall cultivars and more modern semi-dwarf cultivars, and this may in part explain why they detected changes in grains m^{-2} with plant breeding. The presently reported effects are all within semi-dwarf cultivars, released during green and post-green revolution phases. Though there was some tendency to produce more ears per unit area in modern cultivars, the number of grains per unit area did not increase as grains per ear had decreased. The usual reason explaining genetic variation in grains ear^{-1} in wheat is variation in florets per spikelet rather than spikelets per ear, as the latter is less affected by factors after the formation of the terminal spikelet (Evans, 1975 and Acreche *et al.*, 2009). Many researchers mentioned the increased competition for assimilates between the stem and the ear during the period of stem elongation as a reason for reductions in floret fertility and grains per ear (Kirby, 1988), though others such as Bancal (2008) found a positive relation between stem growth and grains per unit land area. One of the strategies suggested to increase grains per unit land area was to extend the stem-elongation phase (Foulkes *et al.*, 2011). In addition, improving the ear partitioning index (proportion of above-ground dry matter allocated to the ear at anthesis) was suggested as an additional way

to increase grains m^{-2}. Austin (1980) reported that HI of 62% can be theoretically obtained by an alteration of the DM partitioning mainly by reducing DM partitioned to the stem-and-leaf-sheaths by 50%. Furthermore, Foulkes *et al.* (2011) suggested that HI might be increased to 64% by increasing AGDM by 10% and decreasing the ratio of chaff to grain by 10% and holding the other assumptions of Austin (1980) the same.

4.4.1.2 Effects of plant breeding on grain weight

Most previous studies on the physiological basis of genetic gains in wheat yield potential in the last decades did not show any change in grain weight (Sayre *et al.*, 1997; Perry and Antuono, 1989; Acreche *et al.*, 2008). With the introduction of the semi-dwarf cultivars during the Green Revolution, there was a tendency for grain weight to decrease (Waddington *et al.*, 1986) and this usually was associated with more grains in distal position in spikelets with lower potential grain weight. A few studies indicated that this yield component has contributed to the progress in yield potential, such as Cox *et al.* (1988). Results in the current study indicated that individual grain weight appeared to track the improvement of the yield potential over the 43-year period. The correlations between grain weight and both year of release and grain yield were significant ($r = 0.79$, $P = 0.01$) and ($r = 0.69$, $P = 0.05$), respectively. However, as expected, the correlation between number of grain m^{-2} and grain weight was negative (Figure 4.10). Compared to the study of Sayre *et al.* (1997), trends in individual grain weight were broadly similar in the common cultivars (Figure 4.14). However, examining more modern genotypes in the present study with heavier grains, there was a strong positive relationship of this trait with both year of release and grain yield. Increasing individual grain weight and not the number of grains per m^2 was the main reason for the increase of HI from 1966 till 1982. Increasing harvest biomass was also partly explained by the increase in the individual grain weight from 1988 until 2009. Singh and Trethowan (2007) reported values of 57 mg in individual grain weight in bread wheat during recent years compared to about 40 mg for most cultivars released during the 1980s and 1990s in Northwest Mexico in CIMMYT germplasm. This increase may have resulted from selecting for end-use market criteria and from

increase seedling vigour. Moreover, many studies showed that possessing the *1BL/1RS* translocation resulted in higher individual grain weight than check cultivars (Zarco-hernands *et al.*, 2005; Villareal *et al.*, 1998 and Moreno-Sevilla *et al.*, 1995). Factors affecting final grain weight and size are not only those affecting the plant post- anthesis but also during a short period pre-anthesis, especially the effect of temperature where negative effects of high temperature on grain weight immediately pre-anthesis were due to reducing the carpel size (Calderini *et al.*, 1999a; Calderini *et al.*, 1999b; Calderini *et al.*, 2001). In addition, Calderini and Reynolds (2000) reported that a de-graining treatment pre-anthesis (at heading) had a larger effect on the grain weight than a post-anthesis treatment, and that this was due to a positive effect on the carpel size with de-graining pre-anthesis. Foulkes *et al.* (2011) suggested that improving our understanding of the factors such as temperature affecting grain size and weight especially the maternal tissues would be a key factor to increase grain weight potential in plant breeding programs.

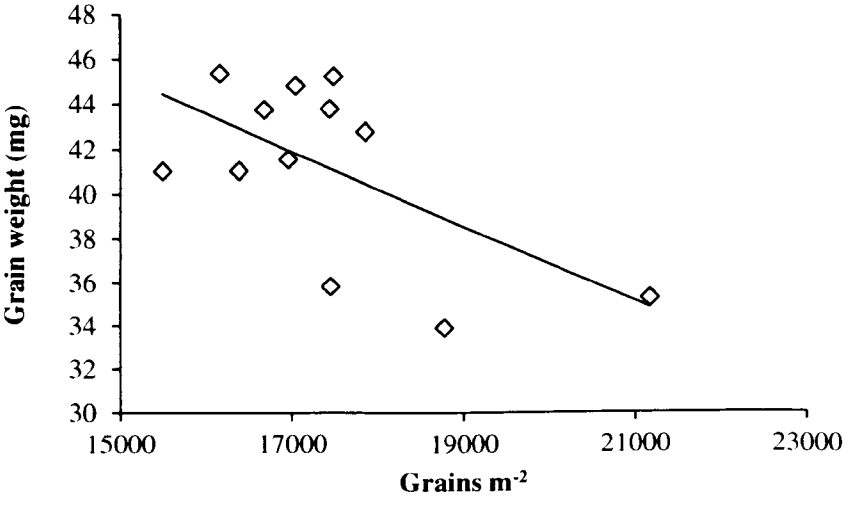
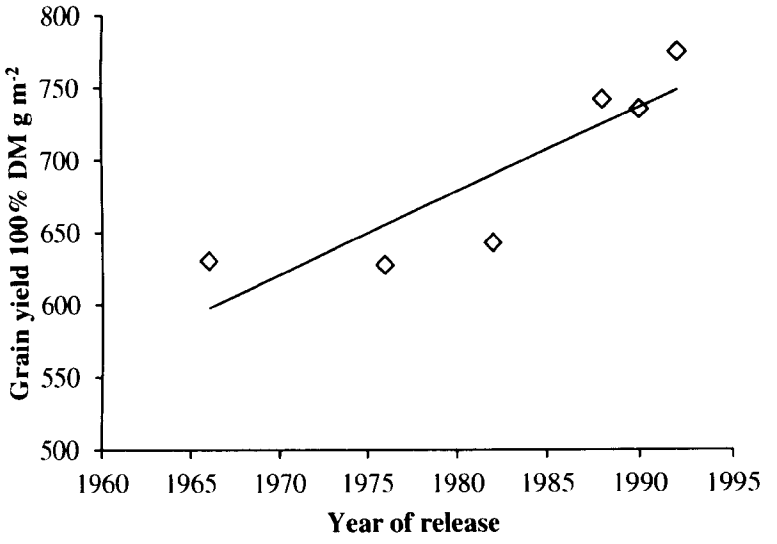


Figure 4.10 Regression of grain weight on grains m^{-2} averaging years Y = - 0.0017x + 70.527 for 12 CIMMYT spring wheat cultivars (R^2 = 0.3689).



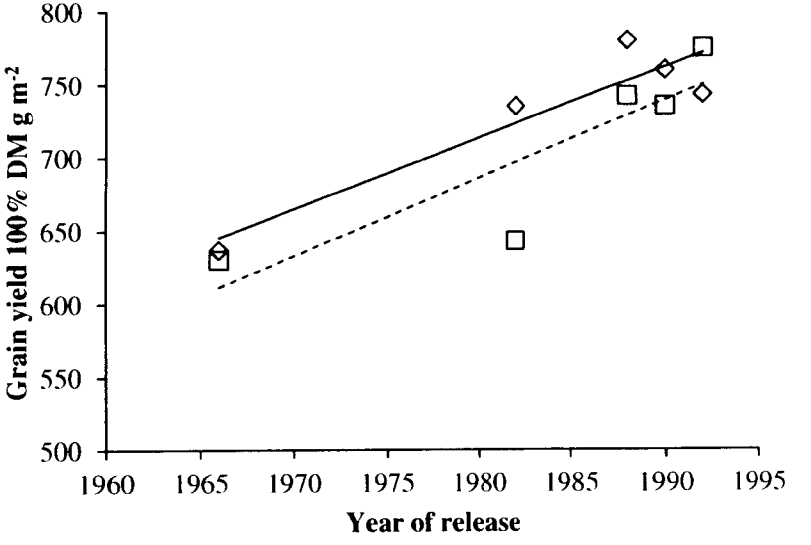
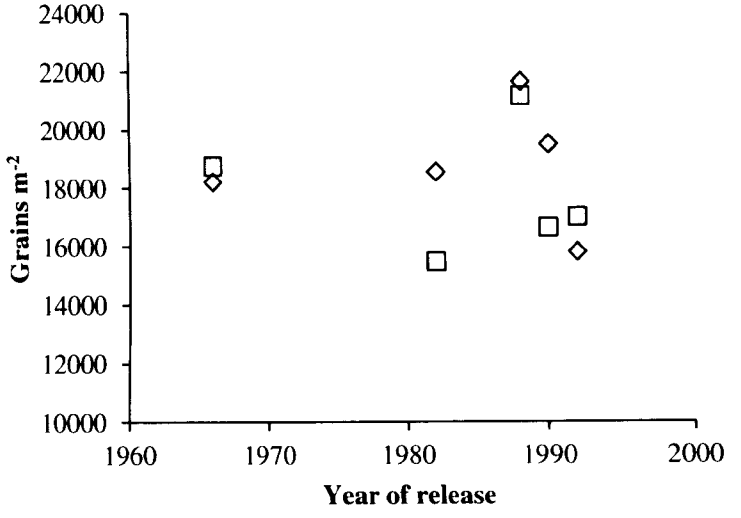


Figure 4.11 Regression of grain yield on year of release for the average of 08/09 and 09/10 y= 5.7928x – 10791 (R^2 = 0.7653) for CIMMYT spring wheat cultivars in present study released from 1966 to 1992. (values are means of 2009 and 2010.

Figure 4.12 Regression of grain yield on year of release for the five common cultivars of Sayre et al (1997) (__◇__) y= 4.8511x – 8891.6 (R^2 = 0.8522), and the present study (---□---) y= 5.3192x - 9846 (R^2 = 0.7567) for 12 CIMMYT spring wheat cultivars.



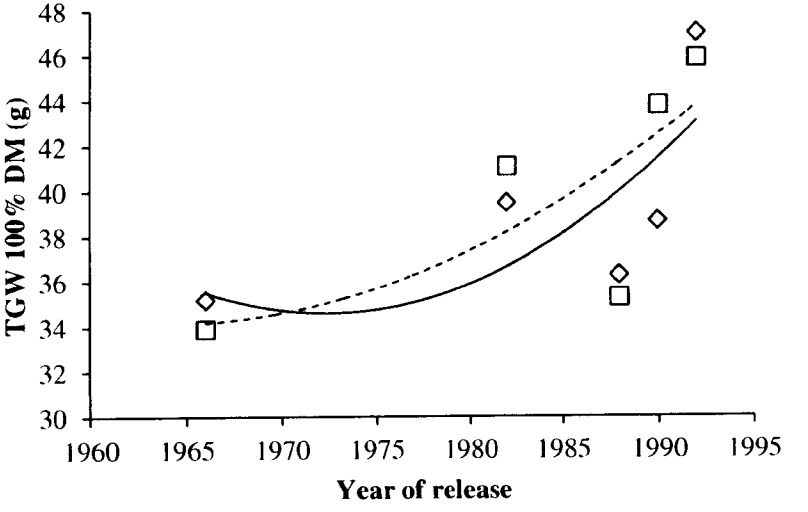


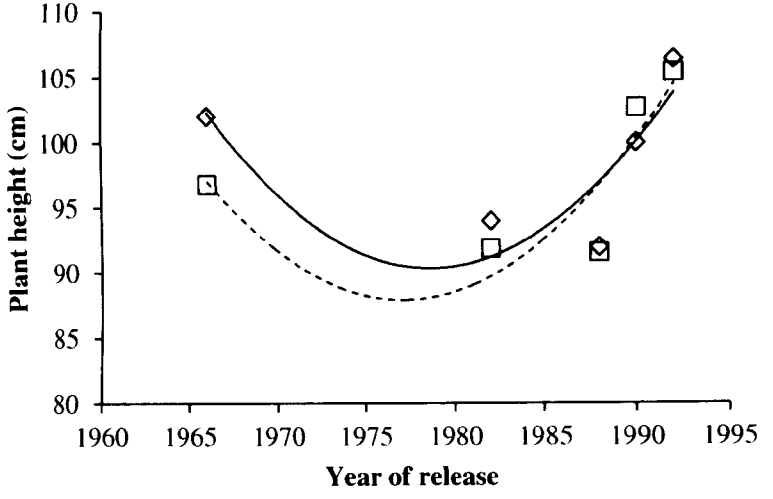
Figure 4.13 Regression of year of release on grains per m^{-2} for the five common cultivars of Sayre et al (1997) (__ ◇__) y= 6.0758x + 6711.4 (R^2 = 0.0009), and the present study (---□---) y= -27.301x + 71984 (R^2 = 0.0169).

Figure 4.14 Regression of year of release on TGW for the five common cultivars of Sayre et al (1997) (__ ◇__) y= 0.0221x^2 – 87.147x + 85979 (R^2 = 0.4778), and the present study (---□---) y= 0.012x^2 – 47.123x + 46299 (R^2 = 0.5416).

4.4.2 Effects of breeding on plant height and physiological yield components

Results showed that plant height has increased significantly with plant breeding, particularly after 1988 (r = 0.58, P = 0.05). This increase is consistent with the increase of above-ground biomass at maturity which appeared to explain most of the genetic progress in grain yield, particularly after 1988 (r = 0.77, P = 0.01). In the study of Sayre *et al.* (1997), plant height was reduced up until Bacanora (1988) and that was associated with an increase in HI and no change in the biomass; consequently yield potential increased. However, in the present study, plant height has increased since Bacanora (1988) associated with an increase in biomass which was proportionately greater than the decrease in HI, hence yield potential has increased.

Results for plant height, biomass and harvest index in this study are in agreement with those in the study of Sayre *et al.* (1997; Fig. 4.15 and 4.16) for the common cultivars in the two studies. Plant height and grain weight were increased in cvs Attila (1990) and Baviacora (1992) released after Bacanora (1988) in the study of Sayre *et al.*, (1997). Moreover, HI and grains per unit area were decreased in the same study. This supports the idea that improving harvest biomass has been a target in recent breeding strategies at CIMMYT since the early 1990s. Nonetheless, and unfortunately, breeders seem to have inadvertently decreased the HI at the same time raising in the harvest biomass.



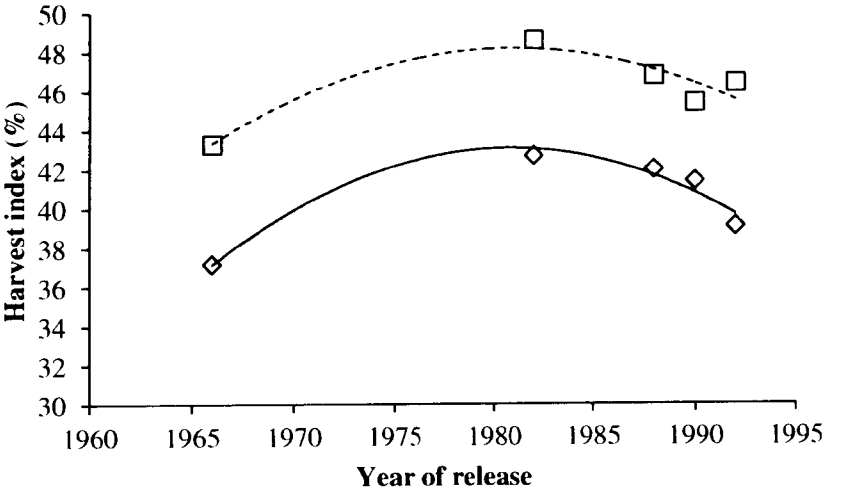


Figure 4.15 Regression of year of release on plant height for the five common cultivars of Sayre et al (1997) (__◇__) $y= 0.0749x^2 - 296.5x + 293416$ (R^2 = 0.7169), and the present study (---□---) $y= 0.0742x^2 - 293.42x + 290147$ (R^2 = 0.7552).

Figure 4.16 Regression of year of release on HI for the five common cultivars of Sayre et al (1997) (__◇__) $y= -0.0271x^2 + 107.16x - 106093$ (R^2 = 0.9548), and the present study (---□---) $y= -0.0216x^2 + 85.57x - 84706$ (R^2 = 0.8648).

4.5 SUMMARY

Results of this chapter show that from 1966 to 2009, the rate of genetic gain in yield potential was 32 kg ha^{-1} yr^{-1} (r = 0.76, P = 0.01). Yield progress was primarily associated with HI in the period from 1966 until about 1982 increasing from 43% (Siete Cerros, 1966) to 49% (Seri, 1982). The increase in the AGDM was evident since the introduction of Seri (1982) from which point it increased rapidly from 1325 to 1776 g m^{-2} (Line1, 2009).

The components of grain number per m^2, ears per m^2 and grains per ear, had a less important effect on genetic progress in yield in this set of cultivars. However, grain weight appeared to track the improvement in yield potential over the 43-year period and increased particularly during the period from 1966 till 1992.

There was a positive association between grain weight and yield amongst the 12 cultivars (r = 0.69, P = < 0.05). This result is consistent with the positive correlation between AGDM and yield (r = 0.90, P < 0.001). In general, these results indicate that grain weight was the main numerical yield component underpinning genetic yield progress since 1966 rather than grains per m^2.

Averaging across the two years the genetic rates of progress for yield and harvest traits during the period from 1966 to 2009 are shown in Table 4.10. The increase in the grain yield of 32 kg ha^{-1} yr^{-1} was associated with an increase in the individual grain weight of 0.23 mg $grain^{-1}$ $year^{-1}$.

Table 4.10 Fitted parameter estimates for changes in crop traits with year of release for 12 CIMMYT spring wheat cultivars released between 1966 and 2009. Linear and quadratic functions were fitted to 2-yr cultivar means (2009 and 2010).

Trait	Parameter estimates linear ($y = a + bx$)		Parameter estimates quadratic		($y = a + bx + cx2$)
	y (as in 1966)	$b \pm$ SE	y (as in 1966)	$b \pm$ SE	$c \pm$ SE
Yield and yield components					
Combine grain yield, g m^{-2}	630.4	3.164 ± 0.852**			
Grains per unit area, m^{-2}	18769.7	-24.32 ± 31.9$^{n.s}$			
Ears per unit area, m^{-2}		1.118 ± 0.930$^{n.s}$	368.8	-220.61 ± 294.0$^{n.s}$	0.0557 ± 0.0739$^{n.s}$
Grains per ear	50.9	-0.1992 ± 0.0876*			
Mean grain weight, mg	33.9	0.2280 ± 0.0552**			
AGDM and HI					
AGDM harvest, g m^{-2}		7.56 ± 1.98**	1457.4	-504.14 ± 624.0*	0.13 ± 0.157*
Harvest index%		-0.0125 ± 0.0391$^{n.s}$	43.3	22.01 ± 10.4$^{n.s}$	-0.00553 ± 0.00262$^{n.s}$
df		10		9	9

*** Significant at 0.05 probability level**
**** Significant at 0.01 probability level**
***** Significant at 0.001 probability level**
n.s Not significant

CHAPTER 5 EFFECTS OF BREEDING ON PRE-ANTHESIS GROWTH

5.1 INTRODUCTION

This chapter examines the physiological processes from the onset of crop emergence until flowering plus seven days in the experiments at CIMMYT Ciudad Obregon in 2008-9 and 2009-10 examining 12 CIMMYT cultivars released from 1966 to 2009. Measurements were carried out to study these physiological processes as follows: i) growth analysis to estimate shoot number and DM production and partitioning at GS31 in 2009 and 2010, GS39 in 2010 only and GS61 + 7d in 2009 and 2010 (sampling was carried out at GS 61 + 7 days rather than at GS 61 to allow a more accurate estimate of stem WSC per m^2 basis); ii) radiation interception and radiation use-efficiency was measured during 2010 only (fractional PAR interception was taken at GS31, GS39 and GS61 + 7d); iii) Normalised Difference Vegetative Index (NDVI) was measured every two weeks from crop emergence to GS61 in 2009 and 2010. Leaf activity traits (canopy temperature, stomatal conductance and SPAD) during the stem-elongation phase were measured in both seasons. In addition, ear traits (rachis length, total and fertile spikelets per ear) were measured in 2009 and 2010; however, ear width and awns length were measured only in 2009.

The main objective of this chapter is to understand the physiological basis of the changes in grains m^{-2} with plant breeding in the set of CIMMYT cultivars as a main yield component, which is determined during this phase and to examine associations with genetic yield progress and quantify the rates of change of physiological traits with year of release. The physiological components of grains m^{-2} are:

Grains m^{-2} = RI x RUE x EPI x EFI

Where RI is the radiation interception from crop emergence to anthesis, (RUE) is the radiation-use efficiency, EPI is the ear partitioning index (ear

DM/AGDM) at anthesis and EFI is the ear fertility index (grains per gram ear DM) at anthesis.

The numerical components of grains m^{-2} are:

Grains m^{-2} = fertile shoots m^{-2} x spikelets ear^{-1} x grains $spikelet^{-1}$

The specific hypotheses tested in this chapter were:

1. The genetic variation amongst the historic set of cultivars in grains m^{-2} is associated with changes in above-ground dry matter accumulation and RUE during the stem-elongation period (GS31-GS61+7d) , in addition to ear partitioning index.
2. The genetic variation in RUE amongst the set of historic cultivars is associated with changes in stomatal conductance and flag leaf 'activity' traits and/or canopy architecture traits (vertical light distribution) during the stem-elongation phase.
3. The genetic variation in grains m^{-2} amongst the 12 cultivars is positively associated each of ears m^{-2}, grains per ear and spikelets per ear and grains per spikelet, and in ear fertility index.

5.2 MATERIALS AND METHODS

The assessments of dry matter growth and light interception at GS31, GS39 and GS61+7d were taken on the actual date that the cultivar reached the GS, i.e. different cultivars were assessed on different calendar dates. At GS31shoots were counted in the plant material sampled from the 0.5 x 0.4 m area and their dry weight recorded separately after drying for 48 hours at 85 °C. Measurements at GS39 were taken in 2009/10 only; in each plot a 50% sub-sample of the plant material sampled (0.5 x 0.4 m area) was taken by fresh weight (FW) and used for the growth analysis. The dry weight of the infertile shoots was recorded. A further 50% sub-sub-sample of the fertile shots by FW

was randomly selected and this material separated into: i) green lamina, ii) stems plus attached leaf sheath, and the dry weight of each fraction recorded after drying at 85°C for 48h. The dry weight of the other 50% remainder sub-sub-sample of the fertile shoots was also recorded. Measurements at GS61 + 7d were taken in both years; the growth analysis was as described for GS39 above, except that: (i) dry matter partitioning was carried out according to five plant components (ear, flag-leaf green lamina, remaining green lamina, remaining non green lamina and stem plus attached leaf sheath) and (ii) ear traits (rachis length, ear width, awns length, and total and fertile number of spikelets per ear) were recorded on an additional sub-sub-sample of 15 fertile shoots from the 50% sub-sample.

5.3 RESULTS

5.3.1 Shoot production and survival

At GS31, fertile-shoot number amongst cultivars in 2009 and 2010 ranged from 468 - 693 and 396 - 611 shoots m^{-2}, respectively (Table 5.1). No significant differences were found amongst the cultivars in both years. Overall, fertile shoot number was similar in both years ($P = 0.248$): (550 m^{-2}) and (518 m^{-2}) for 2009 and 2010, respectively. There was no correlation between fertile shoot number per m^2 and either year of release or grain yield (Table 5.1).

Fertile-shoot number was not measured at GS39 in 2009. However, in 2010 there were differences amongst the cultivars ($P = 0.014$) in the range 310 (Seri, 1982) to 448 m^{-2} (Navojoa, 2007 and Line 1, 2009). No correlation was found between fertile shoot number and either year of release or grain yield. The number of infertile shoots per m^2 did not differ among the cultivars ($P = 0.171$), and again there was no correlation with either the year of release or grain yield (Table 5.1).

More fertile shoots m^{-2} at GS61+7 days were produced in 2009 (427) compared to 2010 (338) ($P < 0.001$). There were differences amongst cultivars in both seasons and for the average across seasons ($P < 0.001$). However, the interaction between year and cultivar was not significant ($P = 0.811$). In 2009,

fertile shoots m^{-2} ranged from 327 (Seri, 1982) to 483 (Navojoa, 2007). A similar result was obtained in 2010; cv Seri (1982) produced the fewest shoots per m^2 (237) and cv Navojoa the most (442). No trends for the relationship between fertile shoots and year of release were found in either year (Table 5.2).

No significant differences were found between year in shoot mortality from GS31 to GS61 ($P = 0.522$; Table 5.2). Cultivars differed in the number of non-surviving shoots on average over the two seasons in the range 73 (Siete Cerros, 1966) to 224 m^{-2} (Baviacora, 1992) ($P = 0.001$; Table 5.2). However, no statistically significant correlations amongst cultivars were found between this trait and either year of release or grain yield.

Table 5.1 Fertile shoots per m^2 at GS31 and GS39 for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2009 and 2010.

Cultivar (Year of release)	Fertile shoots m^{-2} GS31			Fertile shoots m^{-2} GS39	Infertile shoots m^{-2} GS39
	2009	2010	Average	2010	
Siete Cerros (1966)	512.5	395.8	454.2	405.0	40.0
Pavon (1976)	563.8	571.7	567.7	428.3	80.0
Seri (1982)	467.5	475.0	471.3	310.0	88.3
Bacanora (1988)	507.5	491.7	499.6	430.0	90.0
Attila (1990)	605.0	610.8	607.9	428.3	111.7
Baviacora (1992)	545.0	541.7	543.3	325.0	66.7
Tarachi (2000)	607.5	561.7	584.6	385.0	88.3
Tacupeto (2001)	692.5	506.7	599.6	441.7	95.0
Roelfes (2007)	507.5	499.2	503.3	376.7	115.0
Navojoa (2007)	547.5	524.2	535.8	448.3	63.3
Becard (2009)	487.5	550.8	519.2	405.0	68.3
Line 1 (2009)	552.5	486.7	519.6	448.3	60.0
Mean	549.7	518.0	533.8	402.6	80.6
S.E.D (df) (Years)			22.17(3)		
(Cultivars)	65.11(11)	79.00(11)	55.33(33)	37.62(22)	24.58(22)
(Interaction)			79.62(35.98)		
Prob. (Years)			$0.248^{n.s}$		
(Cultivars)	$0.166^{n.s}$	$0.484^{n.s}$	$0.162^{n.s}$	0.014*	$0.171^{n.s}$
(Interaction)			$0.749^{n.s}$		
C.V %	11.8	15.6	16.5	11.4	37.4
Correlation with (Year of release)	n.s	n.s	n.s	n.s	n.s
(Grain yield)	n.s	n.s	n.s	n.s	n.s

* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

Table 5.2 Fertile shoots per m^2 at GS61+7d and non-surviving shoots between GS31 to GS61+7d for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2008/09 and 2009/10

Cultivar (Year of release)	Fertile shoots number m^{-2}			Non-surviving shoots m^{-2} GS31-GS61+7d		
	2009	2010	Average	2009	2010	Average
Siete Cerros (1966)	403.1	333.3	368.2	82.6	62.5	72.6
Pavon (1976)	467.8	326.7	397.2	87.4	245.0	166.2
Seri (1982)	327.0	236.7	281.9	130.9	238.3	184.6
Bacanora (1988)	435.2	338.3	386.8	59.7	153.3	106.5
Attila (1990)	470.7	356.7	413.7	158.2	254.2	206.2
Baviacora (1992)	360.1	295.0	327.5	201.4	246.7	224.0
Tarachi (2000)	440.1	363.3	401.7	171.1	198.3	184.7
Tacupeto (2001)	477.0	390.0	433.5	240.4	116.7	178.5
Roelfes (2007)	372.9	298.3	335.6	146.2	267.5	206.9
Navojoa (2007)	483.1	400.0	441.5	60.0	124.2	92.1
Becard (2009)	420.7	343.3	382.0	59.7	207.5	133.6
Line 1 (2009)	467.6	370.0	418.8	93.2	116.7	104.9
Mean	427.1	337.6	382.4	124.2	185.9	155.1
S.E.D (df) (Years)			8.422(4)			16.79(4)
(Cultivars)	27.317(22)	27.037(22)	19.218(44)	60.511(11)	64.905(22)	17.59(44)
(Interaction)			27.350(47.92)			29.15(26.52)
Prob. (Years)			<0.001***			$0.522^{n.s}$
(Cultivars)	<0.001***	<0.001***	<0.001***	$0.137^{n.s}$	0.053†	0.001***
(Interaction)			$0.811^{n.s}$			0.042*
C.V %	7.8	9.8	8.7	48.7	42.8	26.7
Correlation with (Year of release)	0.21	0.57†	0.48	0.10	0.07	0.10
(Grain yield)	0.11	0.57†	0.29	-0.19	0.10	-0.01

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

5.3.2 Above ground dry matter production

At GS31, results showed differences amongst the cultivars in 2009 in fertile-shoot dry weight which ranged from 92.7 (Bacanora, 1988) to 140.6 g m^{-2} (Navojoa, 2007) (P = 0.002; Table 5.3). No significant differences were found in 2010 (P = 0.427). Results showed that fertile-shoot dry weight was slightly higher in 2009 (122 g m^{-2}) than 2010 (111 g m^{-2}) (P = 0.057).

At GS39 in 2010, there were significant differences amongst cultivars in the dry weight of fertile shoots (P = 0.005) in the range 350 (Seri, 1982) to 508 (Navojoa, 2007), with an overall average of 439 g m^{-2}. There was no change with year of release in fertile-shoot DM per m^2. No statistically significant differences were found amongst the cultivars in infertile shoot DM in the range 5.4 - 22.6 g m^{-2} (Table 5.3).

At anthesis, greater fertile-shoot DM was produced in 2009 (916 g m^{-2}) than 2010 (869 g m^{-2}) (P = 0.046; Table 5.4). Averaging across years, there were differences amongst cultivars in the range 757.3 to 1001.8 g m^{-2} (P < 0.001). The interaction between year and cultivar was significant (P < 0.001). The main interactions were that cv Becard (2009) produced relatively more biomass in 2009 than in 2010; however, Line 1 (2009) produced more biomass in 2010 compared to 2009. There was trend in 2010 for the biomass of fertile shoots at GS61 + 7 days to increase with year of release (P = 0.07).

Table 5.3 Fertile and infertile shoots dry matter at GS31 and GS39 for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2008/09 and 2009/10.

Cultivar (Year of release)	Fertile shoots DM g m^{-2} GS31			Fertile shoots DM g m^{-2} GS39	Infertile shoots DM g m^{-2} GS39
	2009	2010	Average	2010	
Siete Cerros (1966)	134.3	99.4	116.9	463.7	5.4
Pavon (1976)	126.2	113.0	119.6	461.5	14.7
Seri (1982)	98.9	102.8	100.8	349.5	15.3
Bacanora (1988)	92.7	93.1	92.9	427.0	13.5
Attila (1990)	134.7	124.6	129.7	465.0	22.1
Baviacora (1992)	117.6	113.2	115.4	413.5	14.0
Tarachi (2000)	99.2	121.7	110.5	388.1	12.7
Tacupeto (2001)	128.9	118.0	123.5	448.0	15.1
Roelfes (2007)	137.1	125.3	131.2	494.2	22.6
Navojoa (2007)	140.6	109.0	124.8	507.7	8.4
Becard (2009)	117.1	87.8	102.4	373.0	9.0
Line 1 (2009)	136.4	117.7	127.0	477.7	6.1
Mean	122.0	110.5	116.2	439.1	13.2
S.E.D (df) (Years)			3.81(3)		
(Cultivars)	9.27(11)	16.86(22)	11.19(33)	36.61(22)	5.61(22)
(Interaction)			15.92(34)		
Prob. (Years)			0.057†		
(Cultivars)	0.002**	0.427$^{n.s}$	0.035*	0.005**	0.093†
(Interaction)			0.455$^{n.s}$		
C.V %	7.6	18.7	15.4	10.2	51.9
Correlation with (Year of release)	0.19	0.24	0.25	0.12	0.03
(Grain yield)	0.21	0.05	0.09	0.13	0.06

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

Table 5.4 Fertile shoots dry weight per m^{-2} at GS61+7d for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2008/09 and 2009/10

Cultivar (Year of release)	Fertile shoots DM (g m^{-2})			Infertile shoots DM (g m^{-2})		
	2009	2010	Average	2009	2010	Average
Siete Cerros (1966)	740.6	773.9	757.3	31.9	35.9	33.9
Pavon (1976)	1160.4	800.6	980.5	41.2	34.3	37.8
Seri (1982)	926.7	735.4	831.0	29.8	29.9	29.9
Bacanora (1988)	833.3	893.1	863.2	39.3	33.4	36.3
Attila (1990)	833.5	949.6	891.5	28.1	25.8	27.0
Baviacora (1992)	794.8	851.5	823.2	32.4	33.5	32.9
Tarachi (2000)	765.3	864.5	814.9	33.7	26.4	30.1
Tacupeto (2001)	908.5	970.3	939.4	28.5	34.8	31.6
Roelfes (2007)	1134.7	868.8	1001.8	39.7	33.9	36.8
Navojoa (2007)	1027.3	974.0	1000.7	23.7	35.8	29.8
Becard (2009)	1142.9	791.9	967.4	60.9	32.2	46.6
Line 1 (2009)	717.7	952.1	834.9	26.9	24.8	25.8
Mean	915.5	868.8	892.1	34.7	31.7	33.2
S.E.D (df) (Years)			16.372(4)			4.72(4)
(Cultivars)	50.352(22)	83.327(22)	48.679(44)	8.28(22)	7.39(22)	5.55(44)
(Interaction)			67.92(47.60)			8.87(31.53)
Prob. (Years)			0.046*			$0.564^{n.s}$
(Cultivars)	<0.001***	0.094†	<0.001***	0.017*	$0.824^{n.s}$	0.044*
(Interaction)			<0.001***			$0.124^{n.s}$
C.V %	6.7	11.7	9.5	29.2	28.5	29.0
Correlation with (Year of release)	0.25	0.42	0.34	n.s	n.s	n.s
(Grain yield)	0.22	0.26	0.24	n.s	n.s	n.s
(Grains m^{-2})	-0.09	0.23	-0.13	0.27	0.28	0.25

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

5.3.3 Above-ground dry matter partitioning

At GS39, growth analysis of dry matter partitioning was carried out in 2010 only. In this year, differences were found amongst cultivars in both the amount of stem (i.e. stem with attached leaf sheath) DM per m^2 and stem DM partitioning (P = 0.001 and P = 0.008), respectively (Table 5.5). Stem DM ranged from 177 (Seri, 1982) to 295 g m^{-2} (Navojoa, 2007) and stem DM partitioning ranged from 49.1 (Tarachi, 2000) to 58.1% (Navojoa, 2007). Differences amongst cultivars in green lamina DM were not significant. (P = 0.193) However, there were differences amongst cultivars in green lamina DM partitioning from 39.3% (Navojoa, 2007) to 48.0% (Seri, 1982) (P = 0.003). Cultivars differed in both non-green lamina DM and non-green lamina DM partitioning (P < 0.005) and (P < 0.007), respectively. Values of non-green lamina DM ranged from 3.4 g m^{-2} (Becard, 2009) to 29.5 g m^{-2} (Pavon, 1976). Percentage of non-green lamina ranged from 1.4% (both Seri, 1982 and Line 1, 2009) to 6.4% Pavon (1976) (Table 5.5). Regression analysis (Fig 5.1) showed a positive relationship between stem and green-lamina dry weights (R^2 = 0.75). However, as stem and green lamina are the main components of the above-ground DM at this stage, a negative relation was obtained between the stem and green-lamina DM partitioning (R^2 = 0.67) (Fig 5.2). There was no statistically significant change in either stem DM partitioning or lamina DM partitioning at GS39 with year of release (Table 5.5).

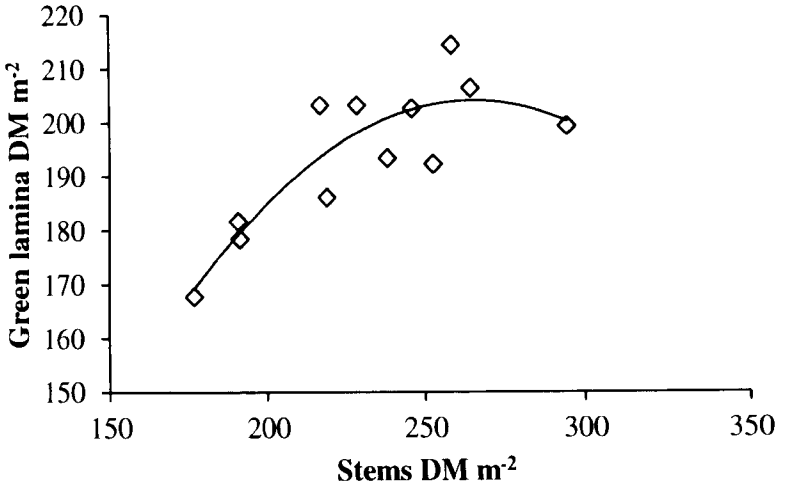
At GS61+7d, growth analysis was carried out in both 2009 and 2010. Results showed differences between the two seasons in the ear DM per m^2 (P = 0.005), with overall slightly more ear biomass produced in 2010 (297 g m^{-2}) than 2009 (264 g m^{-2}). The interaction between year and cultivar was not significant (P = 0.594). Averaging across years, ear DM per m^2 ranged from 241 g m^{-2} (Siete Cerros, 1966) to 362 g m^{-2} (Tacupeto, 2001). There was no association amongst cultivars between ear DM per m^2 and either year of release or grain yield (Table 5.6). For ear partitioning index, there was no effect for year (P < 0.078). Cultivars differ amongst each other (P < 0.001), but the year × cultivar interaction was not significant (P = 0.726). Ear partitioning at GS61+7d was slightly higher in 2010 (26.3%) than in 2009 (24.9%). Averaging over years,

the ear partitioning index ranged from 21.4% (Roelfes, 2007) to 28.4% (Tacupeto, 2001). There was an apparent trend for ear partitioning index (EPI) to increase up to ca. 1990 and to decrease thereafter to 2009 with an overall effect for a slight decrease over the 43-yr period (r = -0.41) (Fig 5.6). This decrease in EPI from ca. 1990 to 2009 appeared to be related mainly to the increase in plant height (r = - 0.61) (Fig 5.7).

Table 5.5 Dry matter (DM) per m^2 and partitioning of DM for stem plus sheath, green lamina and non green lamina at GS39 for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2009/10.

Cultivar (Year of release)	Stems DM g m^{-2}	Green lamina DM g m^{-2}	Non green lamina DM g m^{-2}	% Stems DM	% Green lamina DM	% Non green lamina DM
Siete Cerros (1966)	246.3	202.7	14.7	53.1	43.7	3.2
Pavon (1976)	238.5	193.5	29.5	51.7	41.9	6.4
Seri (1982)	176.8	167.8	4.9	50.6	48.0	1.4
Bacanora (1988)	216.9	203.2	6.8	50.8	47.6	1.6
Attila (1990)	252.9	192.4	19.7	54.4	41.4	4.2
Baviacora (1992)	218.9	186.1	8.5	52.9	45.0	2.0
Tarachi (2000)	190.7	181.7	15.8	49.1	46.8	4.1
Tacupeto (2001)	228.9	203.3	15.9	51.1	45.4	3.5
Roelfes (2007)	258.5	214.4	21.2	52.3	43.4	4.3
Navojoa (2007)	294.8	199.5	13.4	58.1	39.3	2.6
Becard (2009)	191.1	178.5	3.4	51.2	47.8	0.9
Line 1 (2009)	264.6	206.5	6.6	55.4	43.2	1.4
Mean	231.6	194.1	13.4	52.6	44.5	3.0
S.E.D (df) (Years)						
(Cultivars)	22.80(22)	15.44(22)	5.75(22)	1.85(22)	2.02(22)	1.23(22)
(Interaction)						
Prob. (Years)						
(Cultivars)	0.001***	0.193$^{n.s}$	0.005**	0.008**	0.003**	0.007**
(Interaction)						
C.V %	12.1	9.7	52.6	4.3	5.5	51.3
Correlation with (Year of release)	0.18	0.16	-0.27	0.23	-0.03	-0.30
(Grain yield)	0.23	0.16	-0.47	0.40	-0.05	-0.52†
(Grains m^{-2})	0.25	0.40	-0.27	0.23	-0.02	-0.32

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant



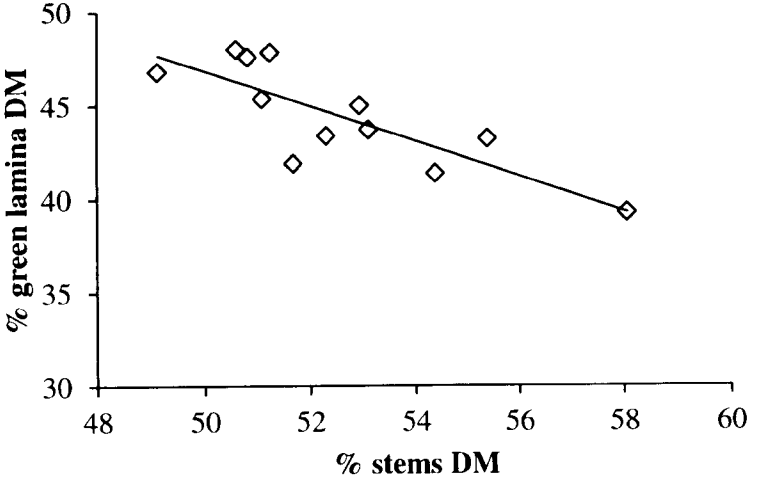


Figure 5.1 Regression of green lamina DM on stems DM at GS39 in 2010 y = 0.0044x2 + 2.3535x – 108.4 (R^2 = 0.7543; P = 0.002) for 12 CIMMYT spring wheat cultivars.

Figure 5.2 Regression of % of green lamina DM on % of stems DM at GS39 in 2010 y = -0.9393x + 93.835 (R^2 = 0.6702; P = 0.001) for 12 CIMMYT spring wheat cultivars.

Similar stem biomass was produced in 2009 and 2010 ($P = 0.224$, Table 5.7). Cultivars differed in the individual years ($P = 0.037$) in 2009 and ($P = 0.014$) in 2010 and for the cross-year mean ($P < 0.001$), but there was no interaction between year and cultivar ($P = 0.457$). Averaging across years, stem DM ranged from 461 (Seri, 1982) to 717 g m^{-2} (Navojoa, 2007). There was a positive association between stem DM and year of release ($r = 0.63$; $P < 0.05$). A similar percentage of AGDM was partitioned to the stems in 2009 (55%) and 2010 (54%). Overall genotype values ranged from 52 (Seri, 1982) to 57% (Roelfes, 2007). Correlation analysis (Table 5.7) showed a positive association between stem DM partitioning at anthesis and both year of release ($r = 0.72$, $P < 0.01$) and grain yield ($r = 0.74$, $P < 0.01$). Regression analysis indicated that this increase in stem biomass with year of release was non-linear and occurred most rapidly since about 1988 (Fig 5.3). The increase in stem biomass was associated positively with plant height (Fig 5.4). Furthermore, there was a negative association between stem DM partitioning and ear partitioning index amongst the cultivars (Fig. 5.5), reflecting competition for assimilates during the stem-elongation phase.

Results showed there were no significant differences between years in the flag-leaf DM ($P = 0.653$). However, there were effects of cultivar ($P < 0.001$) and the interaction between year and cultivar ($P = 0.002$). Overall, cultivars ranged from 51.9 (Seri, 1982) to 95.3 g m^{-2} (Pavon, 1976). No association was found between flag-leaf DM and either year of release or grain yield. Flag leaf DM partitioning did not differ between years (Table 5.8). However, cultivars differed in the range 5.2 (Tarachi, 2000) to 8.5% (Pavon, 1976).

No significant effects were found for year, cultivar or the interaction in the total leaf lamina biomass (Table 5.9), However, for the average of two seasons, there was a positive correlation between lamina DM and both year of release and grain yield ($r = 0.67$; $P < 0.05$) and ($r = 0.76$; $P < 0.01$), respectively. The effect of year on green lamina DM partitioning was not statistically significant ($P = 0.472$). Nevertheless, the effect of cultivar was significant ($P = 0.006$) and values of % green lamina DM at anthesis ranged from 12.1% (Navojoa 2007) to 14.3% (Siete Cerros, 1966).

Table 5.6 Ear dry matter (DM) and partitioning of DM to ears at GS61 + 7d for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2008/09 and 2009/10

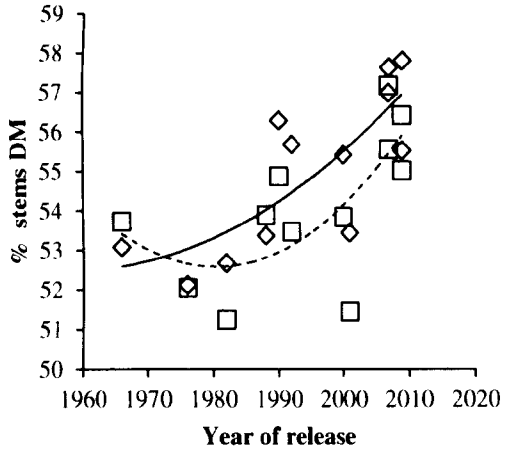
Cultivar (Year of release)	Ear DM g m^{-2}			% ear DM		
	2009	2010	Average	2009	2010	Average
Siete Cerros (1966)	204.4	277.3	240.8	24.4	25.5	24.9
Pavon (1976)	308.2	295.0	301.6	26.4	27.4	26.9
Seri (1982)	231.7	269.0	250.3	26.3	30.1	28.2
Bacanora (1988)	251.7	273.4	262.6	26.7	26.9	26.8
Attila (1990)	306.2	325.2	315.7	25.2	27.3	26.2
Baviacora (1992)	244.9	275.2	260.0	23.9	24.9	24.4
Tarachi (2000)	284.5	303.4	294.0	27.0	26.7	26.8
Tacupeto (2001)	323.5	400.3	361.9	27.4	29.4	28.4
Roelfes (2007)	228.6	251.3	240.0	20.8	22.0	21.4
Navojoa (2007)	295.8	359.1	327.4	24.5	26.7	25.6
Becard (2009)	275.5	264.1	269.8	23.2	24.7	23.9
Line 1 (2009)	206.7	267.1	236.9	22.7	24.0	23.3
Mean	263.5	296.7	280.1	24.9	26.3	25.6
S.E.D (df) (Years)			6.019(4)			0.608(4)
(Cultivars)	35.161(22)	29.856(22)	23.064(44)	1.575(22)	0.744(22)	0.871(44)
(Interaction)			31.803(46.62)			1.327(39.68)
Prob. (Years)			0.005**			$0.078^{n.s}$
(Cultivars)	0.022*	0.001***	<0.001***	0.009**	<0.001***	<0.001***
(Interaction)			$0.594^{n.s}$			$0.726^{n.s}$
C.V %	16.3	12.3	14.3	7.8	3.5	5.9
Correlation with (Year of release)	0.16	0.15	0.16	-0.40	-0.38	-0.40
(Grain yield)	0.02	0.00	-0.01	-0.52†	-0.43	-0.50†

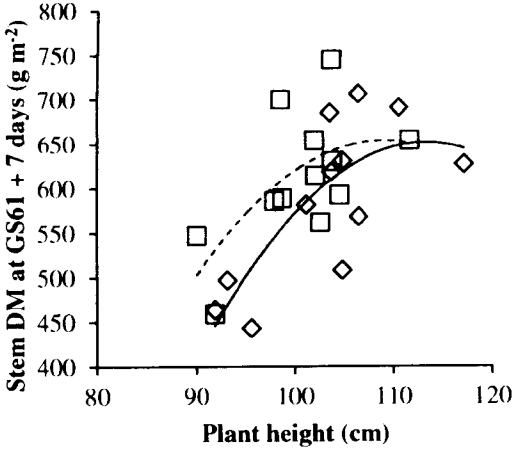
† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

Table 5.7 Stem and leaf sheath dry matter (DM) and partitioning of DM to stem and leaf sheath at GS61+ 7d for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2008/09 and 2009/10

Cultivar (Year of release)	Stems DM g m^{-2}			% stem DM		
	2009	2010	Average	2009	2010	Average
Siete Cerros (1966)	443.2	586.1	514.6	53.1	53.7	53.4
Pavon (1976)	618.2	561.7	590.0	52.1	52.1	52.1
Seri (1982)	463.7	459.0	461.3	52.7	51.3	52.0
Bacanora (1988)	497.0	547.5	522.3	53.4	53.9	53.6
Attila (1990)	684.7	654.0	669.4	56.3	54.9	55.6
Baviacora (1992)	568.5	592.6	580.5	55.7	53.5	54.6
Tarachi (2000)	581.9	614.1	598.0	55.4	53.9	54.6
Tacupeto (2001)	630.6	699.9	665.2	53.4	51.5	52.4
Roelfes (2007)	627.0	654.0	640.5	57.0	57.2	57.1
Navojoa (2007)	690.5	744.4	717.4	57.6	55.6	56.6
Becard (2009)	706.1	589.0	647.5	57.8	55.0	56.4
Line 1 (2009)	508.2	630.3	569.3	55.5	56.4	56.0
Mean	585.0	611.0	598.0	55.0	54.1	54.5
S.E.D (df) (Years)			18.154(4)			0.706(4)
(Cultivars)	81.906(22)	60.940(22)	51.045(44)	1.947(22)	0.838(22)	1.060(44)
(Interaction)			71.459(47.78)			1.599(41.26)
Prob. (Years)			0.224n.s			$0.255^{n.s}$
(Cultivars)	0.037*	0.014*	<0.001***	0.067†	<0.001***	<0.001***
(Interaction)			$0.457^{n.s}$			$0.696^{n.s}$
C.V %	17.1	12.2	14.8	4.3	1.9	3.4
Correlation with (Year of release)	0.56†	0.57†	0.63*	0.77**	0.58*	0.72**
(Grain yield)	0.50†	0.43	0.50†	0.77**	0.60*	0.74**

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant





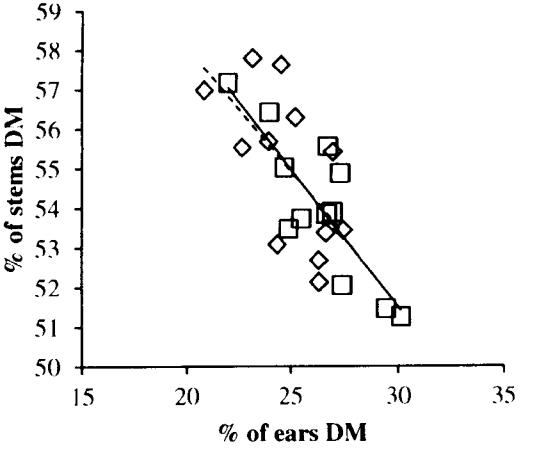


Figure 5.3 Regression of % stem and leaf sheath DM on year of release for 2009 (__◇__) $y = 0.001x^2 - 6.665x + 6577$($R^2 = 0.618$; $P = 0.014$), and 2010 (---□---) $y = 0.004x^2 - 16.04x + 15935$($R^2 = 0.492$; $P = 0.047$) for 12 CIMMYT spring wheat cultivars.

Figure 5.4 Regression of stem and leaf sheath DM on plant height for 2009 (__◇__) $y = -0.4561x^2 + 103.23x - 5190.2$($R^2 = 0.599$; $P = 0.016$), and 2010 (---□---) $y = -0.4255x^2 + 92.632x - 4388.5$ ($R^2 = 0.402$; $P = 0.101$) for 12 CIMMYT spring wheat cultivars.

Figure 5.5 Regression of % stem and leaf sheath DM on % ear DM for 2009 (__◇__) $y = -0.631x + 70.69$ ($R^2 = 0.402$; $P = 0.025$), and 2010 (---□---) $y = -0.691x + 72.24$ ($R^2 = 0.710$; $P < 0.001$) for 12 CIMMYT spring wheat cultivars.

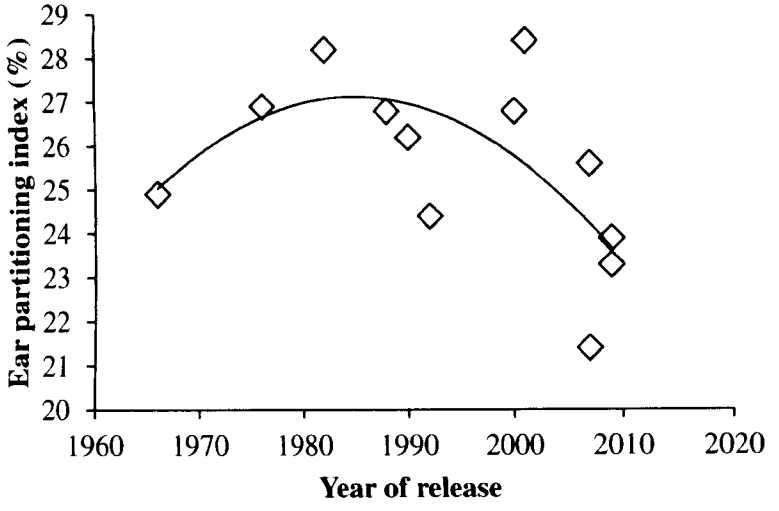


Figure 5.6 Regression of year of release on ear partitioning index averaging of two seasons $y = - 0.0059x^2 + 23.459x - 23254$ ($R^2 = 0.4303$; $P = 0.079$) for 12 CIMMYT spring wheat cultivars.

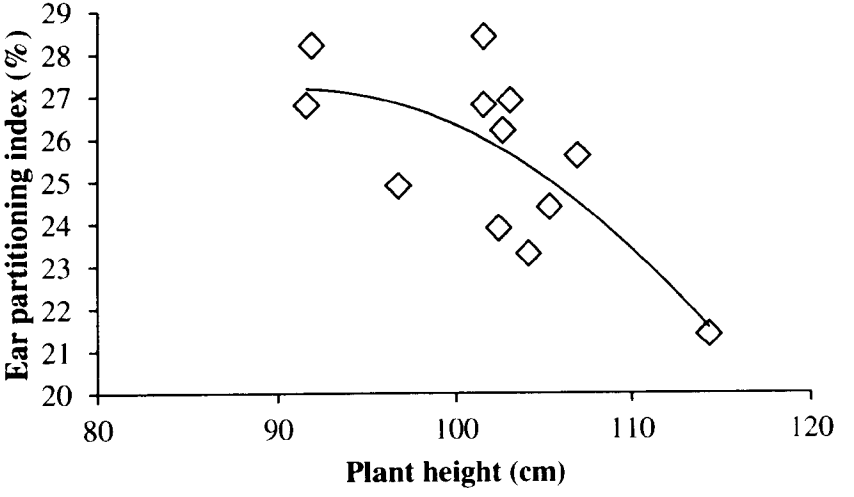


Figure 5.7 Regression of ear partitioning index at GS61 + 7d on plant height averaging of two seasons $y = - 0.0102x^2 + 1.8558x - 57.085$ ($R^2 = 0.5245$; $P = 0.034$) for 12 CIMMYT spring wheat cultivars.

Table 5.8 Flag leaf DM and partitioning of DM to flag leaves at GS61 + 7d for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2009 and 2010

Cultivar (Year of release)	Flag leaf DM g m^{-2}			% Flag leaf DM		
	2009	2010	Average	2009	2010	Average
Siete Cerros (1966)	53.9	91.1	72.5	6.5	8.3	7.4
Pavon (1976)	107.8	82.8	95.3	9.3	7.7	8.5
Seri (1982)	56.9	46.9	51.9	6.5	5.3	5.9
Bacanora (1988)	58.2	56.6	57.4	6.1	5.6	5.8
Attila (1990)	74.4	57.7	66.1	6.1	4.9	5.5
Baviacora (1992)	76.2	77.9	77.1	7.6	7.0	7.3
Tarachi (2000)	51.3	63.0	57.2	4.9	5.5	5.2
Tacupeto (2001)	77.4	90.0	83.7	6.6	6.7	6.7
Roelfes (2007)	87.3	86.7	87.0	8.0	7.6	7.8
Navojoa (2007)	67.6	78.8	73.2	5.7	5.8	5.7
Becard (2009)	74.8	67.6	71.2	6.3	6.3	6.3
Line 1 (2009)	62.4	70.3	66.4	6.9	6.3	6.6
Mean	70.7	72.4	71.6	6.7	6.4	6.6
S.E.D (df) (Years)			3.612(4)			0.291(4)
(Cultivars)	8.703(22)	7.693(22)	5.808(44)	0.714(22)	0.381(22)	0.405(44)
(Interaction)			8.654(43.31)			0.621(38.62)
Prob. (Years)			0.653$^{n.s}$			0.385$^{n.s}$
(Cultivars)	<0.001***	<0.001***	<0.001***	<0.001***	<0.001***	<0.001***
(Interaction)			0.002**			0.011*
C.V %	15.1	13.0	14.1	13.1	7.3	10.7
Correlation with (Year of release)	0.02	0.01	-0.01	-0.24	-0.31	-0.30
(Grain yield)	0.05	-0.15	-0.05	-0. 14	-0.36	-0.26

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

Table 5.9 Lamina DM and partitioning of DM to green lamina at GS61 + 7d for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2008/09 and 2009/10

Cultivar (Year of release)	Lamina DM g m^{-2}			% lamina DM		
	2009	2010	Average	2009	2010	Average
Siete Cerros (1966)	133.3	135.9	134.6	16.1	12.5	14.3
Pavon (1976)	142.5	139.0	140.7	12.3	12.9	12.6
Seri (1982)	127.7	120.0	123.9	14.5	13.4	13.9
Bacanora (1988)	129.6	138.7	134.2	13.9	13.6	13.7
Attila (1990)	151.0	154.9	153.0	12.4	13.0	12.7
Baviacora (1992)	129.2	161.3	145.2	12.8	14.6	13.7
Tarachi (2000)	133.4	159.3	146.4	12.7	14.0	13.3
Tacupeto (2001)	146.7	169.3	158.0	12.5	12.4	12.4
Roelfes (2007)	155.7	151.6	153.6	14.1	13.3	13.7
Navojoa (2007)	145.7	160.0	152.9	12.2	11.9	12.1
Becard (2009)	153.6	150.2	151.9	12.7	14.0	13.4
Line 1 (2009)	137.5	149.5	143.5	15.0	13.3	14.1
Mean	140.5	149.1	144.8	13.4	13.2	13.3
S.E.D (df) (Years)			5.602(4)			0.262(4)
(Cultivars)	34.100(22)	16.908(22)	11.792(44)	1.039(22)	0.612(22)	0.603(44)
(Interaction)			16.921(47.57)			0.858(47.94)
Prob. (Years)			$0.197^{n.s}$			$0.472^{n.s}$
(Cultivars)	$0.689^{n.s}$	$0.287^{n.s}$	$0.185^{n.s}$	0.015*	0.013*	0.006**
(Interaction)			$0.812^{n.s}$			0.004**
C.V %	14.3	13.9	14.1	9.5	5.7	7.8
Correlation with (Year of release)	0.51†	0.62*	0.67*	-0.36	0.15	-0.23
(Grain yield)	0.39	0.55†	0.76**	0.26	0.32	-0.08

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

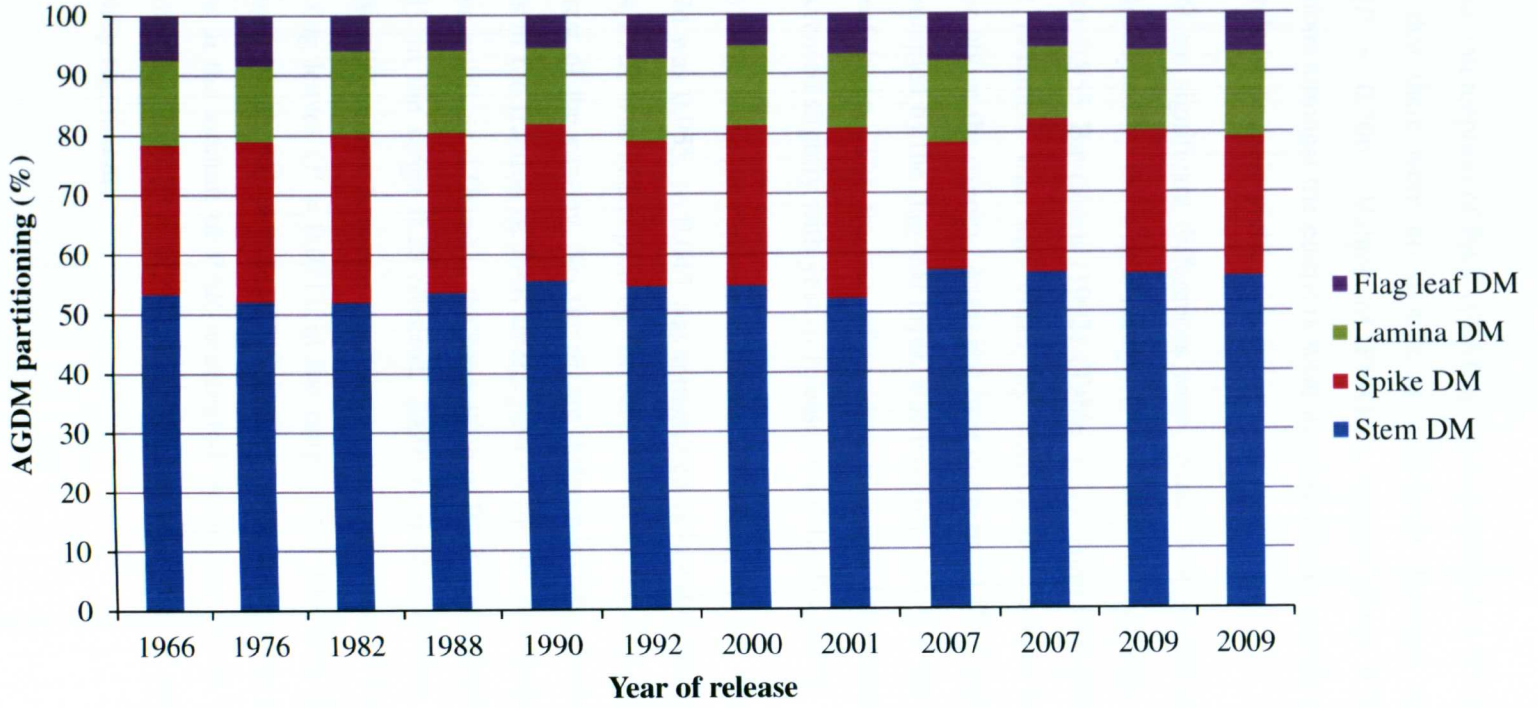


Figure 5.8 – Above-ground dry matter (AGDM) partitioning (%) at GS 61 + 7d for 12 CIMMYT spring wheat cultivars released from 1966 to 2009. Values represent the average of 2008/09 and 2009/10. Note' Lamina DM' is all lamina minus the flag leaf lamina.

5.3.4 Fractional interception of photosynthetically active radiation (PAR)

Fractional interception of PAR ($FPAR_{INT}$) was estimated in 2010 only. Results showed that there were no significant differences amongst the cultivars at GS31 (P = 0.306). Values of $FPAR_{INT}$ ranged from 0.776 to 0.929. Correlations amongst the cultivars were not statistically significant with either year of release or grain yield.

At GS39, no significant differences were found amongst the cultivars in the PAR intercepted by the whole canopy (P = 0.606) in the range of 0.940 Seri (1982) to 0.955 Baviacora (1992) (Table 5.11). Approximately 0.05 of the incident radiation was lost either by transmission below the canopy or reflection above the canopy. Averaged over cultivars, 0.78 of incident radiation was intercepted by the flag-leaf layer, whereas only 0.17 was intercepted by the lower leaf layers. The fraction of incident radiation intercepted by flag-leaf layer increased slightly with year of release (r = 0.40, P > 0.05).

At GS61+7d, averaging across cultivars, $FPAR_{INT}$ by the whole canopy at GS61+7d was 0.955, so 0.045 was transmitted below the canopy. An average of 0.334 PAR was intercepted by the ears, 0.428 by the flag leaves and 0.193 by the rest of the canopy. No significant differences were found amongst the cultivars in the fraction of PAR intercepted by the whole canopy (P = 0.318). However, cultivars differed in the proportion of PAR intercepted by the ears (P = 0.038), in the range 0.20 (Becard, 2009) to 0.427 (Roelfes, 2007). There were also differences between cultivars in the proportion of PAR intercepted by the flag leaves (P = 0.021), in the range 0.571 (Tarachi, 2000) to 0.334 (Bacanora, 1988). No statistically significant differences were found between cultivars in the amount of PAR intercepted by the rest of the canopy (layers below the flag leaf) (P = 0.501). Correlations with year of release were not statistically significant.

Table 5.10 Fraction of Photosynthetically Active Radiation (PAR) intercepted by the canopy at GS31 for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2009/10.

Cultivar (Year of release)	Fraction of PAR intercepted by the canopy
	2010
Siete Cerros (1966)	0.865
Pavon (1976)	0.924
Seri (1982)	0.776
Bacanora (1988)	0.861
Attila (1990)	0.865
Baviacora (1992)	0.929
Tarachi (2000)	0.876
Tacupeto (2001)	0.844
Roelfes (2007)	0.921
Navojoa (2007)	0.888
Becard (2009)	0.871
Line 1 (2009)	0.924
Mean	0.879
S.E.D (df) (Years)	
(Cultivars)	0.055(22)
(Interaction)	
Prob. (Years)	
(Cultivars)	0.306$^{n.s}$
(Interaction)	
C.V %	7.6
Correlation with (Year of release)	0.27
(Grain yield)	0.32

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

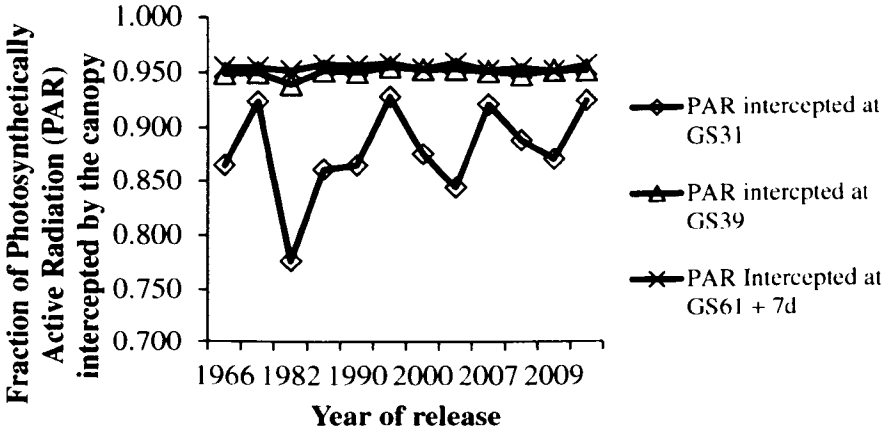


Figure 5.9 – Fraction of Photosynthetically Active Radiation (PAR) intercepted by the canopy at different growth stages pre-anthesis by 12 CIMMYT spring wheat cultivars.

Table 5.11 Fraction of PAR intercepted by the whole canopy, flag leaves and the rest of the canopy at GS39 for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2009/10.

Cultivar (Year of release)	Fraction intercepted PAR at GS39 in 2010		
	By canopy	By flag leaf	By the rest of canopy
Siete Cerros (1966)	0.949	0.654	0.295
Pavon (1976)	0.950	0.810	0.140
Seri (1982)	0.940	0.736	0.204
Bacanora (1988)	0.952	0.795	0.157
Attila (1990)	0.950	0.793	0.157
Baviacora (1992)	0.955	0.853	0.102
Tarachi (2000)	0.953	0.716	0.237
Tacupeto (2001)	0.953	0.833	0.120
Roelfes (2007)	0.951	0.774	0.177
Navojoa (2007)	0.948	0.858	0.090
Becard (2009)	0.951	0.735	0.216
Line 1 (2009)	0.951	0.800	0.151
Mean	0.950	0.780	0.170
S.E.D (df) (Years)			
(Cultivars)	0.00598(33)	0.0641(33)	0.0629(33)
(Interaction)			
Prob. (Years)			
(Cultivars)	$0.606^{n.s}$	$0.103^{n.s}$	$0.101^{n.s}$
(Interaction)			
C.V %	0.9	11.6	52.2
Correlation with (Year of release)	0.30	0.40	-0.39
(Grain yield)	0.41	0.55†	-0.54†

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

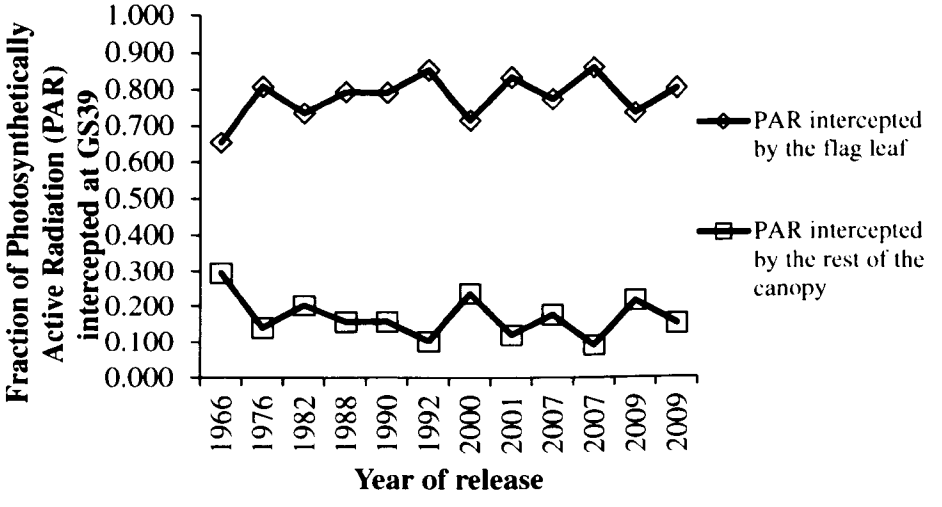


Figure 5.10 Fraction of Photosynthetically Active Radiation (PAR) interception at GS39 by 12 CIMMYT spring wheat cultivars.

Table 5.12 Fraction of PAR intercepted by the whole canopy, ears, flag leaves and the rest of the canopy at GS61+7d for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2009/10.

Cultivar (Year of release)	Fraction PAR intercepted at GS61+7d in 2010			
	By canopy	By ear	By flag leaf	By the rest of canopy
Siete Cerros (1966)	0.955	0.221	0.549	0.185
Pavon (1976)	0.955	0.358	0.442	0.154
Seri (1982)	0.952	0.348	0.374	0.230
Bacanora (1988)	0.958	0.370	0.334	0.254
Attila (1990)	0.956	0.377	0.389	0.191
Baviacora (1992)	0.958	0.392	0.375	0.192
Tarachi (2000)	0.953	0.207	0.571	0.175
Tacupeto (2001)	0.959	0.413	0.396	0.150
Roelfes (2007)	0.952	0.427	0.374	0.150
Navojoa (2007)	0.954	0.406	0.364	0.183
Becard (2009)	0.951	0.201	0.549	0.201
Line 1 (2009)	0.956	0.291	0.418	0.246
Mean	0.955	0.334	0.428	0.193
S.E.D (df) (Years)				
(Cultivars)	0.00345(33)	0.0788(33)	0.0736(33)	0.0509(33)
(Interaction)				
Prob. (Years)				
(Cultivars)	0.318$^{n.s}$	0.038*	0.021*	0.501$^{n.s}$
(Interaction)				
C.V %	0.5	33.4	24.3	37.4
Correlation with (Year of release)	-0.19	0.10	-0.11	-0.01
(Grain yield)	0.16	0.27	-0.39	0.29

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

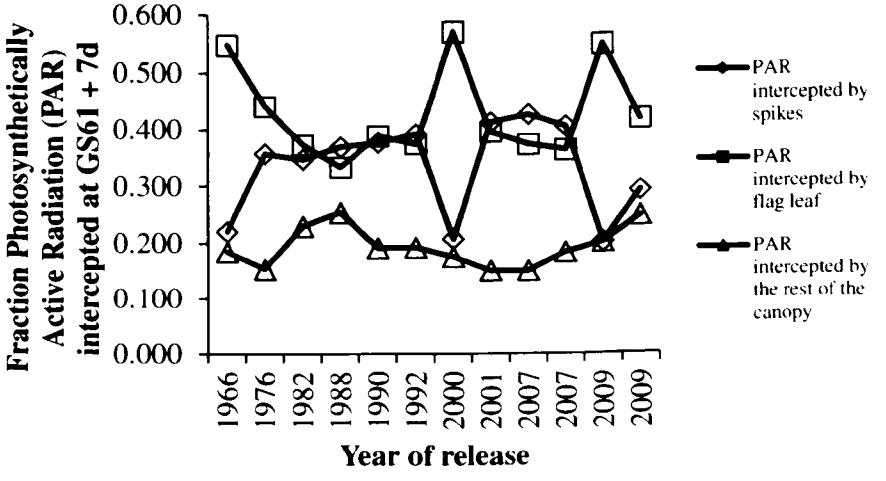


Figure 5.11 Fraction Photosynthetically Active Radiation (PAR) interception at GS61+7d by 12 CIMMYT spring wheat cultivars.

5.3.5 Radiation interception and radiation-use efficiency (RUE)

Radiation-use efficiency (RUE_{PAR}) was calculated over the period from GS31 to GS61 + 7d as the ratio of the cumulative above-ground dry matter (AGDM) to PAR interception. Values of daily fractional PAR interception were obtained by interpolation between readings at GS31, GS39, GS61+7d; these were applied to the daily incident solar radiation to calculate the daily radiation interception, assuming PAR was equal to 0.5 solar radiation (Monteith, 1972). Values for RUE from GS31 to GS61+7d were calculated individually for each plot.

Differences amongst cultivars in the amount of intercepted radiation from GS31 to GS61+7d were significant ($P < 0.001$) in the range 295.4 (Becard, 2009) to 389.4 MJ m^{-2} (Pavon, 1976). No correlations amongst cultivars were found between radiation interception and either year of release or grain yield (r = 0.04 and -0.08, respectively). Results showed that there were significant differences between cultivars in RUE_{PAR} ($P = 0.008$). Values ranged from 1.70 (Pavon, 1976 and Seri, 1982) to 2.56 g MJ^{-1} for (Bacanora, 1988). Although the amount of radiation intercepted during the stem-elongation phase did not change with breeding in this set of cultivars (Fig 5.12), there was an apparent trend for RUE to be increased with year of release (Fig 5.14). One cultivar, however, Bacanora diverged from this apparent trend; if this cultivar was omitted from the analysis, the non-linear increase with year of release according the quadratic polynomial regression became significant (Fig 5.15, P = 0.01). Figure 5.13 show the expected positive relation between RUE_{PAR} and crop growth rate (CGR) over the same period amongst all 12 cultivars.

Table 5.13 Photosynthetically active radiation interception, above-ground dry matter (AGDM) accumulated from GS31 to GS61+7d and PAR radiation use-efficiency (RUE_{PAR}) from GS31 to GS61+7d for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2009/10.

Cultivar (Year of release)	GS31-GS61+7d (2010)		
	Radiation Interception ($MJ\ m^{-2}$)	AGDM ($g\ m^{-2}$)	RUE_{PAR} ($g\ MJ^{-1}$)
Siete Cerros (1966)	317.0	674.5	2.07
Pavon (1976)	389.4	687.6	1.70
Seri (1982)	354.7	632.6	1.70
Bacanora (1988)	297.3	800.1	2.56
Attila (1990)	389.0	824.9	1.94
Baviacora (1992)	353.1	738.3	1.84
Tarachi (2000)	344.9	742.7	2.03
Tacupeto (2001)	363.4	852.3	2.13
Roelfes (2007)	347.2	743.5	2.01
Navojoa (2007)	384.8	865.0	2.08
Becard (2009)	295.4	704.1	2.24
Line 1 (2009)	363.7	834.4	2.13
Mean	350.0	758.3	2.04
S.E.D (df) (Years)			
(Cultivars)	10.47(22)	79.6(22)	0.183(22)
(Interaction)			
Prob. (Years)			
(Cultivars)	<0.001***	$0.110^{n.s}$	0.008**
(Interaction)			
C.V %	3.7	12.9	11.0
Correlation with (Year of release)	0.04	0.57†	0.34
(Grain yield)	-0.08	0.61*	0.44

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

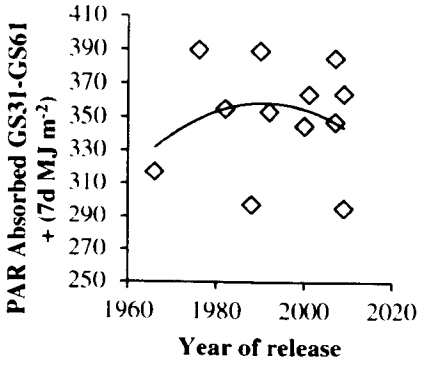


Figure 5.12 PAR absorbed from GS31-GS61 + 7d Versus year of release for 2010. Y = -0.0431x2 + 171.53x – 170389 (R^2 = 0.0591; P = 0.760) for 12 CIMMYT spring wheat cultivars.

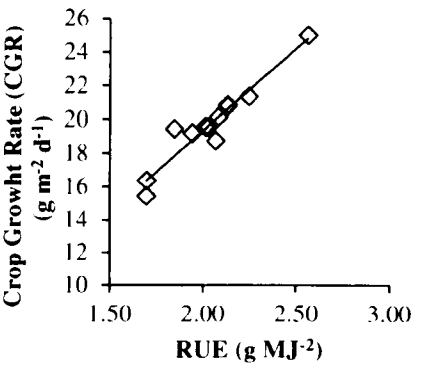


Figure 5.13 Regression of Crop Growth Rate on year of release for 2010. Y = 9.7555x – 0.1645 (R^2 = 0.914; P = 0.140) for 12 CIMMYT spring wheat cultivars.

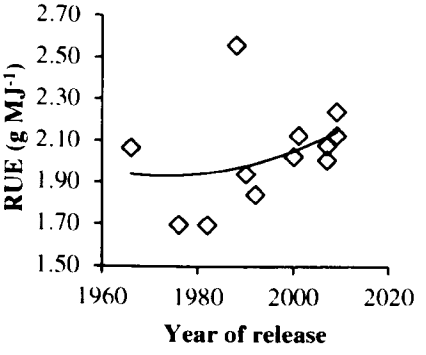


Figure 5.14 Regression of RUE from GS31 to GS61 + 7d on year of release for 2010. Y = 0.0002x^2 – 0.6483x + 641.33 (R^2 = 0.1294; P = 0.546) for 12 CIMMYT spring wheat cultivars (with Bacanora).

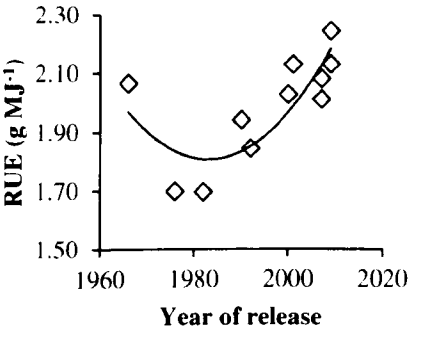


Figure 5.15 Regression of RUE from GS31 to GS61 + 7d on year of release for 2010. Y = 0.0006x^2 – 2.2376x + 2220.5 (R^2 = 0.688; P < 0.01) for 11 CIMMYT spring wheat cultivars (without cultivar Bacanora).

5.3.6 Crop Growth Rate (CGR) and Normalised Difference Vegetative Index (NDVI)

5.3.6.1 Crop growth rate

Cultivars differed in the crop growth rate from GS31 to GS61+7d in both years and averaged across seasons. Crop growth rate was higher in 2010 (19.7 g m^{-2} d^{-1}) than in 2009 (17.4 g m^{-2} d^{-1}) ($P = 0.017$). Overall for cultivars CGR ranged from 16.1 (Attila, 1990) to 24.4 g m^{-2} d^{-1} (Becard, 2009) (Table 5.15). Some cultivars had relatively higher CGR during 2009 compared to 2010 such as Pavon and Becard, whereas others had relatively higher CGR in 2010, e.g Bacanora and Line 1. There was no statistically significant association between crop growth rate and year of release in either year or for the cross year mean (Fig 5.16). There was a positive correlation between the CGR and AGDM at anthesis ($r = 0.63$; $P < 0.05$).

5.3.6.2 The Normalized Difference Vegetation Index (NDVI)

Results showed that NDVI during the pre-anthesis period was higher in 2010 than in 2009 ($P < 0.001$; Table 5.14). In 2009 values ranged from 0.44 (Bacanora, 1988) to 0.54 (Pavon, 1976 and Roelfes, 2007). In 2010, values ranged from 0.54 (Siete Cerros 1966, Bacanora 1988 and Tarachi (2000) to 0.63 for cultivar Pavon (1976). Differences between cultivars averaging across years were significant ($P < 0.001$) and values ranged from 0.50 for cultivar (Siete Cerros, 1966) to 0.58 for cultivars (Pavon, 1976 and Roelfes, 2007). However, no association was found between NDVI and either year of release or grain yield (Fig 5.17).

Table 5.14 Pre-anthesis NDVI and crop growth rate (CGR) from GS31 to GS61+7d for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2009 and 2010. NDVI values are means of measurements on 4, 10, 15 and 29 December in the 2008/09 season and on 18 Dec, 28 Dec, 05 Jan, 11 Jan, 22 Jan and 6 Feb in 2009/10 season.

Cultivar (Year of release)	Pre-anthesis NDVI			CGR g m^{-2} day^{-1}		
	2009	2010	Average	2009	2010	Average
Siete Cerros (1966)	0.47	0.54	0.50	15.2	18.7	17.0
Pavon (1976)	0.54	0.63	0.58	24.0	16.4	20.2
Seri (1982)	0.46	0.55	0.51	17.8	15.4	16.6
Bacanora (1988)	0.44	0.54	0.49	16.9	25.0	21.0
Attila (1990)	0.47	0.56	0.52	13.0	19.2	16.1
Baviacora (1992)	0.52	0.62	0.57	13.7	19.4	16.6
Tarachi (2000)	0.51	0.54	0.52	13.3	19.5	16.4
Tacupeto (2001)	0.50	0.56	0.53	15.5	20.8	18.1
Roelfes (2007)	0.54	0.61	0.58	21.3	19.6	20.4
Navojoa (2007)	0.53	0.59	0.56	17.6	20.1	18.9
Becard (2009)	0.50	0.58	0.54	27.4	21.3	24.4
Line 1 (2009)	0.46	0.56	0.51	13.4	20.9	17.1
Mean	0.49	0.57	0.53	17.4	19.7	18.6
S.E.D (df) (Years)			0.009(6)			0.473(3)
(Cultivars)	0.0267(33)	0.029(33)	0.020(66)	0.965(11)	1.966(22)	1.292(33)
(Interaction)			0.028(71.38)			2.024(35.85)
Prob. (Years)			<0.001***			0.017**
(Cultivars)	0.005**	0.013*	<0.001***	<0.001***	0.013*	<0.001***
(Interaction)			0.744$^{n.s}$			<0.001***
C.V %	7.6	7.2	7.4	5.5	12.2	10.9
Correlation with (Year of release)	0.28	0.11	0.21	0.10	0.43	0.30
(Grain yield)	0.07	0.15	0.12	0.17	0.61*	0.33

* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

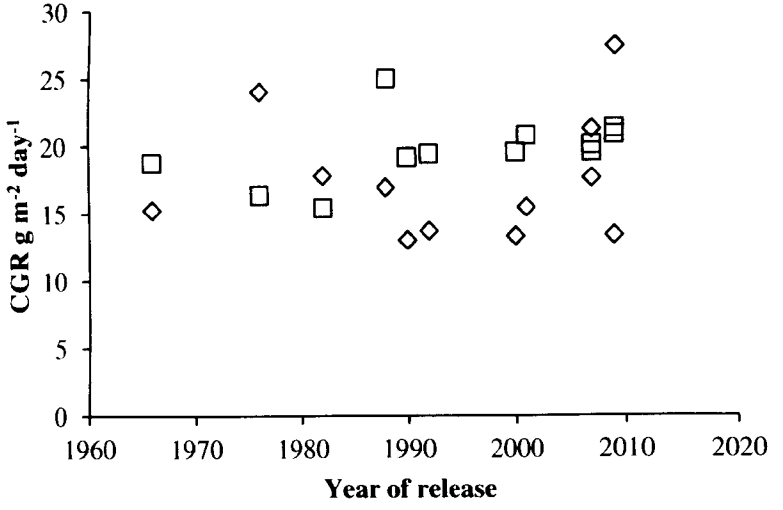


Figure 5.16 Year of release versus crop growth rate (CGR) from GS31 to GS61+7d versus for 2009 (__◇__), and 2010 (---□---) for 12 CIMMYT spring wheat cultivars.

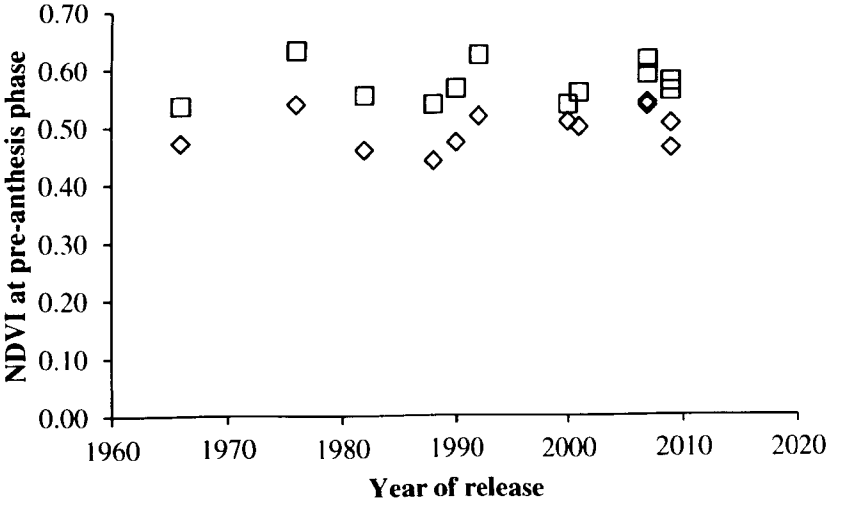


Figure 5.17 Year of release versus averaging pre-anthesis NDVI in 2009 (__◇__), and 2010 (---□---) for 12 CIMMYT spring wheat cultivars.

5.3.7 Ear traits at GS61+7d

5.3.7.1 Rachis length, awns length and ear width

Rachises were longer in 2010 (12.1 cm) compared to 2009 (11.4 cm) (P = 0.001; Table 5.15). Averaging across seasons, there were differences amongst cultivars in the range 10.8 (Siete Cerros, 1966, Bacanora, 1988 and Line 1, 2009) to 13.9 cm (Baviacora, 1992) ($P < 0.001$). However, no association was found between rachis length and either year of release or grain yield. Awn length and ear width were also measured in 2009. Cultivars differed in both awn length and ear width in the ranges 4.47 (Bacanora, 1988) to 7.92 cm (Navojoa, 2007) ($P < 0.001$) and 0.75 (Tarachi, 2000) to 0.93 cm (Seri, 1982) (P = 0.007), respectively. However, no correlation was found between these traits and either year of release or grain yield.

5.3.7.2 Total and fertile spikelets per ear

Total spikelets per ear differed between years (P = 0.008) and amongst cultivars ($P < 0.001$), but there was no effect for the interaction (P = 0.105; Table 5.16). Total spikelet number was slightly greater in 2010 (22.3) than 2009 (21.3). Overall, cultivars differed, with most spikelets produced by Pavon (24.3) and fewest by Navojoa and Line 1 (19.6). Similar results were found for fertile spikelets per ear. Averaged across years, fertile spikelets ranged from 16.8 (Navojoa, 2007) to 21.9 (Pavon, 1976) ($P < 0.001$). There was no change in rachis length with plant breeding (Fig 5.18). Fertile spikelets initially increased with breeding but then decreased from about 1990 (Fig. 5.19); over this latter period the rachis length per fertile spikelet increased with year of release (Fig 5.20). This increase appeared to be associated with an increase in grain weight (Fig 5.21).

Table 5.15 Rachis length, awns length and ear width at GS61 + 7d for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2009 and 2010

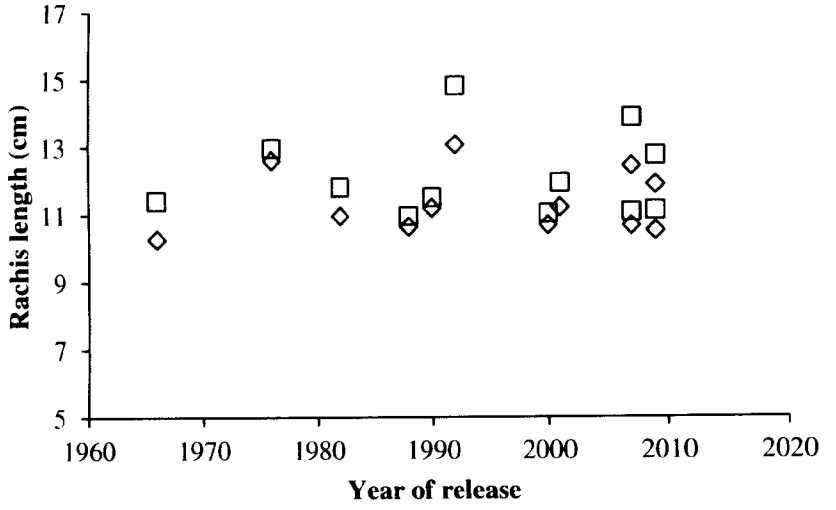
Cultivar (Year of release)	Rachis length (cm)			Awns length (cm)	Ear width (cm)
	2009	2010	Average	2009	2009
Siete Cerros (1966)	10.3	11.4	10.8	7.39	0.86
Pavon (1976)	12.6	13.0	12.8	7.33	0.84
Seri (1982)	11.0	11.8	11.4	6.38	0.93
Bacanora (1988)	10.7	11.0	10.8	4.47	0.78
Attila (1990)	11.2	11.5	11.4	7.26	0.83
Baviacora (1992)	13.1	14.8	13.9	7.46	0.76
Tarachi (2000)	10.7	11.0	10.9	7.29	0.75
Tacupeto (2001)	11.2	11.9	11.6	7.15	0.83
Roelfes (2007)	12.4	13.9	13.2	7.72	0.88
Navojoa (2007)	10.7	11.1	10.9	7.92	0.84
Becard (2009)	11.9	12.8	12.3	6.90	0.91
Line 1 (2009)	10.5	11.1	10.8	7.46	0.78
Mean	11.4	12.1	11.7	7.06	0.83
S.E.D (df) (Years)			0.092(4)		
(Cultivars)	0.32(22)	0.44(22)	0.273(44)	0.231(22)	0.043(22)
(Interaction)			0.381(47.62)		
Prob. (Years)			0.001***		
(Cultivars)	<0.001***	<0.001***	<0.001***	<0.001***	0.007**
(Interaction)			$0.163^{n.s}$		
C.V %	3.5	4.4	4.0	4.0	6.3
Correlation with (Year of release)	0.07	0.04	0.05	0.24	-0.11
(Grain yield)	0.17	0.18	0.18	0.03	-0.13

* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

Table 5.16 Total and fertile spikelets per ear at GS61 + 7d for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2009 and 2010

Cultivar (Year of release)	Total spikelets ear^{-1}			Fertile spikelets ear^{-1}		
	2009	2010	Average	2009	2010	Average
Siete Cerros (1966)	19.6	21.3	20.5	17.8	20.2	19.0
Pavon (1976)	23.6	24.9	24.3	20.8	23.0	21.9
Seri (1982)	21.9	23.9	22.9	20.3	22.5	21.4
Bacanora (1988)	23.1	23.4	23.3	20.8	21.9	21.4
Attila (1990)	22.0	23.1	22.5	18.8	19.9	19.4
Baviacora (1992)	21.8	23.8	22.8	19.4	22.1	20.8
Tarachi (2000)	20.8	21.3	21.1	18.2	19.3	18.7
Tacupeto (2001)	23.5	23.0	23.3	20.9	21.5	21.2
Roelfes (2007)	19.7	21.1	20.4	17.1	19.5	18.3
Navojoa (2007)	19.8	19.4	19.6	16.4	17.1	16.8
Becard (2009)	21.0	22.0	21.5	18.8	20.3	19.5
Line 1 (2009)	19.0	20.3	19.6	16.6	18.4	17.5
Mean	21.3	22.3	21.8	18.8	20.5	19.7
S.E.D (df) (Years)			0.199(4)			0.186(4)
(Cultivars)	0.366(22)	0.825(22)	0.451(44)	0.477(22)	0.790(22)	0.462(44)
(Interaction)			0.643(47.89)			0.652(48)
Prob. (Years)			0.008**			<0.001***
(Cultivars)	<0.001***	<0.001***	<0.001***	<0.001***	<0.001***	<0.001***
(Interaction)			0.105$^{n.s}$			0.275$^{n.s}$
C.V %	2.1	4.5	3.6	3.1	4.7	4.1
Correlation with (Year of release)	-0.34	-0.55†	-0.46	-0.45	-0.59*	-0.53†
(Grain yield)	-0.25	-0.35	-0.32	-0.34	-0.41	-0.39

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant



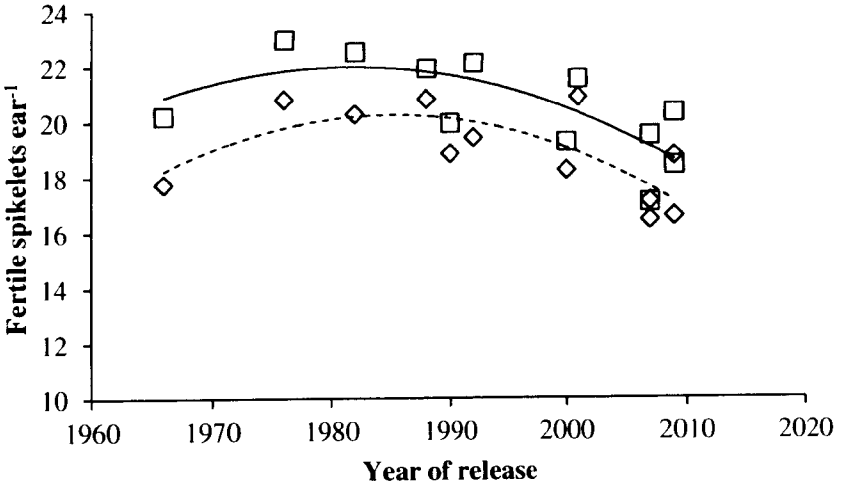


Figure 5.18 Regression of year of release on rachis length for 2009 (__◇__), and 2010 (---□---) for 12 CIMMYT spring wheat cultivars.

Figure 5.19 Regression of year of release on fertile spikelets per ear for 2009 (__◇__) y= -0.005x^2 + 21.78x – 21605 (R^2 = 0.565; *P* = 0.027), and 2010 (---□--) y= -0.004x2 + 17.85x - 17670(R^2 = 0.556; *P* = 0.026) for 12 CIMMYT spring wheat cultivars.

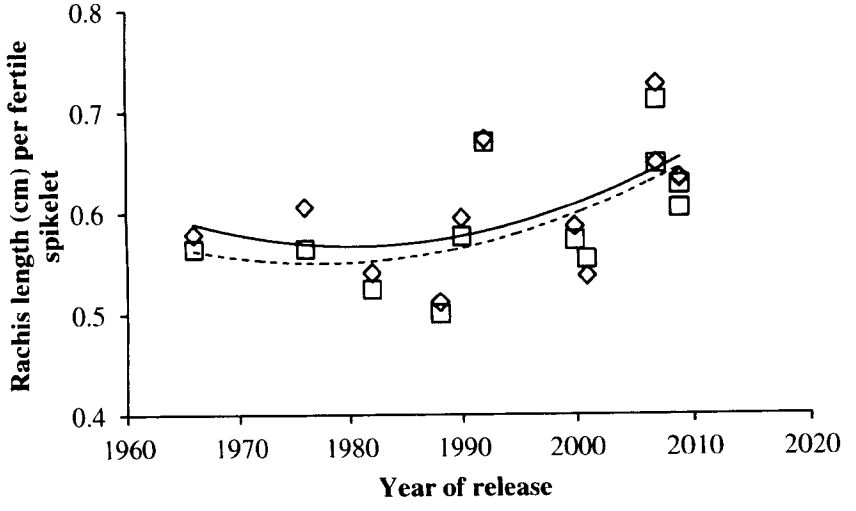


Figure 5.20 Regression of year of release on rachis length per spikelet for 2009 (__◇__) y= $0.000x^2 - 0.42x + 416.4$($R^2 = 0.311$; $P = 0.0186$), and 2010 (---□---) y= $9E - 05x^2 - 0.372x + 368.7$($R^2 = 0.373$; $P = 0.122$) for 12 CIMMYT spring wheat cultivars.

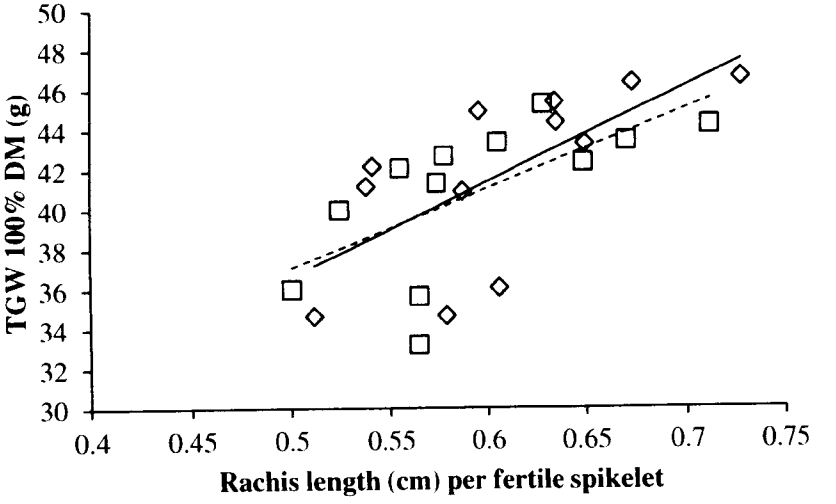


Figure 5.21 Regression of thousand grain weight on year of release for 2009 (__◇__) y= $47.83x + 12.68$($R^2 = 0.453$; $P = 0.016$), and 2010 (---□---) y= $39.88x + 1710$($R^2 = 0.411$; $P = 0.025$) for 12 CIMMYT spring wheat cultivars.

5.3.8 Leaf activity traits

5.3.8.1 SPAD flag leaf assessment

Significant differences were found between years in SPAD values of flag leaves measured once at GS39. Values were 45.4 in 2009 and 41.5 in 2010 ($P < 0.001$) (Table 5.17). Averaging across years, cultivars ranged from 40.1 (Line 1, 2009) to 46.7 (Seri, 1982) ($P < 0.001$). A trend for a negative correlation between SPAD and both year of release ($r = -0.57$; $P < 0.10$) and grain yield ($r = -0.50$; $P < 0.10$) was found.

5.3.8.2 Canopy temperature depression (CTD) during the stem elongation period

Canopy temperature depression averaged over readings during the stem-elongation period was higher in 2010 (6.0 C°) than in 2009 (3.5 C°) ($P < 0.001$). No differences were found amongst cultivars in either years or for the average across the years (Table 5.18; Fig 5.22). The correlation between CTD during the stem-elongation period and both year of release and grain yield amongst the cultivars was not statistically significant.

5.3.8.3 Stomatal conductance during the stem elongation period

Stomatal conductance was measured in both years. However, during the first season 2009, readings were very low due to equipment problems. Nevertheless, cultivar rankings were similar to those in 2010. Averaged over readings during stem elongation in both years, there were differences amongst cultivars in 2010 ($P < 0.001$), and values ranged from 162.4 mmol m^{-2} s^{-1} for (Tacupeto, 2001) to 293.6 mmol m^{-2} s^{-1} for (Becard, 2009) (Table 5.18). There was a positive association between stomatal conductance and grain yield ($r = 0.69$, $P < 0.05$).

Table 5.17 SPAD assessment for flag leaf at GS39 for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2009 and 2010.

Cultivar (Year of release)	SPAD units		
	2009	2010	Average
Siete Cerros (1966)	47.80	44.08	45.94
Pavon (1976)	45.70	41.93	43.81
Seri (1982)	47.83	45.50	46.67
Bacanora (1988)	43.87	40.38	42.12
Attila (1990)	45.47	41.43	43.45
Baviacora (1992)	46.00	41.58	43.79
Tarachi (2000)	46.20	41.95	44.08
Tacupeto (2001)	42.33	40.18	41.25
Roelfes (2007)	45.90	39.85	42.88
Navojoa (2007)	46.57	38.58	42.57
Becard (2009)	46.73	43.38	45.05
Line 1 (2009)	40.93	39.25	40.09
Mean	45.44	41.50	43.47
S.E.D (df) (Years)			0.348(5)
(Cultivars)	0.665(22)	1.006(33)	0.650(55)
(Interaction)			0.955(58.13)
Prob. (Years)			<0.001***
(Cultivars)	<0.001***	<0.001***	<0.001***
(Interaction)			0.001**
C.V %	1.8	3.4	2.8
Correlation with (Year of release)	-0.42	-0.61*	-0.57†
(Grain yield)	-0.33	-0.58*	-0.50†

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

Table 5.18 Canopy temperature depression and stomatal conductance measured before anthesis of 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2010. CTD and stomatal conductance values represent averages of those at GS39 and GS61 in 2009 and in 2010.

Cultivar (Year of release)	Canopy temperature depression (C°)			Stomatal conductance (mmol m^{-2} s^{-1})		
	2009	2010	Average	2009	2010	Average
Siete Cerros (1966)	3.6	6.0	4.8	60.7	316.9	188.8
Pavon (1976)	3.5	5.8	4.7	62.4	337.1	199.8
Seri (1982)	3.0	5.9	4.5	64.5	368.7	216.6
Bacanora (1988)	3.7	6.1	4.9	73.9	419.9	246.9
Attila (1990)	3.8	5.8	4.8	76.0	338.2	207.1
Baviacora (1992)	3.5	6.0	4.7	77.0	467.2	272.1
Tarachi (2000)	3.4	5.9	4.6	73.5	429.0	251.3
Tacupeto (2001)	3.5	5.8	4.7	65.6	259.2	162.4
Roelfes (2007)	3.6	5.8	4.7	71.8	449.5	260.6
Navojoa (2007)	3.4	5.7	4.6	76.1	420.1	248.1
Becard (2009)	3.7	6.2	4.9	64.7	522.5	293.6
Line 1 (2009)	3.8	6.5	5.1	73.9	428.8	251.3
Mean	3.5	6.0	4.7	70.0	396.4	233.2
S.E.D (df) (Years)			0.241(6)			8.94(5)
(Cultivars)	0.301(33)	0.258(33)	0.198(66)	5.71(33)	39.40(22)	16.65(55)
(Interaction)			0.361(26.35)			24.47(58.09)
Prob. (Years)			<0.001***			<0.001***
(Cultivars)	0.565$^{n.s}$	0.182$^{n.s}$	0.130$^{n.s}$	0.042*	<0.001***	<0.001***
(Interaction)			0.721$^{n.s}$			<0.001***
C.V %	12.0	6.1	8.4	11.5	12.2	14.8
Correlation with (Year of release)	0.17	0.24	0.25	0.51†	0.54†	0.56†
(Grain yield)	0.52†	0.28	0.46	0.51†	0.62*	0.69*

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

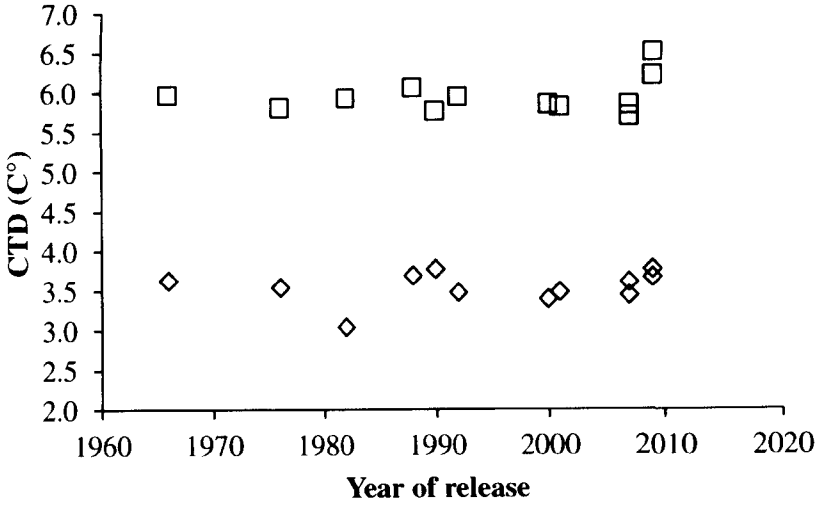


Figure 5.22 Regression of CTD on year of release for 2009 (__◇__), and 2010 (---□---). Values represent averages of GS39 and GS61 in 2009 and in 2010 for 12 CIMMYT spring wheat cultivars.

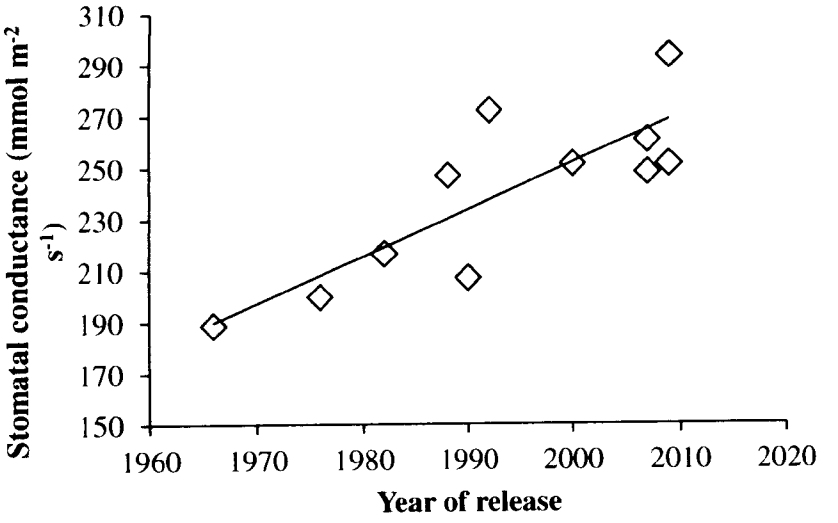


Figure 5.23 Regression of Stomatal conductance pre-anthesis on year of release averaging across years. y = 1.8228x – 3393.7 (R^2 = 0.6688; P = 0.057). Values represent averages of readings at GS39 and GS61 in 2009 and in 2010 for 12 CIMMYT spring wheat cultivars.

Table 5.19 Fitted parameter estimates for changes in crop traits with year of release for 12 CIMMYT spring wheat cultivars released between 1966 and 2009. Linear and quadratic functions were fitted to 2-yr cultivar means (2009 and 2010).

Trait	Parameter estimates linear ($y = a + bx$)		Parameter estimates quadratic		($y = a + bx + cx2$)
	y (as in 1966)	$b \pm$ SE	y (as in 1966)	$b \pm$ SE	$c \pm$ SE
Spike partitioning index GS61 %		-0.0596 ± 0.0426 n.s	24.9	23.46 ± 11.5 †	-0.00591 ± 0.00288 †
Stem + leaf sheath DM GS61 partitioning index		0.0930 ± 0.0286**	53.4	-11.38 ± 8.51*	0.00288 ± 0.00214*
Leaf activity traits					
Stomatal conductance (mmol m^{-2} s^{-1}) pre-anthesis	188.8	1.526 ± 0.709 †			
RUE pre GS61, g MJ^{-1}		0.00554 ± 0.00499 n.s	2.07	-0.66 ± 1.61 n.s	0.000167 ± 0.000406 n.s
Spike traits					
Fertile spikelets $spike^{-1}$		-0.0638 ± 0.0318†	19.0	19.93 ± 7.94*	-0.00502 ± 0.00200*
Spike fertility index		-0.186 ± 0.226 n.s	77.9	-82.19 ± 68.6 n.s	0.0206 ± 0.0172 n.s
df		10		9	9

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Not significant

5.4 DISCUSSION

Results showed that grains per m^2 has not increased with year of release in CIMMYT spring wheat from 1966 to 2009 but there may have been changes in the components of the physiological model explaining grains per m^2. The physiological components of grains per m^2 described in the following equation are now discussed:

Grains m^{-2} = PAR intercepted GS31- GS61+ 7d × RUE (GS31- 61 + 7d) g m^{-2} d^{-1} × Ear partitioning index × Ear fertility index (grains per gram ear DM, at GS61+7d)

The period of stem elongation (from GS31 to GS61) is one of the determinant factors affecting radiation interception and hence number of grains per unit land area. However, in the present study, the duration of this period which ranged only from 36 to 48 days was not statistically correlated with grains per m^2 or with year of release for both seasons.

5.4.1 Fraction PAR intercepted

No differences amongst cultivars were found in the fraction of PAR intercepted by the whole canopy at all growth stages (31, 39 and 61). However, at GS39 the fraction of PAR intercepted by the flag leaves was positively correlated with grain yield (r = 0.55; P < 0.10). Conversely, the fraction of PAR intercepted by the rest of the canopy tended to decrease (r = – 0.39; P > 0.10) with breeding and was negatively correlated with grain yield (r = – 0.54; P < 0.10). At GS61+7d, cultivars differed in the fraction of PAR intercepted by both ears and flag leaves, although no statistically significant correlation was found with either year of release or grain yield. Overall the amount of the radiation intercepted from GS31 to GS61 has not changed with breeding (r = 0.04; P > 0.10) in the present study. A similar result was obtained by Acreche *et al.* (2009) who reported no changes in intercepted radiation in bread wheat released from 1950 to 2006 in the Mediterranean area and Shearman *et al.* (2005), where there was no increase in PAR interception from GS31 to GS61 with breeding.

5.4.2 Crop growth rate and RUE

Although the amount of radiation intercepted by the canopy and number of days to flowering have not changed with breeding, there was some evidence for an increase in the accumulated biomass from GS31 to GS61+7d with year of release ($r = 0.57$; $P < 0.10$) (Table 5.13), and this is explained by the trend for genetic progress in CGR ($r = 0.43$; $P < 0.10$) in 2010. This increase in the CGR was related to the increase in RUE with year of release ($r = 0.95$; $P < 0.001$). Although Acreche *et al.* (2009) and Calderini *et al.* (1997) reported no change in pre-anthesis biomass or RUE with breeding, significant genetic increase through time in RUE in the stem-elongation period was reported by Shearman *et al.* (2005) in UK winter wheat from 1972 to 1995. Bacanora (released 1988) had relatively high RUE in the present study. This may in part be related to better penetration of light through the canopy of Bacanora compared to other cultivars. Bacanora had the highest amount of radiation percentage (25%) transmitted through the ears and flag leaf layer and intercepted by the rest of the canopy. Optimising the canopy photosynthesis maybe obtained by allowing more light to be transmitted to lower levels of the canopy and or reflected to the canopy rather than to the atmosphere (Stoskopf, 1981 and Duncan, 1971). A more uniform vertical distribution of light across the leaf layers may also be associated with reduced light saturation of the upper leaves (Araus *et al.*, 1993).

The relationship between stomatal conductance and canopy temperature depression is usually positive. Present results showed a trend for stomatal conductance to increase with year of release ($R^2 = 0.6688$; $P = 0.057$; Fig 5.23). However, there was no evidence that canopy temperature changed with breeding during the pre-anthesis phase. This difference between the progress in these two traits may be related to the fact that stomatal conductance measurements were done for the flag leaf whereas canopy temperature was measured for the whole canopy. The trend for an increase in stomatal conductance with plant breeding was consistent with a trend for increased accumulation of biomass during stem elongation with year of introduction.

Results of growth analysis for dry matter production at GS31, 39 and 61+7d showed that dry matter production was higher in 2009 compared to 2010. This was associated with the higher number of plants established and fertile shoots produced in 2009 compared to 2010. Although there was a trend for increasing biomass at anthesis with plant breeding in one year, averaged across years, correlations with either year of release or grain yield were not significant. Above-ground dry matter at maturity improved significantly in the present study with breeding, which means that this improvement is mostly attributed to post-anthesis rather than pre-anthesis dry matter accumulation.

5.4.3 Ear partitioning index

Ear DM per unit land area at anthesis +7 d has not changed with year of release in the present study (r = 0.16; P > 0.10). There was a slight tendency to decrease the proportion of assimilate partitioned to the ear; whereas, assimilate partitioning to the stem and leaf sheath increased significantly (Fig 5.7). The decreases in ear partitioning and increases in stem partitioning occurred since about 1990. This increase in stem partitioning was related to the increase in plant height with breeding (Fig 5.4); although all of the cultivars in the current study were semi-dwarfs, they differed in plant height. The competition for assimilates between the stem and ear during the stem-elongation phase has been reported by many authors (Slafer *et al.*, 1990; Austin *et al.*, 1980; Alvaro *et al.*, 2008 and Abbate *et al.*, 1998). Those authors suggest that the higher the DM partitioning to ear during the stem-elongation phase the greater the ear DM at anthesis and the more grains per ear were produced. These findings are generally consistent with the present results in the sense that overall ear DM per m^2 at anthesis was not changed with year of release and grains per m^2 was also not changed with plant breeding. However, stem DM partitioning at anthesis in the present study was positively associated with individual grain weight which was the numerical yield component best explaining the genetic gains in yield in this set of cultivars (see chapter 6).

5.4.4 Ear fertility index

Ear fertility index (EFI: grains per gram ear DM at anthesis) has not changed with breeding amongst the 12 cultivars (r = – 0.25; P > 0.10) (Fig. 5.24). There

was a negative correlation between ear partitioning index and ear fertility index (r = – 0.62; P < 0.05). This negative relationship was also observed by Gonzalez *et al.* (2011b) and Gaju *et al.* (2011). Foulkes *et al.* (2011) suggested that partitioning more ear DM to developing florets rather than the structural parts of the ear (rachis, glumes and paleas) would be one physiological avenue to break this negative relationship.

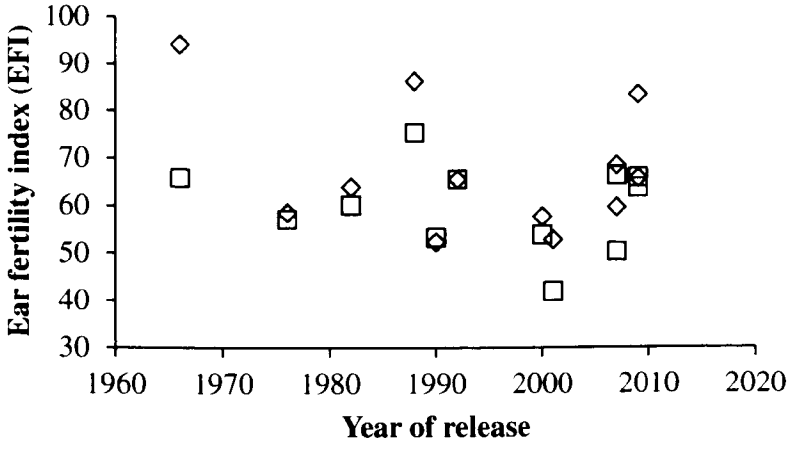


Figure 5.24 of ear fertility index (EFI) on year of release for 2009 (__◇__), and 2010 (---□---).

5.4.5 Shoot production and shoot survival

Averaging across years, cultivars produced similar numbers of fertile shoots at GS31. However, differences were found amongst cultivars in fertile shoot number at GS39 (P = 0.014), but no correlation relationships were found between fertile shoot number and both year of release and grain yield. At GS61, there were more fertile shoots produced in 2009 compared to 2010 (P < 0.001). This was in part because more plants were established in 2009 than 2010. Cultivars differed from each other in shoot mortality, and generally there was a positive relation between the number of fertile shoots produced at GS31 and the number of shoots aborted before anthesis (Fig 5.25). This relation was studied by Shanahan *et al.* (1985), who reported a negative relationship between the maximum shoot number and the final shoot number in

winter wheat in the USA. In addition, Satorre and Slafer (1999) suggested that shoot mortality starts from the onset of the stem-elongation phase due to the increase of competition for assimilates from the stem. It is reported that number of grains per unit area is related more to the shoot survival rather than the maximum number of shoots produced (Shanahan *et al.*, 1985).

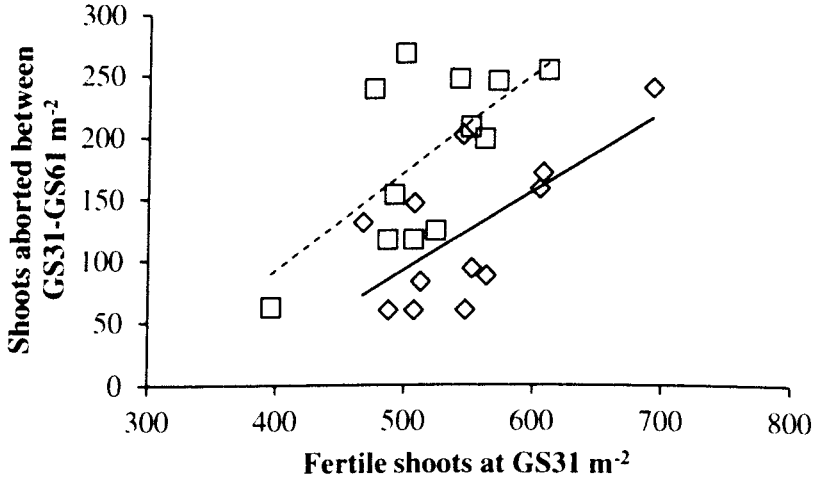


Figure 5.25 Regression of shoots aborted from GS31 to GS61 on fertile shoots at GS31 for 2009 (__◇__) y=0.637x – 226.2 (R^2 = 0.434; *P* = 0.020), and 2010 (---□---) y=0.791x – 224.0 (R^2 = 0.413; *P* 0.024).

Overall present results showed a negative correlation (r = – 0.67, $P < 0.05$) between non-surviving shoots and grains m^{-2}. This negative relation was also reported by Berry *et al.* (2003).

5.4.6 Ear traits

Differences amongst cultivars in rachis length were positively correlated with differences in plant height. Siete Cerros (1966) and Bacanora (1988) the shortest cultivars had rachis length of 10.8 cm, whereas Baviacora (1992) the tallest cultivar produced the longest rachis (13.9 cm). However, no change was found in rachis length with breeding. Fertile spikelets per spike decreased from about 1990 associated with an increase in rachis length per spikelet. This means that more space in the rachis was available for each fertile spikelet and hence potentially more ear photosynthesis per spikelet for the more modern cultivars. This may be one of the factors leading to heavier grains from about 1990 (see chapter 6). The decrease in grains per ear evident from about 1990

with breeding was related more to a decrease in fertile spikelets per ear than in grains per spikelet (Fig 5.19).

5.5 SUMMARY

The physiological basis of genetic gains in yield with year of release in the CIMMYT historic cultivars was not associated with gains in grains m^{-2}. Though the number of ears m^{-2} has increased slightly since 1990, the number of grains m^{-2} has not changed, this was due to a decrease in the number of grains per ear. No change was found in rachis length with breeding; however, fertile spikelet number decreased since about 1990 and was associated with a decrease in grains per ear. The genetic variation amongst the historic set of cultivars in grains m^{-2} was mainly associated with RUE ($r = 0.67$; $P < 0.05$) and CGR ($r = 0.70$; $P < 0.05$) during the stem-elongation period. In addition, the genetic variation in RUE amongst the cultivars appeared to be related to the vertical light distribution, i.e. at GS61+7d RUE was positively correlated with the proportion of PAR transmitted through the ears and flag-leaf layer ($r = 0.40$, $P < 0.10$).

There were statistically significant differences in DM production at all growth stages and a tendency to produce more biomass during the GS31 to GS61+7 days phase with year of release. Differences amongst cultivars were found in the amount of radiation intercepted by the whole canopy in all growth stages, but there was no systematic change with plant breeding. Although not conclusive, since Bacanora was an exception to the trend and RUE was only measured in one season, there was some evidence for a tendency for RUE to increase with year of release. Regression relationship was not significant between RUE and year of release when cv Bacanora was included in the analyses ($R^2 = 0.1294$; $P = 0.546$; Fig 5.14); however, without Bacanora this regression became statistically significant ($R^2 = 0.688$; $P < 0.01$; Fig 5.15). This increase in RUE was consistent with a positive association with CGR and the trend for an increase in biomass accumulation during the stem-elongation phase with plant breeding. Thus there was a trend for an increase in biomass accumulation from GS31-GS61+7d but this was counteracted by a decrease in

EPI so that ear DM per m^2 at GS61+7d and grains per m^2 did not change with plant breeding.

CHAPTER 6 EFFECTS OF BREEDING ON POST-ANTHESIS GROWTH

6.1 INTRODUCTION

This chapter examines the changes in the physiological processes with year of release from anthesis to physiological maturity and their association with yield progress in the historic set of CIMMYT cultivars grown in NW Mexico in 2008-9 and 2009-10. Grain weight is the yield component determined in the post-anthesis phase; this chapter will quantify changes with year of release in potential grain weight and final grain weight and also quantify the trade-off between grains m^{-2} and final grain weight for the set of historic cultivars. The grain source-sink ratio was manipulated at anthesis plus 14 days by imposing a degraining treatment (removal of 50% of spikelets).

The overall objectives were to quantify associations between genetic progress in yield and post-anthesis source and sink type traits and understand the physiological basis of genetic variation in grain weight and grain yield during the period from 1966 to 2009 amongst the 12 CIMMYT cultivars.

The specific hypotheses tested in this chapter were:

1. Genetic variation in grain weight during the period from 1966 to 2009 is positively associated with genetic gains in grain yield with year of release amongst the 12 CIMMYT historic cultivars.
2. Genetic variation in grain weight amongst the 12 CIMMYT historic cultivars is associated with both the duration and rate of grain filling.
3. Genetic variation in duration and rate of grain filling is associated with post-anthesis source type traits such as: Fractional PAR interception, Normalised Difference Vegetative Index, canopy temperature, flag leaf stomatal conductance and flag leaf chlorophyll content (SPAD).

4. The post-anthesis grain source-sink ratio has changed with breeding amongst the CIMMYT cultivars from 1966 to 2009, with the more modern cultivars closer to source limitation.
5. The contribution of stem water soluble carbohydrate to post-anthesis grain growth has increased with year of release amongst the 12 CIMMYT historic cultivars.

6.2 MATERIALS AND METHODS

6.2.1 Experimental measurements

Measurements were carried out to quantify the post-anthesis physiological processes as follows: Normalised Difference Vegetative Index (NDVI) was measured every two weeks during the grain filling period in both seasons; leaf activity traits (canopy temperature, stomatal conductance and SPAD) were measured in both seasons. Stem water soluble carbohydrate analysis was measured at flowering (GS61) plus 7 days and at harvest for both control and sink manipulated shoots.

6.2.2 Post-anthesis source-sink manipulation treatment

This treatment was conducted in the combined yield bed in each plot by randomly selecting and tagging 15 fertile shoots (those with an ear) at heading (GS59) for the degraining treatment and another 15 fertile shoots for the control treatment. At GS 61+14 days, the degraining treatment was implemented by removing all spikelets from one side of the ear (i.e. ca. 50% of the spikletes). At harvest (GS92), all tagged shoots were sampled by cutting at ground level. For each shoot, number of fertile and infertile spikelets was counted, and the bulked 15 ears from each treatment were threshed. Grain and chaff dry weight were recorded separately after drying for 48 h at 85°C. The number of seeds in the threshed grain samples was counted. For the 15 bulked shoots for each treatment, dry weight of the leaf lamina and stem plus leaf sheath was recorded separately.

6.2.3 Stem water soluble carbohydrate (WSC) analysis

This analysis was done in both 2008/09 and 2009/10. The WSC of stems plus attached leaf sheaths was determined by near-infrared spectroscopy in 2008/09 and by colorimetry based on the anthrone reagent (Yemm & Willis, 1954) in 2009/10. In both seasons, 15 fertile shoots were sampled at GS61 + 7 days and again at maturity. After drying the shoots at 85°C for 48 hours, stems plus leaf sheaths were separated from lamina and ears. Then, stem plus leaf sheath was ground to a very fine powder and samples were sent to the plant analysis laboratory in CIMMYT for analysis of %WSC.

6.2.4 Grain growth duration and rate

Grain growth duration and grain growth rate were calculated using final grain weights and assuming grain growth occurred from GS61 to physiological maturity and were calculated on the basis of thermal time using a base temperature of 0°C.

6.3 RESULTS

6.3.1 Stem Water Soluble Carbohydrate (WSC)

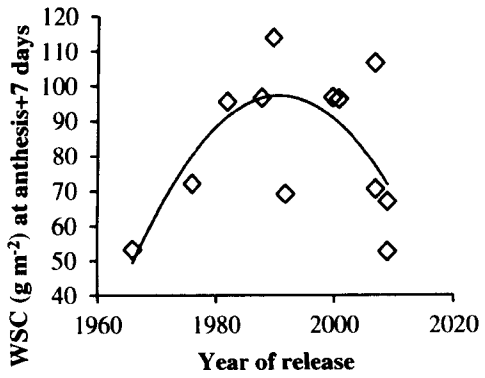
Cultivars differed in the amount of WSC in stems and leaf sheaths at GS61+7d in both years: 2009 ($P < 0.001$) and 2010 ($P = 0.002$) and averaged across years ($P < 0.001$). Stem WSC was not different between 2009 (86.9 g m^{-2}) and 2010 (78.4 g m^{-2}) ($P = 0.282$). Values ranged from 49.2 (Line1, 2009) to 128.8 g m^{-2} (Attila, 1990) in 2009 and from 52.9 (Becard, 2009) to 101.0 g m^{-2} (Tacupeto, 2001) in 2010. Averaging across years, cultivars ranged from 52.6 (Line1, 2009) to 114.0 g m^{-2} (Attila, 1990). The interaction between year and cultivar was not significant ($P = 0.498$). No correlation was found between this trait and either year of release or grain yield. The amount of WSC remaining in the stem at physiological maturity was higher in 2009 (25.0 g m^{-2}) than in 2010 (8.5 g m^{-2}) ($P = 0.016$). No statistically significant cultivar differences were found in either year (significant at 0.10), however, cultivars differed averaging across years ($P = 0.022$). The interaction between years and cultivars was not

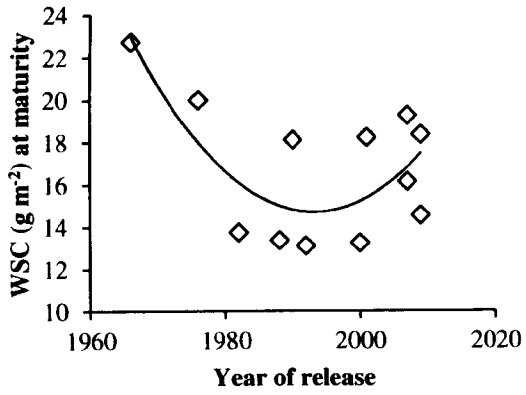
significant (P = 0.108). Averaging across years, values ranged from 13.1 (Baviacora, 1992) to 22.7 g m^{-2} (Siete Cerros, 1966). The utilised amount of WSC (difference between assessments at GS61+7d and physiological maturity) was similar in both years at *ca.* 65 g m^{-2}. There were differences amongst cultivars in 2009 and in 2010 ($P < 0.001$ and $P = 0.001$, respectively), in the range 19.3 (Siete Cerros, 1966) to 101.8 g m^{-2} (Attila, 1990) in 2009 and 41.5 (Siete Cerros, 1966) to 90.3 g m^{-2} (Bacanora, 1988) in 2010. Cultivar differences overall ranged from 30.4 (Siete Cerros, 1966) to 95.9 g m^{-2} (Attila, 1990) ($P < 0.001$). The interaction between year and cultivar was not significant ($P = 0.614$). No correlation was found between utilised stem WSC and either year of release or grain yield. There was a non-linear regression between stem WSC at GS61+7d and year of release, with an increase apparent from 1966 to about 1990, and then a decrease from 1990 to 2009. A similar non-linear relationship was observed between utilised stem WSC and year of release (Figs 6.1 and 6.3, respectively). There was a negative relationship between the duration of grain-filling and both utilised stem WSC and the percentage contribution of stem WSC to grain yield (Figs. 6.5 and 6.6). Differences in stem WSC (g m^{-2}) at anthesis and maturity amongst cultivars were mainly due to stem WSC% ($r = 0.83$ and 0.76; $P < 0.01$) rather than stem DM (g m^{-2}) ($r = 0.33$ and 0.29; $P > 0.05$, respectively) (Fig 6.7 and 6.8, respectively). There was a positive correlation between the WSC accumulated in stems and leaf sheaths at GS61+7d and the ear partitioning index at GS61 + 7d ($r = 0.73$; $P < 0.01$) (Fig 6.9).

Table 6.1 Amount of stem-and-leaf-sheath water-soluble carbohydrate (WSC) at GS61+7days and physiological maturity for 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2010.

Cultivar (Year of release)	Stem Water Soluble Carbohydrates (WSC) g m^{-2}								
	GS61 + 7 days			Physiological maturity			Utilized		
	2009	2010	Average	2009	2010	Average	2009	2010	Average
Siete Cerros (1966)	53.3	53.0	53.1	34.0	11.5	22.7	19.3	41.5	30.4
Pavon (1976)	75.4	68.9	72.1	30.1	9.9	20.0	45.3	59.0	52.1
Seri (1982)	94.9	96.4	95.6	20.0	7.5	13.7	74.9	88.9	81.9
Bacanora (1988)	97.5	96.1	96.8	20.9	5.8	13.4	76.5	90.3	83.4
Attila (1990)	128.8	99.3	114.0	26.9	9.3	18.1	101.8	90.0	95.9
Baviacora (1992)	68.3	70.1	69.2	18.0	8.2	13.1	50.3	61.9	56.1
Tarachi (2000)	105.7	88.1	96.9	18.4	8.1	13.2	87.3	80.0	83.7
Tacupeto (2001)	92.0	101.0	96.5	24.2	12.2	18.2	67.8	88.7	78.3
Roelfes (2007)	78.3	63.1	70.7	22.1	10.2	16.1	56.2	52.9	54.6
Navojoa (2007)	117.9	95.7	106.8	32.7	5.8	19.3	85.2	89.9	87.5
Becard (2009)	81.1	52.9	67.0	23.6	5.5	14.5	57.4	47.5	52.5
Line 1 (2009)	49.2	56.1	52.6	28.6	8.2	18.4	20.7	47.9	34.3
Mean	86.9	78.4	82.6	25.0	8.5	16.7	61.9	69.9	65.9
S.E.D (df) (Years)			6.81(4)			4.123(4)			9.09(4)
(Cultivars)	14.35(22)	13.24(22)	9.76(44)	5.41(22)	2.241(22)	2.927(44)	15.96(22)	13.14(22)	10.34(44)
(Interaction)			14.87(39.7)			5.719(13.74)			16.69(30.1)
Prob. (Years)			0.282			0.016*			0.430
(Cultivars)	<0.001***	0.002**	<0.001***	0.075†	0.089†	0.022*	<0.001***	0.001***	<0.001***
(Interaction)			$0.498^{n.s}$			$0.108^{n.s}$			$0.614^{n.s}$
C.V %	20.2	20.7	20.5	26.5	32.2	30.3	31.6	23.0	27.2
Correlation with (Year of release)	0.17	0.01	0.10	-0.24	-0.36	-0.33	0.21	0.05	0.15
(Grain yield)	0.00	0.04	0.01	-0.07	-0.51	-0.34	0.01	0.10	0.06

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant





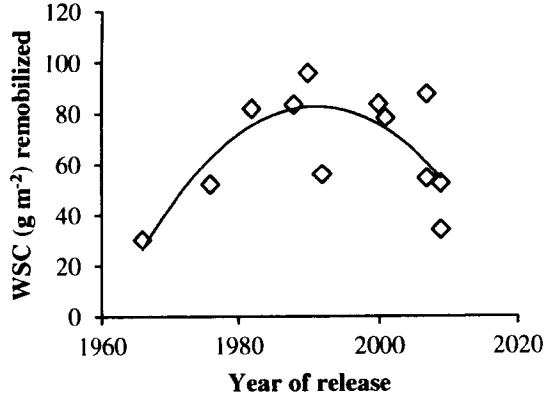
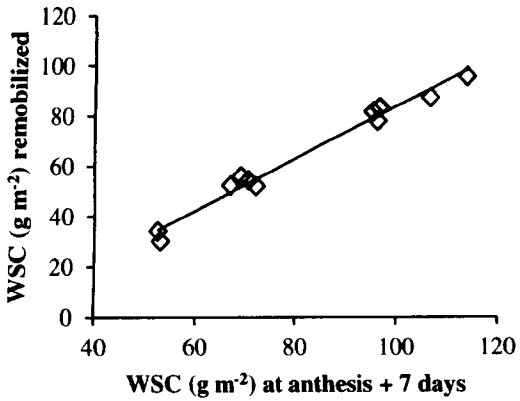
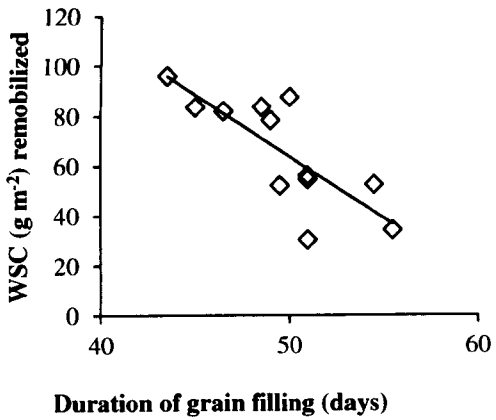


Figure 6.1 Regression of the amount of stem-and-leaf-sheath WSC at GS61 + 7 days on year of release for 12 CIMMYT spring wheat cultivars for the average of two seasons $y = -0.0776x^2 + 308.86x - 307353$ **(**$R^2 = 0.464$, $P = 0.060$**)**

Figure 6.2 Regression of the amount of stem-and-leaf-sheath WSC at physiological maturity on year of release for 12 CIMMYT spring wheat cultivars for the average of two seasons = $0.0112x^2 - 44.546x + 44410$ **(**$R^2 = 0.516$, $P = 0.040$**).**

Figure 6.3 Regression of the amount of stem-and-leaf-sheath WSC remobilized on year of release for 12 CIMMYT spring wheat cultivars for the average of two seasons $y = -0.0887x^2 + 353.41x - 351763$ **(**$R^2 = 0.561$, $P = 0.025$**).**





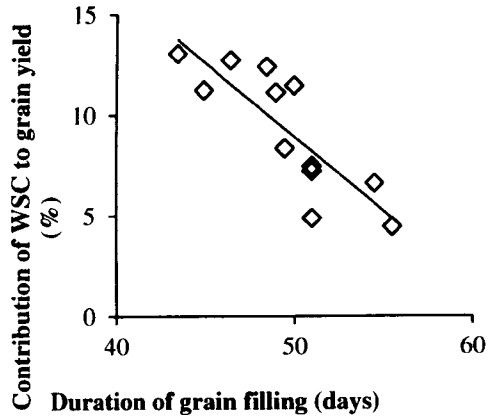


Figure 6.4 Regression of stem WSC utilized on stem WSC at GS61+7d for 12 CIMMYT spring wheat cultivars.. Values represent averages in 2009 and 2010. Y = 1.0381x – 19.885 (R^2 = 0.980, P < 0.001).

Figure 6.5 Regression of stem WSC utilized on duration of grain-filling for 12 CIMMYT spring wheat cultivars.. Values represent averages in 2009 and 2010. Y = -4.9256x + 310.11 (R^2 = 0.620; P = 0.002

Figure 6.6 Regression of stem WSC contribution to grain yield on duration of grain-filling for 12 CIMMYT spring wheat cultivars.. Values represent averages in 2009 and 2010. . Y = -0.7384x + 45.867 (R^2 = 0.694; P < 0.001)

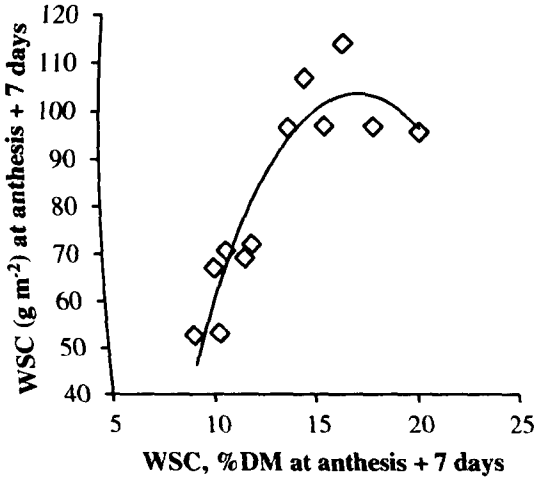


Figure 6.7 Regression of stem WSC (g m^{-2}) at GS61 + 7days on WSC, %DM at GS61+7d for 12 CIMMYT spring wheat cultivars. Values represent averages in 2009 and 2010.. $Y = -0.8037x^2 + 28.478x - 148.6$ ($R^2 = 0.884$, $P < 0.001$)

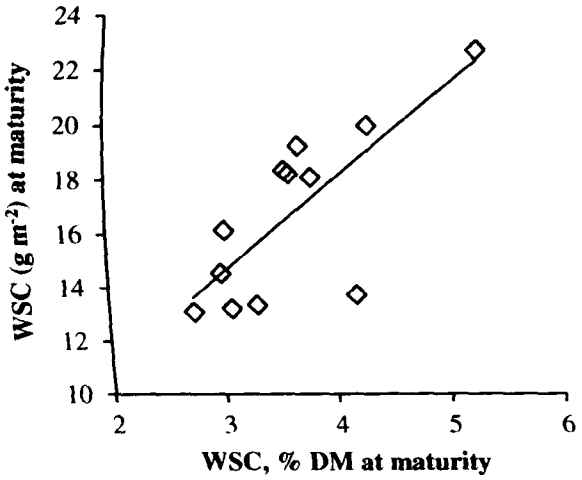


Figure 6.8 Regression of stem WSC (g m^{-2}) at physiological maturity (PM) on WSC, %DM at PM for 12 CIMMYT spring wheat cultivars. Values represent averages in 2009 and 2010. $Y = 3.4219x + 4.2091$ ($R^2 = 0.585$, $P = 0.004$)

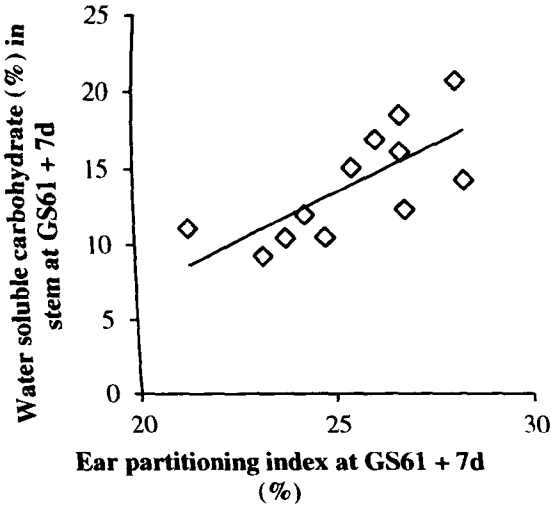


Figure 6.9 Regression of % stem WSC at GS61+7d on ear partitioning index at GS61 + 7d for 12 CIMMYT spring wheat cultivars. Values represent averages in 2009 and 2010. $Y = 1.2685x - 18.496$ ($R^2 = 0.534$, $P = 0.007$)

6.3.2 Canopy and leaf activity traits

6.3.2.1 Flag leaf SPAD value

Post-anthesis SPAD was measured once in 2009 (12 March) and 2010 (6 April), on each occasion around a month after anthesis. SPAD values differed between years with values of 47.2 in 2009 and 44.7 in 2010 ($P < 0.001$). Cultivars ranged from 43.6 (Line1, 2009) to 49.9 (Seri, 1982) in 2009 ($P < 0.001$) and from 41.5 (Line1, 2009) to 47.1 (Siete Cerros, 1966) in 2010 ($P = 0.007$). Averaging across years, cultivars ranged from 42.5 (Line1, 2009) to 48.4 (Seri, 1982) ($P < 0.001$). The interaction between years and cultivars was not statistically significant ($P = 0.410$). Also, the correlation amongst cultivars was not statistically significant with either year of release or grain yield (Table. 6.2).

6.3.2.2 Canopy temperature depression

Canopy temperature depression was measured on 19 and 25 March (around 30d after anthesis) in 2009 and on 29 March (around 30 d after anthesis) in 2010. CTD was higher in 2009 (4.4 C°) than in 2010 (2.6 C°) ($P < 0.001$). No differences were found amongst cultivars in either year or for the average across the years (Table 6.3; Fig 6.10). However, the correlation between CTD and grain yield was positive in 2009 and 2010 and for the average across years ($P < 0.05$; Fig 6.11). Averaging across years, there was a trend for CTD to increase with year of release ($r = 0.56$; $P < 0.10$; Table 6.3).

6.3.2.3 Flag leaf stomatal conductance

Stomatal conductance was measured in both years. However, in 2009, readings were very low due to equipment problems, so readings were more reliable in 2010 where measurements were taken five times after-anthesis during the 30 days after anthesis. Averaged over readings during the post-anthesis period in 2010, there was a trend for differences among cultivars ($P = 0.078$), with values ranging from 253.0 for (Line1, 2009) to 378.3 mmol m^{-2} s^{-1} for (Baviacora, 1992). However, there were no associations between post-anthesis

stomatal conductance and either year of release (r = 0.17) or grain yield (r = 0.03; Table 6.3).

Table 6.2 SPAD units during the post-anthesis period (measured on 12 March 2009 and 6 April 2010) of 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2009 and 2010.

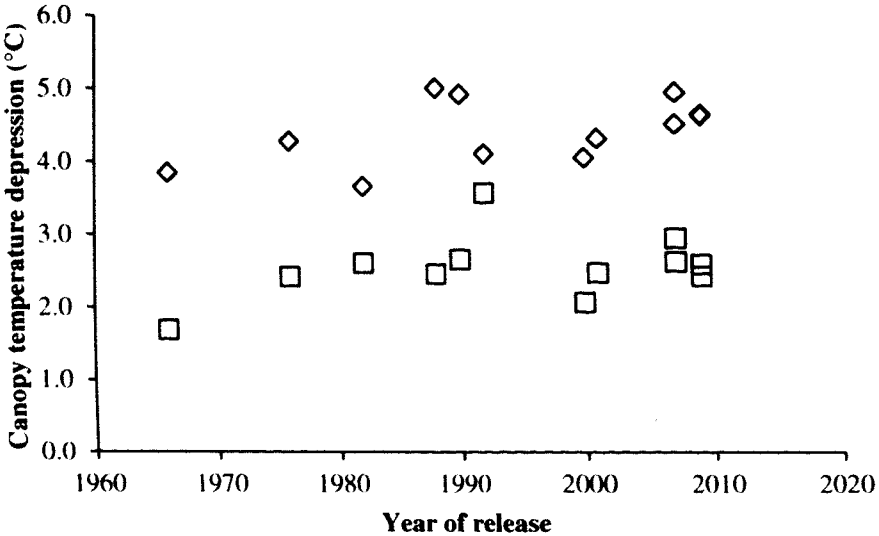
Cultivar (Year of release)	SPAD units		
	2009	2010	Average
Siete Cerros (1966)	46.8	47.1	46.9
Pavon (1976)	46.9	44.8	45.8
Seri (1982)	49.9	46.9	48.4
Bacanora (1988)	45.2	41.9	43.6
Attila (1990)	48.5	45.4	46.9
Baviacora (1992)	49.3	45.7	47.5
Tarachi (2000)	46.3	45.2	45.7
Tacupeto (2001)	45.0	43.1	44.0
Roelfes (2007)	47.7	44.9	46.3
Navojoa (2007)	48.3	45.3	46.8
Becard (2009)	49.5	44.8	47.2
Line 1 (2009)	43.6	41.5	42.5
Mean	47.2	44.7	45.97
S.E.D (df) (Years)			0.262(5)
(Cultivars)	0.767(22)	1.415(33)	0.888(55)
(Interaction)			1.242(58.84)
Prob. (Years)			<0.001***
(Cultivars)	<0.001***	0.007**	<0.001***
(Interaction)			$0.439^{n.s}$
C.V %	2.0	4.5	3.6
Correlation with (Year of release)	-0.11	-0.47	-0.30
(Grain yield)	-0.05	-0.43	-0.19

* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

Table 6.3 Canopy temperature depression measured on 19 and 25 March in 2009 and on 29 March in 2010 and stomatal conductance measured five times after-anthesis during the 30 days after anthesis in 2010 of 12 CIMMYT spring wheat cultivars released from 1966 to 2009.

Cultivar (Year of release)	Canopy temperature depression (°C)			Stomatal conductance (mmol m^{-2} s^{-1})
	2009	2010	Average	2010
Siete Cerros (1966)	3.9	1.7	2.8	273.5
Pavon (1976)	4.3	2.4	3.4	292.9
Seri (1982)	3.7	2.6	3.1	347.9
Bacanora (1988)	5.0	2.5	3.7	268.8
Attila (1990)	4.9	2.7	3.8	327.1
Baviacora (1992)	4.1	3.6	3.8	378.3
Tarachi (2000)	4.1	2.1	3.1	315.3
Tacupeto (2001)	4.3	2.5	3.4	361.4
Roelfes (2007)	4.5	2.6	3.6	307.6
Navojoa (2007)	5.0	3.0	4.0	368.1
Becard (2009)	4.7	2.6	3.6	302.1
Line 1 (2009)	4.7	2.4	3.6	253.0
Mean	4.4	2.6	3.5	316.3
S.E.D (df) (Years)			0.6109(5)	
(Cultivars)	0.587(22)	0.466(33)	0.3655(55)	37.25(11)
(Interaction)			0.7894(13.4)	
Prob. (Years)			<0.028*	
(Cultivars)	$0.373^{n.s}$	0.078†	$0.057^{\dagger}$	0.078†
(Interaction)			$0.369^{n.s}$	
C.V %	16.3	25.8	20.4	11.8
Correlation with (Year of release)	0.51†	0.37	0.56†	0.17
(Grain yield)	0.69*	0.67*	0.82**	0.03

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant



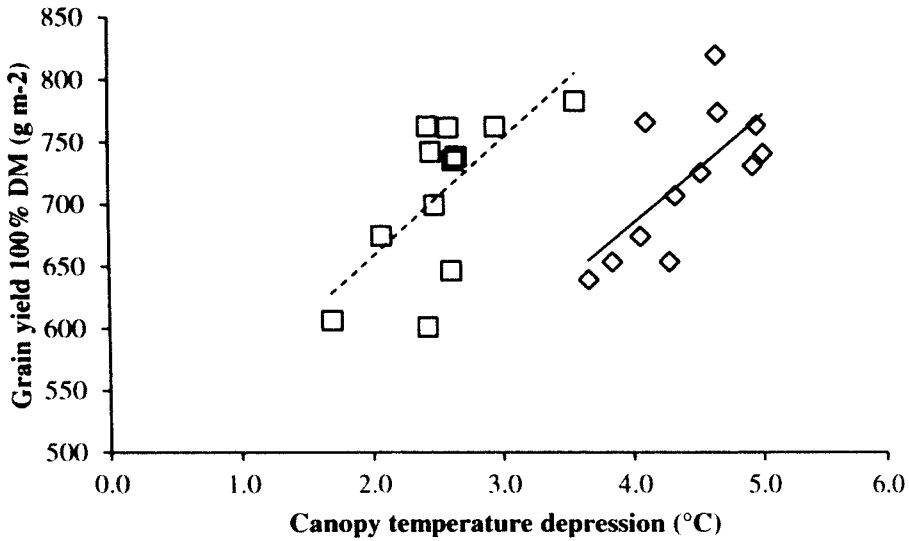
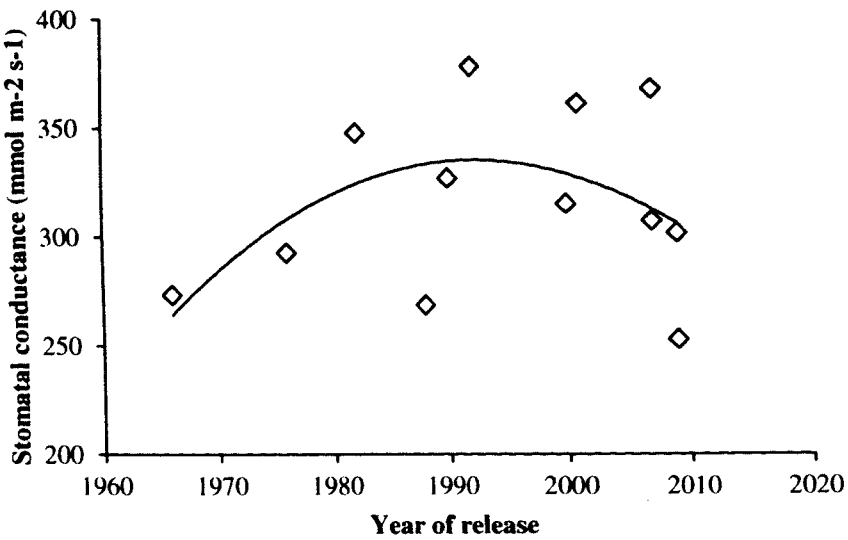


Figure 6.10 canopy temperature depression versus year of release for 2009 (__◇__) and 2010 (---□---) for 12 CIMMYT spring wheat cultivars.

Figure 6.11 Regression of grain yield on canopy temperature depression for 2009 (__◇__) y= 87.264x + 335.31 (R^2 = 0.473; *P* = 0.012), and 2010 (---□---) y= 94.095x + 469.71 for 12 CIMMYT spring wheat cultivars (R^2 = 0.453; *P* = 0.015).



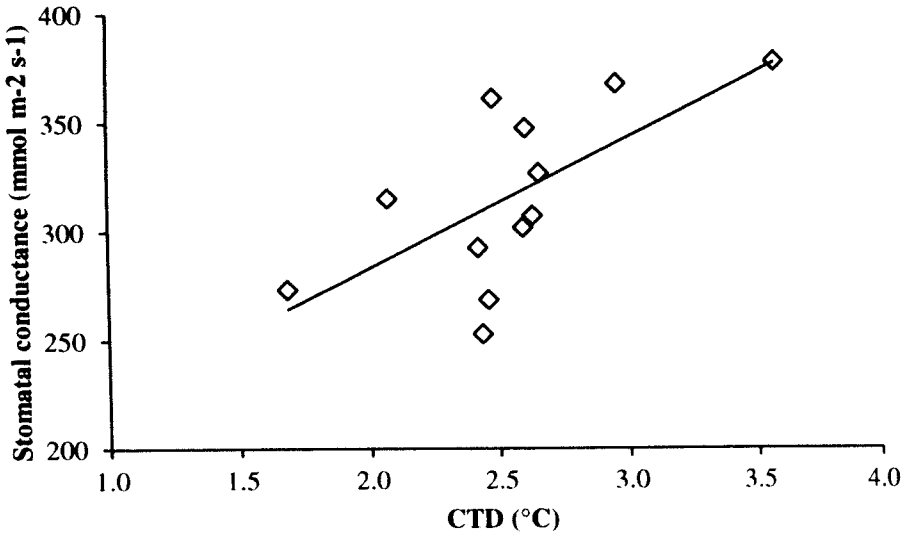


Figure 6.12 Regression of post-anthesis flag-leaf stomatal conductance averaged over five measurements on year of release in 2010 for 12 CIMMYT spring wheat cultivars. y= -0.1031x2 + 410.83x - 408907 (R^2 = 0.234; P = 0.603)

Figure 6.13 Regression of stomatal conductance on CTD in 2010 y= 60.004x + 163.19 for 12 CIMMYT spring wheat cultivars (R^2 = 0.437, P = 0.015).

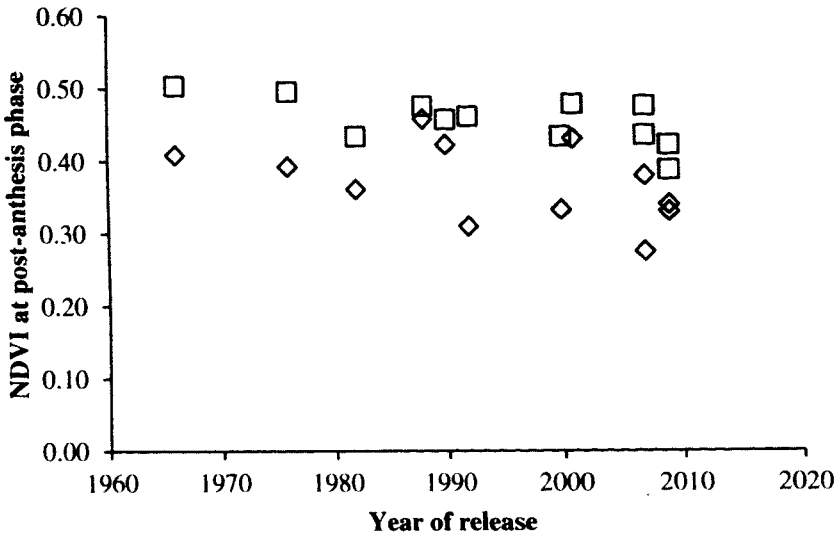
6.3.2.4 The Normalized Difference Vegetation Index (NDVI)

Normalized Difference Vegetation Index was measured once post-anthesis in 2009 and four times in 2010 from about 15-40 days after anthesis. NDVI during the post-anthesis period was higher in 2010 than in 2009 ($P < 0.001$; Table 6.4). Cultivars differed in 2009 and in 2010 ($P < 0.001$), from 0.28 (Roelfes, 2007) to 0.46 (Bacanora, 1988) in 2009, and from 0.39 (Becard, 2009) to 0.50 (Siete Cerros, 1966 and Pavon, 1976) in 2010. NDVI amongst cultivars averaging across years ranged from 0.36 (Roelfes, 2007 and Becard, 2009) to 0.47 (Bacanora, 1988) ($P < 0.001$). Averaging across years, the association between NDVI and year of release ($r = -0.60$, $P < 0.05$) and grain yield ($r = -0.39$) was negative (Table 6.4), indicating canopy green area tended to be negatively associated with yield. There was also a negative relationship between post-anthesis NDVI and thousand grain weight (Fig. 6.15).

Table 6.4 Post-anthesis Normalised Difference Vegetation Index (NDVI) of 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2009 and 2010. Values represent means over one and four readings in 2009 and 2010, respectively.

Cultivar (Year of release)	NDVI		
	2009	2010	Average
Siete Cerros (1966)	0.41	0.50	0.46
Pavon (1976)	0.39	0.50	0.44
Seri (1982)	0.36	0.43	0.40
Bacanora (1988)	0.46	0.48	0.47
Attila (1990)	0.42	0.46	0.44
Baviacora (1992)	0.31	0.46	0.39
Tarachi (2000)	0.33	0.43	0.38
Tacupeto (2001)	0.43	0.48	0.45
Roelfes (2007)	0.28	0.44	0.36
Navojoa (2007)	0.38	0.48	0.43
Becard (2009)	0.34	0.39	0.36
Line 1 (2009)	0.33	0.42	0.38
Mean	0.37	0.46	0.41
S.E.D (df) (Years)			0.016(6)
(Cultivars)	0.022(33)	0.015(33)	0.013(66)
(Interaction)			0.024(25.53)
Prob. (Years)			0.002**
(Cultivars)	<0.001***	<0.001***	<0.001***
(Interaction)			<0.001***
C.V %	8.3	4.7	6.4
Correlation with (Year of release)	-0.46	-0.66*	-0.60*
(Grain yield)	-0.23	-0.48	-0.39

* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant



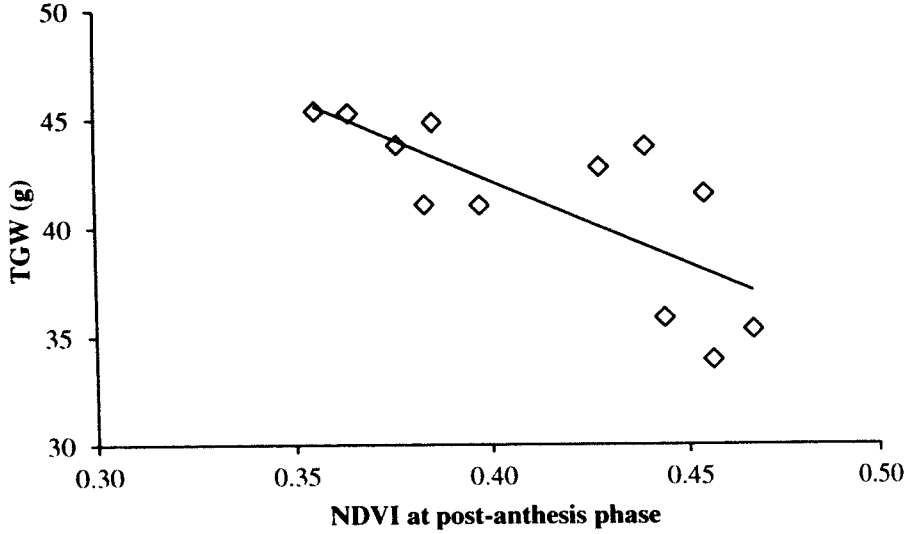


Figure 6.14 Regression of post-anthesis NDVI on year of release for for 12 CIMMYT spring wheat cultivars in 2009 (__◇__) and 2010 (---□---).

Figure 6.15 Regression of thousand grain weight (TGW) on post-anthesis NDVI for 12 CIMMYT spring wheat cultivars. Values represent means across 2009 and 2010. Y = -76.383x + 72.773 (R^2 = 0.558; P = 0.005)

There was a tendency for the NDVI to be decreased with year of release during post anthesis phase, although this reduction was statistically significant amongst cultivars on19 April or about 40 days after anthesis (R^2 = 0.698; P = 0.005; Fig 6.16). NDVI decreased significantly during the period from 1966 to about 1982; however, this decrease levelled off during the period from about 1988 to 2009.

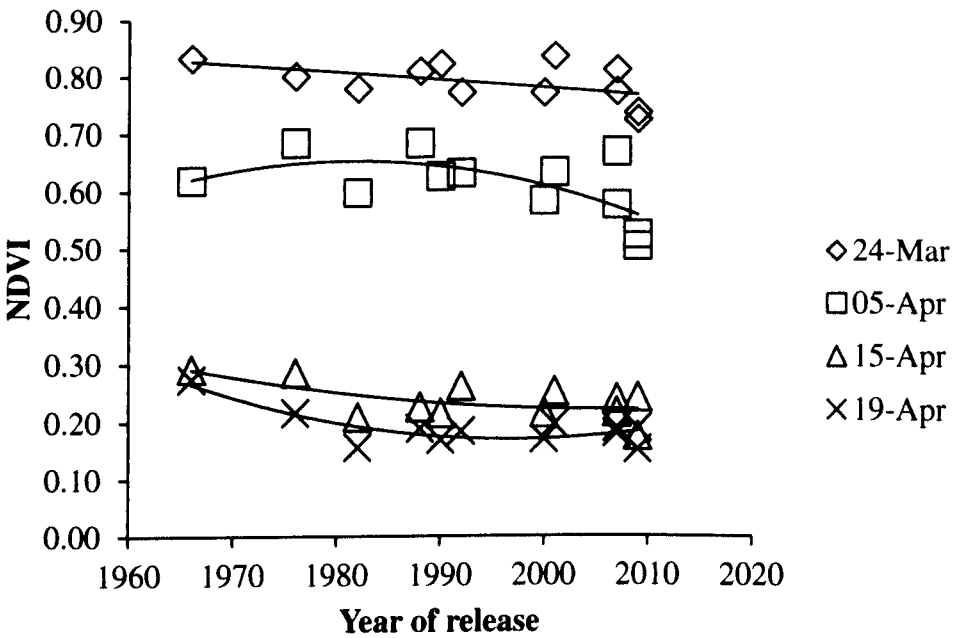


Figure 6.16 Regression of post anthesis NDVI on year of release in 2010 for 12 CIMMYT spring wheat cultivars for 24 Mar y = -0.0014x + 3.5543 (R^2 = 0.29; P = 0.069), 05 Apr y = -0.0001x2 + 0.4976x – 492.36 (R^2 = 0.423; P = 0.084), 15 Apr y = 4E – 05x^2 – 0.1759x + 176.64 (R^2 = 0.406; P = 0.096) and 19 Apr y = 1E – 04x^2 – 0.393x + 392.05 (R^2 = 0.698; P = 0.005).

6.3.3 Responses to source-sink manipulation treatment

The degraining treatment was carried out in 2010 only. As both treatments (control and manipulated ears) were conducted randomly through the same bed, values of the response to the treatments were converted from 15 shoots to per square metre by using the number of the ears m^{-2} obtained at harvest in the each plot. Thus, the same number of ears m^{-2} was used to convert to values per m^2 for both treatments per plot.

Cultivars differed in ear dry weight per m^2 at harvest for the control ears (P = 0.022) in the range from 1026 (Seri, 1982) to 1389 g m^{-2} (Baviacora, 1992). A positive correlation was found between ear dry weight and both year of release and grain yield (r = 0.69 and 0.99, respectively). Cultivars also differed in the ear dry weight in degrained ears (P = 0.007) from 594 (Pavon, 1976) to 817 g m^{-2} (Baviacora, 1992). The correlation between ear dry weight in degrained ears and combine grain yield was significant ($P < 0.001$), and there was a trend for manipulated ear dry weight to increase with year of release (r = 0.47; $P >$ 0.05).

Differences were found amongst cultivars in grain DM per m^2 in control ears (P = 0.009). Values ranged from 754.2 (Seri, 1982) to 1040.3 g m^{-2} (Baviacora, 1992). As expected, the correlation between grain DM per m^2 and year of release was positive and significant (r = 0.73, $P < 0.001$). In the degrained ears, cultivars also differed (P = 0.009) with values ranging from 392 (Pavon, 1976) to 562 g m^{-2} (Baviacora, 1992). There was a trend for grain weight in degrained ears to increase with breeding (r = 0.48; $P > 0.05$).

Cultivars did not differ in the chaff DM per m^2 in control ears (P = 0.115) in the range 272 (Seri, 1982) to 355 g m^{-2} (Navojoa, 2007). No correlation was found amongst cultivars between control ear chaff dry weight and year of release (r = 0.38; $P > 0.05$) However, the correlation was significant with grain yield (r = 0.70; $P < 0.01$). In the degrained ears, cultivars differed in chaff dry weight (P = 0.021) from 185 (Seri, 1982) to 255 g m^{-2} (Baviacora, 1992). No correlation was found amongst cultivars between chaff DM in degrained ears and year of release (r = 0.37; $P > 0.05$) Nevertheless, the correlation was significant with grain yield (r = 0.76; $P < 0.01$) (Table 6.5).

Table 6.5 Effect of sink manipulation degraining treatment on partitioning of DM to ears, grains and chaff at maturity of 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2010.

Cultivar (Year of release)	Ears DM (g m^{-2})		Grains DM (g m^{-2})		Chaff DM (g m^{-2})	
	Control	Manipulated	Control	Manipulated	Control	Manipulated
Siete Cerros (1966)	1094.9	625.7	763.5	413.9	331.4	211.8
Pavon (1976)	1071.9	594.2	776.2	392.4	295.7	201.8
Seri (1982)	1025.9	609.2	754.2	424.5	271.7	184.6
Bacanora (1988)	1215.1	692.0	886.0	461.5	329.2	230.5
Attila (1990)	1198.0	756.6	856.9	509.5	341.1	247.1
Baviacora (1992)	1389.1	816.6	1040.3	561.5	348.9	255.1
Tarachi (2000)	1220.5	649.6	893.6	445.5	326.9	204.1
Tacupeto (2001)	1233.9	705.7	881.0	455.4	352.9	250.3
Roelfes (2007)	1314.3	734.9	968.1	492.4	346.2	242.5
Navojoa (2007)	1345.0	684.5	989.9	459.5	355.1	225.0
Becard (2009)	1186.3	677.1	889.2	471.2	297.1	205.9
Line 1 (2009)	1294.1	725.9	952.1	485.2	342.0	240.7
Mean	1215.8	689.3	887.6	464.4	328.2	225.0
S.E.D (df) (cultivars)	95.270(22)	49.666(22)	71.660(22)	35.533(22)	27.783(22)	19.529(22)
Prob. (Cultivars)	0.022*	0.007**	0.009**	0.009**	$0.115^{n.s}$	0.021*
C.V %	9.6	8.8	9.9	9.4	10.4	10.6
Correlation with (Year of release)	0.69*	0.47	0.73**	0.48	0.38	0.37
(Grain yield)	0.99**	0.97**	1.00	1.00	0.70**	0.76**

* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

Overall, stem-and-leaf-sheath DM at harvest was higher in manipulated shoots (1.79 g shoot^{-1}) than in control shoots (1.64 g shoot^{-2}) ($P < 0.001$). Differences amongst cultivars in stem DM in both control and manipulated shoots were significant ($P < 0.001$; Table 6.6). Values of stem DM ranged from 1.34 (Bacanora, 1988) to 2.08 g shoot^{-1} (Baviacora, 1992) in control shoots and from 1.47 (Bacanora, 1988) to 2.27 g shoot^{-1} (Roelfes, 2007) in manipulated shoots. The interaction between the degraining treatment and cultivar was not significant ($P = 0.228$). The correlation between stem DM in control shoots and year of release was not significant, however, it was significant with grain yield shoot^{-1} ($r = 0.82$; $P < 0.01$). There was also a positive correlation between stem DM in manipulated shoots and grain yield shoot^{-1} ($r = 0.73$; $P < 0.01$). There was a trend for differences amongst cultivars in the % increase in the stem DM in response to degraining ($P = 0.068$). Values in the % increase of the stem dry weight ranged from 2.2 (Tarachi, 2000) to 15.5% (Becard, 2009).

Individual grain weight was slightly higher in degrained ears (45.0 mg) than in control ears (42.7 mg; $P < 0.001$). Values of grain weight ranged from 36.0 (Siete Cerros, 1966) to 48.0 mg (Roelfes, 2007) in control ears and from 36.2 (Siete Cerros, 1966) to 49.3 mg (Roelfes, 2007) in degrained ears ($P < 0.001$; Table 6). There was a trend for an interaction between the degraining treatment and cultivar ($P = 0.087$). Correlations between grain weight and year of release were significant and positive in both treatments ($r = 0.85$ and 0.78; $P < 0.01$). Only weakly significant differences were found amongst cultivars in the percentage increase in grain weight in response to degraining ($P = 0.097$; Table 6.6 and Fig 6.18). Values in the % increase of grain weight ranged from 0.5 (Siete Cerros, 1966) to 13.2% (Baviacora, 1992). The correlation amongst genotypes between the % increase of grain weight and year of release was not significant ($r = 0.16$; $P > 0.10$).

Averaging across cultivars, stem WSC at maturity was 24.5 and 100.6 mg shoot^{-1} in the control and manipulated shoots, respectively ($P < 0.001$; Table 6.7). There were differences amongst cultivars in the control shoots ($P = 0.009$) and also differences in the manipulated shoots ($P < 0.001$) with values ranging from 14.9 (Navojoa, 2007) to 33.7 mg shoot^{-1} (Siete Cerros, 1966) and from

69.6 (Becard, 2009) to 177.1 mg shoot^{-1} (Roelfes, 2007), respectively. The interaction between the degraining treatment and cultivar was significant ($P <$ 0.001). Correlations with year of release and grain yield were not significant in either the control (r = -0.51 and 0.05, respectively) or manipulated shoots (r = -0.15 and 0.37, respectively). Averaging across cultivars, the amount of stem WSC utilized was 211.8 in control shoot stems and 135.6 mg shoot^{-1} in the manipulated shoot stems ($P <$ 0.001). Differences were found amongst cultivars in the amount of stem WSC utilized in the control shoots ($P <$ 0.001) in the range 130.9 (Line 1, 2009) to 378.6 mg shoot^{-1} (Seri, 1982) and the degrained shoots ($P <$ 0.001) in the range 24.4 (Siete Cerros, 1966) to 318.6 mg shoot^{-1}(Seri, 1982). The interaction between the degraining treatment and cultivar was significant ($P <$ 0.001).

Thus, higher amounts of WSC were utilized in the control treatment compared to the manipulated treatment in cultivars e.g. Siete Cerros (1966) and Roelfes (2007), but less WSC values utilized in the control comparing to the manipulated treatment in some other cultivars e.g. Seri (1982) and Tarachi (2000). The correlation amongst cultivars between utilized stem WSC per shoot and either year of release or grain yield was not significant in either control or manipulated shoots (Table 6.7).

The contribution of stem WSC to grain yield was higher in manipulated than control shoots (10.2 and 8.4%, respectively) ($P <$ 0.001). Differences were found amongst cultivars in the percentage contribution of stem WSC to grain yield in control shoots ($P< 0.001$) in the range 5.4 (Line1, 2009) to 14.1% (Seri, 1982), and in the manipulated shoots ($P <$ 0.001) in the range 1.9 (Siete Cerros, 1966) to 21.1% (Seri, 1982). The interaction between manipulation treatment and cultivars was significant ($P <$ 0.001). Correlations with year of release and grain yield were not significant in either the control or manipulated shoots (Table 6.7).

Table 6.6 Effect of sink manipulation degraining treatment on individual grain weight and stem and leaf sheath DM of 12 CIMMYT spring wheat cultivars released from 1966 to 2009 in 2008-9 and 2009-10

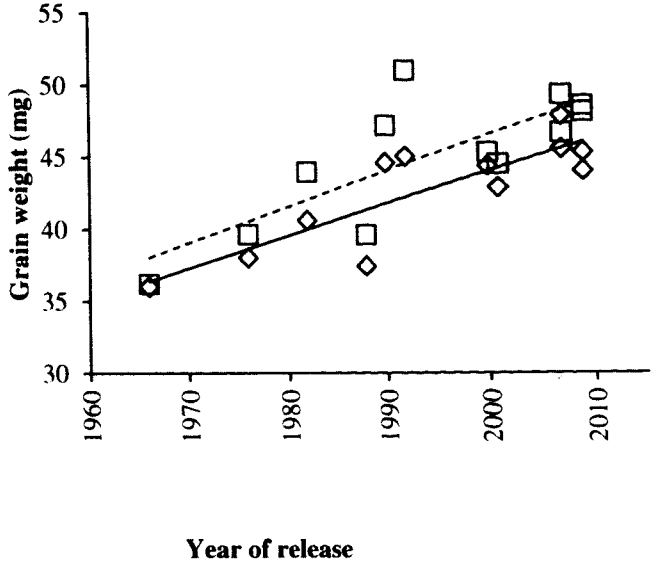
Cultivar (Year of release)	Stem DM (g shoot^{-1})				Grain weight (mg)			
	Control	Manipulated	Average	% increase	Control	Manipulated	Average	% increase
Siete Cerros (1966)	1.62	1.82	1.72	12.5	36.0	36.2	36.1	0.5
Pavon (1976)	1.60	1.72	1.66	7.4	38.0	39.7	38.9	4.2
Seri (1982)	1.58	1.74	1.66	10.8	40.6	44.0	42.3	8.3
Bacanora (1988)	1.34	1.47	1.41	8.7	37.5	39.6	38.6	5.8
Attila (1990)	1.40	1.69	1.54	20.1	44.6	47.2	45.9	5.8
Baviacora (1992)	2.08	2.24	2.16	7.6	45.1	51.0	48.0	13.2
Tarachi (2000)	1.62	1.66	1.64	2.2	44.4	45.4	44.9	2.1
Tacupeto (2001)	1.58	1.67	1.62	5.2	42.9	44.6	43.7	3.8
Roelfes (2007)	2.06	2.27	2.17	10.3	47.9	49.3	48.6	3.0
Navojoa (2007)	1.55	1.66	1.60	7.4	45.6	46.7	46.2	2.4
Becard (2009)	1.55	1.79	1.67	15.5	45.4	48.6	47.0	7.1
Line 1 (2009)	1.70	1.82	1.76	7.3	44.1	48.2	46.1	9.3
Mean	1.64	1.79	1.72	9.6	42.7	45.0	43.9	5.5
S.E.D (df) (Ear treatment)			0.017(24)				0.332(24)	
(Cultivars)	0.085(22)	0.073(22)	0.072(22)	4.647(22)	1.443(22)	0.745(22)	0.852(22)	3.779(22)
(Interaction)			0.083(35.22)				1.178(45.6)	
Prob. (Ear treatment)			<0.001***				<0.001***	
(Cultivars)	< 0.001***	<0.001***	<0.001***	0.068†	<0.001***	<0.001***	<0.001***	0.097†
(Interaction)			0.228$^{n.s}$				0.087†	
C.V %	6.4	5.0	4.1	58.0	4.1	2.0	3.2	82.8
Correlation with								
(Year of release)	0.21	0.16	0.18	-0.18	0.85**	0.78**	0.83**	0.16
(Grain yield shoot^{-1})	0.82**	0.73**	0.79**		0.42	0.50†	0.48	

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

Table 6.7 Effect of sink manipulation degraining treatment on stem water-soluble carbohydrate (WSC) of 12 CIMMYT cultivars released from 1966 to 2009 in 2010.

Cultivar (Year of release)	Water-Soluble Carbohydrates (mg shoot^{-1})						Contribution of WSC in grain yield (%)		
	At maturity			Utilized					
	control	Manipulated	Average	control	manipulated	Average	control	manipulated	Average
Siete Cerros (1966)	33.69	136.55	85.12	127.25	24.39	75.82	5.45	1.87	3.66
Pavon (1976)	29.85	91.71	60.78	178.47	116.62	147.54	7.53	9.68	8.61
Seri (1982)	26.43	86.38	56.40	378.59	318.64	348.61	14.14	21.13	17.63
Bacanora (1988)	16.33	83.66	50.00	267.93	200.59	234.26	10.80	15.51	13.15
Attila (1990)	23.72	102.43	63.08	251.18	172.48	211.83	11.76	13.35	12.55
Baviacora (1992)	26.66	116.88	71.77	210.82	120.60	165.71	6.30	6.69	6.50
Tarachi (2000)	23.55	82.19	52.87	219.30	160.65	189.97	8.46	12.37	10.42
Tacupeto (2001)	30.82	93.21	62.01	226.89	164.50	195.70	10.05	14.41	12.23
Roelfes (2007)	31.01	177.11	104.06	181.36	35.27	108.32	6.14	2.39	4.27
Navojoa (2007)	14.92	77.90	46.41	225.66	162.67	194.17	8.89	13.71	11.30
Becard (2009)	15.48	69.59	42.54	142.84	88.73	115.78	5.72	6.63	6.18
Line 1 (2009)	21.01	89.42	55.22	130.86	62.45	96.66	5.35	5.04	5.19
Mean	24.5	100.6	62.5	211.8	135.6	173.7	8.38	10.23	9.31
S.E.D (df) (Ear treatment)			9.06(22)			3.15(24)			0.407(24)
(Cultivars)	5.08(22)	15.60(22)	3.15(24)	28.33(22)	31.88(22)	29.28(22)	3.006(22)	2.409(22)	1.854(22)
(Interaction)			11.90(44.16)			30.28(25.05)			2.105(33.95)
Prob. (Ear treatment)			<0.001***			<0.001***			<0.001***
(Cultivars)	0.009*	<0.001***	<0.001***	<0.001***	<0.001***	<0.001***	<0.001***	<0.001***	<0.001***
(Interaction)			<0.001***			<0.001***			<0.001***
C.V %	25.5	19.0	21.4	16.4	28.8	7.7	21.2	28.8	18.5
Correlation with:									
(Year of release)	-0.51†	-0.15	-0.23	-0.17	-0.13	-0.15	-0.21	-0.08	-0.12
(Grain yield)	0.05	0.37	0.34	0.10	0.09	0.08	-0.24	-0.11	-0.18

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant



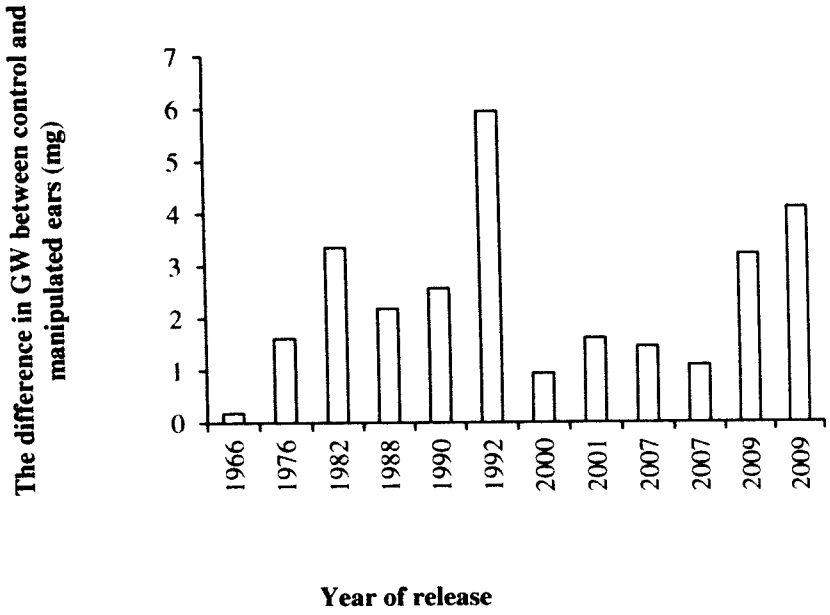


Figure 6.17 Regression of grain weight (mg) on year of release for control treatment (__◇__) y= 0.2257x – 407.39 (R^2 = 0.719; P < 0.001) and degraining treatment (---□---) y= 0.250x – 453.26 (R^2 = 0.615, P = 0.003).

Figure 6.18 Response of grain weight to degraining treatment for 12 CIMMYT spring wheat cultivars released from 1966 to 2009.

6.3.4 Duration and rate of grain filling

There was a trend for grain filling duration to be increased with year of release ($r = 0.41$; $P < 0.10$; Fig. 6.21). The non-linear regression showed duration of grain-filling decreased slightly from 1966 until about 1990, but increased from 1990 to 2009. The correlation between the duration of grain filling and individual grain weight was not significant ($r = 0.31$; $P > 0.10$). However, there was strong positive correlation between grain filling rate and grain weight ($r = 0.73$; $P < 0.01$; Table 6.8 and Fig. 6.19).

Results showed that grain filling rate was higher in 2010 (50.9 μg °C d^{-1}) than in 2009 (47.0 μg °C d^{-1}) ($P < 0.001$). There were differences amongst cultivars in both seasons and averaged across seasons. In 2009, rate of grain filling ranged from 39.1 (Siete Cerros, 1966) to 55.6 μg °C d^{-1} (Attila, 1990) and from 41.0 (Siete Cerros, 1966) to 62.4 μg °C d^{-1} (Attila, 1990) in 2010. Averaging over years, cultivars differed in grain filling in the range 40.0 (Siete Cerros, 1966) to 59.0 μg °C day^{-1} (Attila, 1990). There was an interaction between year and cultivar ($P < 0.001$). Most cultivars had higher grain filling rate in 2010 than in 2009, however, Baviacora and Roelfes had a lower grain filling rate in 2010 than in 2009.

The non-linear regression showed grain-filling rate increased strongly from 1966 until about 1990; however, from 1990 till 2009 there was a decrease in the grain-filling rate (Fig 6.20).

Table 6.8 Rate of grain filling of 12 CIMMYT cultivars released from 1966 to 2009 in 2009 and 2010.

Cultivar (Year of release)	Rate of grain filling (μg °C day^{-1})		
	2009	2010	Average
Siete Cerros (1966)	39.1	41.0	40.0
Pavon (1976)	39.6	45.5	42.6
Seri (1982)	50.1	54.0	52.0
Bacanora (1988)	44.0	48.1	46.1
Attila (1990)	55.6	62.4	59.0
Baviacora (1992)	54.3	46.9	50.6
Tarachi (2000)	45.1	54.9	50.0
Tacupeto (2001)	46.1	52.1	49.1
Roelfes (2007)	54.9	50.0	52.5
Navojoa (2007)	48.5	49.5	49.0
Becard (2009)	45.0	53.2	49.1
Line 1 (2009)	41.6	52.8	47.2
Mean	47.0	50.9	48.9
S.E.D (df) (Years)			0.584(6)
(Cultivars)	0.825(33)	1.758(33)	0.971(66)
(Interaction)			1.438(66.24)
Prob. (Years)			<0.001***
(Cultivars)	<0.001***	<0.001***	<0.001***
(Interaction)			<0.001***
C.V %	2.5	4.9	4.0
Correlation with (Year of release)	0.31	0.46	0.44
(Grain yield)	0.24	0.35	0.40
TGW	0.73**	0.61*	0.73**

* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

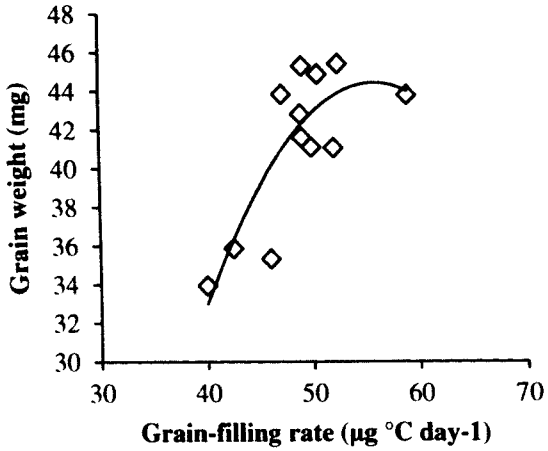


Figure 6.19 Regression of grain weight on grain-filling rate for 12 CIMMYT spring wheat cultivars. Values represent averages across years 2009 and 2010. Y = -0.0454x2 + 5.0794x – 97.52 (R^2 = 0.6869; P = 0.005).

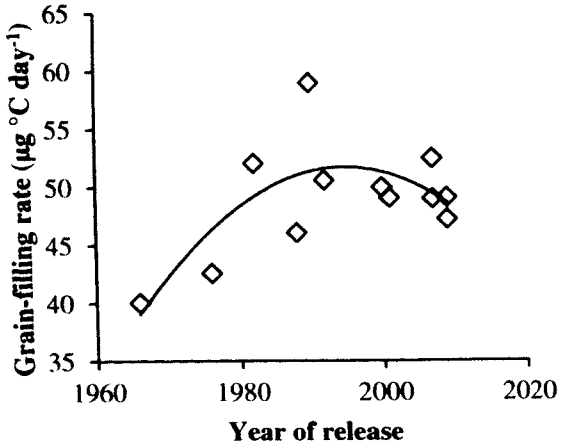


Figure 6.20 Regression of grain-filling rate on year of release for 12 CIMMYT spring wheat cultivars. Values represent averages across years 2009 and 2010. Y = -0.0152x2 + 60.697x - 60490 (R^2 = 0.5194; P = 0.037).

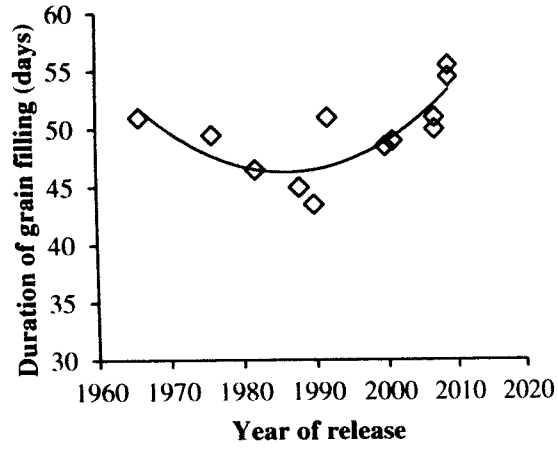


Figure 6.21 Regression of duration of grain-filling on year of release for 12 CIMMYT spring wheat cultivars. Values represent averages across years 2009 and 2010. $y = 0.0136x^2 - 53.994x + 53665$ (R^2 = 0.666; P = 0.007).

6.4 DISCUSSION

6.4.1 Stem water-soluble carbohydrate

Cultivars differed in the amount of stem WSC accumulated at anthesis + 7 days in each year and averaged across years. Overall there was an increase in stem WSC from 1966 to about 1990 and then a decrease to 2009. This relation between the amount of stem WSC and year of release was inversed at maturity, with a decrease from 1966 to 1992 and then a slight increase till 2009 (Fig 6.2). Consequently, the remobilized stem WSC during grain filling was positively correlated with the amount of WSC accumulated at anthesis + 7 days (R^2 = 0.98) (Fig 6.4). A similar positive relationship was reported by Ehdaie *et al.* (2006). The amount of stem WSC accumulated at anthesis + 7 days could therefore be used as a selection criterion to select for cultivars more efficient in the utilization of stem WSC remobilization. Other authors have reported similar findings (e.g. Ruuska *et al.*, 2006). Present results showed that genetic progress in yield potential since about 1990 in NW Mexico has not been associated with increases in stem WSC. The reason may be that modern cultivars, although they had a longer period of grain filling compared to the old ones, had increased source through current photosynthesis post-anthesis. In addition, fractional PAR interception by the ears, flag leaf and the second leaf increased with year of release since about 1990 (Fig 6.22). Consequently, yield increases appear to have been associated with increases in current photosynthesis post-anthesis rather than stem WSC in the modern cultivars. So it may be that source size has increased simultaneously with grain sink size with CIMMYT breeding, but that the increases in source size have been realised through enhanced current photosynthesis.

Shearman *et al.* (2005) found an increase in the stem WSC with year of release from 1972 to 1995 in UK winter wheat. This result was different from the current study where the stem WSC only increased with year of release before about 1990. There was a negative relationship between the duration of grain filling and both the remobilized amount of WSC and the percentage contribution of stem WSC to the grain yield, respectively. This negative relation indicates that cultivars with longer grain filling duration depended

more on the current photosynthesis assimilates rather than the stored reserves. It is feasible that cultivars with a shorter period of grain filling, which usually have high rate of grain filling, may need additional sources of assimilate to supplement the current photosynthesis. The contribution of stem WSC to grain yield in the current study was relatively low varying amongst cultivars in the range 5-13% compared to some other investigations, e.g. 21% reported by Borrell *et al.* (1989) in field experiments in Australia and 19-54% reported by Ehdaie *et al.* (2008) in a glasshouse experiment in the USA. Present results could indicate that under the high radiation environment in NW Mexico, stem WSC is likely to be a less important yield determinant than in lower radiation countries, e.g. UK.

6.4.2 Post-anthesis canopy traits

Present results overall showed a tendency for CTD to increase with year of release (r = 0.56, $P < 0.10$) (Table 6.3), indicating an increase in canopy photosynthesis during grain filling. There was a positive association between CTD and grain yield (r = 0.82, $P < 0.001$). This finding is in agreement with many previous studies showing phenotypic correlations between CTD and yield amongst genotypes in wheat, e.g. Reynolds *et al.* (1994); Gibson and Paulson (1999); Bolta (2008); Ayeneh *et al.* (2002); Fischer and Maurer (1976); Bilge *et al.* (2008) and Fischer *et al.* (1998). Flag-leaf stomatal conductance in the post-anthesis period, however, did not increase after about 1990, though there was slight increase from 1966 to 1990 (Fig 6.12). This is different from the pre-anthesis results where there was a trend for increasing stomatal conductance with year of release across the whole period from 1966 to 2009 (r = 0.56; $P < 0.10$).

Fractional PAR interception at the mid grain filling by the ears, flag leaf and the second leaf increased with year of release since about 1990 (Fig 6.22). This was correlated with greater grain weight and grain yield (r = 0.72; $P < 0.05$; Fig. 6.24 and 6.25, respectively). This likely contributed to the increase in current post-anthesis photosynthesis in the modern cultivars, and further investigation seems justified to quantify more precisely the increase in ear photosynthesis with plant breeding.

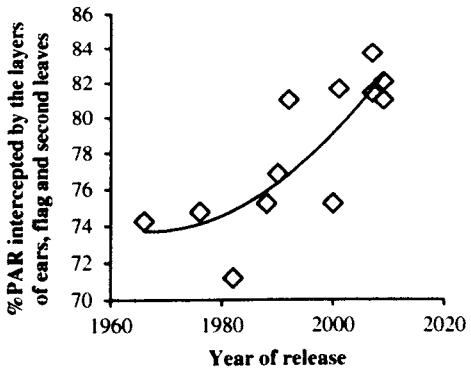


Figure 6.22 Regression of %PAR intercepted by the layers of ears, flag leaf and leaf 2 on year of release for 12 CIMMYT spring wheat cultivars y = 0.0049x2 – 19.408x + 19161 (R^2 = 0.671; *P* = 0.007).

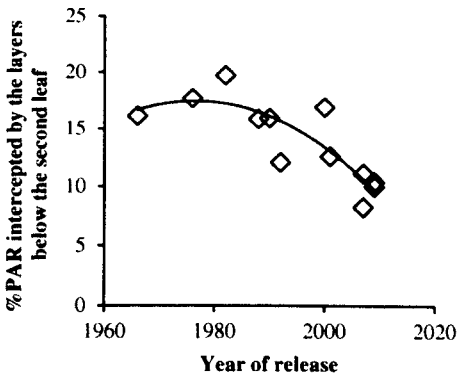
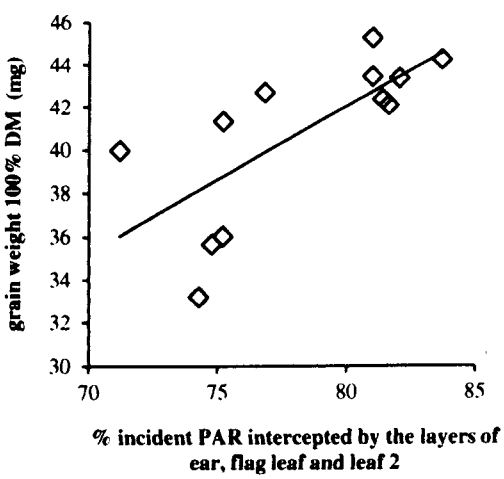


Figure 6.23 Regression of %PAR intercepted by the layers below leaf 2 on year of release for 12 CIMMYT spring wheat cultivars y = -0.0073x2 + 28.93x - 28572 (R^2 = 0.726; *P* = 0.003).



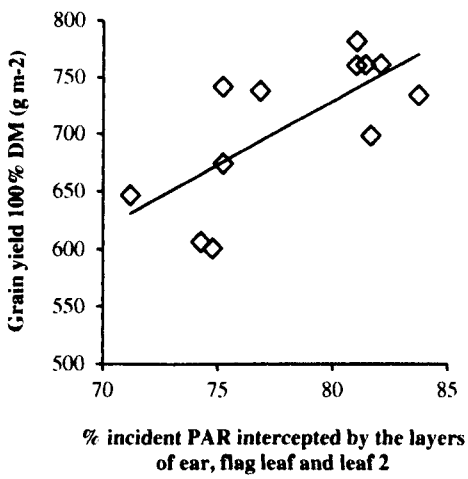


Figure 6.24 Regression of grain weight on %PAR intercepted by ears, flag leaf and leaf 2 for 12 CIMMYT spring wheat cultivars. y = 0.6763x – 12.09 (R^2 = 0.512; *P* = 0.014).

Figure 6.25 Regression of grain yield on %PAR intercepted by ears, flag leaf and leaf 2 for 12 CIMMYT spring wheat cultivars. y = 11.292x – 172.99 (R^2 = 0.518; *P* = 0.008).

6.4.3 Duration and rate of grain filling

Grain filling rate was higher in 2010 (50.9 μg °C day^{-1}) than in 2009 (47.0 μg °C day^{-1}) ($P < 0.001$). This may have been partly because flowering in 2010 started later in the beginning of March rather than the first half of February in 2009. Also, the duration of the grain filling period was longer in the 2009 season (55) days than in 2010 (44) days. Thus, thermal time (base temp 0 °C) from anthesis to physiological maturity was higher in 2009 (892 °C) than in 2010 (805 °C). The shorter grain filling period in 2010 counteracted the faster grain filling rate so that the final grain weight in 2010 (40.8 mg) was similar to that in 2009 (41.7) mg. This inverse relation between grain filling duration and grain weight according to environmental variation in temperature has been previously described in many investigations; for example, by Wiegand and Cuellar (1981), who reported a shortening of 3.1 days in the grain-filling period and 2.8 mg $grain^{-1}$ decrease for each °C increase. The majority of cultivars in the present study had higher grain filling rates in the 2010 although Baviacora (1992) and Roelfes (2007) had similar grain filling rate in both years.

Some researchers have attributed genetic increases in the final grain weight in spring wheat to higher grain filling rate and shorter grain filling period (Duguid and Brule-Babel, 1995). Other investigations have reported a strong correlation between genetic variation in final grain weight and the duration of grain filling e.g. (Wong and Baker, 1986). Talbertet *et al.* (2001) reported low heritability (0.40) for grain filling duration, whereas Mou and Kronstand (1994) reported high heritability (0.89) for grain filling rate in winter wheat. In the current study, averaging across years, grain filling rate increased steadily in the period from 1966 to about 1990, whilst over the same period the duration of grain filling decreased. In the period from about 1990 to 2009, grain filling rate decreased slightly, whilst the duration of grain filling increased steadily. It seems therefore that there is a negative relationship between genetic variation in these two components (r = -0.39 in the present study). Nevertheless, some cultivars were in a balanced position between the rate and duration of grain filling (i.e. showed positive departures from the overall negative relationship between grain filling rate and duration), such as Baviacora (1992) and Roelfes

(2007) which produced the heaviest grains, 44.9 and 45.4 mg, respectively. It was suggested by Gebeyehou *et al.* (1982) and Bruckner and Frohberg (1987) that there was only a weak genetic relationship between the duration and rate of grain filling, so this would offer the possibility to select for high grain weight through increasing the grain filling rate without shortening the duration of grain filling, or vice versa.

Potential grain weight is determined by both the carpel size and the endosperm cell division and expansion (Fischer, 2011). The negative effect of the high temperature pre-anthesis on potential grain weight is mainly due to reducing the carpel size (Calderini *et al.*, 1999a; Calderine *et al.*, 1999b; Calderini *et al.*, 2001). It was suggested that the final number of the endosperm cells which are formed at the end of the cellularization phase is a key factor determining potential DM accumulation in the grain (Brocklehurst, 1977; Foulkes *et al.*, 2011). The determinants of potential grain weight are discussed further below.

6.4.4 Responses to source-sink manipulation treatment

Results showed that stem dry weight at harvest was higher in manipulated shoots (1.79 mg shoot^{-1}) than in control shoots (1.64 mg shoot^{-1}; $P < 0.001$). This was expected since there was less grain sink demand in the manipulated shoots which may relate to reduced utilization of stem WSC. Ma *et al.* (1996) reported that the amount of WSC in stems of shoots in a 75% spikelets removal treatment was higher than in a 100% spikelets removal treatment, but less than a 50 and 25% spikelets removal treatment. In the present study grain weight was overall 5.3% higher in manipulated ears (45.0 mg) than in control ears (42.7 mg) ($P < 0.001$). The interaction for grain weight between the degraining treatment and cultivar was weakly significant ($P = 0.087$), which suggests that there may have been a trend for small differences in source-sink balance amongst some of the cultivars. The percentage increase in grain weight in the manipulated ears ranged from 0.5 to 13.2%. Results indicated that most cultivars in this historic set were generally sink limited rather than source limited. This result is consistent with many previous studies on wheat (Borras *et al.*, 2004; Snyder *et al.*, 1993; Cartelle *et al.*, 2006; Miralles and Slafer, 1995 and Slafer and Savin, 1994). However, Acreche and Slafer (2009) reported

that, in bread wheat genotypes released from 1940 to 2005 in Spain, modifying the source-sink balance by removing all the upper-half of the ear, grain weight was unchanged in the old cultivars and increased in the newest cultivars; they suggested that the modern cultivars in their study exhibited a co-limitation of grain growth by source and sink rather than sink limitation. It is possible that some of the cultivars in the present study with response of grain weight to degraining of > 10% also exhibited co-limitation of grain growth by source and sink, i,e. grain growth may have been limited by sink in approximately the first 28 days of grain filling but limited by source in the latter stages of grain filling. The present results also indicated that potential grain weight has increased with plant breeding and this has underpinned the genetic gains in final grain weight over the 43-year period, since the final grain weight of the grains in the degrained ears increased linearly with year of release. Where source per grain is effectively increased by 100% in the degrained ears, the final grain weight may be taken as an indicator of potential grain weight.

The contribution of stem WSC to the grain yield was slightly higher in the manipulated ears (10.2%) than the control ears (8.4%). This may be explained partly by a feedback inhibition effect of the sink manipulation on the current photosynthesis. This would be consistent with the results of Cruz-Aguado *et al.* (1999) who found that final grain weight in spring wheat decreased when all spikelets were removed except the four central spikelets. The authors attributed this effect to the feedback inhibition of photosynthesis.

From the results of the potential grain weight (as indicated by final grain weight in the degraining treatment), it seems that since this was improved with time of breeding in parallel that the increase in the final grain weight was probably due to an increase in the potential grain weight which related to physiological changes in the period just before anthesis till about two weeks after anthesis.

6.5 SUMMARY

Genetic variation in grain weight during the period from 1966 to 2009 was positively associated with genetic gains in grain yield with year of release amongst the cultivars. Results from the present study showed that the improvement in the individual grain weight from 1966 to 2009 in this set of cultivars was associated with improvements in the grain filling rate from 1966 to 1990 and in the duration of grain filling from 1992 to 2009.

Cultivars with longer grain filling duration appeared to depend more on the current photosynthesis assimilates rather than the stored reserves. Averaging across years, there was a significant positive association between CTD and grain yield. Stomatal conductance at post-anthesis period did not increase significantly during the period from 1990 though it increased slightly from 1966 to 1990. Fractional PAR interception by the layers of ears, flag leaf and the second leaf was increased with year of release since about 1990. This increase in the interception of PAR correlated positively with the grain weight and grain yield.

Grain growth of the cultivars in this historic set was generally sink limited rather than source limited. There was no change in source-sink balance as indicted by grain growth responses to degraining with year of release. Overall the contribution of stem WSC to grain DM growth in the current study was relatively low (4 - 18%) which is consistent with the hypothesis that under the high radiation environment in Northwest Mexico, yields of modern cultivars are more likely to be sink than source limited in high radiation, irrigation conditions.

CHAPTER 7 EFFECTS OF TILLER INHIBITION (*Tin1A*) GENE AND PLANT DENSITY ON YIELD POTENTIAL TRAITS IN DOUBLED HAPLOID LINES OF THE L14 × RIALTO POPULATION OF WHEAT

7.1 INTRODUCTION

This chapter examines the effects of the tiller inhibition (*Tin1A*) gene (tiller inhibition associated with the recessive allele) on yield, yield components and physiological traits measured at anthesis. The effects of the interaction of the presence/absence of the *Tin1A* allele for tiller inhibition on response to plant density are also described. These effects were quantified under two different environments: the UK and NW Mexico. The plant material used in these experiments was DH lines derived from a cross between the UK winter wheat cultivar Rialto and the CIMMYT spring wheat large-ear phenotype advanced line (L14).

The specific hypotheses tested in this chapter in both the UK and N.W Mexico environments are:

1. The *Tin1A* gene reduces ears per m^2 at harvest but increases rachis length, spikelets per ear and grains per ear and hence grains per m^2 in wheat grown under UK rainfed conditions and high radiation, irrigated conditions in NW Mexico when gown at commercial plant density.
2. The *Tin1A* gene increases grain yield in wheat grown UK rainfed conditions and high radiation, irrigated conditions in NW Mexico when grown at commercial plant density.
3. Lines with the *Tin1A* allele produce relatively fewer ears per m^2 than non-*Tin1A* lines under low plant density than under high plant density, so the

economic optimum plant density for *Tin1A* lines is higher than for non *Tin1A* lines.

7.2 MATERIALS AND METHODS

Two field experiments were conducted in the UK, one in 2008/09 at KWS-UK Ltd in Thriplow, Hertfordshire and one in 2009/10 at University of Nottingham Farm, Sutton Bonington campus. The plant material for both of these experiments was selected lines from the CIMMYT spring wheat L14 (+ *Tin1A*) x Rialto winter wheat (-*Tin-1A*) DH population contrasting for the presence/absence of the *Tin1A* allele for tiller inhibition. The groups of lines were selected to be balanced for anthesis date and plant height according to previous data (see chapter 3). In 2008/09 the lines were grown at one seed rate, and in 2009/10 at two seed rates. The other two experiments were conducted at the CIMMYT experimental station at Ciudad Obregon in Northwest Mexico. These experiments examined selected lines from the CIMMYT L14 x Rialto wheat DH population contrasting for the presence/absence of the *Tin1A* allele and their interaction with seed rate in 2008/9 and 2009/10.

Due to the data collection during January to May in 2008/09 and 2009/10 in the experiments in Mexico, experiments in the UK sites were only assessed at harvest. These traits comprised plants m^{-2}, plant height, AGDM, grain yield, HI, yield components, rachis length, ear width and total and fertile spikelets ear^{-1}. ANOVA of data was carried out as well as the analysis of correlation relationships among the traits.

At the CIMMYT site, experiments were assessed at: GS61 + 10 days and harvest. At GS61+10 days, DM of ears, flag leaves, remaining green lamina and stem plus sheaths were measured. In addition, ear traits (rachis length, total and fertile numbers of spikelets per ear) were measured. At harvest, measurements were carried out for the same traits as those assessed at the UK sites.

In the SB 2009/10 experiment, plants m^{-2} was obtained as follows: the number of plants and ears in each grab sample per plot were counted and ears per plant calculated. Then, plants m^{-2} was obtained by dividing the number of ears m^{-2}

(obtained from the harvest growth analysis and the combine harvest grain yield) by the number of ears per plant.

7.3 RESULTS

7.3.1. KWS-UK Ltd Thriplow 2008/9 experiment

7.3.1.1 Environmental and growing conditions

Plants were exposed to a cold winter (December, January and February) (3.3 °C) and to a dry spring (March, April and May) (46.4 mm). This may partly explain the low average yield (485 g m^{-2}).

Table 7.1 Total quarterly temperature, rainfall and total annual rainfall at KWS-UK Ltd in Thriplow, Hertfordshire in 2008/09.

Quarter	Average mean temperature (°C)	Total rainfall (mm)
Autumn	10.4	135.7
Winter	3.3	106.3
Spring	8.4	46.4
Summer	16.6	142.7

7.3.1.2 Grain yield, HI and plant height

Overall non-*Tin1A* lines were slightly taller (65 cm) than *Tin1A* lines (61 cm; $P < 0.001$; Table 7.2). Heights of non *Tin1A* lines ranged from 49 to 82 cm, and for the *Tin1A* lines from 51 to 72 cm. No differences were found between the *Tin1A* and non-*Tin1A* groups in harvest AGDM ($P = 0.182$). Non-*Tin1A* lines ranged from 259 to 1246 g m^{-2}, and *Tin1A* lines from 879 to 1248 g m^{-2} ($P < 0.001$). HI was higher in the *Tin1A* group (0.49) than the non-*Tin1A* group (0.47; $P = 0.015$). HI ranged from 0.34 to 0.54 in non *Tin1A* lines and from 0.42 to 0.54 in *Tin1A* lines ($P < 0.001$). *Tin1A* lines on average yielded more (5.04 t ha^{-1}) than non *Tin1A* lines (4.67 t ha^{-1}) ($P < 0.001$; Table 7.2). Grain yield of non *Tin1A* lines ranged from 259 to 605 g m^{-2} and for *Tin1A* lines from 404 to 594 g m^{-2} ($P < 0.001$)

7.3.1.3 Yield components

There was a strong trend for *Tin1A* to reduce ears m^{-2} from 324 to 304 ears m^{-2} ($P = 0.062$). Non-*Tin1A* lines were in the range of 148 to 420 ears m^{-2} and *Tin1A* lines from 171 to 420 ears m^{-2}. *Tin1A* lines boosted grains per ear (41) compared to the non-*Tin1A* group (33) ($P < 0.001$) (Table 7.3). Grains ear^{-1} ranged amongst non-*Tin1A* lines from 24 to 50 and amongst *Tin1A* lines from 34 to 55 ($P < 0.001$). Overall, *Tin1A* lines produced more grains m^{-2} (11,770) than non *Tin1A* lines (10,279; $P < 0.001$). Grains m^{-2} of non-*Tin1A* lines ranged from 5,934 to 14,246 grains m^{-2} and *Tin1A* lines from 7,513 to 16,349. Non-*Tin1A* lines on average produced heavier grains (46 mg) than the *Tin1A* group (44 mg; $P < 0.001$), with non-*Tin1A* lines ranging from 41 to 53 and *Tin1A* lines ranging from 35 to 54 mg ($P < 0.001$).

Table 7.2 Effect of the tiller inhibition (*Tin1A*) gene on plant height, above-ground dry matter m^{-2}, grain yield m^{-2} and harvest index in 24 DH lines of the Rialto x L14 DH population at Thriplow 2008-9

TIN1A allele	Line	Plant height (cm)	AGDM ($g\ m^{-2}$)	Grain yield 100% DM ($g\ m^{-2}$)	HI
	L14/Rialto-2	56.6	834.0	409.5	0.49
	L14/Rialto-4	68.8	895.2	426.4	0.47
	L14/Rialto-9	51.7	935.1	495.5	0.53
	L14/Rialto-34	75.4	1128.9	384.7	0.34
	L14/Rialto-47	58.7	989.7	495.6	0.50
NO	**L14/Rialto-59**	53.1	1130.3	485.4	0.43
	L14/Rialto-60	64.1	1245.9	604.6	0.48
	L14/Rialto-86	66.9	1072.9	477.5	0.45
	L14/Rialto-93	81.6	1138.0	466.5	0.41
	L14/Rialto-101	48.7	479.6	258.9	0.54
	L14/Rialto-114	73.4	1020.9	515.4	0.51
	L14/Rialto-129	75.3	1181.8	587.3	0.50
	Average	**64.5**	**1004.4**	**467.3**	**0.47**
	L14/Rialto-1	51.1	1112.4	574.6	0.52
	L14/Rialto-24	54.3	879.1	428.6	0.49
	L14/Rialto-25	56.5	904.3	403.9	0.45
	L14/Rialto-30	64.1	1011.8	548.8	0.54
	L14/Rialto-48	52.5	1106.2	594.0	0.54
YES	**L14/Rialto-61**	66.5	988.8	525.6	0.53
	L14/Rialto-65	68.3	1021.1	504.3	0.49
	L14/Rialto-78	61.9	1247.6	548.8	0.44
	L14/Rialto-90	69.3	1016.6	424.2	0.42
	L14/Rialto-110	72.3	1149.1	553.7	0.48
	L14/Rialto-112	55.5	972.6	461.1	0.48
	L14/Rialto-124	60.1	987.4	475.5	0.48
	Average	**61.0**	**1033.1**	**503.6**	**0.49**
	Grand mean	**62.8**	**1018.7**	**485.4**	**0.48**
C.V %		4.0	8.8	8.7	6.0
S.E.D (df)	**Lines**	2.07(46)	73.47(46)	34.46(46)	0.024(46)
	***Tin1A* Groups**	0.60(46)	21.21(46)	9.95(46)	0.0068(46)
Prob.	**Lines**	<0.001***	<0.001***	<0.001***	<0.001***
	***Tin1A* Groups**	<0.001***	0.182n.s	<0.001***	0.015*

* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

Table 7.3 Effect of the tiller inhibition (*Tin1A*) gene on ears m^{-2}, grains ear^{-1}, grains m^{-2} and grain weight (GW) in 24 DH lines of the Rialto x L14 DH population at Thriplow 2008-9

TIN1A allele	Line	Ears m^{-2}	Grains ear^{-1}	Grains m^{-2}	GW 100% DM (mg)
	L14/Rialto-2	297.8	28.8	8599.8	48.0
	L14/Rialto-4	247.9	39.2	9114.5	47.0
	L14/Rialto-9	315.4	36.0	11267.5	44.1
	L14/Rialto-34	371.5	24.1	8886.3	43.3
	L14/Rialto-47	312.4	31.2	9676.0	51.3
NO	**L14/Rialto-59**	420.4	23.6	9690.1	50.1
	L14/Rialto-60	413.0	32.6	13250.7	45.6
	L14/Rialto-86	356.7	33.6	11820.9	40.5
	L14/Rialto-93	380.9	23.6	8888.6	52.5
	L14/Rialto-101	148.3	39.8	5934.1	43.6
	L14/Rialto-114	241.2	49.8	11974.3	43.0
	L14/Rialto-129	383.7	37.4	14246.2	41.2
	Average	**324.1**	**33.3**	**10279.1**	**45.8**
	L14/Rialto-1	480.1	34.1	16349.3	35.3
	L14/Rialto-24	230.5	45.6	9979.2	43.1
	L14/Rialto-25	170.7	44.1	7513.2	53.8
	L14/Rialto-30	213.6	55.1	11566.0	47.5
	L14/Rialto-48	411.9	37.2	15392.3	39.6
YES	**L14/Rialto-61**	296.9	46.2	13734.9	38.3
	L14/Rialto-65	187.7	52.0	9707.8	52.0
	L14/Rialto-78	378.9	33.1	12441.7	44.1
	L14/Rialto-90	277.9	38.3	10525.1	40.3
	L14/Rialto-110	365.8	34.6	12589.7	44.0
	L14/Rialto-112	255.6	39.7	10048.6	45.9
	L14/Rialto-124	371.9	30.7	11389.5	41.8
	Average	**303.5**	**40.9**	**11769.8**	**43.8**
	Grand mean	**313.8**	**37.1**	**11024.4**	**44.8**
C.V %		14.6	15.4	11.7	5.0
S.E.D (df)	**Lines**	37.40(46)	4.66(46)	1048.97(46)	1.820(46)
	***Tin1A* Groups**	10.80(46)	1.35(46)	302.81(46)	0.525(46)
Prob.	**Lines**	<0.001***	<0.001***	<0.001***	<0.001***
	***Tin1A* Groups**	0.062†	<0.001***	<0.001***	<0.001***

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

7.3.1.4 Dry matter partitioning

Tin1A lines produced greater ear dry weight (661 g m^{-2}) than non *Tin1A* lines (616 g m^{-2}) ($P = 0.002$); with non *Tin1A* lines ranging from 331 to 774 g m^{-2} and *Tin1A* lines from 543 to 743 g m^{-2}. In addition, ear DM partitioning was higher with *Tin1A* group (62 vs 64%; $P = 0.014$). Ear DM partitioning ranged from 48 to 72% and from 58 to 68% in non-*Tin1A* and *Tin1A* lines, respectively. No significant differences were found between the *Tin1A* and non-*Tin1A* groups in chaff DM ($P = 0.077$). However, differences among individual lines were significant ($P < 0.001$). Although overall *Tin1A* and non-*Tin1A* lines did not differ in chaff DM partitioning ($P = 0.169$), differences were found among individual lines with non-*Tin1A* lines ranging from 12 to 19% and *Tin1A* lines from 13 to 19% ($P < 0.001$).

No significant differences were found between *Tin1A* and non-*Tin1A* groups in the stem DM ($P = 0.098$) in the range 124 to 492 g m^{-2} in non-*Tin1A* lines and 262- to 420 g m^{-2} in *Tin1A* lines ($P < 0.001$). Non-*Tin1A* lines partitioned more DM to stems (32%) than *Tin1A* lines (30%) ($P = 0.001$). The *Tin1A* and non *Tin1A* groups did not differ in lamina DM ($P = 0.551$), or DM partitioning to lamina ($P = 0.980$). However, there were differences among individual lines in lamina DM ($P < 0.001$) and in lamina DM partitioning ($P = 0.006$).

7.3.1.5 Ear traits

Overall, rachis length for *Tin1A* (9.9 cm) was greater than for than non-*Tin1A* (8.8 cm) lines ($P < 0.001$; Table 7.6). Rachis length of non-*Tin1A* lines ranged from 8.1 to 10.5 cm and of *Tin1A* lines from 8.6 to 11.4 cm ($P < 0.001$). Ears were slightly wider for *Tin1A* (1.5 cm) than non *Tin1A* (1.4 cm) lines ($P = 0.050$; Table 7.6) and *Tin1A* lines produced more total spikelets per ear (20.6) than non-*Tin1A* lines (19.8) ($P < 0.001$). Values ranged from 17.9 to 22.3 in non *Tin1A* lines and from 18.7 to 22.8 in *Tin1A* lines ($P < 0.001$). Similar effects were found for fertile spikelets per ear. *Tin1A* lines produced more fertile spikelets per ear (19.0) than non-*Tin1A* lines (17.5) ($P < 0.001$), with a range of 14.7 to 19.8 in non *Tin1A*-lines and 16.5 to 21.8 in *Tin1A* lines ($P < 0.001$; Table 7.6).

Table 7.4 Effect of the tiller inhibition (*Tin1A*) gene on dry matter and partitioning to ears and chaff at harvest in 24 lines of Rialto x L14 DH population at Thriplow 2008-9

TIN1A allele	Line	Ears DM ($g\ m^{-2}$)	% Ears DM m^{-2}	Chaff DM ($g\ m^{-2}$)	% Chaff DM m^{-2}
	L14/Rialto-2	537.7	64.6	128.2	15.4
	L14/Rialto-4	561.9	62.6	135.5	15.1
	L14/Rialto-9	672.4	72.0	176.9	18.8
	L14/Rialto-34	536.6	47.5	151.9	13.5
	L14/Rialto-47	675.3	68.4	179.7	18.2
NO	**L14/Rialto-59**	658.2	58.2	172.9	14.8
	L14/Rialto-60	774.1	62.1	169.5	13.6
	L14/Rialto-86	618.5	57.9	141.0	13.1
	L14/Rialto-93	623.9	54.9	157.4	13.8
	L14/Rialto-101	331.0	68.6	72.0	15.0
	L14/Rialto-114	638.6	62.8	123.3	12.0
	L14/Rialto-129	761.0	64.4	173.7	14.7
	Average	**615.8**	**62.0**	**148.5**	**14.8**
	L14/Rialto-1	732.3	65.8	157.7	14.1
	L14/Rialto-24	542.9	62.3	114.3	13.2
	L14/Rialto-25	577.6	63.9	173.7	19.2
	L14/Rialto-30	691.4	68.4	142.5	14.1
	L14/Rialto-48	743.1	67.3	149.2	13.5
YES	**L14/Rialto-61**	664.8	67.1	139.2	14.1
	L14/Rialto-65	669.2	65.6	164.9	16.2
	L14/Rialto-78	731.5	58.8	182.7	14.6
	L14/Rialto-90	584.7	57.8	160.6	15.8
	L14/Rialto-110	723.0	63.0	169.3	14.8
	L14/Rialto-112	625.2	64.3	164.2	16.8
	L14/Rialto-124	640.3	64.9	164.8	16.7
	Average	**660.5**	**64.1**	**156.9**	**15.3**
	General mean	**638.1**	**63.0**	**152.7**	**15.0**
C.V %		9.1	5.6	12.9	8.5
S.E.D (df)	**Lines**	47.65(46)	2.868(46)	16.13(46)	1.05(46)
	***Tin1A* Groups**	13.76(46)	0.828(46)	4.66(46)	0.302(46)
Prob.	**Lines**	<0.001***	<0.001***	<0.001***	<0.001***
	***Tin1A* Groups**	0.002**	0.014*	0.077†	0.169$^{n.s}$

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

Table 7.5 Effect of the tiller inhibition (*Tin1A*) gene on dry matter per m^2 and DM partitioning to stem and leaf sheath and lamina in 24 lines of Rialto x L14 DH population at Thriplow 2008-9

TIN1A allele	Name of Line	Stems DM ($g\ m^{-2}$)	% stems DM	Lamina DM ($g\ m^{-2}$)	% lamina DM
	L14/Rialto-2	245.8	29.3	50.4	6.1
	L14/Rialto-4	273.1	30.7	60.3	6.8
	L14/Rialto-9	212.3	22.7	50.3	5.4
	L14/Rialto-34	492.0	43.6	100.3	8.9
	L14/Rialto-47	251.5	25.3	62.9	6.3
NO	**L14/Rialto-59**	392.6	37.9	79.6	7.3
	L14/Rialto-60	389.6	31.3	82.3	6.6
	L14/Rialto-86	386.8	35.9	67.6	6.2
	L14/Rialto-93	444.3	39.0	69.8	6.1
	L14/Rialto-101	124.3	26.3	24.3	5.2
	L14/Rialto-114	322.7	31.4	59.5	5.8
	L14/Rialto-129	354.1	29.9	66.7	5.7
	Average	**324.1**	**31.9**	**64.5**	**6.4**
	L14/Rialto-1	309.3	27.8	70.8	6.4
	L14/Rialto-24	276.6	31.0	59.6	6.7
	L14/Rialto-25	267.2	29.5	59.5	6.5
	L14/Rialto-30	261.7	25.8	58.7	5.8
	L14/Rialto-48	287.0	25.9	76.0	6.8
YES	**L14/Rialto-61**	269.9	27.4	54.1	5.5
	L14/Rialto-65	291.9	28.6	60.0	5.9
	L14/Rialto-78	419.7	33.5	96.3	7.7
	L14/Rialto-90	369.1	36.0	62.8	6.2
	L14/Rialto-110	358.8	31.1	67.4	5.8
	L14/Rialto-112	281.3	28.9	66.1	6.8
	L14/Rialto-124	285.8	28.9	61.4	6.2
	Average	**306.5**	**29.5**	**66.1**	**6.4**
	Grand mean	**315.3**	**30.7**	**65.3**	**6.4**
C.V %		14.0	9.8	16.9	14.3
S.E.D (df)	**Lines**	35.99(46)	2.460(46)	9(46)	0.742(46)
	***Tin1A* Groups**	10.39(46)	0.710(46)	2.60(46)	0.214(46)
Prob.	**Lines**	<0.001***	<0.001***	<0.001***	0.006**
	***Tin1A* Groups**	0.098†	0.001***	$0.551^{n.s}$	$0.980^{n.s}$

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

Table 7.6 Effect of the tiller inhibition (*Tin1A*) gene on ear traits (rachis length, ear width, and total and fertile spikelets per ear) in 24 DH lines of Rialto x L14 population at Thriplow 2008-9

TIN1A allele	Line	Rachis length (cm)	Ear width (cm)	Total spikelets per spike	Fertile spikelets per ear
NO	L14/Rialto-2	8.2	1.5	18.3	16.3
	L14/Rialto-4	9.0	1.3	21.5	18.7
	L14/Rialto-9	8.3	1.2	19.7	16.9
	L14/Rialto-34	8.2	1.3	18.5	16.4
	L14/Rialto-47	9.1	1.3	18.1	16.3
	L14/Rialto-59	8.5	1.6	19.1	17.2
	L14/Rialto-60	10.5	1.4	22.3	19.8
	L14/Rialto-86	8.5	1.3	20.7	18.1
	L14/Rialto-93	8.1	1.4	17.9	14.7
	L14/Rialto-101	8.7	1.7	17.9	17.4
	L14/Rialto-114	9.0	1.6	21.3	18.7
	L14/Rialto-129	9.6	1.2	21.6	19.4
	Average	**8.8**	**1.4**	**19.8**	**17.5**
YES	L14/Rialto-1	8.6	1.4	19.8	18.7
	L14/Rialto-24	11.0	1.5	22.8	21.8
	L14/Rialto-25	10.6	1.6	20.1	18.9
	L14/Rialto-30	11.4	1.6	21.0	20.2
	L14/Rialto-48	9.5	1.5	21.2	19.6
	L14/Rialto-61	9.3	1.3	20.3	18.8
	L14/Rialto-65	10.8	1.5	22.1	20.3
	L14/Rialto-78	9.5	1.5	19.1	16.5
	L14/Rialto-90	9.5	1.2	18.7	17.1
	L14/Rialto-110	9.7	1.2	21.9	20.0
	L14/Rialto-112	9.5	1.9	21.0	19.3
	L14/Rialto-124	9.9	1.3	19.2	17.1
	Average	**9.9**	**1.5**	**20.6**	**19.0**
	Grand mean	**9.4**	**1.4**	**20.2**	**18.3**
C.V %		5.1	6.4	4.1	4.7
S.E.D (df)	**Lines**	0.388(46)	0.074(46)	0.671(46)	0.696(46)
	***Tin1A* Groups**	0.112(46)	0.021(46)	0.194(46)	0.201(46)
Prob.	**Lines**	<0.001***	<0.001***	<0.001***	<0.001***
	***Tin1A* Groups**	<0.001***	0.050*	<0.001***	<0.001***

* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

7.3.1.6 Correlation relationships amongst physiological and yield traits.

Correlations of plant height with grain yield were not significant for either the *Tin1A* or non-*Tin1A* groups. For both groups the correlation between AGDM and grain yield was significant ($P = 0.01$; $r = 0.81$ and 0.76, respectively). The correlation of HI with grain yield amongst DH lines was only significant ($P = 0.05$) in the *Tin1A* group ($r = 0.64$). Nevertheless, the correlation between ears m^{-2} and grain yield was significant ($P = 0.01$) ($r = 0.66$) for both groups. The correlation of grains ear^{-1} with grain yield was not significant for either *Tin1A* or non *Tin1A* groups, whereas that of grains m^{-2} with grain yield was significant ($P < 0.01$) in both groups ($r = 0.92$ and 0.85, respectively). GW did not show any correlation with grain yield amongst DH lines for either the *Tin1A* or non *Tin1A* groups. However, correlations between ear DM per m^2 and grain yield were highly significant in both groups ($r = 0.99$ and 0.96; $P < 0.001$), respectively. No correlation was found amongst lines between chaff DM partitioning at harvest and grain yield in non-*Tin1A* lines, but this correlation was negative in *Tin1A* lines ($r = -0.62$; $P = 0.05$). The correlation of rachis length with grain yield was significant in non *Tin1A* lines ($r = 0.60$; $P = 0.05$), but not in *Tin1A* lines. Ear width did not show any correlation with grain yield in either the *Tin1A* or non *Tin1A* lines. Total spikelets per ear was correlated with grain yield in non *Tin1A* lines ($r = 0.66$; $P = 0.50$), but not in *Tin1A* lines. Fertile spikelets per ear were not correlated amongst lines with grain yield in either the *Tin1A* or non-*Tin1A* groups.

Table 7.7 The phenotypic correlation coefficients at harvest among 12 *Tin-1A* lines (above) and 12 non-*Tin1A* lines (below) of the L14 × Rialto DH population in Thriplow 2008-09.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
AGDM g m^{-2}	1.00	**0.52**	**0.86*****	**-0.42**	**0.62***	**-0.50**	**-0.03**	**0.19**	**0.82*****	**-0.51**	**-0.26**	**0.69***	**0.76****	**-0.32**	**-0.28**	**0.76****
Chaff DM g m^{-2}	0.79**	1.00	**0.33**	**-0.65***	**-0.12**	**-0.46**	**-0.54**	**0.23**	**0.49**	**-0.33**	**0.01**	**0.18**	**0.54**	**0.30**	**-0.51**	**0.06**
Ears DM g m^{-2}	0.85***	0.86***	1.00	**-0.17**	**0.77****	**-0.27**	**0.45**	**0.05**	**0.56**	**-0.42**	**-0.13**	**0.68***	**0.32**	**-0.32**	**-0.07**	**0.96*****
Fertile spikelets ear^{-1}	0.18	-0.02	0.35	1.00	**-0.13**	**0.61***	**0.52**	**-0.12**	**-0.45**	**0.55**	**0.29**	**-0.40**	**-0.57**	**0.26**	**0.95*****	**0.01**
Grains m^{-2}	0.72**	0.59*	0.88***	0.64*	1.00	**-0.39**	**0.58***	**-0.21**	**0.37**	**-0.66***	**-0.33**	**0.87*****	**0.16**	**-0.82*****	**-0.13**	**0.85*****
Grains ear^{-1}	-0.35	-0.43	-0.07	0.62*	0.26	1.00	**0.35**	**0.20**	**-0.57**	**0.74****	**0.33**	**-0.79****	**-0.56**	**0.52**	**0.50**	**-0.16**
HI	-0.53	-0.26	-0.02	0.36	0.12	0.70*	1.00	**-0.28**	**-0.25**	**0.05**	**0.13**	**0.20**	**-0.62***	**-0.29**	**0.43**	**0.63***
Height cm	0.60*	0.19	0.31	0.04	0.35	-0.03	0.54	1.00	**-0.20**	**0.15**	**-0.53**	**-0.26**	**0.37**	**0.20**	**-0.02**	**-0.01**
Lamina DM g m^{-2}	0.86***	0.62*	0.52	0.03	0.38	-0.54	-0.82***	0.54	1.00	**-0.41**	**0.08**	**0.57**	**0.74****	**-0.19**	**-0.30**	**0.46**
Rachis length cm	0.31	0.21	0.52	0.80**	0.60*	0.36	0.34	0.07	0.13	1.00	**0.29**	**-0.79****	**-0.41**	**0.73****	**0.51**	**-0.35**
Ear width cm	-0.47	-0.66*	-0.53	-0.07	-0.50	0.14	0.17	-0.35	-0.36	-0.10	1.00	**-0.39**	**-0.39**	**0.47**	**0.27**	**-0.14**
Ears m^{-2}	0.90	0.82***	0.74**	-0.02	0.54	-0.66*	-0.57	0.33	0.81**	0.15	-0.42	1.00	**0.41**	**-0.79****	**-0.34**	**0.66***
Stem DM g m^{-2}	0.85***	0.47	0.44	-0.05	0.36	-0.52	-0.86***	0.72**	0.92***	0.00	-0.25	0.79**	1.00	**-0.20**	**-0.41**	**0.18**
TGW g	0.06	0.28	0.06	-0.61*	-0.41	-0.54	-0.18	-0.08	0.08	-0.19	0.17	0.18	0.04	1.00	**0.30**	**-0.42**
Total spikelets ear^{-1}	0.43	0.20	0.57	0.91***	0.79	0.53	0.21	0.29	0.21	0.71**	-0.29	0.18	0.17	-0.51	1.00	**0.07**
Grain yield g m^{-2}	0.81**	0.77**	0.99***	0.45	0.92***	0.06	0.06	0.33	0.46	0.60*	-0.46	0.66*	0.41	-0.03	0.66*	1.00

*, **, *** Significant at 0.05, 0.01 and 0.001 probability levels respectively.

1 = AGDM g m^{-2}, 2 = Chaff DM g m^{-2}, 3 = Ears DM g m^{-2}, 4 = Fertile spikelets ear^{-1}, 5 = Grains m^{-2}, 6= Grains ear^{-1}, 7 = HI, 8 = Height cm, 9 = Lamina DM g m^{-2}, 10 = Rachis length cm, , 11 = Ear width cm, 12 = Ears m^{-2}, 13 = Stem DM g m^{-2}, 14 = TGW g, 15 = Total spikelets ear^{-1}, 16 = Grain yield g m^{-2}

7.3.2 Sutton Bonington 2009-10

Although 12 pairs of DH lines (12 + *Tin1A* allele/ 12 – *Tin1A* allele) were sown in this experiment, due to low plant establishment in some plots, only 5 pairs which all exhibited acceptable plant establishment were included in the statistical analysis.

7.3.2.1 Environmental and growing conditions

According to weather data, months of (December, January and February) were colder than the long term mean (LTM). This may partly explain the low plant establishment under low seed density. Plants were exposed to drier conditions during months of (April and May) compared to the LTM (Table 7.8).

Table 7.8 Data of temperature, solar radiation, rainfall and the long term mean (LTM, from 1999 to 2009) in the experimental station at University of Nottingham Farm, Sutton Bonington campus during the season of 2009/10.

Monthly	Temperature (°C)		Rainfall (mm)		Solar radiation (MJ m^2)	
mean	09/10	LTM	09/10	LTM	09/10	LTM
Oct	11.5	11.1	31.8	73.2	189.4	186.0
Nov	8.7	7.6	85.6	53.1	103.1	93.6
Dec	3.5	5.0	51.0	53.4	67.4	58.7
Jan	1.8	5.3	33.0	47.3	77.3	74.4
Feb	2.8	5.0	41.6	43.4	112.4	136.5
Mar	6.2	6.5	36.6	37.4	286.1	260.6
Apr	9.2	8.9	26.6	49.6	444.1	393.9
May	11.1	11.5	15.0	51.7	554.3	428.1
Jun	15.5	15.2	69.2	56.0	624.1	537.4
Jul	17.3	16.6	42.8	83.9	496.3	517.7

7.3.2.2 Plant density (estimated at harvest) and ears per plant

Averaging across genotypes, 248 plants m^{-2} were established at the seed rate of 320 seeds per m^2 (SR320) and 28 plants m^{-2} at the seed rate of 40 seeds per m^2 (SR40) (P = 0.003), and there was no trend for *Tin1A* to show lower plant density than non *Tin1A* lines (P = 0.550; Table 7.9). The seed rate × *Tin1A* interaction was not significant (P = 0.992). Averaging across seed rate treatments, non-*Tin1A* lines produced more ears per plant (4.7) than *Tin1A* lines (4.0) ($P < 0.001$). Also, as expected more ears per plant were found at the lower seed rate (6.9) compared to the higher seed rate (1.8; $P < 0.001$). *Tin1A* and non-*Tin1A* lines responded differently to seed rate ($P < 0.001$), with non-*Tin1A* lines producing slightly more ears per plant (7.5) than *Tin1A* lines (6.2) at SR40, but the groups producing similar ears per plant at SR320 (1.9 and 1.8), respectively (Table 7.9).

7.3.2.3 AGDM and HI

There was a trend for non-*Tin1A* lines to produce more AGDM at harvest than *Tin-1A* lines (P = 0.062), and as expected more AGDM was produced at SR320 (1,289 g m^{-2}) than at SR40 (712.5 g m^{-2}) (P = 0.026). The seed rate x *Tin1A* interaction effect was not significant (P = 0.088). Overall *Tin1A* lines had higher HI (57%) than non-*Tin1A* lines (52%) (P = 0.001) and HI at SR40 (57%) was higher than at SR320 (52%) (P = 0.038). However, the interaction effect was not significant (P = 0.434).

7.3.2.4 Grain yield and yield components

Averaging across seed density treatments, there was no difference between *Tin1A* and non-*Tin1A* groups in grain yield (P = 0.799). There was trend for higher grain yield at the high seed density than at the low seed density (P = 0.051). The interaction effect was statistically significant (P = 0.033); non-*Tin1A* lines produced more grain yield than *Tin1A* lines at SR40 (4.29 and 3.73 t ha^{-1}, respectively), whereas, the *Tin1A* lines had a slightly higher yield than non-*Tin1A* lines at SR320 (6.89 and 6.48 t ha^{-1}, respectively). Overall, non-*Tin1A* lines produced more ears m^{-2} (341.3) than *Tin1A* lines (283.9) (P = 0.019), and ears m^{-2} in the high seed density (440.7) was greater than at the low

seed density (184.4) (P = 0.007). The response of both *Tin1A* and non-*Tin1A* lines to increasing seed density was, however, not different (P = 0.433). Grains per ear was higher in *Tin1A* lines (53.1) than non-*Tin1A* lines (40.0) (P < 0.001); and SR320 resulted in fewer grains ear^{-1} (37.4) than SR40 (55.9) (P = 0.010). The effect of the interaction was significant (P = 0.040). The decrease in the grains ear^{-1} at higher seed density was relatively greater in *Tin1A* (-34%) than in non-*Tin1A* lines (-31%) (Table 7.9). More grains m^{-2} were produced under the high seed rate (15,957) than in the low seed rate (9, 689); P = 0.037). Overall there was no significant effect of *Tin1A* on grains m^{-2} (P = 0.431). However, the interaction for grains m^{-2} was significant (P = 0.009). Non-*Tin1A* lines produced more grains m^{-2} than *Tin1A* lines at SR40 (10,418 and 8,959 respectively); however, *Tin1A* lines produced more grains m^{-2} at SR320 (16,937 and 14,977, respectively) (Table 7.9). Non-*Tin1A* lines produced slightly heavier grains (43.3 mg) than the *Tin1A* lines (42.2 mg) (P = 0.014). There were no differences between seed rates in GW (P = 0.551). However, the interaction effect was significant (P = 0.004). GW was similar for the two groups of lines at SR40 , but GW of non-*Tin1A* lines (44.4 mg) was heavier than that of *Tin1A* lines (41.6 mg) at SR320 (Table 7.9)

7.3.2.5 Dry matter of plant components at harvest

There was a trend for *Tin1A* lines to produce relatively more chaff biomass compared to the non *Tin1A* lines at SR320 than at SR40 (P = 0.059). Overall more lamina biomass was produced by non-*Tin1A* lines (68 g m^{-2}) compared to *Tin1A* lines (50 g m^{-2}; P = 0.005). However, the effect of the interaction between seed rate and *Tin1A* groups was not significant (P = 0.921). Overall, more stem biomass was produced by non-*Tin1A* lines (275 g m^{-2}) than *Tin1A* lines (214 g m^{-2}; P = 0.008) and stem biomass was lower at SR40 (162 g m^{-2}) than at SR320 (327 g m^{-2}) (P = 0.016). The interaction between seed rate and *Tin1A* groups for stem biomass was not statistically significant (P = 0.516).

Table 7.9 Effect of *Tin1A* gene and seed rate on plant height, ears plant^{-1}, above-ground dry matter (AGDM), grain yield (100% DM) and its components and dry matter partitioning in groups of 5 *Tin1A* and 5 non *Tin1A* DH lines of the Rialto x L14 population in 2009/10 season at harvest at Sutton Bonington, UK.

Tin1A allele	Seed rate m^{-2}	Plants m^{-2}	Ears plant^{-1}	AGDM (g m^{-2})	Grain yield (g m^{-2})	HI%	Ears m^{-2}	Grains ear^{-1}	Grains m^{-2}	TGW (g)	Ears DM g m^{-2}	Chaff DM g m^{-2}	Lamina DM g m^{-2}	Stem DM g m^{-2}
No	40	30.4	7.5	792.6	429.0	54	219.7	47.6	10418.2	42.2	554.3	125.3	43.5	194.8
	320	251.3	1.9	1288.8	648.0	50	462.8	32.8	14817.9	44.4	852.8	207.5	90.9	348.8
	Mean	**140.8**	**4.7**	**1040.7**	**535.3**	**52**	**341.3**	**40.0**	**12618.0**	**43.3**	**703.6**	**165.1**	**67.2**	**271.8**
Yes	40	24.5	6.2	632.4	373.2	59	149.1	64.2	8958.9	42.7	477.9	104.7	26.2	128.3
	320	245.1	1.8	1278.2	688.7	54	418.6	42.1	16937.3	41.6	905.0	216.3	74.2	299.0
	Mean	**134.8**	**4.0**	**955.3**	**531.0**	**57**	**283.9**	**53.1**	**12948.1**	**42.2**	**691.5**	**160.5**	**50.2**	**213.7**
Mean of 40		**27.5**	**6.9**	**712.5**	**401.1**	**57**	**184.4**	**55.9**	**9688.6**	**42.5**	**516.1**	**115.0**	**34.9**	**161.5**
Mean of 320		**248.2**	**1.8**	**1283.5**	**668.4**	**52**	**440.7**	**37.4**	**15877.6**	**43.0**	**878.9**	**211.9**	**83.2**	**323.9**
Grand mean		**137.8**	**4.4**	**998.0**	**534.7**	**54**	**312.6**	**46.6**	**12822.7**	**42.7**	**697.5**	**163.5**	**59.0**	**242.7**
C.V%		11.7	2.0	5.8	5.2	1.8	8.4	4.3	5.1	1.1	5.2	5.9	7.7	8.4
S.E.D (df)	(Tin1A)	9.28(4)	0.05(4)	33.29(4)	16.102(4)	0.005(4)	15.17(4)	1.15(4)	377.55(4)	0.269(4)	21.04(4)	5.61(4)	3.02(4)	11.77(4)
	(Seed rate)	12.55(2)	0.10(2)	94.01(2)	61.925(2)	0.010(2)	21.48(2)	1.88(2)	1217.48(2)	0.753(2)	71.05(2)	9.25(2)	2.94(2)	20.97(2)
	(Interaction)	15.6(4.2)	0.07(4)	47.08(4)	22.77(4)	0.008(4)	21.46(4)	1.63(4)	533.93(4)	0.381(4)	29.76(4)	7.94(4)	4.27(4)	16.64(4)
Prob.	(Tin1A)	0.550$^{n.s}$	<0.001***	0.062†	0.799$^{n.s}$	0.001***	0.019*	<0.001***	0.431$^{n.s}$	0.014*	0.651$^{n.s}$	0.353$^{n.s}$	0.005**	0.008**
	(Seed rate)	0.003**	<0.001***	0.026*	0.051†	0.038*	0.007**	0.010**	0.037*	0.551$^{n.s}$	0.037*	0.009**	0.004**	0.016*
	(Interaction)	0.992$^{n.s}$	<0.001***	0.088†	0.033*	0.434$^{n.s}$	0.433$^{n.s}$	0.040*	0.009**	0.004**	0.035*	0.059†	0.921$^{n.s}$	0.516$^{n.s}$

Note: each group consists of 5 lines and data of individual lines is shown in the appendix III

† Significant at 0.10 probability level

* Significant at 0.05 probability level

** Significant at 0.01 probability level

*** Significant at 0.001 probability level

n.s Non significant

7.3.3 CIMMYT, Ciudad Obregon 2009 and 2010.

7.3.3.1 Weather

As described in chapter four, the season 2008/9 was warmer than 2009/10, especially during early tillering in November and December. This may partly explain why more plants were established in 2008-9 compared to 2009-10.

7.3.3.2 Plant establishment, ears per plant and plant height

Plant establishment was higher in 2009 (173 plants m^{-2}) compared to 2010 (111 plants m^{-2}) (P = 0.027). Averaging across years and *Tin1A* groups, plant establishment was 42, 104 and 279 plants m^{-2} at seed rates of 50 (SR50), 150 (SR150) and 450 (SR450) seeds m^{-2}, respectively (P < 0.001). The interaction between year and seed density was significant (P < 0.001). Relatively, more plants were established at SR150 and SR450 than at SR50 seeds m^{-2} in 2008/09 compared to 2009/10. No differences were found between *Tin1A* and non-*Tin1A* lines in plant establishment (P = 0.515). Effects of the interactions of year × *Tin1A*, seed density × *Tin1A* and year × seed density × *Tin1A* were all not significant (P = 0.190, 0.570 and 0.405, respectively; Table 7.10).

The number of ears per plant at harvest was higher in 2010 (4.8) than 2009 (2.3) (P = 0.022; Table 7.9). Averaging across years and *Tin1A* groups, ears per plant were 6.2, 3.1 and 1.3 at SR50, SR150 and SR450, respectively (P < 0.001). The interaction between year and seed density was statistically significant (P < 0.001). Relatively, fewer ears per plant were produced at SR50 in 2009 than in 2010 than at SR150 and SR450. Overall, non *Tin1A* lines produced more ears per plant (3.8) than *Tin1A* lines (3.3) (P = 0.018). Effects of year × *Tin1A*, seed density × *Tin1A* and year × seed density × *Tin1A* were all not significant (P = 0.365, 0.241 and 0.790, respectively; Table 7.9). The difference in plant height between years was not significant (P = 0.197), and plants had the same height under the three seed density levels (P = 0.333). The interaction between year and seed density was not statistically significant (P = 0.120). However, non-*Tin1A* plants were slightly taller (80.6 cm) than *Tin1A* plants (79.8 cm) (P = 0.043). In addition, the interaction between year and *Tin1A* groups was significant (P = 0.017). *Tin1A* and non-*Tin1A* groups

did not differ in height in 2009, but non *Tin1A* plants were slightly taller (82.1 cm) than *Tin1A* plants (80.2) in 2010. No significant effect was found for the interactions of seed density × *Tin1A* or year × density × *Tin1A* ($P = 0.794$ and 0.538, respectively).

Table 7.10 Effects of the *Tin1A* gene and seed rate on plants m^{-2}, ears $plant^{-1}$ and plant height in groups of 4 *Tin1A* and 4 non-*Tin1A* DH lines of the L14 x Rialto population in 2008/09 and 2009/10 at CIMMYT Ciudad Obregon, North West Mexico.

Tin1A Allele	Seed rate m^{-2}	Plants m^{-2}			Ears $plant^{-1}$			Plant height (cm)		
		08/09	09/10	Mean	08/09	09/10	Mean	08/09	09/10	Mean
No	50	49.6	33.5	**41.6**	4.5	8.9	**6.7**	79.4	81.1	**80.2**
	150	132.1	76.5	**104.3**	2.1	4.5	**3.3**	79.4	82.9	**81.2**
	450	339.8	210.2	**275.0**	0.9	1.9	**1.4**	78.5	82.3	**80.4**
	Mean	**173.8**	**106.7**	**140.3**	**2.5**	**5.1**	**3.8**	**79.1**	**82.1**	**80.61**
Yes	50	52.1	32.3	**42.2**	3.9	7.7	**5.8**	80.3	79.0	**79.7**
	150	124.0	82.1	**103.0**	1.9	3.9	**2.9**	79.1	81.6	**80.4**
	450	337.3	229.2	**283.2**	0.8	1.7	**1.2**	78.5	80.0	**79.2**
	Mean	**171.1**	**114.5**	**142.8**	**2.2**	**4.4**	**3.3**	**79.3**	**80.2**	**79.76**
	Mean of 50	**50.8**	**32.9**	**41.9**	**4.2**	**8.3**	**6.2**	79.9	80.0	**79.9**
	Mean of 150	**128.0**	**79.3**	**103.6**	**2.0**	**4.2**	**3.1**	79.3	82.3	**80.8**
	Mean of 450	**338.5**	**219.7**	**279.1**	**0.8**	**1.8**	**1.3**	78.5	81.1	**79.8**
	Grand mean	**172.5**	**110.6**	**141.5**	**2.3**	**4.8**	**3.5**	**79.2**	**81.2**	**80.2**
C.V%		3.9	13.2	8.0	13.8	14.2	14.9	1.3	1.5	1.4
S.E.D (df)	**(Years)**			8.96(4)			0.31(4)			0.74(4)
	(Seed rate)	6.07(4)	9.27(4)	5.54(8)	0.18(4)	0.26(4)	0.16(8)	0.831(4)	0.989(4)	0.646(8)
	(Year*Seed rate)			11.01(8.07)			0.36(6.80)			1.05(10.76)
	(Tin)	3.15(6)	6.86(6)	3.78(12)	0.15(6)	0.32(6)	0.18(12)	0.475(6)	0.584(6)	0.376(12)
	(Year*Tin)			9.73(5.49)			0.36(6.81)			0.83(6.22)
	(Seed rate*Tin)	5.46(6)	11.88(6)	7.22(17.4)	0.26(6)	0.55(6)	0.27(19.73)	0.823(6)	1.011(6)	0.793(15.5)
	(Year*Seed rate*Tin)			12.81(13.62)			0.47(15.65)			1.23(18.25)
Prob.	**(Years)**			0.002**			0.001***			0.058†
	(Seed rate)	<0.001***	<0.001***	<0.001***	<0.001***	<0.001***	<0.001***	$0.365^{n.s}$	$0.194^{n.s}$	$0.333^{n.s}$
	(Year*Seed rate)			<0.001***			<0.001***			$0.120^{n.s}$
	(Tin)	$0.423^{n.s}$	$0.300^{n.s}$	$0.515^{n.s}$	0.081†	0.087†	0.018*	$0.703^{n.s}$	0.018*	0.043*
	(Year*Tin)			$0.190^{n.s}$			$0.365^{n.s}$			0.017*
	(Seed rate*Tin)	$0.439^{n.s}$	$0.513^{n.s}$	$0.570^{n.s}$	$0.474^{n.s}$	$0.442^{n.s}$	$0.241^{n.s}$	$0.564^{n.s}$	$0.738^{n.s}$	$0.794^{n.s}$
	(Year*Seed rate*Tin)			$0.405^{n.s}$			$0.790^{n.s}$			$0.538^{n.s}$

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

7.3.3.3 Grain yield and yield components

Plants suffered from some post-anthesis drought in 2008/9 due to a cessation of irrigation post anthesis at around mid grain filling, whereas in 2009/10, the irrigation was continued through to physiological maturity. Associated differences were found in the overall grain yield between years. Grain yield was 3.49 t ha^{-1} in 2009 compared to 5.94 t ha^{-1} in 2010 ($P < 0.001$). Overall, the main effect of seed density was not significant for grain yield ($P = 0.238$). In addition, the interaction of years × seed density was not significant ($P = 0.865$). Averaging across years and seed densities, non-*Tin1A* lines produced 5.4% more grain yield at 4.84 t ha^{-1} than *Tin1A* lines at 4.59 t ha^{-1} ($P = 0.012$; Table 7.11 and Fig 7.1). Effects of the interactions of year × *Tin1A*, seed density × *Tin1A* and year × seed density × *Tin1A* were all not significant ($P = 0.724$, 0.617 and 0.444, respectively; Table 7.11).

More ears m^{-2} were produced in 2010 (314 m^{-2}) than 2009 (246 m^{-2}; $P = 0.004$; Table 7.12). Ears m^{-2} were 231, 285 and 323 at SR50, SR150 and SR450, respectively ($P < 0.001$; Table 7.12 and Fig 7.4). The interaction between years and seed densities was not significant ($P = 0.357$). Overall, non-*Tin1A* lines produced 298 ears m^{-2}, whereas, *Tin1A* lines produced 261 m^{-2}($P < 0.001$). The interactions of year × *Tin1A*, seed density × *Tin1A* and year × seed density × *Tin1A* were all not significant ($P = 0.912$, 0.847 and 0.074) respectively.

Grains per ear was greater in 2010 (58) than 2009 (44) ($P = 0.001$), and was decreased from 44 to 55 with increasing seed density ($P < 0.001$). The interaction between years and seed density was not significant ($P = 0.225$). *Tin1A* lines produced more grains per ear (58) than non-*Tin1A* lines (43) ($P < 0.001$; Table 7.12 and Fig 7.5). The year × *Tin1A* interaction was significant ($P < 0.001$). In 2009, *Tin1A* lines had relatively higher grains ear^{-1} compared to non-*Tin1A* lines than in 2010. Interactions of seed density × *Tin1A* and year × density × *Tin1A* were not significant ($P = 0.130$ and 0.162, respectively; Table 7.12).

Overall, more grains m^{-2} (17,364) were produced in 2010 than in 2009 (10,445) ($P < 0.001$). Averaging across lines, grains m^{-2} was reduced at SR50 compared to other seed rates in 2009 ($P = 0.037$). However, no differences were found in

grains m^{-2} among seed densities in 2010 or averaging across years (P = 0.618 and 0.272, respectively). Averaging across years and seed densities, *Tin1A* lines produced 18% more grains m^{-2} (15,046) than non-*Tin1A* lines (12,763) (P < 0.001; Table 7.12 and Fig 7.6). In addition, the *Tin1A* lines produced relatively more grains m^{-2} than non-*Tin1A* lines in 2010 compared to 2009 (P < 0.001). Interactions of density × *Tin1A* and year × density × *Tin1A* were not significant (P = 0.283 and 0.200, respectively; Table 7.13).

No significant differences were found between years, seed densities or for the year × seed density interaction in grain weight (P = 0.055, 0.538 and 0.083) respectively. However, averaging across years and seed densities, non-*Tin1A* lines produced heavier grains (37.6 mg) than *Tin1A* lines (30.7 mg) (P < 0.001) (Table 7.13 and Fig 7.7). Interactions of seed density × *Tin1A* and year × seed density × *Tin1A* were not significant (P = 0.282 and 0.495, respectively) (Table 7.13).

7.3.3.4 Above-ground DM and harvest index

Biomass differences were found between 2009 and 2010 (913 vs. 1,328 g m^{-2}, respectively P < 0.001). Averaging across years and lines, AGDM did not differ amongst the three seed densities (P = 0.263). In addition, the interaction of years × seed densities was not significant (P = 0.988). In 2009, non-*Tin1A* lines produced more AGDM (942 g m^{-2}) than *Tin1A* lines (884 g m^{-2}; P = 0.038). However, no differences were found in 2010 (P = 0.563). For the cross-year ANOVA, the main effect of *Tin1A* and the interactions of seed density × *Tin1A* and year × seed density × *Tin1A* were not significant (Table 7.11).

Harvest index was lower in 2009 (38) than in 2009 and (45) (P < 0.001). The effects of density and *Tin1A* and all treatment interactions were not statistically significant for HI (Table 7.11 and Fig 7.3).

Table 7.11 Effects of the *Tin1A* gene and plant density on above-ground dry matter (AGDM), grain yield and harvest index (HI) in groups of 4 *Tin1A* and 4 non-*Tin1A* DH lines of the Ralto x L14 population in 2008/09 and 2009/10 at harvest in CIMMYT Ciudad Obregon , North West Mexico.

Tin1A allele	Seed rate m^{-2}	AGDM ($g\ m^{-2}$)			Grain yield 100% DM ($g\ m^{-2}$)			HI%		
		08/09	09/10	Mean	08/09	09/10	Mean	08/09	09/10	Mean
No	50	875.0	1302.4	**1088.7**	341.1	591.3	**466.2**	39	46	**42**
	150	1006.8	1359.5	**1183.2**	381.7	618.7	**500.2**	37	46	**42**
	450	944.3	1367.2	**1155.8**	366.0	603.5	**484.7**	39	44	**41**
	Mean	**942.1**	**1343.0**	**1142.5**	**362.9**	**604.5**	**483.7**	**38**	**45**	**42**
Yes	50	865.5	1275.5	**1070.5**	323.6	556.4	**440.0**	37	44	**40**
	150	877.0	1339.5	**1108.2**	328.8	602.1	**465.5**	37	45	**41**
	450	910.8	1325.0	**1117.9**	352.1	589.4	**470.8**	39	45	**42**
	Mean	**884.4**	**1313.3**	**1098.9**	**334.9**	**582.6**	**458.8**	**38**	**45**	**41**
	Mean of 50	870.3	1288.9	**1079.6**	332.4	573.8	**453.1**	38	45	**41**
	Mean of 150	941.9	1349.5	**1145.7**	355.2	610.4	**482.8**	37	46	**41**
	Mean of 450	927.6	1346.1	**1136.8**	359.0	596.5	**477.8**	39	44	**42**
	Grand mean	**913.2**	**1328.2**	**1120.7**	**348.9**	**593.6**	**471.2**	**38**	**45**	**41**
C.V%		5.1	7.8	7.1	5.3	5.2	5.4	2.1	4.4	3.6
S.E.D (df)	**(Years)**			17.12(4)			7.397(4)			0.003(4)
	(Seed rate)	41.52(4)	69.12(4)	40.32(8)	8.182(4)	33.23(4)	17.109(8)	0.020(4)	0.0059(4)	0.010(8)
	(Year*Seed rate)			49.60(9.95)			20.63(9.4)			0.012(10.1)
	(Tin)	21.81(6)	48.55(6)	26.61(12)	8.731(6)	14.59(6)	8.503(12)	0.0038(6)	0.0093(6)	0.01(12)
	(Year*Tin)			31.65(15.85)			10.37(15.5)			0.01(12.95)
	(Seed rate*Tin)	37.77(6)	84.10(6)	51.84(17.0)	15.123(6)	25.28(6)	20.03(13.8)	0.0065(6)	0.016(6)	0.012(13.4)
	(Year*Seed rate*Tin)			67.71(21.35)			25.34(17.7)			0.015(18.17)
Prob.	**(Years)**			<0.001***			<0.001***			<0.001***
	(Seed rate)	$0.298^{n.s}$	$0.648^{n.s}$	$0.263^{n.s}$	0.059†	$0.584^{n.s}$	$0.238^{n.s}$	$0.817^{n.s}$	$0.271^{n.s}$	$0.966^{n.s}$
	(Year*Seed rate)			$0.988^{n.s}$			$0.865^{n.s}$			$0.548^{n.s}$
	(Tin)	0.038*	$0.563^{n.s}$	$0.127^{n.s}$	0.018*	$0.184^{n.s}$	0.012*	$0.248^{n.s}$	$0.470^{n.s}$	$0.256^{n.s}$
	(Year*Tin)			$0.610^{n.s}$			$0.724^{n.s}$			$0.817^{n.s}$
	(Seed rate*Tin)	$0.135^{n.s}$	$0.982^{n.s}$	$0.685^{n.s}$	$0.212^{n.s}$	$0.821^{n.s}$	$0.617^{n.s}$	$0.274^{n.s}$	$0.674^{n.s}$	$0.346^{n.s}$
	(Year*Seed rate*Tin)			$0.568^{n.s}$			$0.444^{n.s}$			$0.984^{n.s}$

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

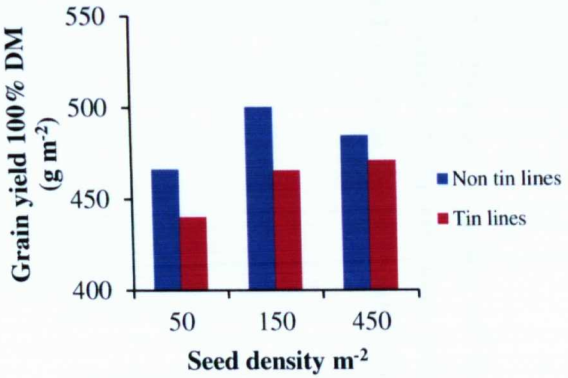


Figure 7.1 Response of grain yield (g m^{-2}) to seed density (seeds m^{-2}) in DH lines with and without *Tin1A* gene. For SEDs see Table 7.11

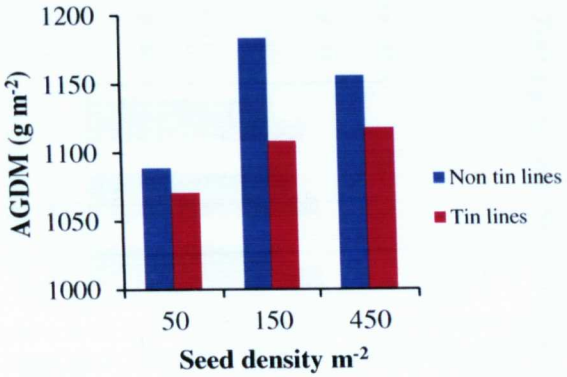


Figure 7.2 Response of AGDM (g m^{-2}) to seed density (seeds m^{-2}) in DH lines with and without *Tin1A* gene. For SEDs see Table 7.11

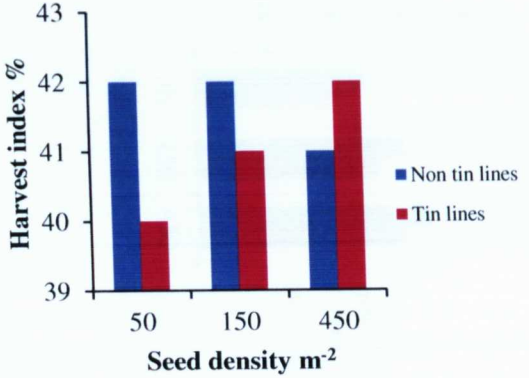


Figure 7.3 Response of harvest index to seed density (seeds m^{-2}) in DH lines with and without *Tin1A* gene. For SEDs see table 7.11

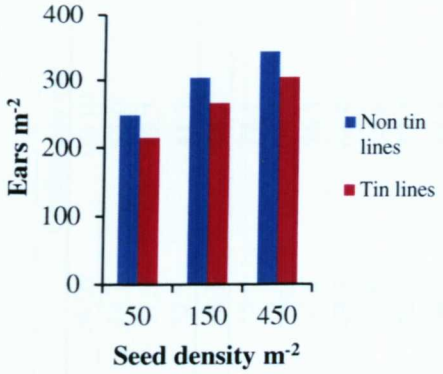


Figure 7.4 Response of ears m^{-2} to seed density (seeds m^{-2}) in DH lines with and without *Tin1A* gene. For SEDs see Table 7.12

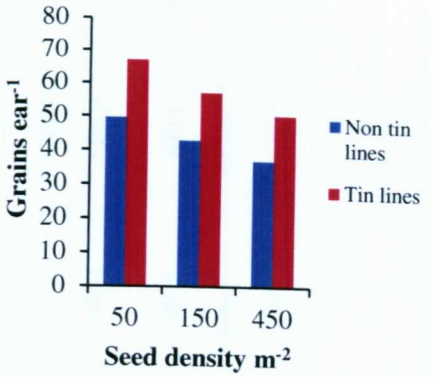


Figure 7.5 Response of grains ear^{-1} to seed density (seeds m^{-2}) in DH lines with and without *Tin1A* gene. For SEDs see Table 7.12

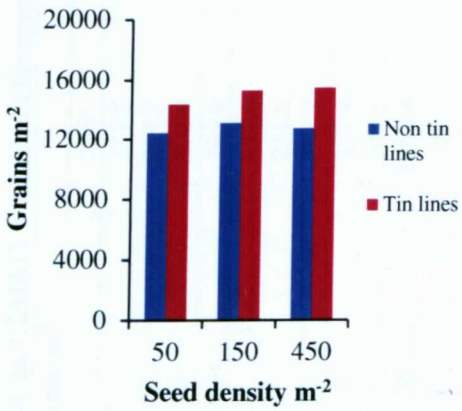


Figure 7.6 Response of grains m^{-2} to seed density (seeds m^{-2}) in DH lines with and without *Tin1A* gene. For SEDs see Table 7.13

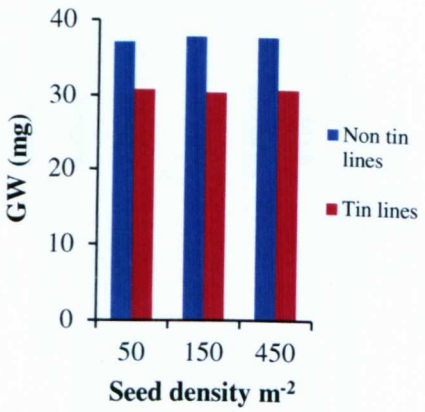


Figure 7.7 Response of grain weight (mg) to seed density (seeds m^{-2}) in DH lines with and without *Tin1A* gene. For SEDs see Table 7.14

Table 7.12 Effects of the *Tin1A* gene and plant density on ears m^{-2} and grains per ear in groups of 4 *Tin1A* and 4 non-*Tin1A* DH lines of the Rialto x L14 DH population in 2008/09 and 2009/10 at harvest in CIMMYT Cuidad Obregon, North West Mexico.

Tin1A allele	Seed rate m^{-2}	Ears m^{-2}			Grains per ear		
		08/09	09/10	Mean	08/09	09/10	Mean
No	50	211.5	283.8	**247.7**	44.1	55.0	**49.5**
	150	277.2	330.0	**303.6**	37.3	48.3	**42.8**
	450	302.9	382.3	**342.6**	32.8	41.2	**37.0**
	Mean	**263.9**	**332.1**	**298.0**	**38.1**	**48.2**	**43.1**
Yes	50	194.6	234.6	**214.6**	55.9	78.1	**67.0**
	150	231.6	299.4	**265.5**	48.0	66.2	**57.1**
	450	257.2	350.9	**304.0**	44.6	56.3	**50.5**
	Mean	**227.8**	**295.0**	**261.4**	**49.5**	**66.9**	**58.2**
	Mean of 50	**203.1**	**259.2**	**231.2**	**50.0**	**66.6**	**58.3**
	Mean of 150	**254.4**	**314.7**	**284.6**	**42.7**	**57.3**	**50.0**
	Mean of 450	**280.1**	**366.6**	**323.3**	**38.7**	**48.8**	**43.7**
	Grand mean	**245.8**	**313.5**	**279.7**	**43.8**	**57.5**	**50.7**
C.V%		4.6	4.6	4.7	3.7	5.1	4.7
S.E.D (df) (Years)				3.37(4)			0.86(4)
(Seed rate)		8.993(4)	19.56(4)	10.762(8)	1.356(4)	3.26(4)	1.766(8)
(Year*Seed rate)				13.202(9.56)			2.21(10.45)
(Tin)		5.326(6)	6.86(6)	4.344(12)	0.774(6)	1.392(6)	0.796(12)
(Year*_Tin_)				5.50(14.76)			1.17(11.1)
(Seed rate*_Tin_)		9.225(6)	11.89(6)	12.005(11.9)	1.340(6)	3.681(6)	2.018(12.8)
(Year*Seed rate*_Tin_)				14.91(15.07)			2.61(17.79)
Prob. (Years)				<0.001***			<0.001***
(Seed rate)		0.003**	0.014*	<0.001***	0.003**	0.014*	<0.001***
(Year*Seed rate)				$0.357^{n.s}$			$0.225^{n.s}$
(Tin)		<0.001***	0.002**	<0.001***	<0.001***	<0.001***	<0.001***
(Year*_Tin_)				$0.912^{n.s}$			<0.001***
(Seed rate*_Tin_)		$0.110^{n.s}$	$0.499^{n.s}$	$0.847^{n.s}$	$0.790^{n.s}$	$0.131^{n.s}$	$0.130^{n.s}$
(Year*Seed rate*_Tin_)				0.074†			$0.162^{n.s}$

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

Table 7.13 Effects of the *Tin1A* gene and seed rate on grains m^{-2} and grain weight in groups of 4 *Tin1A* and 4 non-*Tin1A* DH lines of the Rialto x L14 DH population in 2008/09 and 2009/10 at CIMMYT Ciudad Obregon, North West Mexico.

Tin1A allele	Seed rate m^{-2}	Grains m^{-2}			GW (mg)		
		08/09	09/10	Mean	08/09	09/10	Mean
No	50	9314.8	15555.1	**12434.9**	36.1	38.2	**37.1**
	150	10337.1	15898.2	**13117.6**	36.3	39.3	**37.8**
	450	9809.9	15665.2	**12737.6**	36.7	38.7	**37.7**
	Mean	**9820.6**	**15706.1**	**12763.4**	**36.4**	**38.7**	**37.6**
Yes	50	10736.3	17977.7	**14357.0**	30.2	31.4	**30.8**
	150	11092.3	19510.9	**15301.6**	29.7	31.1	**30.4**
	450	11381.1	19574.9	**15478.0**	31.0	30.6	**30.8**
	Mean	**11069.9**	**19021.2**	**15045.5**	**30.3**	**31.1**	**30.7**
	Mean of 50	**10025.5**	**16766.4**	**13396.0**	**33.1**	**34.8**	**34.0**
	Mean of 150	**10714.7**	**17704.5**	**14210.0**	**33.0**	**35.2**	**34.1**
	Mean of 450	**10595.5**	**17620.1**	**14107.8**	**33.9**	**34.7**	**34.3**
	Grand mean	**10445.2**	**17363.7**	**13904.5**	**33.3**	**34.9**	**34.1**
C.V%		**5.7**	**3.6**	**4.4**	**1.3**	**2.9**	**2.3**
S.E.D (df)	**(Years)**			**118.83(4)**			**0.34(4)**
	(Seed rate)	**180.47(4)**	**995.35(4)**	**505.79(8)**	**0.324(4)**	**0.420(4)**	**0.265(8)**
	(Year*Seed rate)			**596.00(8.65)**			**0.45(9.91)**
	(Tin)	**282.59(6)**	**293.34(6)**	**203.66(12)**	**0.211(6)**	**0.485(6)**	**0.26(12)**
	(Year*Tin)			**235.79(16.00)**			**0.43(9.25)**
	(Seed rate*Tin)	**489.46(6)**	**508.08(6)**	**563.95(11.9)**	**0.365(6)**	**0.840(6)**	**0.419(20)**
	(Year*Seed rate*Tin)			**692.56(14.48)**			**0.64(21.73)**
Prob.	**(Years)**			**<0.001*** **			**0.010** **
	(Seed rate)	**0.037***	**0.618$^{n.s}$**	**0.272$^{n.s}$**	**0.112$^{n.s}$**	**0.468$^{n.s}$**	**0.528$^{n.s}$**
	(Year*Seed rate)			**0.955$^{n.s}$**			**0.081†**
	(Tin)	**0.004** **	**<0.001*** **	**<0.001*** **	**<0.001*** **	**<0.001*** **	**<0.001*** **
	(Year*Tin)			**<0.001*** **			**0.011** **
	(Seed rate*Tin)	**0.497$^{n.s}$**	**0.172$^{n.s}$**	**0.283$^{n.s}$**	**0.251$^{n.s}$**	**0.438$^{n.s}$**	**0.283$^{n.s}$**
	(Year*Seed rate*Tin)			**0.200$^{n.s}$**			**0.497$^{n.s}$**

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

7.3.3.5 Dry matter growth and partitioning at flowering

In 2010, ear DM was greater (463 g m^{-2}) than in 2009 (296 g m^{-2}; $P = 0.001$). Ear DM increased from SR50 (328 g m^{-2}) to SR450 (426 g m^{-2}; $P < 0.001$). The interaction of year × seed density was not significant ($P = 0.643$). Overall non-*Tin1A* lines produced more ear DM (410 g m^{-2}) than *Tin1A* lines (349 g m^{-2}; $P < 0.001$). Differences in ear DM between *Tin1A* and non-*Tin1A* lines were not significant in 2009; however, in 2010 non-*Tin1A* lines produced greater ear DM (511 g m^{-2}) than *Tin1A* lines (416 g m^{-2}). The interactions of seed density × *Tin1A* or year × seed density × *Tin1A* were not significant ($P = 0.286$ and 0.541) respectively.

Flag leaf DM at flowering was greater in 2010 (77 g m^{-2}) than 2009 (61 g m^{-2}; $P = 0.011$). Amongst seed densities, differences were only significant between SR50 and SR450 ($P = 0.004$). The interaction between year and seed density was not significant ($P = 0.722$). Overall, *Tin1A* lines produced slightly more flag leaf DM (71 g m^{-2}) than non-*Tin1A* lines (67 g m^{-2}; $P = 0.046$). Differences in flag leaf DM between *Tin1A* and non *Tin1A* lines were not significant in 2009 ; however, *Tin1A* lines produced greater flag leaf DM (80 g m^{-2}) than non *Tin1A* lines (74 g m^{-2}) in 2010. No significant differences were found in either the interactions of seed density × *Tin1A* or year × density × *Tin1A*. Similar effects were observed for the total lamina DM of the culm leaves.

Stem DM at flowering was overall greater in 2010 (654 g m^{-2}) than in 2009 (349 g m^{-2}; $P = 0.003$). Differences in stem DM between seed densities 50 and 150 and between 50 and 450 were found ($P = 0.012$); however, differences between 150 and 450 were not significant. Non *Tin1A* lines produced more stem DM (514 g m^{-2}) than *Tin1A* lines (489 g m^{-2}) ($P = 0.032$). The interactions of year × *Tin1A*, density × *Tin1A* and year × density × *Tin1A* were not significant ($P = 0.332$, 0.265 and 0.548, respectively).

Ear partitioning index (EPI) at anthesis + 7 days was greater in 2009 (0.37) than in 2010 (0.34) ($P = 0.01$). EPI increased from SR50 (0.34) to SR450 (0.37; $P < 0.001$). The interaction of year × density was not significant ($P = 0.08$). Non-*Tin1A* lines partitioned a higher proportion of above-ground biomass to the ear (0.37) than *Tin1A* lines (0.34; $P < 0.001$). Differences in

EPI between *Tin1A* and non-*Tin1A* lines were not significant in 2009; however, non-*Tin1A* lines had higher EPI (0.36) than *Tin1A* lines (0.31) in 2010. The interactions of seed density × *Tin1A* or year × seed density × *Tin1A* were not significant.

No differences were found between years in the ear fertility index (i.e. grains per gram of ear DM at anthesis (P = 0.068). Nevertheless, there were differences amongst seed densities (P < 0.001). EFI decreased from 41.4 grains g^{-1} in SR 50 to 33.5 grains g^{-1} in SR450. The interaction between year and seed density was not significant (P = 0.37). Overall *Tin1A* lines had higher EFI (43.0) than non *Tin1A* lines (31.8; P < 0.001). Also the interaction between year and *Tin1A* was significant (P = 0.002). *Tin1A* and non-*Tin1A* lines had similar EFI in 2009; however, *Tin1A* lines had higher EFI than non-*Tin1A* lines in 2010. The interactions of seed density × *Tin1A* and year × seed density × *Tin1A* were not significant (P = 0.633 and 0.911) respectively.

Table 7.14 Effects of the *Tin1A* gene and seed rate on ear and flag-leaf dry weight per m at GS61 in groups of 4 *Tin1A* and 4 non-*Tin1A* DH lines of Rialto x L14 population in 2008/09 2009/10 at CIMMYT Ciudad Obregon, North West Mexico

Tin1A allele	Seed rate m^{-2}	Ears DM ($g\ m^{-2}$)			Flag leaves ($g\ m^{-2}$)		
		08/09	09/10	Mean	08/09	09/10	Mean
No	50	244.2	451.5	**347.8**	49.9	69.2	**59.5**
	150	333.4	507.0	**420.2**	65.6	74.2	**69.9**
	450	352.8	573.7	**463.3**	65.8	79.2	**72.5**
	Mean	**310.1**	**510.7**	**410.4**	**60.4**	**74.2**	**67.3**
Yes	50	242.7	372.6	**307.7**	57.7	72.2	**65.0**
	150	281.0	418.2	**349.6**	61.5	79.6	**70.5**
	450	319.9	456.2	**388.0**	66.2	87.0	**76.6**
	Mean	**281.2**	**415.7**	**348.5**	**61.8**	**79.6**	**70.7**
	Mean of 50	243.5	412.1	**327.8**	53.8	70.7	**62.3**
	Mean of 150	307.2	462.6	**384.9**	63.5	76.9	**70.2**
	Mean of 450	336.4	514.9	**425.7**	66.0	83.1	**74.6**
	Grand mean	**295.7**	**463.2**	**379.4**	**61.1**	**76.9**	**69.0**
C.V%		**8.8**	**6.4**	**7.4**	**8.5**	**5.0**	**6.6**
S.E.D (df)	**(Years)**			**11.99(4)**			**2.07(4)**
	(Seed rate)	**5.53(4)**	**23.44(4)**	**12.04(8)**	**3.37(4)**	**3.739(4)**	**2.517(8)**
	(Year*Seed rate)			**18.36(11.55)**			**3.57(12)**
	(Tin)	**12.32(6)**	**14.02(6)**	**9.33(12)**	**2.45(6)**	**1.824(6)**	**1.527(12)**
	(Year*Tin)			**15.19(9.19)**			**2.57(8.68)**
	(Seed rate*Tin)	**21.34(6)**	**24.28(6)**	**16.6(18.8)**	**4.24(6)**	**3.160(6)**	**3.135(16.01)**
	(Year*Seed rate*Tin)			**24.46(23.06)**			**4.44(22.12)**
Prob.	**(Years)**			**<0.001*** **			**0.002***
	(Seed rate)	**<0.001*** **	**0.030***	**<0.001*** **	**0.046***	**0.071†**	**0.004** **
	(Year*Seed rate)			**0.643$^{n.s}$**			**0.722$^{n.s}$**
	(Tin)	**0.057†**	**<0.001*** **	**<0.001*** **	**0.600$^{n.s}$**	**0.024***	**0.046***
	(Year*Tin)			**0.004** **			**0.205$^{n.s}$**
	(Seed rate*Tin)	**0.306$^{n.s}$**	**0.539$^{n.s}$**	**0.286$^{n.s}$**	**0.218$^{n.s}$**	**0.597$^{n.s}$**	**0.446$^{n.s}$**
	(Year*Seed rate*Tin)			**0.541$^{n.s}$**			**0.166$^{n.s}$**

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

Table 7.15 Effects of the *Tin1A* gene and plant density on lamina and stem and sheath dry weight per m^2 at GS61 in groups of 4 *Tin1A* and 4 non-*Tin1A* DH lines of the Rialto x L14 population 2008/09 and 2009/10 seasons at CIMMYT Ciudad Obregon, North West Mexico

Tin1A allele	Seed rate m^{-2}	Lamina DM ($g\ m^{-2}$)			Stem and leaf sheath DM ($g\ m^{-2}$)		
		08/09	09/10	Mean	08/09	09/10	Mean
No	50	81.6	153.0	**117.3**	316.1	608.4	**462.2**
	150	90.5	164.5	**127.5**	381.9	667.0	**524.4**
	450	87.2	167.7	**127.5**	400.5	707.1	**553.8**
	Mean	**86.4**	**161.7**	**124.1**	**366.2**	**660.8**	**513.5**
Yes	50	104.2	178.0	**141.1**	315.5	608.5	**462.0**
	150	96.7	183.0	**139.8**	322.0	659.5	**490.8**
	450	98.3	181.4	**139.9**	356.3	671.2	**513.8**
	Mean	**99.7**	**180.8**	**140.3**	**331.3**	**646.4**	**488.9**
	Mean of 50	92.9	165.5	**129.2**	315.8	608.5	**462.1**
	Mean of 150	93.6	173.8	**133.7**	352.0	663.2	**507.6**
	Mean of 450	92.8	174.6	**133.7**	378.4	689.1	**533.8**
	Grand mean	**93.1**	**171.3**	**132.2**	**348.7**	**653.6**	**501.2**
C.V%		**9.9**	**8.4**	**9.1**	**7.0**	**5.4**	**6.1**
S.E.D (df)	**(Years)**			**1.68(4)**			**11.82(4)**
	(Seed rate)	**5.26(4)**	**9.08(4)**	**5.25(8)**	**9.94(4)**	**34.9(4)**	**18.14(8)**
	(Year*Seed rate)			**6.29(9.17)**			**24.06(11.56)**
	(Tin)	**4.33(6)**	**6.80(6)**	**4.03(12)**	**11.43(6)**	**16.75(6)**	**10.14(12)**
	(Year*Tin)			**4.37(15.17)**			**15.58(10.21)**
	(Seed rate*Tin)	**7.50(6)**	**11.77(6)**	**7.20(18.7)**	**19.79(6)**	**29.02(6)**	**21.99(15.1)**
	(Year*Seed rate*Tin)			**9.40(21.16)**			**29.79(21.33)**
Prob.	**(Years)**			**<0.001*** **			**<0.001*** **
	(Seed rate)	**0.986$^{n.s}$**	**0.587$^{n.s}$**	**0.634$^{n.s}$**	**0.008****	**0.175$^{n.s}$**	**0.012***
	(Year*Seed rate)			**0.659$^{n.s}$**			**0.846$^{n.s}$**
	(Tin)	**0.022***	**0.031***	**0.002****	**0.022***	**0.424$^{n.s}$**	**0.032***
	(Year*Tin)			**0.489$^{n.s}$**			**0.332$^{n.s}$**
	(Seed rate*Tin)	**0.353$^{n.s}$**	**0.801$^{n.s}$**	**0.437$^{n.s}$**	**0.171$^{n.s}$**	**0.669$^{n.s}$**	**0.265$^{n.s}$**
	(Year*Seed rate*Tin)			**0.856$^{n.s}$**			**0.548$^{n.s}$**

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

Table 7.16 Effects of the *Tin1A* gene and seed rate on ear partitioning index at flowering and ear fertility index in groups 4 *Tin1A* and 4 non-*Tin1A* DH lines of a Rialto x L14 population during 20008/09 and 20009/10 seasons at CIMMYT experimental station in Ciudad Obregon, North West Mexico

Tin1A allele	Seed rate m^{-2}	Ear partitioning index (EPI)			Ear fertility index (EFI grains g^{-1})		
		08/09	09/10	Mean	08/09	09/10	Mean
No	50	0.35	0.35	**0.35**	38.4	34.5	**36.5**
	150	0.38	0.36	**0.37**	31.0	31.4	**31.2**
	450	0.39	0.38	**0.38**	28.0	27.3	**27.7**
	Mean	**0.38**	**0.36**	**0.37**	**32.5**	**31.0**	**31.8**
Yes	50	0.34	0.30	**0.32**	44.3	48.5	**46.4**
	150	0.37	0.31	**0.34**	39.9	46.7	**43.3**
	450	0.38	0.33	**0.35**	35.6	42.9	**39.3**
	Mean	**0.36**	**0.31**	**0.34**	**39.9**	**46.0**	**43.0**
	Mean of 50	0.35	0.33	**0.34**	41.3	41.5	**41.4**
	Mean of 150	0.38	0.34	**0.36**	35.5	39.0	**37.2**
	Mean of 450	0.39	0.35	**0.37**	31.8	35.1	**33.5**
	Grand mean	**0.37**	**0.34**	**0.35**	**36.2**	**38.6**	**37.4**
C.V%		**4.1**	**3.5**	**3.8**	**9.8**	**4.8**	**7.6**
S.E.D (df) (Years)				**0.006(4)**			**1.441(4)**
(Seed rate)		**0.00821(4)**	**0.00327(4)**	**0.0044(8)**	**0.935(4)**	**2.343(4)**	**1.261(8)**
(Year*Seed rate)				**0.008(9.34)**			**2.049(10.74)**
(Tin)		**0.00716(6)**	**0.00550(6)**	**0.00452(12)**	**1.671(6)**	**0.878(6)**	**0.944(12)**
(Year*_Tin_)				**0.008(8.78)**			**1.723(7.70)**
(Seed rate*_Tin_)		**0.01241(6)**	**0.00952(6)**	**0.00708(20.0)**	**2.895(6)**	**1.521(6)**	**1.711(18.4)**
(Year*Seed rate*_Tin_)				**0.011(21.00)**			**2.621(21.11)**
Prob. **(Years)**				**0.007****			**0.176$^{n.s}$**
(Seed rate)		**0.017***	**0.005****	**<0.001*****	**0.001*****	**0.120$^{n.s}$**	**<0.001*****
(Year*Seed rate)				**0.078†**			**0.366$^{n.s}$**
(Tin)		**0.123$^{n.s}$**	**<0.001*****	**<0.001*****	**0.004****	**<0.001*****	**<0.001*****
(Year*_Tin_)				**0.002****			**0.002****
(Seed rate*_Tin_)		**0.933$^{n.s}$**	**0.958$^{n.s}$**	**0.934$^{n.s}$**	**0.762$^{n.s}$**	**0.761$^{n.s}$**	**0.633$^{n.s}$**
(Year*Seed rate*_Tin_)				**0.937$^{n.s}$**			**0.911$^{n.s}$**

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

7.3.4.6 Ear traits at flowering

Rachis length was 12.2 cm in 2009 and 14.6 cm in 2010 ($P < 0.001$). Rachis length decreased with increasing seed rate from 14.3 cm at SR50 to 12.5 cm at SR450 ($P < 0.001$). Rachis length of *Tin1A* shoots was longer (13.9 cm) than non-*Tin1A* plants (12.9 cm; $P < 0.001$). The interaction between year and *Tin1A* was not significant ($P = 0.693$); however, the interaction between seed density and *Tin1A* was significant ($P = 0.047$). The decrease in rachis length with increasing plant density was relatively larger in *Tin1A* lines than the non-*Tin1A* lines. The year × density × *Tin1A* interaction was not significant ($P = 0.851$).

Total spikelet number was higher in 2010 (29.3) than in 2009 (27.0) ($P = 0.002$). Spikelets ear^{-1} decreased with increasing plant density from 30.3 at SR50 to 25.9 at SR450 ($P < 0.001$). Overall, *Tin1A* lines produced more spikelets ear^{-1} (28.8) than non *Tin1A* lines (27.5) ($P < 0.001$). The difference between *Tin1A* and non-*Tin1A* lines was relatively greater in 2009 than in 2010. Moreover, the decrease in total spikelets with increasing plant density was relatively greater in *Tin1A* lines than non-*Tin1A* lines ($P = 0.042$). The interaction of year × seed density × *Tin1A* was not statistically significant ($P = 0.533$). Similar effects were observed for the fertile spikelets ear^{-1}, for which overall *Tin1A* lines produced more fertile spikelets ear^{-1} (28.1) than non-*Tin1A* lines (25.2); and there was a trend for the decrease in spikelets ear^{-1} with increasing plant density to be relatively greater in *Tin1A* lines than non-*Tin1A* lines ($P = 0.089$) (Table 7.17).

Table 7.17 Effects of the *Tin1A* gene and plant density on rachis length, total and fertile spikelets spike^{-1} at GS61 in groups of 4 *Tin1A* and 4 non-*Tin1A* DH lines of the Rialto x L14 population during 2008/09 2009/10 at CIMMYT Ciudad Obregon, North West Mexico.

Tin1A allele	Seed rate m^{-2}	Rachis length (cm)			Total spikelets spike^{-1}			Fertile spikelets spike^{-1}		
		08/09	09/10	Mean	08/09	09/10	Mean	08/09	09/10	Mean
No	50	12.5	14.8	**13.6**	28.1	30.5	**29.3**	25.6	28.8	**27.2**
	150	11.7	14.1	**12.9**	26.3	29.3	**27.8**	23.5	27.0	**25.2**
	450	10.8	13.3	**12.0**	24.2	26.8	**25.5**	21.7	24.5	**23.1**
	Mean	**11.7**	**14.1**	**12.9**	**26.2**	**28.9**	**27.5**	**23.6**	**26.8**	**25.2**
Yes	50	13.7	16.1	**14.9**	30.4	31.9	**31.2**	29.8	31.6	**30.7**
	150	12.7	15.1	**13.9**	27.8	29.9	**28.9**	26.9	29.2	**28.0**
	450	11.7	14.1	**12.9**	25.2	27.6	**26.4**	24.1	26.9	**25.5**
	Mean	**12.7**	**15.1**	**13.9**	**27.8**	**29.8**	**28.8**	**26.9**	**29.2**	**28.1**
	Mean of 50	13.1	15.5	**14.3**	29.3	31.2	**30.3**	27.7	30.2	**28.9**
	Mean of 150	12.2	14.6	**13.4**	27.1	29.6	**28.3**	25.2	28.1	**26.6**
	Mean of 450	11.2	13.7	**12.5**	24.7	27.2	**25.9**	22.9	25.7	**24.3**
	Grand mean	**12.2**	**14.6**	**13.4**	**27.0**	**29.3**	**28.2**	**25.3**	**28.0**	**26.6**
C.V%		1.6	1.0	1.3	1.7	1.4	1.6	1.8	2.0	1.9
S.E.D (df)	**(Years)**			0.15(4)			0.12(4)			0.18(4)
	(Seed rate)	0.0812(4)	0.1676(4)	0.0931(8)	0.129(4)	0.5154(4)	0.2657(8)	0.135(4)	0.469(4)	0.2439(8)
	(Year*Seed rate)			0.18(8.21)			0.33(10.21)			0.33(11.88)
	(Tin)	0.0901(6)	0.0666(6)	0.560(12)	0.217(6)	0.1991(6)	0.1471(12)	0.217(6)	0.263(6)	0.1706(12)
	(Year*Tin)			0.16(5.20)			0.19(14.15)			0.25(11.49)
	(Seed rate*Tin)	0.1560(6)	0.1153(6)	0.1157(15.9)	0.375(6)	0.3449(6)	0.3210(14.9)	0.376(6)	0.456(6)	0.3212(17.7)
	(Year*Seed rate*Tin)			0.21(12.79)			0.42(19.98)			0.45(23.51)
Prob.	**(Years)**			<0.001***			<0.001***			<0.001***
	(Seed rate)	<0.001***	0.001***	<0.001***	<0.001***	0.004**	<0.001***	<0.001***	0.002**	<0.001***
	(Year*Seed rate)			0.816$^{n.s}$			0.579$^{n.s}$			0.738$^{n.s}$
	(Tin)	<0.001***	<0.001***	<0.001$^{n.s}$	<0.001***	0.004**	<0.001***	<0.001***	<0.001***	<0.001***
	(Year*Tin)			0.693$^{n.s}$			0.037*			0.032*
	(Seed rate*Tin)	0.352$^{n.s}$	0.095†	0.047*	0.114$^{n.s}$	0.291$^{n.s}$	0.042*	0.050*	0.741$^{n.s}$	0.089†
	(Year*Seed rate*Tin)			0.851$^{n.s}$			0.533$^{n.s}$			0.253$^{n.s}$

† Significant at 0.10 probability level
* Significant at 0.05 probability level
** Significant at 0.01 probability level
*** Significant at 0.001 probability level
n.s Non significant

7.4 DISCUSSION

7.4.1 Effects of the tiller inhibition *Tin1A* gene, plant density and their interaction on number of ears per plant.

In the UK environment (SB site), non *Tin1A* lines produced more ears per plant than *Tin1A* lines (7.5 and 6.2, respectively), under low seed density of 40 seeds m^{-2}. However, both *Tin1A* and non-*Tin1A* lines produced a similar number of ears per plant (1.8 and 1.9, respectively), under the high seed density of 320 seed m^{-2}. Similar results were observed in the Northwest Mexico environment, where ears per plant of non-*Tin1A* lines (6.7) was significantly higher than *Tin1A* lines (5.8) under low seed density of 50 seeds m^{-2} , with no significant differences between *Tin1A* and non *Tin1A* groups under higher seed densities of 150 and 450 seeds m^{-2}.

The negative effect of the tiller inhibition *Tin1A* allele on the tillering process was described by Richards (1988). In addition, Duggan *et al.* (2005) found that *Tin1A* decreased fertile ears per m^2 by 11% in four near-isogenic lines of spring wheat (Bodallin ± *Tin1A*, Banks ± *Tin1A*, Kite ± *Tin1A* and Osprey ± *Tin1A*) under terminal drought conditions in Australia. The effects of environmental factors such as light amount and quality as affected by plant density on the tillering process were also described by Evers *et al.* (2006), who reported that increasing plant density caused an earlier cessation of tillering and that under high radiation conditions, this cessation starts later in development when approximately 4.8 phyllochrons had occurred. This effect of light on tiller production was observed by Sparkes *et al.* (2006) and Thorne and Wood (1987).

Results showed differences in ears $plant^{-1}$ between *Tin1A* and non-*Tin1A* lines were expressed to their greatest extent under low seed densities. Under high seed densities as inter-plant competition increased, the decrease in ears per plant was greater for *non-Tin1A* lines compared to *Tin1A* lines. At high seed rates, possibly tillering cessation started earlier due to increased light competition and tillers may also have aborted earlier due to competition for light and nitrogen, in the *non-Tin1A* lines compared to the *Tin1A* lines.

7.4.2 Effects of the tiller inhibition *Tin1A* gene, plant density and their interaction on grain yield and its components

At the KWS Thriplow site, grain yield was overall relatively low at ca. 5 t ha^{-1}. The *Tin1A* lines produced more grain yield than the non-*Tin1A* lines (5.04 and 4.67 t ha^{-1}, respectively). There was strong trend for fewer ears m^{-2} with *Tin1A* (- 6.4%) (P = 0.062). The *Tin1A* allele, however, boosted grains per ear by 24%, which was the main component explaining more grains per m^2 (+ 14.5%) for the *Tin1A* lines than non-*Tin1A* lines. Heavier individual grains in non-*Tin1A* lines compared to *Tin1A* lines (46 and 44 mg $grain^{-1}$ respectively), did not therefore fully counteract the boost in grains m^{-2}. Similar results were obtained by Duggan *et al.* (2005) in Australia, who reported that the *Tin1A* allele decreased fertile ears per m^{-2} by 11%, but increased grains per ear by 9%, and grain weight by 2% averaged across four pairs of isolines in bread wheat.

The reduction in the number of ears m^{-2} under at KWS site due to the presence of *Tin1A* allele was not statistically significant; however, in SB site the decrease in the ears m^{-2} due to the presence of *Tin1A* allele was -17% overall and the interaction between the *Tin1A* gene and the seed rate was not statistically significant (P = 0.433, Table 7.9).

Under low seed density at Sutton Bonington in 2010, non-*Tin1A* lines produced greater yield (+13%) than *Tin1A* lines. Although *Tin1A* lines produced more grains ear^{-1} (+ 33%) than non-*Tin1A* lines under low seed density, more ears m^{-2} for non *Tin1A* lines led to more grains m^{-2} in non *Tin1A* lines (+ 14%) compared to *Tin1A* lines and increased grain yield. Relationships between these components changed under high seed density. *Tin1A* lines produced more yield (+ 6%) than non-*Tin1A* lines, and the seed density x *Tin1A* interaction was statistically significant. This was associated with an increase in grains ear^{-1} (+ 27%) and grains m^{-2} (+ 13%) in *Tin1A* lines compared to non *Tin1A* lines. Thus, the production of fewer grains in non-*Tin1A* lines was not compensated by their heavier grains compared to *Tin1A* lines (44 and 42 mg $grain^{-1}$, respectively). It was reported by Gaju *et al.* (2009) that the increase in the spikelets per ear in the large-spike phenotype L14 line was related to a longer

thermal time duration for spikelet primordia, compared to the check cultivar Bacanora.

A similar interaction between plant density and genotype was reported by Reynolds *et al.* (1994), who found that low-yield potential lines were more responsive to decreasing inter-plant competition at low seed rates than high yield potential lines. They suggested that the high yield potential lines have better adaptation to high plant densities. Tillering economy with *Tin1A* is therefore possibly a trait associated with better adaptation to high plant density.

At CIMMYT, grain yield was 3.49 t ha^{-1} in 2009, whereas it was 5. 94 t ha^{-1} in 2010 and this seasonal difference was significant ($P < 0.001$). In 2009, irrigation was not applied from around 10 days post-flowering since the experiment was located in the middle of any irrigation field and all the surrounding experiments had reached maturity earlier than the current experiment, examining lines of the winter (Rialto) x spring (L14) wheat DH population. Consequently, some incidence of late-season drought likely led to this lower yield in 2009.

Averaging across years and lines, seed density levels produced similar grain yield ($P = 0.238$). Despite the increase of ears per m^2 with seed density, grains m^{-2} did not change due to the decrease in grains per ear under higher densities. Number of grains per ear was 58, 50 and 44 in the densities of 50, 150 and 450, respectively. The negative effect of increasing seed density on grains per ear was reported by Yu *et al.* (1988), who indicated that grains per ear was decreased from 51 to 28 at plant densities of 18 and 229 plants m^{-2}, respectively, with a positive correlation between floret abortion rate and plant density. Similar results were reported by other investigation in wheat (Done and Whittington, 1980; Carr *et al.*, 2003; Whaley *et al.*, 2000; Lloveras *et al.*, 2004 and Geleta *et al.*, 2002). Under Mexican conditions, there was a larger reduction in the individual grain weight in *Tin1A* lines compared to the-non *Tin1A* lines (31 and 38 mg, respectively) than in the UK environment (42 and 43.5 mg), respectively. This larger reduction in the high temperature environment at CIMMYT compared to the UK might be related to the shorter grain filling period in Mexico combined with a larger positive effect of *Tin1A* on grains per ear and grains per m^2 in Mexico than in the UK . A significant

negative association between grains per ear and potential and final grain weight in NW Mexico was previously shown by Gaju *et al.* (2009).

7.4.3 Effects of the tiller inhibition *Tin1A* gene, plant density and their interaction on AGDM, DM partitioning, plant height, HI and ear traits

Tin1A and non-*Tin1A* lines produced a similar amount of AGDM, in both UK experiments. However, assimilate was partitioned differently according to the tillering ability and to the plant density.

The *Tin1A* allele reduced assimilate partitioning to stems and leaf sheaths compared to non-*Tin1A* lines (30 vs 32%) at KWS site. As a result, *Tin1A* lines had higher harvest index than non-*Tin1A* lines (49 and 47%, respectively). This effect was also reported by Duggan *et al.* (2005), who observed that the *Tin1A* allele increased harvest index by 2% and *Tin1A* lines were more efficient than non *Tin1A* lines in partitioning DM to ears at harvest (64 vs 62%, respectively).

Results in the SB experiment also showed *Tin1A* lines had a higher harvest index (57 vs 52%, respectively). Also, *Tin1A* lines partitioned relatively more DM to the grains under high compared to low seed density.

At CIMMYT, averaging across years and lines, seed density levels produced similar amounts of AGDM (a non-significant increase from 1080 to 1137 g m^{-2} from 50 to 450 seeds per m^2) and HI (P = 0.263 and 0.966, respectively). This stability in HI under different seed densities was also reported by Sharma and Smith (1987), who studied the effect of two seed rates (standard and low) on ten genotypes and reported no significant effects of plant density on HI. More generally, however, small increases in HI have been reported with plant densities below ca. 80 plants m^{-2} compared to conventional plant density (e.g. Whalley *et al.*, 2000).

At KWS Thriplow, *Tin1A* lines as expected had a longer rachis (+ 12.5%), wider ears (+ 7%) and more fertile spikelets per ear (+ 8.6%) than the non-*Tin1A* lines. At CIMMYT, the *Tin1A* allele resulted in an increase in rachis length of + 9.6, + 7.8 and + 7.5% under seed densities of 50, 150 and 450 seed

m^{-2}, respectively. In these two experiments, increasing seed density decreased ear traits (rachis length, total and fertile spikelets per ear). In addition, the *Tin1A* allele resulted in an increase in the fertile spikelets ear^{-1} by + 12.9, + 11.1 and + 10.2% under seed densities of 50, 150 and 450 seed m^{-2}, respectively. This result is consistent with the findings of Motzo *et al.* (2004) who found that the increased grains ear^{-1} with the *Tin1A* allele in the progenies of inter-specific bread wheat × durum wheat crosses was due to increases in both fertile spikelets ear^{-1} and grains $spikelet^{-1}$.

In the CIMMYT experiments, possessing the *Tin1A* allele resulted in a reduction in ear partitioning index by - 8.1% and in an increase in ear fertility index by 35.2%. This negative relationship between these two components was also observed by Gonzalez *et al.* (2011b). Foulkes *et al.* (2011) suggested that partitioning more DM to developing florets rather than the structural parts of the ear (rachis, glumes and paleas) would be a way to break this negative relationship. EPI increased with seed density for both *Tin1A* groups. However, increasing seed density from 50 to 150 and 450 seeds m^{-2} led to a reduction in EFI by - 14.5% and 24.1% in non *Tin1A* lines and - 6.7% and 15.3% in *Tin1A* lines, respectively.

Results showed higher EFI in *Tin1A* lines compared to non-*Tin1A* lines and at the same time non-*Tin1A* lines had higher EPI. The increase in grains per ear and grains per m^2 was associated more with higher EFI than EPI in the present study. These results are in contrast to those of Gaju *et al.* (2009) who reported that the parental lines L14 has reduced EFI compared to the check cultivar Bacanora of conventional ear morphology in NW Mexico. Those authors found no advantage for grain yield of the *Tin1A* allele at plant density of ca. 150 plants m^{-2}, and suggested that higher plant densities from 200 to 400 plants m^{-2} would be required to exploit commercially lines possessing the *Tin1A* allele in Mexico. The present results indicated that the *Tin1A* lines yielded relatively higher than the non-*Tin1A* at higher compared to lower seed rates and likely had high a higher economic optimum seed rate. However, the absolute grain yields of the two groups were not significantly different at the highest seed rate of 450 seeds m^{-2}.

7.5 SUMMARY

Results of these experiments showed that under the UK environment, *Tin1A* lines produced more grain yield than non *Tin1A* lines under high seed densities. The main yield component explaining this was grains per m^2. Increasing grains m^2 was as expected not due to more ears per m^2, but was a consequence of more grains per ear. *Tin1A* lines had a longer rachis, a wider ear, and more total and fertile spikelets per ear. Non-*Tin1A* lines produced more ears per plant than *Tin1A* lines under low seed density; however, both groups of lines had similar ears per plant under high seed density. Non-*Tin1A* lines produced heavier grains than *Tin1A* lines either under high or low seed density, and the difference between the groups in individual grain weight was not affected by the increase of seed density.

Under the Mexican environment, there was a slight increase in the yield of non-*Tin1A* compared to *Tin1A* lines at SR50 but not at SR 450 where yields of the groups were similar. This increase at SR 50 was attributed mainly to heavier individual grains in non-*Tin1A* than *Tin1A* lines. Though non-*Tin1A* lines overall produced more ears m^{-2} than *Tin1A* lines, *Tin1A* lines produced more grains m^{-2} and this resulted from a longer rachis, more total and fertile spikelets per ear and thus more grains per ear. No differences were found among seed densities in yield. All ear traits (rachis length, total and fertile number of spikelets) were affected negatively with the increase of seed density. This led to a decrease in grains per ear with increasing of seed density. However, these negative effects on grains per ear did not affect grains m^{-2} and hence yield. Increasing ears per m^2 at higher seed densities with maintenance of GW compensated this loss. In contrast to the UK environment, it seemed that under high radiation, irrigated environment in NW Mexico, possessing the *Tin1A* gene may not be an advantage compared to the freely tillering lines even under high seed rates.

CHAPTER 8 GENERAL DISCUSSION

8.1 INTRODUCTION

There is no doubt that yield potential has increased with plant breeding in bread wheat worldwide in the last decades (Reynolds *et al.*, 2011). Studying the changes in the morphological and physiological traits in cultivars released in different eras is very helpful to guide the future strategies of wheat breeding programs. However, these kinds of experiments which are conducted with a relatively small number of cultivars released at different times and exposed to similar environments may not give unequivocal results. Moreover, it was suggested that modern cultivars sometimes do not show any progress compared to the old ones in yield potential when grown under unfavourable conditions (Sancaran *et al.*, 2000).

This chapter explains the effects of plant breeding in the CIMMYT program on yield and its components, plant height, biomass production, HI, pre-anthesis physiological traits and post-anthesis physiological traits, and then considers the effects of the tiller inhibition *Tin1A* gene to boost grain number and yield potential and the optimum plant density for the expression of physiological traits associated with *Tin1A* gene. Finally, the development of a wheat ideotype with physiological traits optimised to increase yield potential is set out and discussed.

8.2 EFFECTS OF BREEDING ON YIELD, YIELD COMPONENTS, BIOMASS AND HARVEST INDEX

The genetic progress of yield potential of spring wheat cultivars released in CIMMYT from 1966 to 2009 was 37 kg ha^{-1} yr^{-1} (0.59% yr^{-1}). This improvement in yield was slightly less than values obtained from some previous studies conducted at the same site such as Waddington *et al.* (1986) with progress of 59 kg ha^{-1} (1.1 %) yr^{-1} from 1950 to 1982 and Sayre *et al.* (1997) with progress of 67 kg ha^{-1} yr^{-1} from 1962 to 1988. Waddington *et al.*

(1987) also reported a significant gain from 3.7 to 8.4 t ha^{-1} in yield potential in durum wheat released in Northwest Mexico from 1960 to 1984. Similar results were obtained by Slafer and Andrade (1993) in three bread wheat cultivars released from 1920 to 1980, where yield potential increased from 4.6 to 7.6 t ha^{-1}, as well as by Underdahl *et al.* (2008), Perry and Antuono (1989), Siddique *et al.* (1989), Royo *et al.* (2007) and Xiao *et al.*, (2012) in winter wheat from 1969 to 2006 in China.

Winter wheats similarly showed linear genetic progress of grain yield potential with year of release, e.g. Austin *et al.* (1980), Austin *et al.* (1989), Zhou *et al.* (2007), Brancourt-Hulmel *et al.* (2003), Sherman *et al.* (2005), Donmez *et al.* (2001) and Cox *et al.* (1988).

On the other hand, some other researchers suggested that yield potential of wheat may be reaching its plateau in some countries, e.g. in the Great Plains of North America since 1983 (Graybosch and Peterson, 2010); Finland (Peltonen-Sainio *et al.*, 2009) since 1995; Turkey (Barutcular *et al.*, 2006) since 1990s. However, it was reported that climate changes (e.g. high temperatures during grain filling and drought during stem elongation) and the exchange of legumes with the oilseed rape in cereal rotation rather than the genetic progress has been the reasons for the yield decline since the middle of the 1990s (Brisson *et al.*, 2010). Indeed, in the current study, although non-linear functions did not account for a higher proportion of variation in yield compared to a linear function with year of release, grain yield potential had almost levelled off since 1992, with only a slight tendency for an increase with year of release after 1992 and at the same time biomass increased since 1992 so increased straw production would have economic value.

Present results showed no systematic improvement in grains m^{-2} during the period from 1966 till 2009, although there were differences between individual cultivars, e.g. Bacanora (1988; 21,175 m^{-2}) compared to Seri (1982; 15,490 m^{-2}). This result contradicts many previous studies where yield progress was attributed to the improvement of grains m^{-2}, such as Slafer and Andrade (1993) in three bread wheat cultivars released from 1920 to 1980, Slafer and Andrade (1989) in a set of wheat cultivars released from 1912 to 1980 in Argentina,

Sayre *et al.* (1997) in NW Mexico, Perry and D'Antuono (1989) in Australia, Waddington *et al.* (1986) in NW Mexico and Abbate *et al.* (1998) in spring bread wheat in Argentina. Similar results for a positive association between genetic progress in grain yield and grains m^{-2} were obtained by Waddington *et al.* (1987) who reported that grains m^{-2} (specifically grains $spikelet^{-1}$) was the yield component most closely associated with yield potential progress in the durum wheat in the Northwest Mexico from 1960 to 1984.

Although there was a slight increase in ears m^{-2} with year of release in the present study of 1.12 ears m^{-2} yr^{-1}, no progress was observed in grains m^{-2} due to a reduction in grains ear^{-1} of – 0.20 grains ear^{-1} yr^{-1} ($r = -0.58$; $P = 0.05$). Fewer grains ear^{-1} was not associated with a reduction in rachis length which did not change with breeding, but was associated with fewer fertile spikelets ear^{-1} (- 0.06 spikelets ear^{-1} yr^{-1}; $r = -0.53$; $P < 0.10$).

In the present study, the yield component most closely associated with the genetic gains in yield potential was the individual grain weight. Again this has not been the usual result of the majority of the previous studies of the physiological basis of genetic progress in wheat yield potential (Sayre *et al.*, 1997; Perry and Antuono, 1989; Brancourt-Hulmet *et al.*, 2003; Shearman *et al.*, 2005; Acreche *et al.*, 2008). Nevertheless, a few previous studies did indicate genetic progress in grain weight, e.g. Underdahl *et al.* (2008) in the Great Plains from 1968 to 2006, Cox *et al.* (1988) in Kansas from 1874 to 1987, and Morgounov *et al.* (2010) who reported genetic gains in grain weight and grains m^{-2} in spring wheat from 1900 to 2008 in Western Siberia of 20.5% and 41.1%, respectively, underpinning grain yield progress of 0.7% yr^{-1}. In addition, Tian *et al.* (2011) in thirty five winter wheat cultivars released from 1950 to 2005 and Zheng *et al.* (2011) in 18 cultivars of winter wheat released from 1981 to 2008 in China showed associations between grain weight and genetic progress in yield.

Present results indicated grain weight appeared to track the improvement of the yield potential over the period from 1966 to 2009, with a linear gain of 0.23 mg $grain^{-1}$ yr^{-1} ($P < 0.001$). Breeders at CIMMYT may have been directly selecting for larger grains preferred by growers in developing countries as well as for

stability in grain weight; and this may have inadvertently selected against increases in grains m^{-2}; e.g. high grains m^{-2} may be associated with shrivelled grains in seasons with low radiation/high temperatures during the grain filling period.

Reduction in the plant height during the second half of the last century occurred in many wheat breeding programs worldwide due to the introduction of the semi-dwarfing genes from the Japanese source of Norin 10 during the Green Revolution (Hedden, 2003). This reduction in plant height led to an increase in the dry matter partitioned to the ear at anthesis and consequently increased spikelet fertility, grains m^{-2} and HI. This may in part explain why the majority of these previous studies examining trends amongst sets of historic cultivars including tall and semi-dwarf genotypes found that the main yield component explaining yield progress was grains per unit land area, in turn, associated with higher HI , e.g. in spring wheat (Sayre *et al.*, 1997; Perry and Antuono, 1989; Ortiz-Monasterio *et al.*, 1997; Miri, 2008; Sener *et al.*, 2009 and Acreche *et al.*, 2008) and in winter wheat (Austin *et al.*, 1980; Austin *et al.*, 1989; Brancourt-Hulmet *et al.*, 2003; Zhou *et al.*, 2007; Siddique *et al.* 1989). However, some investigations (e.g. Waddington *et al.*, 1986; Shearman *et al.*, 2005) have reported that the HI is beginning to plateau, so future increases in yield through this avenue may be harder to achieve. It was concluded by Foulkes *et al.* (2007) that the main way to increase the yield potential in future may be through enhancing biomass whilst maintaining the HI. Although Slafer and Andrade (1989) found no changes in AGDM from 1912 to 1980 in bread wheats in Argentina, yield potential improvement in the most modern wheat cultivars showed the highest above-ground biomass; statistically significant genetic gains in biomass were also reported in a few other studies (Waddington *et al.*, 1986; Waddington *et al.*, 1987; Shearman *et al.*, 2005).

In the present study, results showed that the above-ground-biomass at maturity has increased significantly with year of release, particularly after ca. 1988 and this increase was associated with an increase of plant height. Biomass appeared to explain most of the genetic progress in grain yield since 1988 rather than HI.

The increase in the above-ground biomass at maturity was much higher than the decrease in HI; hence, yield potential has increased in the last decades.

8.3 EFFECTS OF BREEDING ON PRE-ANTHESIS GROWTH

It has been suggested that increasing the thermal duration of the period of the stem-elongation phase as a proportion of the thermal time to anthesis is an effective way to improve ear DM production at anthesis and hence grains m^{-2} (Reynolds *et al.*, 2005; Garcia *et al.*, 2011). In addition, it was suggested by Foulkes *et al.* (2007) that this extension of the stem-elongation period should be done by advancing the time of GS31 and maintaining anthesis date to avoid yield loss due to late harvesting under the Northwest Europe conditions (although increased frost risk must also be taken into consideration with advanced onset of stem elongation in some environments). The sensitivity to photoperiod is one of the main factors controlling the length of developmental phases of wheat in spring wheat. Miralles and Richards (2000) demonstrated that extending the photoperiod during the spikelet primordia production phase caused a decrease in the number of spikelets initiated and that variation in the duration of the spikelet primordia production phase was clearly independent from the vegetative phase providing an opportunity to manipulate the durations of these phases genetically for higher grain number and yield.

In the present study, there were no associations between year of release and the date of onset of stem extension, flowering or physiological maturity. The range between cultivars for these stages was relatively small at 8, 10 and 7 days, respectively, hence, the duration of each period was generally similar in all the cultivars and did not show trends with year of release. However, the duration of the grain filling period tended to increase with year of release especially after 1990.

Under high radiation environments such as Northwest of Mexico, approximately 5% of the incident radiation may be lost either by transmission below the canopy or reflection above the canopy during the flag-leaf emergence to anthesis phase. During this period, present results showed there

was a tendency for increased fractional PAR interception by the flag-leaf canopy layer with year of release which was positively correlated with grain yield ($r = 0.55$; $P < 0.10$). Consequently the fractional PAR interception by the rest of the canopy decreased with breeding. Greater interception by the flag-leaf layer was positively associated with leaf lamina DM per m^2. Leaf lamina area was not measured in the present study, but it is feasible that flag-leaf specific DM (leaf lamina DM per cm^2 of lamina area) may have also increased with plant breeding and that this may have reduced any potential increase in light saturation of photosynthesis of flag leaves associated with increased fractional interception by this layer. Further work seems justified to test this hypothesis. However, there was no increase with breeding in the amount of PAR intercepted from GS31 to GS61 by the whole canopy and similar findings were reported by Acreche *et al.* (2009) and Shearman *et al.* (2005).

Several authors reported no change in pre-anthesis RUE and related traits with wheat breeding. For example, Fischer *et al.* (1998) reported no change in the CGR from 1962 to 1988 in spring wheat and other investigations observed no change in pre-anthesis biomass or RUE with breeding (Acreche *et al.*, 2009; Calderini *et al.*, 1997). However, in the current study, there was an apparent trend for an increase in the accumulated biomass from GS31 to GS61+7d with year of release ($r = 0.57$; $P < 0.10$; Table 5.13), and this was associated with an increase in the CGR over the same phase ($r = 0.60$; $P < 0.05$). The CGR was positively correlated with RUE during the stem-elongation phase in 2010, the one year in which pre-anthesis RUE was measured ($r = 0.95$; $P < 0.001$). In 2010, RUE showed a positive association with year of release only amongst 11 of the 12 cultivars, excluding Bacanora (1988) which had the highest RUE (2.56 g MJ^{-1}). These findings although not conclusive suggested a tendency for CGR and RUE to increase in the more modern cultivars, and further work seems justified to test whether this is the case. If these trends could be confirmed over more experimental years, it would indicate that CIMMYT plant breeders may have been inadvertently selecting for higher pre-anthesis RUE as has been the case for UK winter wheat in recent years (Shearman *et al.*, 2005). Yunusa *et al.* (1993) have also reported increases in RUE with date of cultivar introduction in Australia, and suggested that the increases in k values (which is

the light extinction coefficient of the canopy) underlying progress in RUE were associated with larger awned ears in the modern wheats. In the present study, trends for an increase in CGR and RUE were also associated with increase in pre-anthesis stomatal conductance and canopy temperature depression.

Cultivar 'Bacanora' (1988) had the highest RUE. With regard to enhancing RUE, it was suggested by Sinha *et al.* (1981) that one of the advantages of the semi-dwarf cultivars compared to the tall ones is their higher efficiency of photosynthesis through higher activity of RuBP and stomatal conductance. However, this may relate to an increase in post-anthesis RUE associated with increased grain sink strength rather than intrinsic increases in pre-anthesis RUE.

Present results showed a positive relationship between maximum shoot number at GS31 and the number of the shoots aborted. However, there were no trends with either year of release or grain yield. One of the traits that has been suggested for an improved wheat ideotype is a single culm with a large ear. Several studies support this idea of restricted tillering as a beneficial trait for yield. For example, Mohamed and Marshall (1979) observed that removing tillers from just before the appearance of the flag leaf till 10 days post-anthesis led to an increase in the main-shoot yield by increasing grains per spikelet in spring wheat. Typically most of the yield in wheat crops is produced in the main shoot and first two primary tillers (Rawson, 1971), so it could be beneficial to allocate more resource to these shoots by restricting the production of higher order tillers. For example, Thorne and Wood (1988) reported that 96% of grain yield was produced by the main stem (60%), the first tiller (22%) and the second tiller (14%). Using genotypes with restricted tillering to minimize effects of intra-plant competition has been an important target in the breeding programs. The tiller inhibition (*Tin1A*) allele on the short arm of chromosome 1A is a major recessive allele on chromosome 1A restricting tillering (Richards, 1988). Effects of the *Tin1A* gene have been reported previously in Mexico (Gaju, 2007; Gaju *et al.*, 2009) and Australia (Duggan *et al.*, 2005), but not in the UK. The main potential advantages of wheat genotypes possessing the *Tin1A* allele are higher grains per ear through both a longer rachis with more spikelets per ear and higher spikelet fertility

associated with an increased ear partitioning index at anthesis (Gaju *et al.*, 2009). The specific effects of the *Tin1A* genes in the UK and Mexico environments will be discussed in a later section of this chapter.

More generally with regard to ear anatomy traits, despite differences among the CIMMYT historic cultivars in rachis length, ear width and awn length, no associations were found with either year of release or grain yield. However, over the 43-year period both total and fertile spikelets initially increased with breeding but then decreased from about 1990. Generally longer awns would not be expected to give any advantages under irrigated conditions according to a study of Olugbemi and Bush (1987) who reported that awns contribute to grain yield ear^{-1} more when plants are grown under temperature and/or water stress and there were no advantages of awns when plants grown under favourable conditions.

The present results showed a small decrease in fertile spikelets per ear with no change of the rachis length with breeding over the 43-year period which results in an increase rachis length per fertile spikelet. This provided more space for each spikelet on the ear, and a significant positive correlation was found between rachis length per fertile spikelet and grain weight. So it is possible additional light interception by the ear and increased ear photosynthesis may have favoured increased endosperm cell division in the first 14 days post-anthesis and an increase in potential grain weight, or potential grain weight may have increased associated with a reduction in physical restrictions to grain size by the glumes, paleas and lemmas.

In the present study, the proportion of above-ground DM partitioned to the ear at anthesis tended to decrease very slightly with breeding of the 43 year period, initially increasing to ca. 1990 and decreasing thereafter. The phase of the decrease was associated with an increase in plant height. Ear DM per m^2 did not change with plant breeding. Ear DM partitioning as expected was inversely linearly related to stem-and-leaf-sheath DM partitioning.

This result was not in general in agreement with many other reports worldwide of increases in ear DM partitioning at anthesis positively associated with yield progress with breeding, e.g. in bread wheat released from 1920 to 1980 in

Argenitina (Slafer and Andrade, 1993). In the current study, there was a decrease in grains ear^{-1} with plant breeding associated with a tendency for increased ears m^{-2}, but no change in ear DM per m^2 with plant breeding. Bancal (2008) reported that grains per m^2 (or per ear) for six winter wheats (chosen for their differences in ear: stem DM ratio) was positively correlated not only to the ear DM but also to the stem DM. On the other hand, it was concluded that the onset of floret death was associated with onset of rapid stem growth in 80% of the six independent experiments reviewed by Gonzalez *et al.* (2011), supporting the relationship between assimilate supply to the ear and grains per ear, consistent with results in the present study. Present results showed that a decrease in grains ear^{-1} amongst the cultivars was related to an increase in stem DM partitioning and stem biomass at anthesis.

Present findings showed a negative correlation between the ear partitioning index and the ear fertility index, which was also observed by Gonzalez *et al.* (2011b). In the current study, both indices changed little over the whole 43-year period; however, up to about 1990 there was a slight increase in EPI and at the same time a decrease in EFI. Since about 1990 this negative relationship between these two parameters was also observed as EFI increased slightly but EPI decreased. It seems that improvements in one of these determinants of grains m^{-2} may to some extent be offset by a reduction in the other one. This negative correlation could potentially be broken by partitioning more DM to developing florets rather than the structural parts of the spike (rachis, glumes and paleas) (Foulkes *et al.*, 2011).

8.4 EFFECTS OF BREEDING ON POST-ANTHESIS GROWTH

In the present study, the duration of grain filling decreased from 1966 to ca. 1990 with an increase in the rate of grain filling over the same period. From ca. 1990 to 2009 there was a slight decrease in the rate and an increase in the duration of the grain filling. However, genetic variation in grain filling duration and rate are not intrinsically negatively related, as indicated by the weak relationships between the duration and the rate of grain filling reported by Gebeyehou *et al.* (1982) and Bruckner and Frohberg (1987). Furthermore, in

the current study Baviacora (1992) and Roelfes (2007) which produced the heaviest grains (44.9 and 45.4 mg, respectively) had relatively high grain filling rates associated with long durations of grain filling. According to Evans *et al.* (1975) and Austin (1982) genotypes which have longer grain filling duration are more effective than those with shorter grain filling duration (and higher grain filling rates) in favourable conditions where water and the heat stresses are absent. In Northwest Mexico, even though ambient temperature increases continuously after anthesis, small increases in the thermal duration of grain filling were positively associated with grain weight and grain yield over the 43-year period.

Present results showed increases in the post-anthesis CTD with year of release and this trait was positively correlated with grain yield ($r = 0.82$, $P < 0.001$). It seems possible that increasing the duration of grain filling period from current anthesis dates in the NW Mexico environment could potentially introduce some heat stress into the grain fill phase i.e, during the latter stages of grain filling. However, if this was combined with a high CTD, any negative effect of higher temperature during grain filling could potentially be counteracted.

Fractional PAR intercepted by the ear, flag-leaf and leaf 2 layers during the post-anthesis phase was positively correlated with both the grain weight and grain yield ($r = 0.72$; $P < 0.05$). Presumably this was associated with increased current photosynthesis by these canopy components which are the latest to senesce. In addition, these canopy layers are the nearest sources to the sink (grains), hence assimilate partitioning could be more efficient with reduced translocation costs.

The contribution of the stem-and-leaf-sheath WSC to the grain yield in modern wheat cultivars under different favourable environments was shown to be ca. 20-30% (Pheloung and Siddique, 1991; Shearman *et al.,* 2005; Ruuska *et al.,* 2006). However, in this study, the contribution of stem WSC to the grain yield ranged only from 5 to 14%. The variation in the amount of WSC remobilised to the grains didn't show any correlation with year of release after ca. 1990. This was possibly a consequence of improvements in the current photosynthesis in this latter phase, as indicated by higher CTD and an

increased fractional PAR interception by the upper canopy layers during post anthesis phase. Genetic variation of stem WSC remobilized (i.e. maximum %WSC - %WSC at physiological maturity) in wheat was reported to range from 3.3 to 22.2% in NW Mexico amongst lines of RIL populations derived from crosses of synthetic derived wheats developed in the CIMMYT program (Reynolds *et al.,* 2007b), hence it seems there is an opportunity to breed and select for this trait in the CIMMYT program. However, present results suggested this trait may not be a priority for raising yield potential in the high radiation, irrigated environment of NW Mexico.

The percentage increase in the grain weight in the manipulated degrained ears ranged amongst cultivars from 0.5 to 13.2%; the differences were not statistically different. This result indicated that grain growth of wheat under NW Mexico irrigated conditions is primarily sink limited, in agreement with other investigations on wheat carried out under favourable conditions (Borras *et al.,* 2004; Snyder *et al.,* 1993; Cartelle *et al.,* 2006; Miralles and Slafer 1995; Slafer and Savin 1994). The similar GW responses to degraining of cultivars with different years of release indicated that, although the grain sink size increased with year of release due to an increase in the potential grain weight, the modern cultivars were still not primarily source limited. It is recognised that it could be argued that Baviacora with a response to degraining of 13% may have been co-limited by source and sink; with grain growth sink limited through most of the grain filling period but source limited during the latter stages of grain filling associated with rapid senescence.

8.5 EFFECTS OF THE TILLER INHIBITION *TIN1A* GENE, PLANT DENSITY AND THEIR INTERACTION

The reduction in tillers per plant with *Tin1A* was relatively larger when plants were grown under low seed density compared to high seed density. This interaction effect was obtained in the UK site (Table 7.9) but not in the Mexico site (Table 7.10). The effects of the *Tin1A* gene in spring wheat in Australia were described by Richards (1988) and Duggan *et al.* (2005).

Under the UK conditions, *Tin1A* lines produced more grain yield (7.8% at KWS and 6.3% at SB site) at high seed density than non-*Tin1A* lines. Nevertheless, this result was not obtained in Mexico where *Tin1A* lines yielded less than non-*Tin1A* lines at low seed density and similarly to non-*Tin1A* lines at high seed densities. Thus, the trend of the grain yield with increasing seed density in Mexico was not the same for *Tin1A* and non-*Tin1A* lines. There was a reduction in the grain yield at SR450 in non-*Tin1A* lines comparing to at SR150 . However, *Tin1A* lines continued to increase grain yield with increasing seed density. This result therefore supported the hypothesis that *Tin1A* lines yield relatively better under high seed density than non *Tin1A* lines.

Under high seed density at the KWS, Thriplow site (300 seeds m^{-2}) and the SB site (320 seeds m^{-2}) in the UK, the reduction in ears m^{-2} with the *Tin1A* allele was relatively small (- 6.4 and – 9.5%, respectively). Similar effects of *Tin1A* were obtained at the CIMMYT site. Though grains ear^{-1} and grains m^{-2} was higher with the *Tin1A* allele in both the UK and Mexico experiments, more grain yield with *Tin1A* was found only in the UK. Producing heavier grains in non-*Tin1A* lines than *Tin1A* lines did not compensate for fewer grains m^{-2} in the UK; however, in Mexico heavier grains in non-*Tin1A* lines (even with fewer grains m^{-2}) led to higher or similar yield compared to *Tin1A* lines at the respective seed rates. At the SB site, *Tin1A* lines produced relatively lighter grains at 320 than at 80 seeds m^{-2} compared the *non-Tin1A* lines. This likely reflected reduced intra-plant competition in the *Tin1A* lines particularly under the low seed density. A negative relationship between seed density and GW is widely reported in wheat, e.g. by Geleta *et al.* (2002), Carr *et al.* (2003), Arduini *et al.* (2006) and Blue *et al.* (1990).

Above-ground DM at harvest did not differ for *Tin1A* and non-*Tin1A* groups of lines in the UK environment. However, HI for *Tin1A* was higher than non-*Tin1A* lines. *Tin1A* lines also partitioned more DM to the ears at harvest compared to the non-*Tin1A* lines under high seed density. The reduction in height in the *Tin1A* lines may have partly contributed to this difference. The increase in ear partitioning at harvest for *Tin1A* in the SB experiment is consistent with the findings of Gaju *et al.* (2009), who reported on the *Tin1A*

L14 parental line compared to the conventional check cultivar Bacanora in NW Mexico. However, in the present study, in Mexico, above-ground DM produced and HI did not differ significantly between the *Tin1A* and non-*Tin1A* lines at all seed density levels, and *Tin1A* lines partitioned slightly less DM to ears at anthesis, associated with slightly increased DM partitioning to the lamina. The *Tin1A* allele conferred a longer rachis, more total and fertile spikelets per ear in all experiments under all seed densities. This may need to increase lodging resistance in new *Tin1A* cultivars with large ear phenotype.

Increasing seed density decreased expression of these traits. It is reported that DH lines possessing the *Tin1A* allele had similar root DM compared to freely tillering lines (Palta *et al.,* 2007), but root DM was not measured in the present study.

The *Tin1A* lines had a slightly lower ear partitioning index than the non-*Tin1A* lines in the experiments in NW Mexico. *Tin1A* lines had higher ear fertility index than the non-*Tin1A* lines. The *Tin1A* lines were therefore more efficient at partitioning the DM to the grains rather than the other ear components (rachis, glumes and paleas) (Foulkes *et al.*, 2011). The negative effect between the ear fertility index and the increase of seed density might be partly explained by the increase of infertile spikelets ear^{-1} under high seed density.

Tillering is one of the most important agronomic traits in wheat crops because tillers $plant^{-1}$ determines ears $plant^{-1}$, a key component of grain yield. In wheat, tillering is controlled by a number of minor QTL (Li & Gill, 2004), in addition to the single gene (*Tin1A*) investigated in the present study (Spielmeyer & Richards, 2004). The biological mechanisms underlying tiller inhibition with *Tin1A* are not known. After formation, axillary buds require one or more of a wide range of cues before outgrowth ensues. Depending on a range of developmental, environmental and genetic conditions, cytokinin can promote branching, whereas auxin may inhibit branching (Beveridge, 2006); cytokinin acts to increase the flow of assimilates within the shoot to the axillary bud site. Recent work in Arabidopsis has shown that a long-distance branching signal other than cytokinin or auxin might act as an inhibitor of shoot branching (Beveridge, 2006).

Present findings in the L14 x Rialto DH population show *Tin1A* decreased ears m^{-2} from 324 to 304 (-6.4%) at the KWS site under high density and from 220 to 149 (-32%) and from 463 to 419 (-9.6%) at SB site under low and high seed density, respectively. The percentage decreases in ears m^{-2} at CIMMYT site were similar under all seed densities (-13.4, -12.5 and -11.3%, respectively) under seed densities of 50, 150 and 450 seed m^{-2}, respectively. A wide range of quantitative variation for tillering within the *Tin1A* group amongst the individual *Tin1A* lines was observed in the present study. This suggested that axillary buds can be at least partially released from tiller inhibition in *Tin1A* lines during tiller development, and demonstrated that the upper end of the range of ears m^{-2} for *Tin1A* DH lines represents commercial ear population densities. Positive effects of *Tin1A* on both spikelets ear^{-1} and grains ear^{-1} were observed. It can be proposed that the *Tin1A* allele in the presence of modifying tiller promoting QTL(s) may represent a beneficial allele to introduce into UK wheat germplasm for improved grains m^{-2} and grain yield. However, further work is required to test the effects of the *Tin1A* allele more precisely than in the present study. This would require the development of sets of near isogenic lines (NILs) for *Tin1A* in both elite spring and winter wheat backgrounds to investigate the pleiotropic effects of restricted tillering with *Tin1A* on yield components more precisely than in the present study against more uniform genetic backgrounds in the sets of NILs.

8.6 DEVELOPING A WHEAT IDEOTYPE WITH PHYSIOLOGICAL TRAITS TO INCREASE YIELD POTENTIAL

Breeders have been very successful in the past in direct selections for higher yield potential. Those selections were made directly for grain yield (or visually for agronomic ear type in earlier generations) and with limited consideration for the physiological processes limiting grain yield potential and therefore the mechanisms responsible for yield progress could not be identified with certainty in breeding programs.

Designing strategies for future yield improvement would not be an easy task without understanding the physiological processes determining yield and breeders and physiologists are aware of this issue (Jackson *et al.,* 1996). Studying traits from the physiological level to the gene level may be more effective way to improve yield by combining yield-enhancing traits in new genotypes than direct empirical selection for yield (Fischer, 2011). Furthermore, because the genetic gain in yield potential resulting from traditional breeding has slowed down recently, improving the understanding of physiology has now become more important (Fischer, 2007; Reynolds *et al.,* 2007).

Introducing trait selection may complement traditional direct selection methodologies for wheat and improve the efficiency of breeding programs. Ideotype breeding has been defined by Rasmusson (1991) as the method of breeding to improve genetic yield potential by optimising individual target traits for specific environments. Since the report of Donald (1968) who described a wheat ideotype for yield in New South Wales Australia as a plant with a short single culm, few small erect leaves and a large, awned, erect ear, there has been more need to design ideotypes for specific environments to accelerate yield progress. It was concluded that the gap between breeding and physiology could be narrowed by implementing crop modelling to predict the joint optimization of physiological traits (Shorter *et al.,* 1991).

Using the ideotype approach in rice breeding was an effective way to produce the second generation of the new plant type of rice in China which yielded as high as 12 t ha^{-1} in farmers' fields (Peng *et al.,* 2009). Moreover, it is very important to focus on the traits which are limiting yield and combine work between physiology and molecular studies to identify markers for selection for important yield-enhancing traits and to identify synergies between traits to improve wheat yield potential. Moreover, knowledge of the genes that regulate these traits will facilitate their assembly in new genotypes. Trait-based physiological breeding has been used successfully to improve drought adaptation of wheat in Australia and by the International Maize and Wheat Improvement Centre (CIMMYT), including higher transpiration efficiency,

greater early vigour, reduced tillering, and dehydration avoidance (Richards *et al.*, 2002; Reynolds and Tuberosa, 2008).

The presently reported genetic gains in yield in the CIMMYT historic set were associated with improvement in harvested biomass and individual grain weight and mechanisms to raise these two traits further in future breeding programs will now be considered further.

8.6.1 Physiological avenues to increase biomass

The increase in grain yield potential in the historic set of CIMMYT cultivars was associated with the increase of above-ground biomass at maturity which appeared to explain most of the genetic progress in grain yield since ca. 1990 rather than HI. This supports the idea that improving harvest biomass has been a direct selection target in breeding strategies at CIMMYT breeding programs since the early1990s. Straw biomass is an important product with a significant economic value in many developing countries.

Improving radiation interception is one strategy to boost biomass by either promoting more rapid canopy area expansion and/or extending the period of vegetative growth to anthesis (Parry *et al.*, 2011) (or delaying canopy senescence during grain filling where grain growth is source-limited). Because leaf lamina are the main organs intercepting radiation (Slafer *et al.*, 1999), light interception increases up the point when any further increase in the leaf area of the upper lamina would only shade the lower leaves, thus decreasing the CGR (Gardner *et al.*, 1985). GAI and leaf inclination affect the amount of radiation transmitted through the canopy to ground level (Gardner *et al.*, 1985), and optimizing the distribution of the incident radiation within the canopy by reducing the light extinction coefficient will improve the RUE. It seemed that this was the case in cultivar Bacanora (1988) which had the highest percentage of radiation (25%) transmitted through the ears and flag-leaf layer and intercepted by the rest of the canopy and the highest RUE.

In the current study, HI increased only from 1966 to about 1982 and during this time biomass was not increasing. HI then decreased with year of release. However, the increase in biomass after 1990 was proportionally greater than

the decrease in HI and consequently grain yield continued to increase from 1990 to 2009. This trade-off between biomass production and HI is one of the main challenges to wheat breeders. In this historic set of cultivars, no significant differences were found amongst the cultivars in the fraction of PAR intercepted by the whole canopy at all growth stages measured (GS31, GS39 and GS61 + 7d); similar findings were observed by Acreche *et al.* (2009) and Shearman *et al.* (2005). However, cultivars differed in the proportion of PAR intercepted by the ears and by the flag leaves, with higher yield potential associated with greater interception in the upper canopy. The other avenue for increasing biomass production is the RUE. This could be achieved by improving the efficiency of leaf photosynthesis, improving respiration efficiency, optimizing the distribution of the radiation within the canopy and/or optimizing the distribution of the nitrogen within the canopy with respect to the vertical distribution of radiation (Slafer *et al.*, 1999; Foulkes *et al.*, 2009).

Phenotyping germplasm for stomatal conductance is an indirect way to assess leaf photosynthesis. There was a positive association between pre-anthesis stomatal conductance and grain yield ($r = 0.62$, $P < 0.05$) and a positive trend with year of release. There was an apparent tendency for RUE to be increased with year of release as described above. Cultivar Bacanora (1988) which had the highest RUE also had the best light penetration through the canopy where 25% of light was penetrated below the flag leaf. So potentially there may still be some scope to modify the vertical distribution of light within the canopies of modern cultivars to increase RUE. However, present results appeared to contradict this in that a positive association was seen between fractional interception in the upper canopy in the pre-anthesis period and grain yield. More studies are therefore required to examine if the N content of the upper canopy leaves has increased to potentially increase the light-saturated rate of photosynthesis and decrease the extent of light saturation in the upper leaves of the canopy of modern cultivars. The apparent increase in the RUE with year of release in this study was associated with an increase in CTD and stomatal conductance during pre-anthesis phase. Present results showed that increases in biomass have been associated with increases in plant height within the semi-dwarf cultivars. However, it seems likely that crop height could not be

increased significantly above current values of ca. 105 cm in future without increasing lodging susceptibility as well resulting in decreases HI that may not be compensated by proportionally greater increases in biomass.

Modern cultivars with higher biomass may require larger roots systems to take up more N and water especially with the climate changes. Indeed, restricted water uptake was the main reason for the most susceptible wheat cultivar to drought under the UK conditions (Foulkes *et al.*, 2001).

8.6.2 Physiological avenues to increase grain weight

Results in the current study indicated that individual grain weight tracked closely the improvement of the yield potential over the 43y period. The correlation between grain weight and both year of release and grain yield was highly significant ($r = 0.79$, $P = 0.01$) and ($r = 0.69$, $P = 0.05$), respectively. From the results of the sink manipulation treatment (Fig. 8.1), there were no differences between the control and manipulated treatments in the slope of the linear relationship between final grain weight and year of release; in the degrained shoots the increase in grain weight indicated that the potential grain weight also increasing linearly with plant breeding; presumably related to changes in physiological processes in the period just before anthesis until about two weeks after anthesis.

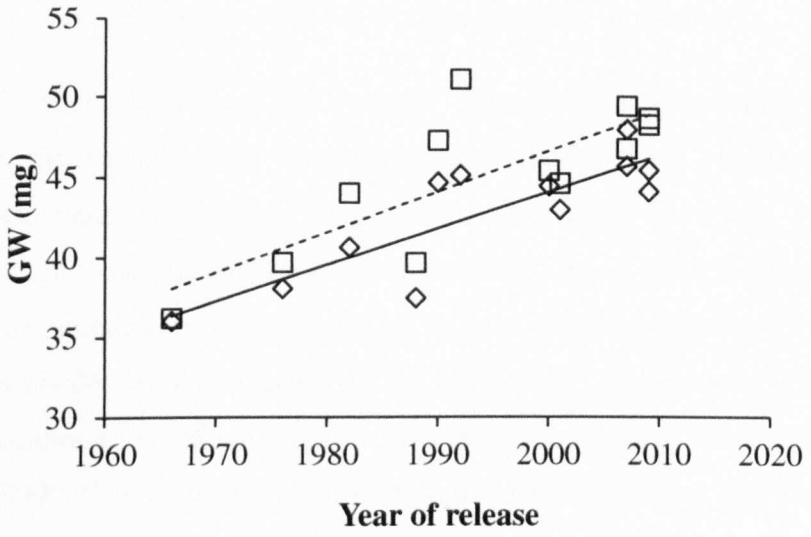


Figure 8.1 Regression of grain weight (mg) on year of release for control ears (__◇__) y= 0.2257x – 407.39 (R^2 = 0.719; P < 0.001), and manipulated ears (degrained at GS61 + 14 days) (---□---) y= 0.250x – 453.26 (R^2 = 0.615, P = 0.003).

Traits such as earlier flowering, economic tillering, high stem WSC and more grains per spikelets were suggested as ideotype traits for improving grain weight and grain yield for environments under heat stress during the grain-filling period in lines derived from the cross of Seri/Babax in Australia (Rattey *et al.*, 2009).

However, in the experiments investigating the effects of the *Tin1A* gene, there was a negative effect of the *Tin1A* gene on the individual grain weight under both environments. This indicates the well established negative relationship between grain number per m^2 and grain size. To break this negative trade-off will require a better understanding of the physiological and genetic bases of potential grain size, especially by considering the period immediately pre-flowering which accounts for both grain number and grain size (Ugarte *et al.*, 2007). It is encouraging in this regard that for a range of different wheat crosses, some QTL controlling grain yield have been found to work primarily through individual grain weight without pleiotropic effects on grain number

(Snape *et al.,* 2007; Gegas *et al.,* 2010; McIntyre *et al.,* 2010). Relevant processes for future investigation on the mechanistic basis of the genetic increases in potential grain weight in the present study would be:

- *Grain endosperm cell division and expansion.* The total number of cells in the endosperm at the end of the cellularization phase is closely associated with final grain weight controlling the rate of starch accumulation during the linear grain-filling phase (Brocklehurst, 1977). The expansion of maternally derived tissues delimits a volume available for the growth of the endosperm and for the subsequent accumulation of starch in wheat and other crops (Calderini *et al.,* 1999a; Cantagallo *et al.,* 2004; Haughn and Chaudhury, 2005; Berger *et al.,* 2006; Yang *et al.,* 2009).
- *Mechanical constraints to grain size.* The correlation coefficient ranging from 0.40 to 0.76 between final grain size and the volume of the floret cavity (Millet, 1986) also suggests that the early development of the grain may be influenced by physical constraints.

Table 8.1 Main physiological traits relevant to grain yield potential for 12 CIMMYT spring wheat cultivars released from 1966 to 2009

Trait	Effects relevant to yield	Correlation with yield	Rate of genetic variation
Harvest biomass g m^{-2}	Increased season-long photosynthetic capacity	($r = 0.90$, $P < 0.001$)	1325-1777 g m^{-2}
Stomatal conductance (mmol m^{-2} s^{-1}) pre-anthesis	Increase photosynthesis capacity	($r = 0.69$, $P < 0.05$)	162.4-293.6 mmol m^{-2} s^{-1}
Radiation use efficiency (g MJ^{-1} ; RUE) pre-anthesis	Increase crop growth rate and biomass	($r = 0.44$, $P < 0.10$)	1.70-2.56 g MJ^{-1}
Increased crop growth rate pre-anthesis	Increased photosynthesis capacity	($r = 0.33$, $P < 0.10$)	16.4-24.4 g m^{-2} d^{-1}
Above-ground dry matter (g m^{-2}; AGDM) accumulated from GS31 to GS61+7d	Increased source size	($r = 0.61$, $P < 0.05$)	632.6-865.0 g m^{-2}
Lamina DM (g m^{-2}) at GS 61	Increase photosynthesis capacity	($r = 0.76$, $P < 0.01$)	123.9-158.0 g m^{-2}
Post anthesis canopy temperature depression (^{o}C)	Increase photosynthesis capacity post-anthesis	($r = 0.82$, $P < 0.01$)	2.8-4.0 °C
Potential grain weight (mg)	Increase grain sink-size and harvest biomass	($r = 0.69$, $P < 0.05$)	36.2-48.6 mg

8.7 OVERALL CONCLUSIONS

With regard to the original hypotheses which were stated at the end of chapter 2, the following can be concluded based on the results of the present study:

1. Grain yield potential has increased in spring wheat cultivars released in CIMMYT in the period from 1966 to 2009 by 37 kg ha^{-2} yr^{-1} (0.59 % yr^{-1})
2. There was no association between this genetic progress in grain yield and grains m^{-2}. In addition; genetic gains in grain yield potential was related to the increase in the HI during the period from 1966 to about 1990; however, HI decrease slightly since about 1990.
3. Although there was an increase in the number of ears m^{-2} from ca. 1990 to 2009, this did not lead to more grains m^{-2} with plant breeding because grains ear^{-1} decreased over the same period.
4. The decrease in grains ear^{-1} with plant breeding was not associated with a decrease in rachis length, but was associated with a decrease in the number of fertile spikelets ear^{-1}.
5. Genetic yield progress from 1966 to 2009 was associated with grain weight improvement and since there was no systematic change over the same period in grains m^{-2}, individual grain weight was the principal numerical yield component explaining the genetic progress in yield.
6. Genetic progress in above-ground biomass was mainly apparent since ca,. 1990 and HI increased only from 1966 until ca. 1990, i.e. during the phase that biomass was not increasing. HI then decreased with year of release since ca. 1990. The increase in biomass after 1990 was proportionally greater than the decrease in HI and consequently grain yield continued to increase from 1990 to 2009.
7. There was a non-linear increase in the plant height with year of release, with height increasing from ca. 1990.
8. There was no association amongst cultivars between ear DM at GS61 + 7d and either year of release or grain yield.
9. There was a positive association between stem DM partitioning at anthesis and both year of release ($r = 0.72$, $P < 0.01$) and grain yield (r

= 0.74, $P < 0.01$). Regression analysis indicated that this increase in stem biomass with year of release was non-linear and occurred mostly since ca. 1990. The increase in stem biomass was associated positively with plant height.

10. There was a negative association between stem DM partitioning and ear partitioning index amongst the cultivars (r = - 0.79; $P < 0.01$), reflecting competition for assimilates during the stem-elongation phase.
11. The amount of radiation intercepted during the stem-elongation phase did not change with breeding from 1966 to 2009; however, there was an apparent tendency for RUE to increase with year of release.
12. The correlation between CTD during the stem-elongation period and both year of release and grain yield was not statistically significant. Nevertheless, there was a positive association between stomatal conductance and grain yield ($r = 0.62$, $P < 0.05$). Overall there was an increase in stem WSC accumulated at anthesis + 7 days from 1966 to ca. 1992 and then a decrease to 2009. This relation was inversed at maturity, with a decrease from 1966 to ca. 1992 and then a slight increase till 2009. Consequently, the remobilized stem WSC during grain filling was positively correlated with the amount of stem WSC accumulated at anthesis + 7 days ($R^2 = 0.98$).
13. The percentage increase in the grain weight in the degrained ears compared to control ears ranged from 0.5 to 13.2%, cultivar differences were not statistically different, and there was no association between the response and year of release. Consequently all 12 CIMMYT spring wheat cultivars in the historic set were generally sink limited rather than source limited.
14. Under both NW Mexico (all seed densities) and the UK environments (high density only), *Tin1A* lines overall produced more grains m^{-2} than non*Tin1A* lines. Increased grains m^{-2} was as expected not due to more ears m^{-2}, but was a consequence of more grains per ear. *Tin1A* lines had a longer rachis, a wider ear, and more total and fertile spikelets per ear than non-*Tin1A* lines. However, under low seed density (in the UK only), non-*Tin1A* lines produced more grains m^{-2} than *Tin1A* lines and this was associated with more ears $plant^{-1}$ in non-*Tin1A* lines.

15. *Tin1A* lines yielded higher than the non-*Tin1A* lines when grown under the high seed density in the UK. However, under NW Mexico environment, *Tin1A* lines yielded lower than non-*Tin1A* lines at the lower seed densities and similarly compared to non-*Tin1A* lines at the high seed rate.
16. Lines with the *Tin1A* allele produced relatively fewer ears per m^2 (and lower grain yield) than non-*Tin1A* lines under low plant density than under high plant density under the UK conditions, indicating the economic optimum plant density for *Tin1A* lines may be higher than for non-*Tin1A* lines. The interaction for grain yield from the cross-year analysis of the CIMMYT experiments also indicated that the economic optimum seed density was higher for the *Tin1A* compared to the non-*Tin 1A* group of lines.
17. Non-*Tin1A* lines on average produced heavier grains (46 mg) than *Tin1A* lines (44 mg) at the KWS site. At the SB site, GW of the two groups was similar at the low seed density; however, GW of non-*Tin1A* lines was statistically higher than the *Tin1A* lines at the high seed density. At the CIMMYT site, non-*Tin1A* lines produced heavier grains than *Tin1A* lines at all seed densities; and the difference between the two groups was proportionally similar at all seed densities.
18. At the CIMMYT site, the *Tin1A* allele overall resulted in a reduction in the ear partitioning index and in an increase in the ear fertility index. Ear partitioning index increased with seed density for both *Tin1A* groups, whereas ear fertility index decreased with seed density for both *Tin1A* groups.

8.8 FUTURE WORK

8.8.1 The physiological basis of the genetic progress in yield potential.

In order to accelerate the rate of genetic progress observed in the present study in the last decades, it will be important to conduct future physiological experiments to investigate further the basis of genetic yield progress and trends in traits determining yield potential. Though the genetic progress in yield

potential observed in the present study was expected, it was not expected from previous studies that the main physiological basis of this increase of yield would relate to harvest biomass and individual grain weight.

Despite the major role of the introduction of the semi-dwarfing genes into the breeding programs at CIMMYT and their advantages of reducing plant height, increasing the DM partitioned to the ear, and hence, higher HI, it is reported by many authors that this direction of breeding would not add any more advantages to grain yield. The present strategy to increase yield in the CIMMYT irrigated, high potential mega-environment has been to increase the harvest biomass production while maintaining HI values. Although this strategy has led to a slight decrease in the HI and consequently fewer grains ear^{-1}, it has resulted in raising yield potential through heavier grains and hence higher quality. However, the more modern cultivars may have an increased lodging susceptibility and an increased requirement for N.

With the availability of new in-field high-throughput phenotyping tools for phenotyping canopy photosynthetic capacity underpinning biomass, such as:

- NDVI, (canopy size and architecture) and other spectral reflectance indices, e.g. NIR Water Index (Biomass)
- CTD, (canopy photosynthesis)
- stomatal conductance, (leaf photosynthetic rate)
- Chlorophyll fluorescence (leaf photosynthetic efficiency)

there is likely potential for application of these phenotyping tools in breeders' trials to quantify canopy architecture and photosynthetic efficiency. However, future work is required to refine phenotyping protocols to maximize precision of measurements, e.g. identify the optimum developmental stages, time of day, weather conditions for assessments, as well as number of readings per plot for the respective phenotyping techniques.

The following points would be useful for future studies to improve understanding of traits determining yield potential in wheat and for their application in breeding programs to raise yield potential based on the findings of the present study:

1. More detailed physiological studies to examine the physiological basis of apparent increases in RUE with plant breeding; Licor 6400 gas-exchange analysis and measurements of Rubisco content will be valuable.
2. More detailed studies on the physiological basis of the increase in potential grain weight (see above for priority mechanisms for further study).
3. Screen wider ranges of novel germplasm (synthetic wheats, landraces, introgression lines, diploid progenitors etc) to identify genetic variation in key traits.
4. It will be essential to understand the genetic control of key target traits through analysis of mapping populations (biparental populations and association panels) segregating for target traits. Also the development of near-isogenic lines through back-crossing will be crucial for precise physiological studies and fine mapping to develop molecular markers for the key traits for use in marker-assisted selection. Markers can be used for progeny selection and to identify parental crosses with synergistic combinations of traits. The use of cop simulation to model to predict the joint optimization of traits in new ideotypes will be important in this context.
5. Future Research approaches should also combine physiological and genetic analysis to strengthen understanding of the genetic controls of ear fertility index It may be useful to place some emphasis on defining the nature and impact of hormonal signalling (meristem/spikelet hormone concentration (ABA,ACC, IAA, cytokinins) in determining thresholds of assimilate requirement for floret survival in the spikelets.
6. Also there is a requirement to develop high-throughput field phenotyping screens for key traits as described above.

Specific points for future work on experiments examining sets of historic cultivars would include:

1. Cultivars used in the studies of investigation the physiological basis of yield progress should be representative of the period of study with approximately similar time intervals between successive introductions in the set of cultivars.

2. To allow for detailed measurements of source- and sink-type traits, the number of cultivars should not be more than ten cultivars; this would also facilitate increasing the number of replications to more than three.
3. It would be very useful to apply more source and sink manipulation treatments to benchmark source sink balance, e.g. shading or light treatments during booting to decrease/increase ear DM growth and grains m^{-2} compared to control treatments and to examine effects post-anthesis on the upregulation of RUE.
4. Sampling the roots in addition to shoots in the growth analysis measurements would be important and add valuable information to fully understand the genetic gains in biomass. It will also be important to measure the N content of the plant samples at the respective samplings to examine whether enhanced biomass with plant breeding is associated with higher N requirements and if so whether changes in rooting depth, root biomass and root length density (root length per unit soil volume; RLD) or the distribution of root DM and RLD with depth are associated with genetic increases in N uptake.
5. As the individual grain weight was positively associated with the genetic yield progress it will be useful to apply further measurements to investigate the mechanistic basis of the increases in potential grain weight (especially during the 7 d prior to anthesis focused on carpel DM growth and during the first 14 d after anthesis focused on endosperm cell number).

8.8.2 The effect of the tiller inhibition (*Tin1A*) gene and the interaction with plant density

To study the interaction between the effect of the *Tin1A* gene and the plant density it would be better to apply at least four seed densities to allow response curves for the yield versus plant establishment to be fitted and the economic optimum seed rates estimated according to latest grain prices and costs of seed.

Under the UK conditions, it will be important to add higher seed densities than the maximum examined in this study (300 seeds m^{-2}) e.g (450 and 600 seeds m^{-2}) to quantify the response of the *Tin1A* groups to these densities. Future

work should also be based on the analysis of the effects of the *Tin1A* gene in near isogenic lines as described above. Following fine mapping, next generation sequencing and candidate gene analysis approaches could be taken to clone the *Tin1A* gene to allow the development of a perfect marker for the gene for application in worldwide breeding programs.

CHAPTER 9 REFERENCES

ABBATE, P. E., ANDRADE. D. H., LAZARO. L., BARAITTI. J. H., BERADOCCO. H. G., INZA. V. H., AND MARTURANO, F. (1998). Grain yield in recent Argentine wheat cultivars. *Crop Science.* **38**, 1203–1209.

ABELEDO, L. G., CALDERINI, D. F., AND SLAFER, G. A. (2003). Genetic improvement of barley yield potential and its physiological determinants in Argentina (1944–1998). *Euphytica* **130**, 325–334.

ABELEDO, L. G., CALDERINI, D. F., AND SLAFER, G. A. (2004). Leaf appearance, tillering and their coordination in old and modern barleys from Argentina. *Field Crops Research*, **86**, 23-32.

ACRECHE, M. M., AND SLAFER, G. A. (2009). Grain weight, radiation interception and use efficiency as affected by sink-strength in Mediterranean wheats released from 1940 to 2005. *Field Crops Research.* **110**, 98–105.

ACRECHE, M. M., BRICENO-FELIX. G., MARTIN SANCHEZ, J. A., AND SLAFER, G. A., (2008a). Physiological bases of genetic gains in Mediterranean bread wheat yield in Spain. *European Journal of Agronomy* **28**, 162–170.

ACRECHE, M. M., AND SLAFER, G. A., (2006). Grain weight response to increases in number of grains in wheat in a Mediterranean area. *Field Crops Research* **98**, 52–59.

ACRECHE, M., BRICENO-FELIX, G., MARTIN SANCHEZ, J.A. AND SLAFER, G. A. (2009). Grain number determination in an old and a modern Mediterranean wheat as affected by pre-anthesis shading. *Crop & Pasture Science.* **60**, 271–279.

ACRECHE, M., BRICENO-FELIX, G., MARTIN SANCHEZ, J.A., AND SLAFER, G. A. (2008b). Radiation interception and use efficiency as affected by breeding in Mediterranean wheat. *Field Crops Research.* **110**. 91-97.

ACUNA, T. B., DEAN, G., AND RIFFKIN, P,. (2011). Constraints to achieving high potential yield of wheat in a temperate, high-rainfall environment in south-eastern Australia. *Crop & Pasture Science.* **62**, 125–136.

AGGARWAL, P. K., CHATURVEDI, G. S., SINGH, A. K. AND SINHA, S. K. (1986). Performance of wheat and triticale cultivars in a variable soil-water environment. III. Source-sink relationships. *Field Crops Research.* **13**, 317-330.

AGGARWAL, P. K., FISCHER, R. A., AND LIBOON, S. P. (1990). Source-sink relations and effects of post-anthesis canopy defoliation in wheat at low latitudes. *Journal of Agricultural Science*, Cambridge.**114**, 93-99.

AHMADI, A., JOUDI, M., AND JANMOHAMMADI, M. (2009). Late defoliation and wheat yield: Little evidence of post-anthesis source limitation. *Field Crops Research*. **113**, 90–93.

ALLAN, R. E. (1983). Harvest Indexes of Backcross-Derived Wheat Lines Differing in Culm Height. *Crop Science*. **23**, 1029-1032.

ALLAN, R. E. (1986). Agronomic Comparisons Among Wheat Lines Nearly Isogenic for Three Reduced-Height Genes. *Crop Science*. **26**, 707-710.

ALVARO, F., ISIDRO, J., VILLEGAS, D., GARCIA DEL MORAL, L. F., AND ROYO, C. (2008a). Old and modern durum wheat varieties from Italy and Spain differ in spike components. *Field Crops Research*. **106**, 86–93.

ALVARO, F., ISIDRO, J., VILLEGAS, D., GARCIA DEL MORAL, L. F., AND ROYO, C. (2008b). Breeding effects on grain filling, biomass partitioning, and remobilization in Mediterranean durum wheat. *Agronomy Journal*. **100**, 361–370.

ALVARO. F., ROYO, C., GARCIA DEL MORAL, L. F., AND VILLEGAS, D. (2008c). Grain Filling and Dry Matter Translocation Responses to Source–Sink Modifications in a Historical Series of Durum Wheat. *Crop Science*. **48**, 1523–1531.

AMANI, I., FISCHER, R. A., REYNOLDS, M. P., (1996). Canopy temperature depression associated with yield of irrigated spring wheat cultivars in a hot climate. *Journal of Agronomy and Crop Science*. **176**, 119-129.

ANDRADE, F., RODRIGO, H., SALA, G., PONTAROLI, A. C., AND LEON, A., (2009). Integration of biotechnology, plant breeding and crop physiology: dealing with complex interactions from a physiological perspective. In: SADRAS, V. O., AND CALDERINI D, eds. Crop physiology applications for genetic improvement and agronomy. The Netherlands: Elsevier, 267-276.

ARAUS, J. L., SLAFER, G. A., REYNOLDS, M. P., AND ROYO, C. (2002). Plant breeding and water relations in C3 cereals: what should we breed for?. Annals of Botany. 89, 925–940.

ARDUINI, I., MASONI, A., ERCOLI, L., AND MARIOTTI, M. (2006). Grain yield, and dry matter and nitrogen accumulation and remobilization in durum wheat as affected by variety and seeding rate. *European Journal of Agronomy*. **25,** 309–318.

ASANA, R. D AND WILLIAMS, R. F. (1965). The Effect of Temperature Stress on Grain Development in Wheat. *Australian Journal of agricultural Research*. 16, 1-13.

ASSENG, S., CAO, W., ZHANG, W., AND LUDWIG, F., (2009). Crop Physiology, Modelling and Climate Change: Impact and Adaptation Strategies. In: SADRAS, V. O., CALDERINI, D. F, eds. Crop physiology: applications for genetic improvement and agronomy. The Netherlands: Elsevier, 511-543.

AUSTIN, R. B., BINGHAM, J., BLACKWELL, R. D., EVANS, L., FORD, M. A., MORGAN, C.L., AND TAYLOR, M. (1980a). Genetic improvements in winter wheat yields since 1900 and associated physiological changes. *Journal of Agricultural Science*. (Cambridge). **94,** 675–689.

AUSTIN, R. B. (1980b). Physiological limitations to cereals yields and ways of reducing them by breeding. p. 319. In R.G. Hurd et al. (ed.) Opportunities for increasing crop yields: *Association of Applied Biology*. Pitman, Boston, London.

AUSTIN, R. B. (1982). Crop characteristics and the potential yield of wheat. *Journal of Agricultural Science*. (Cambridge). **98**, 447–453.

AUSTIN, R. B. (1999). Yield of Wheat in the United Kingdom: Recent Advances and Prospects. *Crop Science*. **39**, 1604–1610.

AUSTIN, R. B., FORD, M. A., AND MORGAN, C. L. (1989). Genetic improvement in the yield of winter wheat: A further evaluation. *Journal of Agricultural Science*. (Cambridge). **112**, 295–301.

AYENEH, A., M. GINKEL, V., REYNOLDS, M. P., AND AMMAR, K. (2002). Comparison of leaf, spike, peduncle and canopy temperature depression in wheat under heat stress. *Field Crops Research*. **79**, 173-184.

BABAR, M. A., VAN GINKEL, M., KLATT, A. R., PRASAD, B., AND REYNOLDS, M. P. (2006). The potential of using spectral reflectance indices to estimate yield in wheat grown under reduced irrigation. *Euphytica*. **150**, 155–172.

BALOTA. M., PAYNE, W. A., EVETT, S. R., AND LAZAR, M. D. (2007). Canopy Temperature Depression Sampling to Assess Grain Yield and Genotypic Differentiation in Winter Wheat. *Crop Science*. **47**, 1518–1529.

BANCAL, P. (2008). Positive contribution of stem growth to grain number per spike in wheat. *Field Crops Research*. **105**, 27–39.

BANCAL, P. (2009). Early development and enlargement of wheat floret primordia suggest a role of partitioning within spike to grain set. *Field Crops Research.* **110**, 44–53.

BARUTCULAR, C., KOC, M., TIRYAKIOGLU, M., AND YAZAR, A. (2006). Trends in performance of Turkish durum wheats derived from the International Maize and Wheat Improvement Center in an irrigated West Asian and North African environment. *Journal of Agricultural Science*, **144**, 317–326.

BELL, M. A., FISCHER, R. A., BYERLEE, D., AND SAYRE, K. (1995). Genetic and agronomic contribution to yield gains: A case study for wheat. *Field Crops Research.* **44**, 55-65.

BERGER, F., GRINI, P. E., SCHNITTGER, A. (2006). Endosperm: an integrator of seed growth and development. *Current Opinion in Plant Biology.* **9**, 664–670.

BERRY, P. M., SPINK, J. H., FOULKES, M. J., AND WADE, A. (2003). Quantifying the contributions and losses of dry matter from non-surviving shoots in four cultivars of winter wheat. *Field Crops Research.* **80**, 111–121.

BERZONSKY W. A., AND LAFEVER, H. N. (1993). Progress in Ohio Soft Red Winter Wheat Breeding: Grain Yield and Agronomic Traits of Cultivars Released from 1871 to 1987. *Crop Science.* **33**, 1382-138.

BEVERIDGE, C. A. (2006). Axillary bud outgrowth: sending a message. *Current Opinion in Plant Biology.* **9**, 35-40

BHATT. G. M. (1972). Inheritance of Heading Date, Plant Height, and Kernel Weight in Two Spring Wheat Crosses. *Crops Science.* **12**, 95-98.

BHULLAR, S. S., AND JENNER, C. F. (1985). Differential Responses to High Temperatures of Starch and Nitrogen Accumulation in the Grain of Four Cultivars of Wheat. *Australian Journal of Plant Physiology.* **12**, 363-75.

BILGE, B., YILDIRIM, M., BARUTCULAR, C., AND GENC, I. (2008). Effect of Canopy Temperature Depression on Grain Yield and Yield Components in Bread and Durum Wheat. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca.***1**, 34-37.

BINDRABAN, P. S., SAYRE, K. D., SOLIS-MOYA, E. (1998). Identifying factors that determine kernel number in wheat. *Field Crops Research.* **58**, 223-234.

BINGHAM, I. J., BLAKE, J., FOULKES, M. J., AND SPINK, J. (2007a). Is barley yield in the UK sink limited? I. Post-anthesis radiation interception, radiation-use efficiency and source–sink balance. *Field Crops Research.* **101**, 198-211.

BINGHAM, I. J., BLAKE, J., FOULKES, M. J., AND SPINK, J. (2007b). Is barley yield in the UK sink limited? II. Factors affecting potential grain size. *Field Crops Research*. **101**, 212-220.

BITSCH, C., GROGER, S., AND LELLEY, T. (1998). Effect of parental genotypes on haploid embryo and plantlet formation in Wheat × maize crosses. *Euphytica*. **103**, 319–323.

BLAKE, N. K., LANNING, S. P., MARTIN, J. M., DOYLE, M., SHERMAN, J. D., NARUOKA, Y., AND TALBERT, L. E. (2009). Effect of Variation for Major Growth Habit Genes on Maturity and Yield in Five Spring Wheat Populations. *Crop Science*. **49**,1211–1220.

BLUE, E. N., MASON, S. C., AND SANDER, D. H. (1990). Influence of Planting Date, Seeding Rate, and Phosphorus Rate on wheat yield. Agronomy Journal. **82**, 762-768.

BLUM, A. (1990). Variation among wheat cultivars in the response of leaf gas exchange to light. *Journal of Agricultural Science*. **115**, 305-311.

BLUM. A., SINMENA, B., MAYER, J., GOLAN, G., AND SHPILER, L., (1994). Stem Reserve Mobilisation Supports Wheat-grain Filling Under Heat Stress. *Australian Journal of Plant Physiology*. **21**, 771-81.

BORRAS, G., ROMAGOSA, I., VAN EEUWIJK, F., AND SLAFER, G. A. (2009). Genetic variability in duration of pre-heading phases and relationships with leaf appearance and tillering dynamics in a barley population. *Field Crops Research*. **113**, 95–104.

BORRAS, L., SLAFER, G. A., AND OTEGUI, M. E. (2004). Seed dry weight response to source–sink manipulation in wheat, maize, and soybean: A quantitative reappraisal. *Field Crops Research*. **86**, 131–146.

BORRELL, A. K., INCOLL, L. D., AND DALLING, M. J. (1993). The influence of the *Rht1* and *Rht2* Alleles on the deposition and use of stem reserves in wheat. *Annals of Botany*. **71**, 317-326.

BORRELL, A. K., INCOLL, L. D., AND DALLING, M. J. (1991). The Influence of the *Rht1* and *Rht2* Alleles on the Growth of Wheat Stems and Ears. *Annals of Botany*. **67**, 103-110.

BORRELL, A. K., INCOLL, L. D., SIMPSON, R. J., AND DALLING, M. J. (1989). Partitioning of Dry Matter and the Deposition and Use of Stem Reserves in a Semi-dwarf Wheat Crop. *Annals of Botany*. **63**, 527-539.

BOTWRIGHT, T., REBETZKE, G., CONDON, T., AND RICHARDS, R. (2001). The effect of *rht* genotype and temperature on coleoptile growth and dry matter partitioning in young wheat seedlings. *Australian Journal of Plant Physiology*. **28**, 417–423.

BOUKERROU, L., AND RASMUSSON, D. D. (1990). Breeding for High Biomass Yield in Spring Barley. *Crop Science*. **30**, 31-35.

BRANCOURT-HULMEL, M., DOUSSINAULT, G., LECOMTE, C., BERARD, P., LE BUANEC, B., AND TROTTET, M. (2003). Genetic improvement of agronomic traits of winter wheat cultivars released in France from 1946 to 1992. *Crop Science*. **43**, 37–45.

BRAZAUSKAS, G., PADAKINSKIENE, I., AND RUZGAS, V. (2005). Improved approaches in wheat × maize crossing for wheat doubled haploid production. *Biologija*. **4**, 15–18.

BREMNER, P. M., AND RAWSON, H. M. (1978). The Weights of Individual Grains of the Wheat Ear in Relation to their Growth Potential, the Supply of Assimilate and Interaction between Grains. *Australian Journal of Plant Physiology*. **5**, 61-72.

BRIGGS, J. (2009). Development: the Green Revolution. In Kitchen, R. and Thrift, N. (eds.) *International Encyclopaedia of Human Geography*. 634-638. (Elsevier, Oxford).

BRIM, C. A. (1966). A modified pedigree method of Selection in soybeans. *Crop Science*. **6**, 220.

BRISSON, N., GATE, P., GOUACHE, D., CHARMET, G., OURY, F., AND HUARD, F. (2010). Why are wheat yields stagnating in Europe? A comprehensive data analysis for France. Field Crop Research. 119, 201-212.

BROCKLEHURST, P. A. (1977). Factors controlling grain weight in wheat. *Nature*. **226**, 348–349.

BROOKING, I. R. AND KIRBY, E. J. M. (1981). Interrelationships between stem and ear development in winter wheat: the effects of a Norin 10 dwarfing gene, Gai/Rht2. *Journal of Agricultural Science*. (Cambridge). **97**, 373-381.

BRUCKNERA, P. L., AND FROHBERG, R. C. (1987). Rate and Duration of Grain Fill in Spring Wheat. *Crop Science*. **27**, 451-455.

BUTLER, J. D., BYRNE, P. F., MOHAMMADI, V., CHAPMAN, P. L., AND HALEY, S. D. (2005). Agronomic Performance of *Rht* Alleles in a Spring Wheat Population across a Range of Moisture Levels. *Crop Science*. **45**, 939–947.

CALDERINI, D. F., AND SLAFER, G. A. (1998). Changes in yield and yield stability in wheat during the 20th century. *Field Crops Research*. **57**(3), 335-347.

CALDERINI, D. F., ABELEDO, L. G., SAVIN, R., and SLAFER, G. A. (1999). Effect of temperature and carpel size during pre-anthesis on potential grain weight in wheat. *Journal of Agricultural Science*. **132**, 453-459.

CALDERINI, D. F., ABELEDO, L. G., SAVIN, R., and SLAFER, G. A. (1999b). Final grain weight in wheat as affected by short periods of high temperature during pre- and post-anthesis under field conditions. *Australian Journal of Plant Physiology*. **26**, 453–458.

CALDERINI, D. F., SAVIN, R., ABELEDO, L. G., REYNOLDS, M. P., AND SLAFER, G. A. (2001). The importance of the period immediately preceding anthesis for grain weight determination in wheat. *Euphytica*. **119**, 199–204.

CALDERINI, D. F., REYNOLDS, M. P., SLAFER, G. A., (1999a). Genetic gains in wheat yield and main physiological changes associated with them during the 20th century. In: SATORRE, E. H, SLAFER, G. A, eds. Wheat: ecology and physiology of yield determination. New York: Food Product Press, 351–377.

CALDERINI, D.F., and REYNOLDS, M. P. (2000). Changes in grain weight as a consequence of degraining treatments at pre- and post anthesis in synthetic hexaploid lines of wheat (*Triticum durum* × *T. tauschii*). *Australian Journal of Plant Physiology*. **27**, 183–191.

CALDERINI, D. F., AND SLAFER, G. A. (1999). Has yield stability changed with genetic improvement of wheat yield? *Euphytica*. **107**, 51–59.

CALDERINI, D. F., DRECCER, M. F., AND SLAFER G. A. (1997). Consequences of breeding on biomass, radiation interception and radiation-use efficiency in wheat. *Field crops research*. **52**, 271-281.

CAMPBELL, A. W., GRIFFIN, W. B., BURRITT, D. J. AND CONNER A. J. (2001). The Importance of Light Intensity for Pollen Tube Growth and Embryo Survival in Wheat × Maize Crosses. *Annals of Botany*. **87**, 517-522.

CAMPBELL, A. W., GRIFFIN, W. B., BURRITT, D. J. AND CONNER A. J. (2000). Production of wheat doubled haploids via wide crosses in New Zealand wheat. *New Zealand Journal of Crop and Horticultural Science*. **28**, 185-194.

CANTAGALLO, J. E., MEDAN, D., HALL, A. J. (2004). Grain number in sunflower as affected by shading during floret growth, anthesis and grain setting. *Field Crops Research*. **85**, 191–202.

CARR, P. M., HORSLEY, R. D., AND POLAND, W. W. (2003). Tillage and Seeding Rate Effects on Wheat Cultivars: II. Yield Components. *Crop Science*. **43**, 210–218.

CARTELLE, J., PEDRO, A., SAVIN, R., AND SLAFER, G. A. (2006). Grain weight responses to post-anthesis spikelet-trimming in an old and a modern wheat under Mediterranean conditions. *European Journal of Agronomy*. **25**, 365–371.

CECCARELLI, S., VALKOUN, J., ERSKINE, W., WEIGAND, S., MILLER, R. AND VAN LEUR, J. A. G. (1992). Plant genetic resources and plant improvement as tools to develop sustainable agriculture. *Experimental Agricultural*. **28**, 89-98.

CHAPMAN, S. C., MATHEWS, K. L., TRETHOWAN, R. M., AND SINGH R. P. (2007). Relationships between height and yield in near-isogenic spring wheats that contrast for major reduced height genes. *Euphytica*. **157**, 391–397.

CHEN, C., NEILL, K., WICHMAN, D., AND WESTCOTT, M. (2008). Hard Red Spring Wheat Response to Row Spacing, Seeding Rate, and Nitrogen. *Agronomy Journal*. **100**, 1296 –1302.

COMMURI, P. D., AND JONES, R. J. (2001). High Temperatures during Endosperm Cell Division in Maize: A Genotypic Comparison under In Vitro and Field Conditions. *Crop Science*. **41**, 1122–1130.

COSSANI, C. M., SLAFER, G. A., AND SAVIN, R. (2009). Yield and biomass in wheat and barley under a range of conditions in a Mediterranean site. *Field Crops Research*. **112**, (2-3), 205-213.

COSSANIA, C. M., SLAFER, G. A., AND SAVIN, R. (2011). Do barley and wheat (bread and durum) differ in grain weight stability through seasons and water–nitrogen treatments in a Mediterranean location? *Field Crops Research*. **121**, 240–247.

COX, T. S., SHROYER, J. P., BEN-HUI, L., SEARS, R. G., AND MARTIN, T. J. (1988). Genetic Improvement in Agronomic Traits of Hard Red Winter Wheat Cultivars from 1919 to 1987. *Crop Science*. **28**, 756-76.

CRUZ-AGUADO, J. A., REYES, F., RODES, R., PEREZ, I., AND DORADO, M. (1999). Effect of Source-to-sink Ratio on Partitioning of Dry Matter and 14C-photoassimilates in Wheat during Grain Filling. *Annals of Botany*. **83**, 655-665,

CRUZ-AGUADOA, J. A., RODES, R., PEREZ, I. P., DORADO, M. (2000). Morphological characteristics and yield components associated with accumulation and loss of dry mass in the internodes of wheat. *Field Crops Research*. **66**, 129-139.

DARWINKEL, A. (1978). Ear size in relation to tiller emergence and crop density. *Proceedings of Eucarpia workshop*. Wageningen, the Netherlands, 14-16 November, 1978. Editors: J. H. J. Spiertz and Th. Kramer.

DAS, T. K., AND YADURAJU, N. T. (2011). Effects of missing-row sowing supplemented with row spacing and nitrogen on weed competition and growth and yield of wheat. *Crop & Pasture Science*. **62**, 48–57.

DAVIDSON, D. J., AND CHEVALIER, P. M. (1990). Pre-anthesis Tiller Mortality in Spring Wheat. *Crop Science*. **30**, 832-836.

DAVIDSON, D. J., AND CHEVALIER, P. M. (1992). Storage and Remobilization of Water-Soluble Carbohydrates in Stems of Spring Wheat. *Crop Science*. **32**, 186-190.

DEMOTES-MAINARDA, S., JEUFFROYA, M., AND ROBIN, S. (1999). Spike dry matter and nitrogen accumulation before anthesis in wheat as affected by nitrogen fertilizer: relationship to kernels per spike. *Field Crops Research*. **64**, 249-259.

DIXON, J., NALLEY, L., KOSINA, P., LA ROVERE, R., HELLIN, J., AND AQUINO, P. (2006). Adoption and economic impact of improved wheat varieties in the developing world. *Journal of Agricultural Science*. **144**, 489–502.

DONALD, C. M. (1968). The breeding of crop ideotypes. *Euphytica*. **17**, 385-403.

DONE, A. A., AND WHITTINGTON, W. J. (1980). Effect of plant density and nitrogen on wheat F_1 hybrids and their parents. *Annals of Applied Biology*. **95**, 391-398.

DONMEZ, E., SEARS, R. G., SHROYER, J. P., AND PAULSEN, G. M. (2001). Genetic gain in yield attributes of winter wheat in the Great Plains. *Crop Science*. **41**, 1412–1419.

DRECCER, M. F., VAN HERWAARDEN, A. F., AND CHAPMAN, S. C. (2009). Grain number and grain weight in wheat lines contrasting for stem water soluble carbohydrate concentration. *Field Crops Research*. **112**, 43–54

DUGGAN, B. L., RICHARDS, R. A., AND VAN HERWAARDEN, A. F. (2005b). Agronomic evaluation of a tiller inhibition gene (tin) in wheat. II. Growth and partitioning of assimilate. *Australian Journal of Agricultural Research*. **56**, 179-186.

DUGGAN, B. L., RICHARDS, R. A., VAN HERWAARDEN, A. F., AND FETTELL, N. A. (2005a). Agronomic evaluation of a tiller inhibition gene (tin) in wheat: I. Effect on yield, yield components, and protein content. *Australian Journal of Agricultural Research*. **56**, 169–178.

DUGGAN, B. L., RICHARDS, R. A., AND TSUYUZAKI, H. (2002). Environmental effects on stunting and the expression of a tiller inhibition (tin) gene in wheat. *Functional Plant Biology*. **29**, 45–53.

DUGUID, S. D., AND BRULE-BABELL, A. L. (1994). Rate and duration of grain filling in five spring wheat (Triticum aestivum L.) genotypes. *Canadian Journal of Plant Science*. **74**, 681-686.

DUNCAN, W. G. (1971). Leaf Angles, Leaf Area, and Canopy Photosynthesis. *Crop Science*, **11**, 482-485.

EHDAIE, B., ALLOUSH, G. A., AND WAINES, J. G. (2008). Genotypic variation in linear rate of grain growth and contribution of stem reserves to grain yield in wheat. *Field Crops Research*. **106**, 34-43.

EHDAIE, B., ALLOUSH, G. A., MADORE, M. A., AND WAINES, J. G. (2006). Genetic variation of stem reserves and mobilization in wheat: II. Post anthesis changes in internode water-soluble carbohydrate. *Crop Science*. **46**, 2093-2103.

ELHANI, S., MARTOS, V., RHARRABTI, Y., ROYO, C., DEL MORAL, L.F. G. (2007). Contribution of main stem and tillers to durum wheat (Triticum turgidum L. var. durum) grain yield and its components grown in Mediterranean environments. *Field Crops Research*. **103**, 25–35.

ELLIS, M. H., REBETZKE, G. J., CHANDLER, P., BONNETT, D., SPIELMEYER, W., AND RICHARDS, R. A. (2004). The effect of different height reducing genes on the early growth of wheat. *Functional Plant Biology*. **31**, 583-589.

EVANS L. T., AND DUNSTONE, R. L. (1970). Some physiological aspects of evolution in wheat. *Australian Journal of biological Sciences*. **23**, 725-41.

EVANS, L. T., AND FISCHER, R. A. (1999). Yield potential: its definition, measurement, and significance. *Crop Science*. **39**, 1544–1551.

EVANS, L. T., WARDLAW, I. F., AND FISCHER, R. A. (1975). Wheat. In L. T. Evans, ed. Crop Physiology, p. 101-149. Cambridge, UK, Cambridge University Press.

EVANS, L.T. (1993). Crop Evolution, adaptation and yield. Cambridge Univ. Press, Cambridge.

EVERS, J. B., VOS, J., ANDRIEU, B., AND STRUIK, P. C. (2006). Cessation of Tillering in Spring Wheat in Relation to Light Interception and Red: Far-red Ratio. *Annals of Botany*. **97**, 649–658.

FARIS, D. G., AND DE PAUW, R. M. (1980). Effect of seeding rate on growth and yield of three spring wheat cultivars. *Field Crops Research*. **3**, 289-301.

FARQUHAR, G. D., AND SHARKEY, T. D. (1982). Stomatal conductance and photosynthesis. *Annual Reviews Inc*. P 317-345.

FAOSTAT (2009). (http://faostat.fao.org/site/339/default.aspx).

FERRIS, R., ELLIS, R. H., WHEELER, T. R., AND HADLEY, P. (1998). Effect of High Temperature Stress at Anthesis on Grain Yield and Biomass of Field-grown Crops of Wheat. *Annals of Botany*. **82**, 631-639.

FISCHER R. A., REES, D., SAYRE, K. D., LU, Z-M., CONDON, A.G., AND SAAVEDRA, A. L. (1998). Wheat yield progress associated with higher stomatal conductance and photosynthetic rate and cooler canopies. *Crop Science*. **38**, 1467–1475.

FISCHER, R. A. (2007). Understanding the physiological basis of yield potential in wheat. *Journal of Agricultural Science*. **145**, 99–113.

FISCHER, R. A. (2008). The importance of grain or kernel number in wheat: A reply to Sinclair and Jamieson. *Field Crops Research*. **105**, 15–21.

FISCHER, R. A. (2011). Wheat physiology: a review of recent developments. *Crop & Pasture Science*. **62**, 95–11.

FISCHER, R. A., AND LAING, D. R. (1976). Yield potential in a dwarf spring wheat and response to crop thinning. *Journal of Agricultural Science* (Cambridge). **87**, 113-122.

FISCHER, R. A., AND EDMEADES, G. O. (2010). Breeding and Cereal Yield Progress. *Crop Science*. **50**, S-85–S-98.

FISCHER, R. A., AND MAURER, R. (1976). Crop temperature modification and yield potential in a dwarf spring wheat. *Crop Science*. **16**, 855-859.

FISCHER, R. A., AND STOCKMAN, Y. M. (1986). Increased Kernel Number in Norin 10-derived Dwarf Wheat: Evaluation of the Cause. *Australian Journal of Plant Physiology*. **13**, 767-84.

FISCHER, R. A., AGUILAR, M., MAURBR, R., AND RIVAS, A. (1976). Density and row spacing effects on irrigated short wheats at low latitude. *Journal of Agricultural Science*. (Cambridge). **87**, 137-147.

FOULKES, M. J., J. W. SNAPE., V. J. SHERMAN., M. P. REYNOLDS., O. GAJU AND R. SYLVESTER-BRADLEY. (2007). Genetic progress in yield potential in wheat: recent advances and future prospects. *Journal of Agricultural Science*. **145**, 17-29.

FOULKES, M. J., SCOTT, R. K., AND SYLVESTER-BRADLEY, R. (2002). The ability of wheat cultivars to withstand drought in UK conditions: formation of grain yield. *Journal of Agricultural Science*. (Cambridge). **138**, 153–169.

FOULKES, M. J., SLAFER, G. A., DAVIES, W. J., BERRY, P. M., SYLVESTER-BRADLEY, R., MARTRE, P., CALDERINI, D. F., GIFFITHS, S., AND REYNOLDS, M. P. (2011). Raising yield potential of wheat. (III) Optimizing partitioning to grain while maintaining lodging resistance. *Journal of Experimental Botany*. **62**, 469–486.

FOULKES, M. J. SCOTT, R. K., AND SYLVESTER-BRADLEY, R. (2001). The ability of wheat cultivars to withstand drought in UK conditions: resource capture. *Journal of Agricultural Science.* **137**, 1-16.

FOULKES, M. J., SPINK, J. H., SCOTT, R. K., AND CLARE, R.W. (1998). Varietal typing trials and NIAB additional character assessments. *Home-Grown Cereals Authority Final Project Report* No. 174, vol. V. HGCA, London.

FOULKES, M. J., SYLVESTER-BRADLEY, R., WEIGHTMAN, R., AND SNAPE, J. (2007). Identifying physiological traits associated with improved drought resistance in winter wheat. *Field Crops Research.* **103**, 11–24.

FOULKES, M. J., REYNOLDS, M. P., and SYLVESTER-BRADLEY, R. (2009). Genetic improvement of grain crops: Yield Potential. In: SADRAS V. O., AND CALDERINI, D, eds. Crop physiology applications for genetic improvement and agronomy. The Netherlands: Elsevier, 355-385.

FREDERICK, J. R., AND BAUER, P. J. (1999). Physiological and numerical components of wheat yield. In: SATORRE, E. H., SLAFER, G. A, eds. Wheat: ecology and physiology of yield determination. New York: Food Products Press. 45-65.

GAJU, O., REYNOLDS, M. P., SPARKES, D. L., AND FOULKES, M. J. (2009). Relationships between large-spike phenotype, grain number and yield potential in spring wheat. *Crop Science.* **49**, 961–973.

GAO, X., FRANCIS, D., JOHN, ORMROD, C., AND BENNETT, M. D. (1992). Changes in Cell Number and Cell Division Activity during Endosperm Development in Allohexaploid Wheat, Triticum aestivum L. *Journal of Experimental Botany.* **43**, (257) 1603-1609.

GARCIA, G. A., ROMAN, A., SERRAGO, M. L., LOMBARDO, A. L. A., VANZETTI, L. S., HELGUERA, M., AND MIRALLES, D. J. (2011). Variability of duration of pre-anthesis phases as a strategy for increasing wheat grain yield. *Field Crops Research.* **124**, 408–416.

GARDNER, F. P., PEARCE, R. B., MITCHELL, R. L. (1985) (ed.): Physiology of Crop Plants. Iowa State University Press, Ames. 327 pp.

GEBEYEHOU, G., KNOTT, D. R., AND BAKER, R. J. (1982). Rate and Duration of Grain Filling in Durum Wheat Cultivars. *Crop Science.* **22**, 337-340.

GEGAS, V. C., NAZARI, A., GRIFFITHS, S., SIMMONDS, J., FISH, L., ORFORD, S., SAYERS, L., DOONAN, J. H., AND SNAPE, J. W. 2010. A genetic framework for grain size and shape variation in wheat. *Plant Cell.* **22**, 1046–56.

GELETA, B., ATAK, M., BAENZIGER, P. S., NELSON, L. A., BALTENESPERGER, D. D., ESKRIDGE, K. M., SHIPMAN, M. J., AND SHELTON, D. R. (2002). Seeding Rate and Genotype Effect on Agronomic Performance and End-Use Quality of Winter Wheat. *Crop Science*. **42**, 827-832.

GIBSON, L. R., AND PAULSEN, G. M. (1999). Yield components of wheat grown under high temperature stress during reproductive growth. *Crop Science*. **39**, 1841-1846.

GILL, B. S., AND FRIEBE, B. (2002). Cytogenetics, phylogeny and evolution of cultivated wheats. In: B.C. Curtis, S. Rajaram and H. Gomez Macpherson. Bread wheat, improvement and introduction. Food and agriculture organization of the United Nations. Rome.

GLEADOW, R. M., DALLING, M. J., AND HALLORAN, G. M. (1982). Variation in Endosperm Characteristics and Nitrogen Content in Six Wheat Lines. *Australian Journal of Plant Physiology*. **9**, 539-551.

GONZALEZ, F. G., TERRILE, I. I., AND FALCON, M. O. (2011b). Spike Fertility and Duration of Stem Elongation as Promising Traits to Improve Potential Grain Number (and Yield): Variation in Modern Argentinean Wheats. *Crop Science*. **51**,1693–1702.

GONZALEZ, F. G., MIRALLES, D. J., AND SLAFER, G. A. (2011a). Wheat floret survival as related to pre-anthesis spike growth. *Journal of Experimental Botany*. **62**, 1-13.

GRAYBOSCH, R. A., AND PETERSON, C. J. (2010). Genetic Improvement in Winter Wheat Yields in the Great Plains of North America, 1959–2008. *Crop Science*. **50**, 1882–1890.

GREEN, C. F. (1989). Genotypic differences in the growth of Triticum aestivum in relation to absorbed solar radiation. *Field Crops Research*. **19**, 285-295.

HAUGHN, G., CHAUDHURY, A., (2005). Genetic analysis of seed coat development in Arabidopsis. *Trends in Plant Science*. **10**, 472–477.

HAY, R. K. M., AND WALKER, A. J. (1989). An introduction to the physiology of crop yield. Longman scientific & technical.

HEDDEN, P. (2003). The genes of the Green Revolution. *Trends in Genetics*.**19**, (1). 6-9.

HEISEY, P. W. (2002). International Wheat Breeding and Future Wheat Productivity in Developing Countries. Wheat Yearbook/WHS-2002/March. Economic Research Service/USDA.

HEMMAT, A., AND TAKI, O. (2001). Grain yield of irrigated winter wheat as affected by stubble-tillage management and seeding rates in central Iran. *Soil & Tillage Research*. **63**, 57-64.

HUANG, X., WOLF, M., GANAL, M. W., ORFORD, S., KOEBNER, R. M. D., AND RODER, M. S. (2007). Did Modern Plant Breeding Lead to Genetic Erosion in European Winter Wheat Varieties? *Crop Science*. **47**, 343–349.

HUCL, P., AND BAKER, R. J. (1989). Tiller Phenology and Yield of Spring Wheat in a Semiarid Environment. *Crop Science*. **29**, 631-635.

ISHAG, H. M., AND AGEEB, O. A. A. (1991). The physiology of grain yield in wheat in an irrigated tropical environment. *Experimental Agriculture*. **27**, 71-77.

ISIDRO, J., ALVARO, F., ROYO, C., VILLEGAS, D., MIRALLES, D. J., AND GARCIA DEL MORAL, L. F. (2011). Changes in duration of developmental phases of durum wheat caused by breeding in Spain and Italy during the 20th century and its impact on yield. *Annals of Botany*. **107**, 1355–1366.

JACKSON, P., ROBERTSON, M., COOPER, M., AND HAMMER, G. (1996). The role of physiological understanding in plant breeding: from a breeding perspective. *Field Crops Research*. **49**, 11–37.

JENNER, C. F., AND RATHJEN, A. J. (1975). Factors Regulating the Accumulation of Starch in Ripening Wheat Grain. *Australian Journal of Plant Physiology*. **2**, 311-322.

JENNER, C. F., AND RATHJEN, A. J. (1978). Physiological Basis of Genetic Differences in the Growth of Grains of Six Varieties of Wheat. *Australian Journal of Plant Physiology*. **5**, 249-62.

JONES, R. J., ROESSLER, J., AND OUATTAR, S. (1985). Thermal Environment During Endosperm Cell Division in Maize: Effects on Number of Endosperm Cells and Starch Granules. *Crop Science*. **25**, 830-834.

KARANJA, L., KINYUA, M., AND MALINGA, J. (2002). Development of doubled haploid system for wheat through wheat × maize crosses in Kenya. *African Crop Science Journal*. **10**, 311-316.

KEMP, D. R., AND WHINGWIRI, E. E. (1980). Effect of tiller removal and shading on spikelets development and yield components of the main shoot of wheat and on the sugar concentration of the ear and flag leaf. *Australian Journal of Plant Physiology*. **7**, 501-510.

KHUSH, G. (2001). Challenges for meeting the global food and nutrient needs in the new millennium. *Proceedings of the Nutrition Society*. **60**, 15–26.

KIRBY, E. J. M. (1988). Analysis of leaf, stem and ear growth in wheat from terminal spikelet initiation to anthesis. *Field Crops Research*. **18**, 127–140.

KIRBY, E. J. M., AND APPLEYARD, M. (1984). Cereal plant development and its relation to crop management. In. E. J. Callagher, Cereal Production, p. 161-173. Anchor Brendon Ltd, Tiptree, Essex. England.

KOSHKIN, E. I., AND TARARINA, V. V. (1989). Yield and source/sink relations of spring wheat cultivars. *Field Crops Research.* **22**, 297-306.

KRUK, B. C., CALDERINI, D. F., AND SLAFER, G. A., (1997). Grain weight in wheat cultivars released from 1920 to 1990 as affected by post-anthesis defoliation. *Journal of Agricultural Science.* (Cambridge). **128**, 273–281.

LELLEYA, T. C., AND GRAUSGRUBER, E. H. (2004). Influence of 1BL.1RS wheat-rye chromosome translocation on genotype by environment interaction. *Journal of Cereal Science.* **39**, 313–320.

LI, H. L., LUO, Y., AND MA, J. H. (2011). Radiation-use efficiency and the harvest index of winter wheat at different nitrogen levels and their relationships to canopy spectral reflectance. *Crop & Pasture Science.* **62**, 208–217.

LI, W., AND GILL, B. S. (2004). Genomics for cereal improvement. In: Gupta PK, Varshney RK (eds) Cereal Genomics. Kuwer Academic Pub. 585–634.

LIZANA, X. C., RIEGEL, R., GOMEZ, L. D., HERRERA, J. ISLA., A. MCQUEEN-MASON S. J., AND CALDERINI, D. F. (2010). Expansins expression is associated with grain size dynamics in wheat (Triticum aestivum L.). *Journal of Experimental Botany.* **61**, (4), 1147–1157.

LLOVERAS, J., MANET, J., VIUDAS, J., LOPEZ A., AND SANTIVERI, P. (2004). Seeding Rate Influence on Yield and Yield Component of Irrigated Winter Wheat in a Mediterranean Climate. *Agronomy Journal.* **96**, 1258-1265.

LOOMIS, R. S., AND WILLIAMS, W. A. (1963). Maximum Crop Productivity: An Estimate. *Crop Science.* **3**, 67-72.

LOSS, S. P., KIRBY, E. J. M., SIDDIQUE, K. H. M.., AND PERRY, M. W. (1989). Grain growth and development of old and modern Australian wheats. *Field Crops Research.* **21**, 131-146.

LU, Z. (1989). Ratio of stomatal resistance on two sides of wheat leaves as affected by soil water content. *Field Crops Research.* **49**, 1-7.

MA, Y., MACKOWN, C. T., AND VAN SANFORD, D. A. (1996). Differential effects of partial spikelet removal and defoliation on kernel growth and assimilate partitioning among wheat cultivars. *Field Crops Research.* 47, 201-209.

MALUSZYNSKI, M., KASHA, K. J., FORSTER, B. P., AND SZAREJKO, I. (2003). Doubled haploid production in crop plants-A Manual. Kluwer Academic Publisher, The Netherlands. ISBN 1-4020-1544-5.

MARTINEZ-CARRASCO, R., AND THORNE, G. N. (1979). Physiological factors limiting grain size in wheat. *Journal of Experimental Botany*. **30**, 669-679.

MARTINEZ-CARRASCO, R., PEREZ, P., MARTIN DEL MOLINO, I., ULLOA, M., AND ROJO, B. (1988). Regulation of Grain Weight by Supply of Assimilates and Starch Granule Development in Three Winter Wheat Varieties. *Journal of Experimental Botany*. **39**, (209), 1723-1733.

MATHEWS, K. L., CHAPMAN, S. C., TRETHOWAN, R., SINGH, R. P., CROSSA, J. PFEIFFER, W., GINKEL, M. V., AND DELACY, I. (2006). Global Adaptation of Spring Bread and Durum Wheat Lines Near-Isogenic for Major Reduced Height Genes. *Crop Science*. **46**, 603–613.

MCINTYRE, C. L., MATHEWS, K. L., RATTEY, A., CHAPMAN, S. C., DRENTH, J., GHADERI, M., REYNOLDS, M. P., AND SHORTER, R. (2010). Molecular detection of genomic regions associated with grain yield and yield-related components in an elite bread wheat cross evaluated under irrigated and rainfed conditions. *Theoretical and Applied Genetics*. **120**, 527–541.

MILLET, E. (1986). Relationships between grain weight and the size of floret cavity in the wheat spike. *Annals of Botany*. **58**, 417–423.

MILTHORPE. F. L., AND MOORBY, J. (1979). An introduction to crop physiology. Cambridge university press.

MIRALLES, D. J. AND RICHARDS, R. A. (2000). Responses of Leaf and Tiller Emergence and Primordium Initiation in Wheat and Barley to Interchanged Photoperiod. *Annals of Botany*. **85**, 655-663.

MIRALLES, D. J., AND SLAFER, G. A. (1995). Individual grain weight responses to genetic reduction in culm length in wheat as affected by source–sink manipulations. *Field Crops Research*. **43**, 55–66.

MIRALLES, D. J., KATZ, S. D., COLLOCA, A., AND SLAFER, G. A. (1998). Floret development in near isogenic wheat lines differing in plant height. *Field Crops Research*. **59**, 21–30.

MIRI, H. R. (2008). Grain yield and morpho-physiological changes from 60 years of genetic improvement of wheat in Iran. Experimental Agriculture. **45**, 149–163.

MISHRA, S. P., AND MOHAPATRA, P. K. (1987). Soluble Carbohydrates and Floret Fertility in Wheat in Relation to Population Density Stress. *Annals of Botany*. **60**, 269-277.

MITCHELL, J. H., CHAPMAN, S. C., REBETZKE, G. J., AND SHU, F. (2006). Reduced tillering wheat lines maintain kernel weight in dry environments. The 13th of Australian Agronomy Conference. 10-14 September 2006 Perth, Western Australia.

MOHAMED, G. B. S., AND MARSHALL, C. (1979). Physiological aspects of tiller removal in spring wheat. *Journal of Agricultural Science.* (Cambridge). **93**, 457-463.

MONTEITH, J. R. (1972). Solar radiation and productivity in tropical ecosystems. *Journal of Applied Ecology*. **9**, 747–766.

MORENO-SEVILLA, B., BAENZIGER, P. S., PETERSON, C. J., GRAYBOSCH, R. A., AND MCVEY, D. V. (1995). The 1BL/1RS Translocation: Agronomic Performance of F_3-Derived Lines from a Winter Wheat Cross. *Crop Science*. **35**, 1051-1055.

MORGOUNOV, A., ZYKIN, V., BELAN, I., ROSEEVA, L., ZELENSKIY, YU., GOMEZ-BECERRA, H. F., BUDAK, H., AND BEKES, F. (2010). Genetic gains for grain yield in high latitude spring wheat grown in Western Siberia in 1900–2008. *Field Crops Research.* **117**, 101–112.

MOTZO, R., GIUNTA, F., AND DEIDDA, M. (2004). Expression of a tiller inhibitor gene in the progenies of inter-specific crosses *Triticum aestivum* L. × *T. turgidum* subsp. durum. *Field Crops Research.* **85**, 15–20.

MOTZO, R., GIUNTA, F., AND PRUNEDDU, G. (2010). The response of rate and duration of grain filling to long-term selection for yield in Italian durum wheats. *Crop & Pasture Science.* **61**, 162–169.

MOU, B., AND KRONSTAD, W. E. (1994). Duration and Rate of Grain Filling in Selected Winter Wheat Populations: I. Inheritance. *Crop Science*. **34**, 833-837

MURCHIE, E. H., YANG, J., HUBBART, S., HORTON, P., AND PENG, S. (2002). Are there associations between grain-filling rate and photosynthesis in the flag leaves of field-grown rice?. *Journal of Experimental Botany*. **53**, (378), 2217-2224.

NA, T., YING, J., BEI-RU, H., AND YIN-GANG, H. (2009). The Effects of Dwarfing Genes (Rht-B1b, Rht-D1b, and Rht8) with Different Sensitivity to GA3 on the Coleoptile Length and Plant Height of Wheat. *Agricultural Sciences in China.* **8**, 1028-1038.

NICOLAS, M. E., GLEADOW, R., AND DALLING, M. J. (1984). Effects of Drought and High Temperature on Grain Growth in Wheat. *Australian Journal of Plant Physiology.***11**, 553-66.

OLUGBERNI, L. B., AND BUSH, M. G. (1987). The Influence of Temperature on the Contribution of Awns to Yield in Wheat. *Australian Journal of Plant Physiology.* **14**, 299-310.

ORTIZ-MONASTERIO, J. I. R., SAYRE, K. D., RAJARAM, S., AND MCMAHON, M. (1997). Genetic Progress in Wheat Yield and Nitrogen Use Efficiency under Four Nitrogen Rates. *Crop Science*. **37**, 898-904.

OTTESON, B. N., MERGOUM, M., RANSOM, J. K., AND SCHATZ, B. (2008). Tiller Contribution to Spring Wheat Yield under Varying Seeding and Nitrogen Management. Agronomy Journal. **100**, 406–413.

OTTESON, B. N., MERGOUM, M., AND RANSOM, J. K. (2007). Seeding Rate and Nitrogen Management Effects on Spring Wheat Yield and Yield Components. Agronomy Journal. **99**, 1615–1621.

PALTA, J. A., FILLERY, I. R. P., AND REBETZKE, G. J. (2007). Restricted-tillering wheat does not lead to greater investment in roots and early nitrogen uptake. *Field Crops Research*. **104**, 52–59.

PARRY, M., MADGWICK. P. J., CARVAHLO, J. F. C., ANDRALOJC, P. J. (2007). Prospects for increasing photosynthesis by overcoming the limitations of Rubisco. *Journal of Agricultural Science*. **145**, 31–43.

PARRY, M. A. J., REYNOLDS, M., SALVUCCI, M. E., RAINES, C., ANDRALOJC, J. P., ZHU, X., PRICE, G. D., CONDON, A. G., AND FURBANK, R. T. (2011). Raising yield potential of wheat. II. Increasing photosynthetic capacity and efficiency. *Journal of Experimental Botany*. **62**, (2), 453–467.

PEAKE, A. S., GILMOUR, A., AND COOPER, M. (2011). The 1BL/1RS translocation decreases grain yield of spring wheat germplasm in low yield environments of north-eastern Australia. *Crop & Pasture Science*. **62**, 276–288.

PELTONEN, J. (1992). Ear Developmental Stage Used for Timing Supplemental Nitrogen Application to Spring Wheat. *Crop Science*. **32**, 1029-1033.

PELTONEN-SAINIO, P., JAUHIAINEN, L., AND LAURILA, I. P. (2009). Cereal yield trends in northern European conditions: Changes in yield potential and its realisation. *Field Crops Research*. **110**, 85–90.

PENG, S., KHUSH, G. S., VIRK, P., TANG, Q., AND ZOU, Y. (2009). Progress in ideotype breeding to increase rice yield potential. *Field Crops Research*. **108**, 32–38.

PERRY, M. W., AND D'ANTUONO, M. F. (1989). Yield Improvement and Associated Characteristics of some Australian Spring Wheat Cultivars Introduced between 1860 and 1982. *Australian Journal of Agricultural Research*. **40**, 457-72.

PHELOUNG, P. C., AND SIDDIQUE, K. H. M. (1991). Contribution of Stem Dry Matter to Grain Yield in Wheat Cultivars. *Australian Journal of Plant Physiology*. **18**, 53-64.

PINTER J. P. J., ZIPOLI, G., REGINATO, R. J., JACKSON, R. D., IDSO, S. B., AND HOHMAN, J. P. (1990). Canopy temperature as an indicator of differential water use and yield performance among wheat cultivars. *Agricultural water management*. **18**, 35-48.

POELHAM, J. M., AND SLEPER, D. A. (1995). Breeding field crops. (4th ed.). Iowa State Univ. Pr., Ames. 494P.

RADLEY, M. (1976). The Development of Wheat Grain in Relation to Endogenous Growth Substances. *Journal of Experimental Botany*. **27**, (100), 1009-1021.

RAJARAM, S. (1994). Wheat Germplasm Improvement: Historical Perspectives, Philosophy, Objectives, and Missions. In: Wheat Breeding at CIMMYT: Commemorating 50 Years of Research in Mexico for Global Wheat Improvement. Editors: S. Rajaram and G.P. Hettel. Ciudad Obregon, Sonora, Mexico 21-25 March. International Maize and Wheat Improvement Center, (CIMMYT).

RASMUSSON, D. C. (1991). A plant breeder's experience with ideotype breeding. *Field Crops Research*. **26**, 191-200.

RATTEY, A., SHORTER, R., CHAPMAN, S., DRECCER, F., AND VAN HERWAARDEN, A. (2009). Variation for and relationships among biomass and grain yield component traits conferring improved yield and grain weight in an elite wheat population grown in variable yield environments. *Crop & Pasture Science*. **60**, 717–729.

RAWSON, H. M., AND GOMEZ, H. M. (2000). Irrigated wheat, managing your crop. Food and Agriculture Organization of the United Nation. Rome. Italy.

REIF, J. C., ZHANG, P., DREISIGACKER, S., WARBURTON, M. L., VAN GINKEL, M., HOISINGTON, D., BOHN, M., MELCHINGER, A. E. (2005). Wheat genetic diversity trends during domestication and breeding. *Theoretical and Applied Genetics*. **110**, 859–864.

REYNOLDS, M. P., AND BORLAUG, N. E. (2006). Impacts of breeding on international collaborative wheat improvement. *Journal of Agricultural Science*. **144**, 3–17.

REYNOLDS, M. P., DRECCER, F., TRETHOWAN, R. (2007). Drought-adaptive traits derived from wheat wild relatives and landraces. *Journal of Experimental Botany*. **58**, 177–186.

REYNOLDS, M. P., ACEVEDO, E., SAYRE, K. D., AND FISCHER, R. A. (1994). Yield potential in modern wheat varieties: its association with a less competitive ideotype. *Field Crops Research*. **37**, 149-160.

REYNOLDS, M. P., SAYRE, K. D., AND RAJARAM, S. (1999). Physiological and genetic changes in irrigated wheat in the post green revolution period and approaches for meeting projected global demand. *Crop Science*. **39**, 1611–1621.

REYNOLDS, M. P., BALOTA, M., DELGADO, M. I. B., AMANI, I., AND FISCHER, R. A. (1994). Physiological and morphological traits associated with spring wheat yield under hot, irrigated conditions. *Australian Journal of Plant Physiology*. **21**,717–730.

REYNOLDS, M. P., AGEEB, O. A. A., NAGARAJAN, S., RAZZAQUE, M. A., AND RAJARAM, S. (1997). Analysis of the Relationship between Physiological Traits and International Yield Data In: M.P. Reynolds, S. Nagarajan, M.A. Razzaque, and Ageeb. 1997. Using Canopy Temperature Depression to Select for Yield Potential of Wheat in Heat-Stressed Environments. pp 6-18.

REYNOLDS, M. P., HOBBS, P. R., AND BRAUN, H. J. (2007). Challenges to international wheat improvement. *Journal of Agricultural Science*. **145**, 223–227.

REYNOLDS, M. P., PELLEGRINESCHI, A., SKOVMAND, B. (2005). Sink-limitation to yield and biomass: a summary of some investigations in spring wheat. *Annals of Applied Biology*. **146**, 39–49.

REYNOLDS, M., FOULKES, M. J., SLAFER, G., BERRY, P., PARRY, MAJ., SNAPE, J. W., ANGUS, W. J. (2009). Raising yield potential in wheat. *Journal of Experimental Botany*. **60**, 1899–1918.

REYNOLDS, M., BONNETT, D., CHAPMAN, S. C., YANN, MANES R. T. F., MATHER, D. E., AND PARRY, M. A. J. (2011). Raising yield potential of wheat. I. Overview of a consortium approach and breeding strategies. *Journal of Experimental Botany*. **62**, (2), 439–452.

REYNOLDS. M. P., DELGADO, M. I. B., GUTIERREZ-RODRIGUEZ, M., AND LARQUE-SAAVEDRA, A. (2000). Photosynthesis of wheat in a warm, irrigated environment I: Genetic diversity and crop productivity. *Field Crops Research*. **66**, 37-50.

REYNOLDS, M., AND TUBEROSA, R. (2008). Translational research impacting on crop productivity in drought-prone environments. *Current Opinion in Plant Biology*. **11**, 171–179.

RICHARDS, R. A. (1988). A tiller inhibition gene in wheat and its effect on plant growth. *Australian Journal of Agricultural Research*. **39**, 749–757.

RICHARDS, R. A., REBETZKE, G. A., CONDON, A. G., AND VAN HERWAARDEN, A. F. (2002). Breeding opportunities for increasing the efficiency of water use and crop yield in temperate cereals. *Crop Science* **42**, 111–121.

ROYO, C., ALVARO, F., MARTOS, V., RAMDANI, A., ISIDRO, J., VILLEGAS, D., LUIS, F., AND DEL MORAL, G. (2007). Genetic changes in durum wheat yield components and associated traits in Italian and Spanish varieties during the 20th century. *Euphytica*. **155**, 259–270.

RUUSKA, S, A., REBETZKE, G. J., VAN HERWAARDEN, A. F., RICHARDS, R. A., FETTELL, N. A., TABE, L., AND JENKINS, C. L. D. (2006). Genotypic variation in water-soluble carbohydrate accumulation in wheat. *Functional Plant Biology*. **33**, 799–809.

SANKARAN, V. M., AGGARWAL, P. K., AND SINHA, S. K. (2000). Improvement in wheat yields in northern India since 1965: measured and simulated trends. *Field Crops Research*. **66**, 141-149.

SAYRE, K.D., RAJARAM, S., AND FISCHER, R. A. (1997). Yield potential progress in short bread wheats in northwest Mexico. *Crop Science*. **37**, 36–42.

SENER, O., ARSLAN, M., SOYSALAND, Y., AND ERAYMAN, M. (2009). Estimates of relative yield potential and genetic improvement of wheat cultivars in the Mediterranean region. *Journal of Agricultural Science*. **147**, 323–332.

SHANAHAN, F. K., DONNELLY, J., SMITH, D. H., AND SMIKA, D. E. (1985). Shoot Developmental Properties Associated with Grain Yield in Winter Wheat. *Crop Science*. **25**, 770-775.

SHARMA, R. C. (1995). Tiller mortality and its relationship to grain yield in spring wheat. *Field Crops Research*. **41**, 55-60.

SHARMA, R. C., AND SMITH, E. L. (1987). Effects of Seeding Rates on Harvest Index, Grain Yield, and Biomass Yield in Winter Wheat. *Crop Science*. **27**, 528-531.

SHEARMAN, V. J., SYLVESTER-BRADLEY, R., SCOTT, R. K., AND FOULKES, M. J. (2005). Physiological processes associated with wheat yield progress in UK. *Crop Science*. **45**, 175–185.

SHORTER, R., R. J. LAWN., AND G. L. HAMMER. (1991). IMPROVING GENOTYPIC ADAPTATION IN CROPS – A ROLE FOR BREEDERS, PHYSIOLOGISTS AND MODELLERS. *Experimental Agriculture*. **27**, 155-175.

SIDDIQUE, K. I. F. M., BELFBRD, R. K., PERRY, M. W., AND TENNANT, D. (1989). Growth, Development and Light Interception of Old and Modern Wheat Cultivars in a Mediterranean-type Environment. *Australian Journal of Agricultural Research*. **40**, 473-87.

SINCLAIR, T. R., AND BAIB, Q. (1997). Analysis of High Wheat Yields in Northwest China. *Agricultural Systems*. **53**, 373-385.

SINCLAIR, T. R., JAMIESON, P. D. (2006). Grain number, wheat yield, and bottling beer: An analysis. *Field Crops Research.* **98**, 60–67.

SINGH, R. P., AND TRETHOWAN, R. (2007). Breeding Spring Bread Wheat for Irrigated and Rainfed Production Systems of the Developing World. In: Breeding Major Food Staples. Edited by Manjit S. Kang and P.M. Priyadarshan. Blackwell. Publishing Ltd. 109-140.

SINHA, S. K., AGGARWAL, P. K., CHATURVEDI, G. S., KOUNDAL, K. R., AND A-CHOPRA, R. K. A. (1981). A comparison of physiological and yield characters in old and new wheat varieties. *Journal of Agricultural Science.* (Cambridge). **97**, 233-236.

SLAFER, A. G., AND RAWSON, H. M. (1994). Does temperature affect final numbers of primordia in wheat? *Field Crops Research.* **39**, 111-117.

SLAFER, G. A., AND ANDRADE, F. H. (1993). Physiological attributes related to the generation of grain yield in bread wheat cultivars released at different eras. *Field Crops Research.* **31**, 351–367.

SLAFER, G. A., AND SAVIN, R. (1994a). Grain mass change in a semi-dwarf and a standard height wheat cultivar under different sink-source relationships. *Field Crops Research.* **37**, 39–49.

SLAFER, G. A., ARAUS, J. L., AND RICHARDS, R. A. (1999). Physiological traits that increase the yield potential of wheat. In: Satorre EH, Slafer GA, eds. Wheat: ecology and physiology of yield determination. New York: Food Products Press, 379–415.

SLAFER, G. A., CALDERINI, D. F., AND MIRALLES, D. J. (1996). Yield components and compensation in wheat: opportunities for further increasing yield potential. In M.P. Reynolds, S. Rajaram & A. McNab, eds. Increasing Yield Potential in Wheat: Breaking the Barriers. Workshop Proc., Cd. Obregon, Mexico, 28-30 Mar. 1996. Mexico, DF, CIMMYT.

SLAFER, G. A., KANTOLIC, A. G., APPENDINO, M. L., MIRALLES, D. J., AND SAVIN, R. (2009). Crop development: genetic control, environmental modulation and relevance for genetic improvement of crop yield. In: Sadras VO, Calderini DF, eds. Crop physiology: applications for genetic improvement and agronomy. The Netherlands: Elsevier, 277–308.

SLAFER, G. A., ANDRADE, F. H., AND SATORRE, E. H. (1990). Genetic-Improvement Effects on Pre-Anthesis Physiological Attributes Related to Wheat Grain- Yield. *Field Crops Research.* **23**, 255-263.

SLAFER, G. A., AND ANDRADE, F. H. (1989). Genetic improvement in bread wheat (Triticum aestivum) yield in Argentina. *Field Crop research*. **21**, 289-296.

SMALE, M., REYNOLDS, M. P., WARBURTON, M., SKOVMAND, B., TRETHOWAN, R., SINGH, R. P., ORTIZ-MONASTERIO, I., AND CROSSA, J. (2002). Dimensions of Diversity in Modern Spring Bread Wheat in Developing Countries from 1965. *Crop Science*. **42**, 1766–1779.

SNAPE, J. W., FOULKES, M. J., SIMMONDS, J., LEVERINGTON, M., FISH, L. J., WANG, Y., AND CIAVARRELLA, M. (2007). Dissecting gene3environmental effects on wheat yields via QTL and physiological analysis. *Euphytica*. **154**, 401–408.

SNYDER, G. W., SAMMONS, D. J., AND SICHER, R. C. (1993). Spike removal effects on dry matter production, assimilate distribution and grain yields of three soft red winter wheat genotypes. *Field Crops Research*. **33**, 1-11.

SPARKES, D. L., HOLME, S. J., GAJU, O. (2006). Does light quality initiate tiller death in wheat? *European Journal of Agronomy*. **24**, 212-217

SPIELMEYER, W., AND RICHARDS, R. A. (2004) Comparative mapping of wheat chromosome 1AS which contains the tiller inhibition gene (tin) with rice chromosome 5S. *Theoretical and Applied Genetics*. **109**, 1303–1310.

STEPHEN, R. C., SAVILLE, D. J., AND DREWITT, E. G. (2005). Effects of wheat seed rate and fertiliser nitrogen application practices on populations, grain yield components and grain yields of wheat (Triticum aestivum). *New Zealand Journal of Crop and Horticultural Science*. **33**, 125-138.

STOCKLE, C. O., AND KEMANIAN, A. R. (2009). Crop radiation capture and use efficiency: A frame work for crop growth analysis. In: SADRAS, V. O., CALDERINI, D, eds. Crop physiology applications for genetic improvement and agronomy. The Netherlands: Elsevier, 145-170.

STOSKOPF, N. C. (1981). Understanding Crop Production. Reston Publishing Company, Inc. Reston, Virginia. 433 pp.

SUN P. L. F., SHANDS, H. L., AND FORSBERG, R. A. (1972). Inheritance of Kernel Weight in Six Spring Wheat Crosses. *Crop Science*. **12**, 1-5.

TALBERT L. E., LANNING, S. P., MURPHY, R. L., AND MARTIN, J. M. (2001). Grain Fill Duration in Twelve Hard Red Spring Wheat Crosses: Genetic Variation and Association with Other Agronomic Traits. *Crop Science*. **41**, 1390–1395.

TASHIRO, T., AND WARDLAW, I. F. (1989). A Comparison of the Effect of High Temperature on Grain Development in Wheat and Rice. *Annals of Botany.* **64**, 59-65.

THORNE, G. N. AND WOOD, D. W. (1987). Effects of Radiation and Temperature on Tiller Survival, Grain Number and Grain Yield in Winter Wheat. *Annals of Botany.* **59**, 413-426.

THORNE, G. N., AND WOOD, D. W. (1988). Contributions of shoot categories to growth and yield of winter wheat. *Journal of Agricultural Science.* (Cambridge).**111**, 285-294.

TIAN, Z., JING, Q., DAI, T., JIANG, D., AND CAO, W. (2011). Effects of genetic improvements on grain yield and agronomic traits of winter wheat in the Yangtze River Basin of China. *Field Crops Research.* **124**, 417–425

TOTTMAN, R. (1987). The decimal code for growth stages of cereals with illustrations. *Annals of Applied Biology.* **110**, 441–454.

UGARTE, C., CALDERINI, D. F., SLAFER, G. A.(2007). Grain weight and grain number responsiveness to pre-anthesis temperature in wheat, barley and triticale. *Field Crops Research.* **100**, 240–248.

UNDERDAHL, J., MERGOUM, M., RANSOM, J. K., AND SCHATZ, B. G. (2008). Agronomic Traits Improvement and Associations in Hard Red Spring Wheat Cultivars Released in North Dakota from 1968 to 2006. *Crop Science.* **48**, 158–166.

VERMA. V., BAINS, N. S., MANGAT ,G. S., NANDA, G. S., GOSAL, S. S., AND SINGH, K. (1999). Maize Genotypes Show Striking Differences for Induction and Regeneration of Haploid Wheat Embryos in the Wheat × Maize System. *Crop Science.* **39**, 1722–1727.

VILLAREAL, R. L., BANUELOS, O., MUJEEB-KAZI, A., AND RAJARAM, S. (1998). Agronomic performance of chromosomes 1B and T1BL.1RS near-isolines in the spring bread wheat Seri M82. *Euphytica.* **103**, 195–202.

WADDINGTON, S. R., RANSOM, J. K., OSMANZAI, M., AND SAUNDERS, D. A. (1986). Improvement in the yield potential of bread wheat adapted to northwest Mexico. *Crop Science.* **26**, 698–703.

WADDINGTON, S. R., OSMANZAI, M., YOSHIDA, M., AND RANSOM, J. K. (1987). The yield of durum wheats released in Mexico between 1960 and 1984. *Journal of Agricultural Science.* **108**, 469-477.

WALPOLE, P. R., AND MORGAN, D. G. (1974). The Influence of Leaf Removal upon the Development of the Grain of Winter Wheat. *Annals of Botany.* **38**, 779-782.

WARDLAW, I. F., SOFIELD, I., AND CARTWRIGHT, P. M. (1980). Factors Limiting the Rate of Dry Matter Accumulation in the Grain of Wheat Grown at High Temperature. *Australian Journal of Plant Physiology.* **7**, 387-400.

WARDLAW, I. F. (1994). The Effect of High Temperature on Kernel Development in Wheat: Variability Related to Pre-heading and Post-anthesis Conditions. *Australian Journal of Plant Physiology.* **21**, 731-739.

WATSON D. J., THORNE, G., AND FRENCH, S. A. W. (1963). Analysis of Growth and Yield of Winter and Spring Wheats. *Annals of Botany.* **27**, 1-22.

WELSH, J. (1981). Fundamentals of plant genetics and breeding. John Wiley & sons. Inc. USA.

WHALEY, J. M., SPARKES, D. L., FOULKES, M. J., SPINK, J. H., SEMERE, T., AND SCOTT, R. K. (2000). The physiological response of winter wheat to reductions in plant density. *Annals of Applied Biology.* **137**, 165–177.

WIEGAND, C. L., AND CUELLAR, J. A. (1981). Duration of Grain Filling and Kernel Weight of Wheat as Affected by Temperature. *Crop Science.* **21**, 95-101.

WIERSMA, J. J., BUSCH, R. H., FULCHER, G. G., AND HARELAND, G. A. (2001). Recurrent Selection for Kernel Weight in Spring Wheat. *Crop Science.* **41**, 999–1005.

WONG, L. S. L., AND BAKER, R. J. (1986). Developmental Patterns in Five Spring Wheat Genotypes Varying in Time to Maturity. *Crop Science*, **26**, 1167-1170.

WOUW, M. V., KIK, C., HINTUM, T. V., TREUREN, R. V., AND VISSER, B. (2009). Genetic erosion in crops: concept, research results and challenges. *Plant Genetic Resources: Characterization and Utilization* **8**, 1–15.

WSON, H. M. R. (1971). Tillering patterns in wheat with special reference to the shoot at the coleoptile node. *Australian Journal of Biological Sciences.* **24**, 829-841.

XIAO, Y. G., QIAN, Z. G., WU, K., LIU, J. J., XIA, X. C., JI, W. Q., AND HE, Z. H. (2012). Genetic Gains in Grain Yield and Physiological Traits of Winter Wheat in Shandong Province, China, from 1969 to 2006. *Crop Science.* **52**, 44–56

YANG, Z., VAN, O. E. J., JORDAN, D. R., AND HAMMER, G. L. (2009). Pre-anthesis ovary development determines genotypic differences in potential kernel weight in sorghum. *Journal of Experimental Botany*. **60**, 1399–1408.

YEMM, E. W., AND WILLIS, A. J. (1954). The estimation of carbohydrates in plant extracts by anthrone. *Biochemical Journal*. **57**, 508–514.

YIN, X., GUO, W., SPIERTZ, J. H. (2009) A quantitative approach to characterize sink–source relationships during grain filling in contrasting wheat genotypes. *Field Crops Research*. **114**, 119–126.

YU, Z., VAN SANFORD, D. A., AND EGLIF, D. B. (1988). The Effect of Population Density on Floret Initiation, Development and Abortion in Winter Wheat. *Annals of Botany*. **62**, 295-302.

YUNUSA, I. A. M., SIDDIQUE, K. H. M., BELFORD, R. K., AND KARIMI, M. M. (1993). Effect of canopy structure on efficiency of radiation interception and use in spring wheat cultivars during the pre-anthesis period in a Mediterranean-type environment. *Field Crops Research*. **35**, 113-122.

ZADOKS, J. C., CHANG, T. T., AND KONZAK, C. F. (1974). A decimal code for the growth stages of cereals. *Weed Research*. **14**, 415-421.

ZARCO-HERNANDEZ. J. A., SANTIVERI, F., MICHELENA, A., PENA, R. J. (2005). Durum wheat (Triticum turgidum, L.) carrying the 1BL/1RS chromosomal translocation: agronomic performance and quality characteristics under Mediterranean conditions. *European Journal of Agronomy*. **22**, 33–43.

ZHANG, H., TURNER, N. C., AND POOLE, M. L. (2010). Source–sink balance and manipulating sink–source relations of wheat indicate that the yield potential of wheat is sink limited in high-rainfall zones. *Crop & Pasture Science*. **61**, 852–861.

ZHENG, T. C., ZHANG, X. K., YIN, G. H., WANG, L. N., HAN, Y. L., CHEN, L., HUANG, F., TANG, J. W., XIA, X. C., AND HE, Z. H. (2011). Genetic gains in grain yield, net photosynthesis and stomatal conductance achieved in Henan Province of China between 1981 and 2008. *Field Crops Research*. 122, 225–233.

ZHOU, Y., HE, Z. H., SUIC, X. X., XIAA, X. C., ZHANG, X. K., AND ZHANG, G. S. (2007). Genetic improvement of grain yield and associated traits in the northern china winter wheat Region from 1960 to 2000. *Crop Science*. **47**, 245–253.

ZOHARYI, D., HARLAN, J. R., AND VARDI, A. (1969). The wild diploid progenitors of wheat and their breeding value. *Euphytica*. **18**, 58-65.

CHAPTER 10 APPENDICES

10.1 Appendix I: Field experimental designs

10.1.1 Experiments at CIMMYT C. Obregon Mexico

10.1.1.1 CIMMYT wheat historic releases experiments 2008/09 and 2009/10

Table A1 A randomized complete block design with four replications and 16 cultivars within each replicate.

15	11	7	12	6	3	13	2	Rep 4
16	1	14	9	8	4	10	5	
3	14	10	7	4	11	16	6	Rep 3
8	13	12	1	9	15	5	2	
14	15	4	12	1	2	16	7	Rep 2
13	5	11	10	8	9	6	3	
16	15	14	13	12	11	10	9	Rep 1
1	2	3	4	5	6	7	8	

10.1.1.2 CIMMYT L14 x Rialto DH population (*Tin1A*) experiments 2008/09 and 2009/2010

Table A2 A split plot randomised complete block design with three main plots (seed rates) and 12 sub-plots (lines) randomized in three replications (Yellow plots are *Tin1A* lines and blue are non *Tin1A* lines)

97 L 124	98 L 36	99 L 67	100 L 96	101 L 48	102 L 1	103 L 93	104 L 87	105 L 61	106 L 90	107 L 31	108 L 51	D 150	Rep III
96 L 51	95 L 31	94 L 90	93 L 61	92 L 87	91 L 93	90 L 1	89 L 48	88 L 96	87 L 67	86 L 36	85 L 124	D 50	
73 L 124	74 L 36	75 L 67	76 L 96	77 L 48	78 L 1	79 L 93	80 L 87	81 L 61	82 L 90	83 L 31	84 L 51	D 450	
72 L 51	71 L 96	70 L 87	69 L 93	68 L 61	67 L 36	66 L 1	65 L 67	64 L 48	63 L 31	62 L 90	61 L 124	D 150	Rep II
49 L 124	50 L 90	51 L 31	52 L 48	53 L 67	54 L 1	55 L 36	56 L 61	57 L 93	58 L 87	59 L 96	60 L 51	D 450	
48 L 51	47 L 96	46 L 87	45 L 93	44 L 61	43 L 36	42 L 1	41 L 67	40 L 48	39 L 31	38 L 90	37 L 124	D 50	
25 L 1	26 L 31	27 L 36	28 L 48	29 L 51	30 L 61	31 L 67	32 L 87	33 L 90	34 L 93	35 L 96	36 L 124	D 450	Rep I
24 L 124	23 L 96	22 L 93	21 L 90	20 L 87	19 L 67	18 L 61	17 L 51	16 L 48	15 L 36	14 L 31	13 L 1	D 150	
1 L 1	2 L 31	3 L 36	4 L 48	5 L 51	6 L 61	7 L 67	8 L 87	9 L 90	10 L 93	11 L 96	12 L 124	D 50	

10.1.2 Experiments at the UK

10.1.2.1 Experiment at Thriplow, Hertfordshire UK 2008/09

Table A3 A randomized complete block design with three replications and 135 DH lines within each replicate.

Rep 1

237 RxL14 #36	270 RxL14 #70	328 RxL14 #137	222 RxL14 #21	282 RxL14 #84	254 RxL14 #54	204 RxL14 #2	316 RxL14 #125	298 RxL14 #104	251 RxL14 #51	228 RxL14 #27	336 RxL14 #120	260 RxL14 #60	218 RxL14 #17	292 RxL14 #95	319 RxL14 #128	220 RxL14 #19	301 RxL14 #107	299 RxL14 #105	249 RxL14 #49	272 RxL14 #73	221 RxL14 #20	321 RxL14 #130	209 RxL14 #7	327 RxL14# 136	231 RxL14 #30	257 RxL14 #57
217 RxL14 #16	289 RxL14 #92	240 RxL14 #39	311 RxL14 #118	330 Rialto ex Comme rcial	302 RxL14 #109	203 RxL14 #1	280 RxL14 #82	268 RxL14 #68	309 RxL14 #116	213 RxL14 #11	239 RxL14 #38	306 RxL14 #113	290 RxL14 #93	273 RxL14 #74	234 RxL14 #33	324 RxL14 #133	259 RxL14 #59	294 RxL14 #100	333 RxL14 #76	265 RxL14 #65	262 RxL14 #62	224 RxL14 #23	201 Rialto ex CPBT	232 RxL14# 310	325 RxL14 #134	253 RxL14 #53
236 RxL14 #35	261 RxL14 #61	227 RxL14 #26	322 RxL14 #131	208 RxL14 #6	329 RxL14 #138	247 RxL14 #47	271 RxL14 #71	297 RxL14 #103	335 RxL14 #98	313 RxL14 #121	291 RxL14 #94	269 RxL14 #69	245 RxL14 #45	207 RxL14 #5	225 RxL14 #24	286 RxL14 #89	248 RxL14 #48	283 RxL14 #85	304 RxL14 #111	318 RxL14 #127	210 RxL14 #8	238 RxL14 #37	235 RxL14 #34	315 RxL14# 124	279 RxL14 #81	256 RxL14 #56
246 RxL14 #46	206 RxL14 #4	293 RxL14 #96	219 RxL14 #18	267 RxL14 #67	312 RxL14 #119	243 RxL14 #42	332 RxL14 #88	285 RxL14 #87	215 RxL14 #14	202 Humbe r	241 Rialto ex NIJ	334 RxL14 #13	288 RxL14 #91	317 RxL14 #126	308 RxL14 #115	275 RxL14 #77	264 RxL14 #64	287 RxL14 #90	266 RxL14 #66	211 RxL14 #9	331 RxL14 #122	278 RxL14 #80	310 RxL14 #117	205 RxL14# 3	242 RxL14 #41	303 RxL14 #110
281 RxL14 #83	284 RxL14 #86	216 RxL14 #15	314 RxL14 #123	263 RxL14 #63	229 RxL14 #28	326 RxL14 #135	300 RxL14 #106	244 RxL14 #43	295 RxL14 #101	305 RxL14 #112	226 RxL14 #25	276 RxL14 #78	250 RxL14 #50	255 RxL14 #55	214 RxL14 #12	230 RxL14 #29	320 RxL14 #129	274 RxL14 #75	212 RxL14 #10	233 RxL14 #32	307 RxL14 #114	323 RxL14 #132	296 RxL14 #102	258 RxL14# 58	252 RxL14 #52	223 RxL14 #22

Table A3 continued

Rep 2

252 RxL 14# 52	277 RxL 14# 79	318 RxL 14# 127	230 RxL 14#2 9	224 Rx L14 #23	310 RxL 14# 117	300 RxL 14# 106	290 RxL 14# 93	208 Rx L14 #6	259 RxL 14# 59	233 Rx L14 #32	214 Rx L14 #12	284 RxL 14# 86	311 RxL 14# 118	304 RxL 14# 111	331 RxL 14#1 22	227 RxL 14# 26	251 RxL 14# 51	220 RxL 14# 19	335 RxL 14# 98	244 RxL 14# 43	234 Rx L14 #33	279 RxL 14# 81	266 RxL 14# 66	312 RxL 14# 119	289 Rx L14 #92	308 RxL 14# 115
222 RxL 14# 21	314 RxL 14# 123	292 RxL 14# 95	232 RxL 14#3 1D	276 Rx L14 #78	209 RxL 14# 7	258 RxL 14# 58	324 RxL 14# 133	247 Rx L14 #47	296 RxL 14# 102	204 Rx L14 #2	255 Rx L14 #55	309 RxL 14# 116	301 RxL 14# 107	271 RxL 14# 71	219 RxL 14#1 8	231 RxL 14# 30	253 RxL 14# 53	262 RxL 14# 62	243 RxL 14# 42	305 RxL 14# 112	254 Rx L14 #54	297 RxL 14# 103	323 RxL 14# 132	272 RxL 14# 73	215 Rx L14 #14	207 RxL 14# 5
322 RxL 14# 131	299 RxL 14# 105	203 RxL 14# 1	241 Rialt o ex NU	211 Rx L14 #9	248 RxL 14# 48	333 RxL 14# 76	282 RxL 14# 84	267 Rx L14 #67	281 RxL 14# 83	287 Rx L14 #90	218 Rx L14 #17	302 RxL 14# 109	313 RxL 14# 121	239 RxL 14# 38	334 RxL 14#1 3	223 RxL 14# 22	256 RxL 14# 56	320 RxL 14# 129	294 RxL 14# 100	246 RxL 14# 46	245 Rx L14 #45	329 RxL 14# 138	257 RxL 14# 57	270 RxL 14# 70	217 Rx L14 #16	202 Hu mbe r
250 RxL 14# 50	326 RxL 14# 135	236 RxL 14# 35	274 RxL 14#7 5	221 Rx L14 #20	306 RxL 14# 113	260 RxL 14# 60	315 RxL 14# 124	201 Rial to ex CP PT	242 RxL 14# 41	264 Rx L14 #64	293 Rx L14 #96	280 RxL 14# 82	321 RxL 14# 130	216 RxL 14# 15	328 RxL 14#1 37	286 RxL 14# 89	235 RxL 14# 34	295 RxL 14# 101	307 RxL 14# 114	319 RxL 14# 128	261 Rx L14 #61	265 RxL 14# 65	225 RxL 14# 24	206 RxL 14# 4	237 Rx L14 #36	249 RxL 14# 49
210 RxL 14# 8	327 RxL 14# 136	298 RxL 14# 104	240 RxL 14#3 9	285 Rx L14 #87	325 RxL 14# 134	205 RxL 14# 3	269 RxL 14# 69	275 Rx L14 #77	263 RxL 14# 63	228 Rx L14 #27	283 Rx L14 #85	273 RxL 14# 74	226 RxL 14# 25	212 RxL 14# 10	330 Rialt o ex Com merc	317 RxL 14# 126	303 RxL 14# 110	291 RxL 14# 94	268 RxL 14# 68	278 RxL 14# 80	288 Rx L14 #91	332 RxL 14# 88	316 RxL 14# 125	229 RxL 14# 28	238 Rx L14 #37	213 RxL 14# 11

Table A3 continued

Rep 3

309 RxL14 #116	310 RxL14 #117	311 RxL14 #118	312 RxL14 #119	313 RxL14 #121	314 RxL14 #123	315 RxL14 #124	316 RxL14 #125	317 RxL14 #126	318 RxL14 #127	319 RxL14 #128	320 RxL14 #129	321 RxL14 #130	322 RxL14 #131	323 RxL14 #132	324 RxL14 #133	325 RxL14 #134	326 RxL14 #135	327 RxL14 #136	328 RxL14 #137	329 RxL14 #138	330 Rialto ex Commercial	331 RxL14# 122	332 RxL14 #88	333 RxL14 #76	334 RxL14 #13	335 RxL14 #98
308 RxL14 #115	307 RxL14 #114	306 RxL14 #113	305 RxL14 #112	304 RxL14 #111	303 RxL14 #110	302 RxL14 #109	301 RxL14 #107	300 RxL14 #106	299 RxL14 #105	298 RxL14 #104	297 RxL14 #103	296 RxL14 #102	295 RxL14 #101	294 RxL14 #100	293 RxL14 #96	292 RxL14 #95	291 RxL14 #94	290 RxL14 #93	289 RxL14 #92	288 RxL14 #91	287 RxL14 #90	286 RxL14# 89	285 RxL14 #87	284 RxL14 #86	283 RxL14 #85	282 RxL14 #84
255 RxL14 #55	256 RxL14 #56	257 RxL14 #57	258 RxL14 #58	259 RxL14 #59	260 RxL14 #60	261 RxL14 #61	262 RxL14 #62	263 RxL14 #63	264 RxL14 #64	265 RxL14 #65	266 RxL14 #66	267 RxL14 #67	268 RxL14 #68	269 RxL14 #69	270 RxL14 #70	271 RxL14 #71	272 RxL14 #73	273 RxL14 #74	274 RxL14 #75	275 RxL14 #77	276 RxL14 #78	277 RxL14# 79	278 RxL14 #80	279 RxL14 #81	280 RxL14 #82	281 RxL14 #83
254 RxL14 #54	253 RxL14 #53	252 RxL14 #52	251 RxL14 #51	250 RxL14 #50	249 RxL14 #49	248 RxL14 #48	247 RxL14 #47	246 RxL14 #46	245 RxL14 #45	244 RxL14 #43	243 RxL14 #42	242 RxL14 #41	241 Rialto ex NU	240 RxL14 #39	239 RxL14 #38	238 RxL14 #37	237 RxL14 #36	236 RxL14 #35	235 RxL14 #34	234 RxL14 #33	233 RxL14 #32	232 RxL14# 310	231 RxL14 #30	230 RxL14 #29	229 RxL14 #28	228 RxL14 #27
201 Rialto ex CPBT	202 Humber	203 RxL14 #1	204 RxL14 #2	205 RxL14 #3	206 RxL14 #4	207 RxL14 #5	208 RxL14 #6	209 RxL14 #7	210 RxL14 #8	211 RxL14 #9	212 RxL14 #10	213 RxL14 #11	214 RxL14 #12	215 RxL14 #14	216 RxL14 #15	217 RxL14 #16	218 RxL14 #17	219 RxL14 #18	220 RxL14 #19	221 RxL14 #20	222 RxL14 #21	223 RxL14# 22	224 RxL14 #23	225 RxL14 #24	226 RxL14 #25	227 RxL14 #26

10.1.2.2 - Experiment at Sutton Bonington, Leicestershire UK 2009/10

Table A4 A split plot randomised complete block design with two main plots (seed rates) and 25 sub-plots (lines) randomized in three replications

Rep 1

Discard	78	114	34	129	48	93	110	1	65	101	30	2	24	25	4	60	47	9	59	124	Rialto	86	112	61	90	Discard
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
Discard	112	2	86	24	65	1	9	25	30	114	59	93	34	60	Rialto	90	61	4	48	129	101	78	110	124	47	Discard
	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	

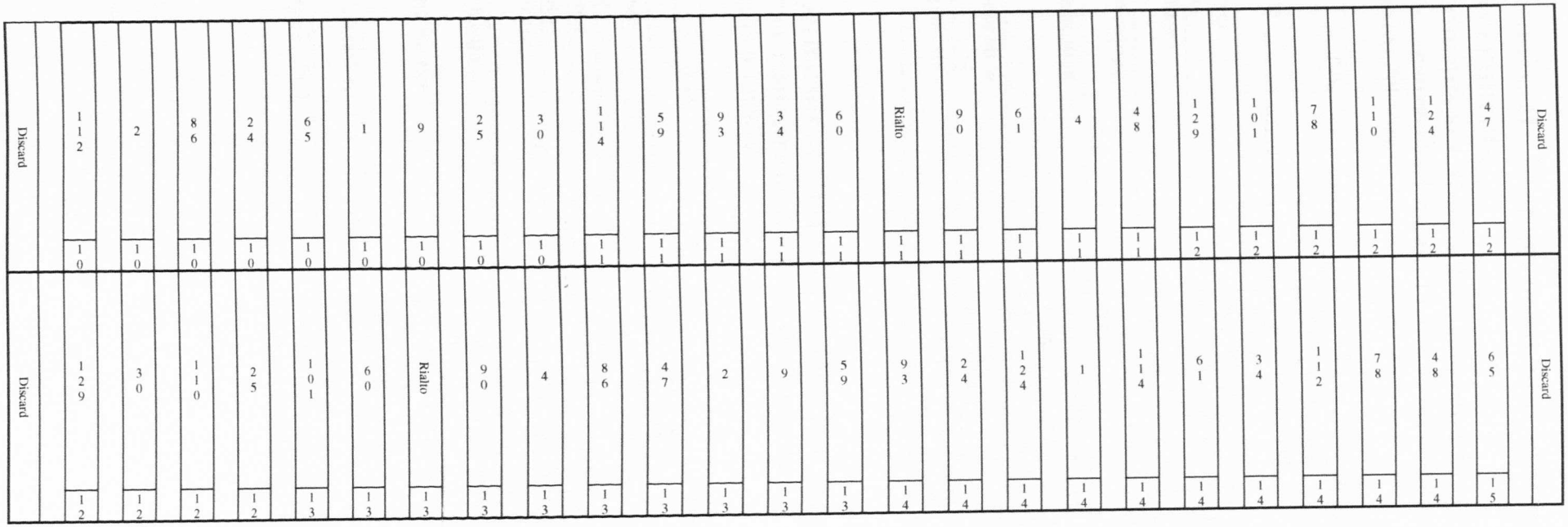
Table A4 continued

Rep 2

Discard	78	114	34	129	48	93	110	1	65	101	30	2	24	25	4	60	47	9	59	124	Rialto	86	112	61	90	Discard
	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	
Discard	129	30	110	25	101	60	Rialto	90	4	86	47	2	9	59	93	24	124	1	114	61	34	112	78	48	65	Discard
	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	10	

Table A4 continued

Rep 3



10.2 Appendix II: Management and cultural practices in field experiments

10.2.1 Experiments at CIMMYT C. Obregon Mexico 2008/09

Table A5 Plot management details of the Experiments at CIMMYT C. Obregon Mexico 2008/09

Title	Details
Sowing date	18 November 2008
Emergence date	28 November 2008
Previous crop	Wheat
Irrigation system	gravity-based system
Irrigation times	at 19 Dec, 15 Jan, 13 Feb and 7 Mar
Nitrogen fertilizer	Urea (50 kg N ha^{-1}) in Oct 2008 Urea (50 kg N ha^{-1}) in Dec 2008
Phosphorous fertilizer	Triple Super Phosphate (40 kg N ha^{-1}) in Oct 2008
Herbicides application	Buctril (1300 ml ha^{-1}) at 15/12/2008 Estrane (750 ml ha^{-1}) at 15/12/2008 Axial (500 ml ha^{-1}) at 10/12/2008
Fungicides application	Folicur (500 ml ha^{-1}) at 9 Jan, 4 Feb, 3 Mar and 25 Mar.
Insecticides application	Aflix (1 l ha^{-1}) at 14/01/2009 Lorsban (1400 ml ha^{-1}) at 30/01/2009

10.2.2 Experiments at CIMMYT C. Obregon Mexico 2009/10

Table A6 Plot management details of the Experiments at CIMMYT C. Obregon Mexico 2009/10

Title	Details
Sowing date	3 December 2009
Emergence date	13 December 2009
Previous crop	Wheat
Irrigation system	gravity-based system
Irrigation dates	at 13 Jan, 20 Feb, 3 Mar and 31 Mar
Nitrogen fertilizer	Urea (50 kg N ha^{-1}) in Oct 2009 Urea (50 kg N ha^{-1}) in Dec 2009
Phosphorous fertilizer	Triple Super Phosphate (40 kg N ha^{-1}) in Oct 2009
Herbicides application	Buctril (1300 ml ha^{-1}) at 11/01/2010 Estrane (750 ml ha^{-1}) at 11/01/2010 Axial (500 ml ha^{-1}) at 04/01/2010
Fungicides application	Folicur (500 ml ha^{-1}) at 13 Jan, 8 Feb, 10 Mar and 26 Mar.
Insecticides application	Aflix (1 l ha^{-1}) at 12/01/2010 Lorsban (1400 ml ha^{-1}) at 02/02/2010

10.2.3 Experiment at Thriplow, Hertfordshire UK 2008/09

Table A7 Plot management details of the Experiment at Thriplow, Hertfordshire UK 2008/09

Title	Date	Details
Sowing date	28/10/2008	
Fertilizer application	End of March	Multisulph 200kg/ha Nitram 230 kg/ha Nitram 440-500 kg/ha
Fungicides application	GS 26-30	Bravo @ 1 l ha^{-1}
		Tracker @ 0.5 l ha^{-1}
		Flexity @ 0.25 l ha^{-1}
		Mirage @ 1 l ha^{-1}
	GS 30-31	Tracker @ 1.5 l ha^{-1}
		Bravo @ 1 l ha^{-1}
		Talius @ 0.15 l ha^{-1}
	GS 39-45	Opus @ 0.75 l ha^{-1}
		Comet @ 0.75 l ha^{-1}
		Bravo @ 1 l ha^{-1}
	GS 51-61	Fandango @ 1.25 l ha^{-1}

10.2.4 Experiment at Sutton Bonington, Leicestershire UK 2009/10

Table A8 Plot management details of the Experiment at Sutton Bonington, Leicestershire UK 2009/10

Title	Date	Details
Field		S04
Previous crop		Winter Oats
SNS N Index	12/11/2009	101.4 kg/ha, SNS Index 2
Soil Indices		P:5, K:4, Mg:6, pH:6.8
Cultivations	16/09/2009	Plough
	16/10/2009	Power Harrow
	23/10/2009	Roll after drilling
Crop/variety		Various (see seedrates tab)
TGW (g)		Various (see seedrates tab)
Seed treatment		Redigo Deter
Sowing	23/10/2009	
Seed rate (m-2)		40 and 320 seeds m^2
Drill type		Oyjard
Row width (cm)		12.5
Plot length (m)		12
Plot width (m)		1.625
Fertiliser	12/11/2009	Manganese Jett @ 1.0 l/ha
	03/03/2010	148kg/ha 27N, 9 SO_3 (40kg/ha N, 13.3kg/ha, SO_3)
	08/04/2010	Human Extra @).75l/ha
	08/04/2010	232kg/ha 34.5% Nitram (80kg/ha N)
	28/04/2010	Human Extra @ 1l/ha
	14/05/2010	174kg/ha 34.5% Nitram (60kg/ha N)
Herbicide	12/11/2009	Picona SC @ 3.0 l/ha
	28/04/2010	Hatra @ 1.2l/ha + Biopower @ 1l/ha
Fungicide	08/04/2010	Alto Elite @ 0.75l/ha
	28/04/2010	Proline @ 0.65l/ha + Amistar Opti @ 0.75l/ha
	09/07/2010	Folicur @ 0.25l/ha + Corbel @ 0.5l/ha + Justice @ 0.15l/ha
Insecticide	12/11/2009	Permasect C @ 0.25 l/ha
	09/07/2010	Aphox @ 0.25kg/ha
PGR	08/04/2010	Chlormequat @1.5l/ha
	28/04/2010	Chlormequat @ 0.75/ha + Moddus @ 0.2l/ha

10.3 Appendix III: Additional results tables from SB site in 2007/08 and 2009/10 seasons and from CIMMYT C. Obregon site in 2008/09 and 2009/10.

Table A9 Effect of the interaction between the TIN gene and seed density on plants m^{-2} and spikes $plant^{-1}$ in some DH lines in 2009/10 season at harvest GS in SB campus, Nottingham University.

Tin1A allele	Line	Plants m^{-2}			Ears $plant^{-1}$		
		40	320	Mean	40	320	Mean
	34	38.0	325.2	**181.6**	6.2	1.5	**3.9**
	59	26.4	209.4	**117.9**	8.9	2.3	**5.6**
No	**60**	30.4	208.0	**119.2**	7.5	2.1	**4.8**
	93	25.0	266.4	**145.7**	8.1	1.7	**4.9**
	114	32.4	247.3	**139.8**	6.7	1.9	**4.3**
Mean		**30.4**	**251.3**	**140.9**	**7.5**	**1.9**	**4.7**
	48	38.3	190.1	**114.2**	4.1	2.5	**3.3**
	61	18.6	266.3	**142.4**	4.4	1.6	**3.0**
Yes	**65**	17.8	265.2	**141.5**	7.2	1.3	**4.3**
	78	16.6	188.5	**102.5**	6.5	1.7	**4.1**
	110	31.1	315.4	**173.3**	9.0	1.8	**5.4**
Mean		**24.5**	**245.1**	**134.8**	**6.2**	**1.8**	**4.0**
General means		**27.5**	**248.2**	**137.8**	**6.9**	**1.8**	**4.4**
C.V %				**35.2**			**18.9**
LSD for Densities				124.5**			0.98**
LSD for lines				**n.s**			**1.29****
LSD for Tins				**n.s**			**
LSD (Lines* densities)				n.s			1.75**
LSD (Tins*densities)				**n.s**			*

* Significant differences at the 0.05 probability level
** Significant differences at the 0.01 probability level
n.s Non significant differences

Table A10 Effect of the interaction between the TIN gene and seed density on above-ground dry matter m^{-2}, grain yield m^{-2} and harvest index in some DH lines in 2009/10 season at harvest GS in SB campus, Nottingham University.

Tin1A allele	Line	AGDM (g m^{-2})			Grain yield (g m^{-2})			HI		
		40	320	Mean	40	320	Mean	40	320	Mean
	34	798.8	1330.2	**1064.5**	406.0	609.7	**507.9**	0.51	0.46	**0.48**
	59	696.5	1095.7	**896.1**	397.3	526.2	**461.8**	0.57	0.48	**0.53**
No	**60**	855.0	1411.7	**1133.4**	467.2	753.0	**610.1**	0.54	0.53	**0.54**
	93	722.4	1227.2	**974.8**	378.7	572.4	**475.6**	0.52	0.47	**0.50**
	114	890.4	1432.0	**1161.2**	496.0	778.7	**637.3**	0.56	0.54	**0.55**
Mean		**792.6**	**1299.4**	**1040.7**	**429.0**	**648.0**	**535.3**	**0.54**	**0.50**	**0.52**
	48	707.2	1391.3	**1049.2**	438.1	790.9	**614.5**	0.62	0.57	**0.59**
	61	335.6	1224.6	**780.0**	209.1	704.2	**456.6**	0.62	0.58	**0.60**
Yes	**65**	686.5	1169.6	**928.0**	396.6	642.8	**519.7**	0.58	0.55	**0.56**
	78	615.5	1335.9	**975.7**	352.6	729.0	**540.8**	0.57	0.54	**0.56**
	110	817.4	1269.9	**1043.6**	469.7	576.6	**523.1**	0.57	0.45	**0.51**
Mean		**632.4**	**1278.2**	**955.3**	**373.2**	**688.7**	**531.0**	**0.59**	**0.54**	**0.57**
General means		**712.5**	**1288.8**	**1000.7**	**401.1**	**668.4**	**534.7**	**0.57**	**0.52**	**0.54**
C.V %				14.9			**13.5**			**3.1**
LSD for Densities				382.27*			253.21*			0.041*
LSD for lines				233.73**			113.23**			0.027**
LSD for Tins				*			**n.s**			**
LSD (Lines* densities)				n.s			**285.12****			**0.049****
LSD (Tins*densities)				n.s			*			n.s

* Significant differences at the 0.05 probability level
** Significant differences at the 0.01 probability level
n.s Non significant differences

Table A11 Effect of the interaction between the TIN gene and seed density on ears m^{-2}, grains ear^{-1}, grains m^{-2} and thousand grain weight (TGW) in some DH lines in 2009/10 season at harvest GS in SB campus, Nottingham University.

Tin1A allele	Line	Ears m^{-2}			Grains ear^{-1}			Grains m^{-2}			TGW (g)		
		40	320	Mean	40	320	Mean	40	320	Mean	40	320	Mean
	34	233.7	497.2	**365.5**	40.1	27.9	**34.0**	9378.7	13639.0	**11508.8**	43.3	44.5	**43.9**
	59	229.2	468.1	**348.6**	39.1	23.1	**31.1**	8834.3	10798.7	**9816.5**	45.0	48.8	**46.9**
No	**60**	229.8	430.3	**330.1**	55.3	43.7	**49.5**	12733.7	18823.9	**15778.8**	36.5	40.0	**38.3**
	93	192.3	463.6	**328.0**	40.1	24.7	**32.4**	7630.4	11370.9	**9500.7**	49.7	50.3	**50.0**
	114	213.6	454.7	**334.2**	63.3	44.6	**53.9**	13514.0	20249.9	**16881.9**	36.7	38.4	**37.5**
Mean		**219.7**	**462.8**	**341.3**	**47.6**	**32.8**	**40.0**	**10418.2**	**14976.5**	**12618.0**	**42.2**	**44.4**	**43.3**
	48	156.4	466.2	**311.3**	80.6	49.5	**65.0**	12499.6	23050.9	**17775.3**	35.1	34.2	**34.6**
	61	77.4	410.4	**243.9**	68.3	47.1	**57.7**	5317.4	19197.9	**12257.7**	39.3	36.7	**38.3**
Yes	**65**	124.2	351.8	**238.0**	63.0	42.0	**52.5**	7823.2	14593.9	**11208.5**	50.7	43.9	**47.3**
	78	108.5	318.0	**213.2**	65.8	47.5	**56.6**	7144.4	14833.7	**10989.0**	49.3	49.1	**49.2**
	110	278.8	546.9	**412.8**	43.1	24.2	**33.7**	12010.0	13010.1	**12510.0**	39.1	44.3	**41.7**
Mean		**149.1**	**418.6**	**283.9**	**64.2**	**42.1**	**53.1**	**8958.9**	**16937.3**	**12948.1**	**42.7**	**41.6**	**42.2**
General means		**184.4**	**440.7**	**312.6**	**55.9**	**37.4**	**46.6**	**9688.6**	**15956.9**	**12822.7**	**42.5**	**43.0**	**42.7**
C.V %				**21.3**			**10.0**			**12.5**			**3.3**
LSD for Densities				213.61**			17.16**			4913.94*			n.s
LSD for lines				104.72**			7.33**			2522.65**			2.23**
LSD for Tins				**			**			**n.s**			**
LSD (Lines* densities)				n.s			n.s			5509.06**			3.88**
LSD (Tins*densities)				**n.s**			**			**			**

* Significant differences at the 0.05 probability level
** Significant differences at the 0.01 probability level
n.s Non significant differences

Table A12 Effect of the interaction between the TIN gene and seed density on dry matter partitioning m^{-2} in some DH lines in 2009/10 season at harvest GS in SB campus, Nottingham University.

Tin1A allele	Line	Ears DM m^{-2}			Chaff DM m^{-2}			Lamina DM m^{-2}			Stems DM m^{-2}		
		40	320	Mean	40	320	Mean	40	320	Mean	40	320	Mean
	34	531.5	821.8	**676.6**	125.4	212.1	**168.8**	48.9	105.0	**77.0**	218.5	403.4	**310.9**
	59	520.8	748.6	**634.7**	123.5	222.4	**173.0**	37.4	77.0	**57.2**	138.2	270.0	**204.1**
No	60	603.5	949.6	**776.6**	136.4	196.6	**166.5**	45.8	100.5	**73.1**	205.8	361.7	**283.7**
	93	498.3	785.9	**642.1**	119.6	213.5	**166.6**	35.5	81.6	**58.5**	188.6	359.7	**274.1**
	114	617.5	958.1	**787.8**	121.5	179.4	**150.5**	50.0	96.7	**73.3**	222.9	377.2	**300.0**
Mean		**554.3**	**852.8**	**703.6**	**125.3**	**204.8**	**165.1**	**43.5**	**92.2**	**67.9**	**194.8**	**354.4**	**274.6**
	48	548.3	1013.8	**781.0**	110.3	222.9	**166.6**	31.0	84.0	**57.5**	127.9	293.5	**210.7**
	61	261.6	893.8	**577.7**	52.5	189.6	**121.0**	9.8	66.5	**38.2**	64.3	264.3	**164.3**
Yes	65	521.4	850.7	**686.1**	124.9	208.0	**166.4**	24.8	61.7	**43.3**	140.2	257.2	**198.7**
	78	453.8	930.3	**692.0**	101.2	201.2	**151.2**	27.6	78.2	**52.9**	134.1	327.4	**230.8**
	110	604.4	836.4	**720.4**	134.7	259.8	**197.2**	37.9	80.7	**59.3**	175.1	352.8	**263.9**
Mean		**477.9**	**905.0**	**691.5**	**104.7**	**216.3**	**160.5**	**26.2**	**74.2**	**50.2**	**128.3**	**299.0**	**213.7**
General means		**516.1**	**878.9**	**697.5**	**115.0**	**210.5**	**162.8**	**34.9**	**83.2**	**59.0**	**161.5**	**326.7**	**244.1**
C.V %				**13.8**			**18.9**			**20.1**			**18.4**
LSD for Densities				**298.10***			**45.11***			**22.95****			**78.21***
LSD for lines				**150.90****			**35.95***			**18.67****			**70.58****
LSD for Tins				**n.s**			**n.s**			**			**
LSD (Lines* densities)				**231.51***			**n.s**			**n.s**			**n.s**
LSD (Tins*densities)				*			**n.s**			**n.s**			**n.s**

* Significant differences at the 0.05 probability level
** Significant differences at the 0.01 probability level
n.s Non significant differen

Table A13 Effect of the interaction between tiller inhibition (TIN) gene and seed density on plant establishment and ears plant^{-1} in some DH lines during 08/09, 09/10 seasons at CIMMYT experimental station in Ciudad Obregon, North West Mexico.

Tin1A allele	Seed density m^{-2}	Line	Plants m^{-2}			Ears plant^{-1}		
			08/09	09/10	Mean	08/09	09/10	Mean
		36	58.3	36.7	**47.5**	4.1	8.1	**6.1**
	50	**51**	46.7	35.0	**40.8**	4.5	7.9	**6.2**
		87	43.3	26.7	**35.0**	4.7	11.7	**8.2**
		93	50.0	35.8	**42.9**	4.6	8.0	**6.3**
	Mean		**49.6**	**33.5**	**41.6**	**4.5**	**8.9**	**6.7**
		36	139.2	72.5	**105.8**	2.0	4.7	**3.4**
	150	**51**	130.0	71.7	**100.8**	2.3	4.7	**3.5**
No		**87**	125.8	76.7	**101.3**	2.1	4.7	**3.4**
		93	133.3	85.0	**109.2**	2.1	3.8	**3.0**
	Mean		**132.1**	**76.5**	**104.3**	**2.1**	**4.5**	**3.3**
		36	351.7	191.7	**271.7**	0.8	1.9	**1.3**
	450	**51**	354.2	221.7	**287.9**	0.9	1.7	**1.3**
		87	301.7	235.0	**268.3**	1.0	1.7	**1.3**
		93	351.7	192.5	**272.1**	1.0	2.2	**1.6**
	Mean		**339.8**	**210.2**	**275.0**	**0.9**	**1.9**	**1.4**
Mean of non tin lines			**173.8**	**106.7**	**140.3**	**2.5**	**5.1**	**3.8**
		1	52.5	25.0	**38.8**	4.3	10.9	**7.6**
	50	**61**	56.7	33.3	**45.0**	4.0	7.7	**5.9**
		90	56.7	33.3	**45.0**	2.8	5.6	**4.2**
		124	42.5	37.5	**40.0**	4.4	6.7	**5.5**
	Mean		**52.1**	**32.3**	**42.2**	**3.9**	**7.7**	**5.8**
		1	126.7	73.3	**100.0**	1.9	4.4	**3.2**
	150	**61**	112.5	92.5	**102.5**	2.4	3.9	**3.1**
Yes		**90**	121.7	89.2	**105.4**	1.7	3.1	**2.4**
		124	135.0	73.3	**104.2**	1.6	4.2	**2.9**
	Mean		**124.0**	**82.1**	**103.0**	**1.9**	**3.9**	**2.9**
		1	355.8	204.2	**280.0**	0.8	2.1	**1.5**
	450	**61**	317.5	263.3	**290.4**	0.9	1.5	**1.2**
		90	370.8	184.2	**277.5**	0.6	1.8	**1.2**
		124	305.0	265.0	**285.0**	0.7	1.2	**1.0**
	Mean		**337.3**	**229.2**	**283.2**	**0.8**	**1.7**	**1.2**
Mean of tin lines			**171.1**	**114.5**	**142.8**	**2.2**	**4.4**	**3.3**
Mean of 50			**50.8**	**32.9**	**41.9**	**4.16**	**8.32**	**6.24**
Mean of 150			**128.0**	**79.3**	**103.6**	**2.01**	**4.19**	**3.10**
Mean of 450			**338.5**	**219.7**	**279.1**	**0.84**	**1.76**	**1.30**
General mean			**172.5**	**110.6**	**141.5**	**2.34**	**4.76**	**3.55**
C.V%					**19.6**			**31.7**
	Year				**44.23***			**1.58***
	Density				**18.59****			**0.52****
	Year × Density				**58.84****			**2.36****
	Lines				**n.s**			**0.99****
	TINs				**n.s**			*
	Year × Lines				**35.14***			**n.s**
LSD	**Year × TINs**				**n.s**			**n.s**
	Density × Lines				**n.s**			**1.25***
	Density × TINs				**n.s**			**n.s**
	Year × Density × Lines				**49.28***			**n.s**
	Year × Density × TINs				**n.s**			**n.s**

Table A14 Effect of the interaction between tiller inhibition (TIN) gene and seed density on AGDM and grain yield m^{-2} in some DH lines during 08/09, 09/10 seasons at CIMMYT experimental station in Ciudad Obregon, North West Mexico

Tin1A allele	Seed density m^{-2}	Line	AGDM ($g\ m^{-2}$)			Grain yield ($g\ m^{-2}$)		
			08/09	09/10	Mean	08/09	09/10	Mean
		36	766.6	1201.4	**984.0**	297.1	581.4	**439.2**
		51	1006.4	1455.4	**1230.9**	416.4	638.1	**527.2**
	50	87	637.6	1069.6	**853.6**	216.8	484.3	**350.6**
		93	1089.5	1483.1	**1286.3**	434.0	661.6	**547.8**
	Mean		**875.0**	**1302.4**	**1088.7**	**341.1**	**591.3**	**466.2**
		36	931.7	1303.5	**1117.6**	385.3	635.1	**510.2**
		51	1169.4	1510.7	**1340.1**	447.6	634.7	**541.1**
	150	87	749.2	1202.5	**975.8**	232.4	546.4	**389.4**
No		93	1176.8	1421.5	**1299.2**	461.4	658.6	**560.0**
	Mean		**1006.8**	**1359.5**	**1183.2**	**381.7**	**618.7**	**500.2**
		36	852.4	1244.9	**1048.6**	374.5	610.9	**492.7**
		51	1060.9	1515.1	**1288.0**	405.6	603.6	**504.6**
	450	87	690.7	1106.6	**898.7**	221.2	488.6	**354.9**
		93	1173.3	1602.1	**1387.7**	462.5	711.0	**586.8**
	Mean		**944.3**	**1367.2**	**1155.8**	**366.0**	**603.5**	**484.7**
Mean of non tin lines			**942.0**	**1343.0**	**1142.5**	**362.9**	**604.5**	**483.7**
		1	813.5	1354.0	**1083.8**	255.5	556.2	**405.8**
		61	997.7	1344.6	**1171.2**	402.1	620.2	**511.2**
	50	90	983.2	1351.0	**1167.1**	389.5	600.8	**495.2**
		124	667.7	1052.4	**860.0**	247.5	448.2	**347.8**
	Mean		**865.5**	**1275.5**	**1070.5**	**323.6**	**556.4**	**440.0**
		1	799.6	1307.4	**1053.5**	270.6	612.2	**441.4**
		61	1051.7	1372.9	**1212.3**	412.2	681.6	**546.9**
Yes	150	90	964.8	1525.7	**1245.3**	379.8	606.6	**493.2**
		124	691.8	1151.9	**921.8**	252.7	508.0	**380.4**
	Mean		**877.0**	**1339.5**	**1108.2**	**328.8**	**602.1**	**465.5**
		1	878.3	1363.7	**1121.0**	299.9	632.1	**466.0**
		61	1056.6	1517.2	**1286.9**	439.6	682.9	**561.3**
	450	90	1047.3	1322.7	**1185.0**	411.7	572.1	**491.9**
		124	661.1	1096.5	**878.8**	257.4	470.6	**364.0**
	Mean		**910.8**	**1325.0**	**1117.9**	**352.1**	**589.4**	**470.8**
Mean of tin lines			**884.4**	**1313.3**	**1098.9**	**334.8**	**582.6**	**458.7**
Mean of 50			**870.3**	**1288.9**	**1079.6**	**332.4**	**573.8**	**453.1**
Mean of 150			**941.9**	**1349.5**	**1145.7**	**355.2**	**610.4**	**482.8**
Mean of 450			**927.6**	**1346.1**	**1136.8**	**359.0**	**596.5**	**477.8**
General mean			**913.2**	**1328.2**	**1120.7**	**348.9**	**593.6**	**471.2**
C.V%					**11.8**			**9.7**
	Year				**188.26****			**73.41****
	Density				**n.s**			**n.s**
	Year × Density				**n.s**			**n.s**
	Lines				**116.11****			**40.35****
	TINs				**n.s**			******
	Year × Lines				**n.s**			**57.30****
LSD	**Year × TINs**				**n.s**			**n.s**
	Density × Lines				**n.s**			**n.s**
	Density × TINs				**n.s**			**n.s**
	Year × Density × Lines				**n.s**			**n.s**
	Year × Density × TINs				**n.s**			**n.s**

Table A15 Effect of the interaction between tiller inhibition (TIN) gene and seed density on harvest index in some DH lines during 08/09, 09/10 seasons at CIMMYT experimental station in Ciudad Obregon, North West Mexico

Tin1A allele	Seed density m^{-2}	Line	HI		
			08/09	09/10	Mean
No	50	36	0.39	0.49	**0.44**
		51	0.41	0.44	**0.43**
		87	0.34	0.46	**0.40**
		93	0.40	0.45	**0.42**
	Mean		**0.39**	**0.46**	**0.42**
	150	36	0.41	0.49	**0.45**
		51	0.38	0.42	**0.40**
		87	0.31	0.46	**0.38**
		93	0.39	0.46	**0.43**
	Mean		**0.37**	**0.46**	**0.42**
	450	36	0.44	0.49	**0.47**
		51	0.38	0.40	**0.39**
		87	0.32	0.44	**0.38**
		93	0.39	0.44	**0.42**
	Mean		**0.39**	**0.44**	**0.41**
Mean of non tin lines			**0.38**	**0.45**	**0.42**
Yes	50	1	0.32	0.41	**0.36**
		61	0.40	0.46	**0.43**
		90	0.40	0.45	**0.42**
		124	0.37	0.43	**0.40**
	Mean		**0.37**	**0.44**	**0.40**
	150	1	0.34	0.47	**0.40**
		61	0.39	0.50	**0.45**
		90	0.39	0.40	**0.40**
		124	0.36	0.44	**0.40**
	Mean		**0.37**	**0.45**	**0.41**
	450	1	0.35	0.47	**0.41**
		61	0.42	0.45	**0.44**
		90	0.39	0.43	**0.41**
		124	0.39	0.43	**0.41**
	Mean		**0.39**	**0.45**	**0.42**
Mean of tin lines			**0.38**	**0.45**	**0.42**
Mean of 50			**0.38**	**0.45**	**0.41**
Mean of 150			**0.37**	**0.46**	**0.41**
Mean of 450			**0.39**	**0.44**	**0.42**
General mean			**0.38**	**0.45**	**0.41**
C.V%					**7.1**

LSD	**Year**	**0.030****
	Density	**n.s**
	Year × Density	**n.s**
	Lines	**0.026****
	TINs	**n.s**
	Year × Lines	**0.035****
	Year × TINs	**n.s**
	Density × Lines	**n.s**
	Density × TINs	**n.s**
	Year × Density × Lines	**n.s**
	Year × Density × TINs	**n.s**

Table A16 Effect of the interaction between tiller inhibition (TIN) gene and seed density on ears m^{-2} and grains ear^{-1} in some DH lines during 08/09, 09/10 seasons at CIMMYT experimental station in Ciudad Obregon, North West Mexico

Tin1A allele	Seed density m^{-2}	Line	Ears m^{-2}			Grains ear^{-1}		
			08/09	09/10	Mean	08/09	09/10	Mean
No	50	36	209.5	283.0	**246.3**	39.8	53.4	**46.6**
		51	209.7	265.6	**237.6**	50.2	56.2	**53.2**
		87	200.0	304.1	**252.1**	40.0	54.6	**47.3**
		93	226.8	282.6	**254.7**	46.3	55.7	**51.0**
	Mean		**211.5**	**283.8**	**247.7**	**44.1**	**55.0**	**49.5**
	150	36	280.1	337.9	**309.0**	37.7	47.8	**42.7**
		51	292.1	334.8	**313.5**	37.2	44.0	**40.6**
		87	258.8	334.1	**296.4**	33.0	53.5	**43.2**
		93	277.9	313.4	**295.6**	41.5	48.0	**44.7**
	Mean		**277.2**	**330.0**	**303.6**	**37.3**	**48.3**	**42.8**
	450	36	262.9	353.5	**308.2**	38.6	44.9	**41.7**
		51	319.3	366.1	**342.7**	31.4	38.4	**34.9**
		87	291.4	404.1	**347.8**	27.9	41.3	**34.6**
		93	338.1	405.6	**371.8**	33.4	40.2	**36.8**
	Mean		**302.9**	**382.3**	**342.6**	**32.8**	**41.2**	**37.0**
Mean of non tin lines			**263.9**	**332.0**	**298.0**	**38.1**	**48.2**	**43.2**
Yes	50	1	213.8	265.7	**239.7**	53.7	84.2	**69.0**
		61	221.5	250.9	**236.2**	55.8	72.6	**64.2**
		90	156.7	181.1	**168.9**	68.1	90.5	**79.3**
		124	186.6	240.8	**213.7**	46.1	65.3	**55.7**
	Mean		**194.6**	**234.6**	**214.6**	**55.9**	**78.1**	**67.0**
	150	1	234.4	312.7	**273.5**	48.3	75.7	**62.0**
		61	272.3	334.5	**303.4**	49.1	59.4	**54.3**
		90	207.3	268.6	**238.0**	54.4	65.1	**59.7**
		124	212.3	281.9	**247.1**	40.3	64.5	**52.4**
	Mean		**231.6**	**299.4**	**265.5**	**48.0**	**66.2**	**57.1**
	450	1	279.6	399.1	**339.3**	44.5	62.5	**53.5**
		61	297.9	402.1	**350.0**	46.2	48.7	**47.4**
		90	229.8	284.4	**257.1**	49.6	56.3	**53.0**
		124	221.3	318.1	**269.7**	38.2	57.7	**48.0**
	Mean		**257.2**	**350.9**	**304.0**	**44.6**	**56.3**	**50.5**
Mean of tin lines			**227.8**	**295.0**	**261.4**	**49.5**	**66.9**	**58.2**
Mean of 50			**203.1**	**259.2**	**231.1**	**50.0**	**66.6**	**58.3**
Mean of 150			**254.4**	**314.7**	**284.6**	**42.7**	**57.2**	**50.0**
Mean of 450			**280.0**	**366.6**	**323.3**	**38.7**	**48.7**	**43.7**
General mean			**245.8**	**313.5**	**279.7**	**43.8**	**57.5**	**50.7**
C.V%					**13.2**			**11.6**
LSD	**Year**				**44.26****			**5.24****
	Density				**36.11****			**5.93****
	Year × Density				**n.s**			**n.s**
	Lines				**32.39****			**5.15****
	TINs				******			******
	Year × Lines				**n.s**			**6.95****
	Year × TINs				**n.s**			******
	Density × Lines				**n.s**			**9.59****
	Density × TINs				**n.s**			**n.s**
	Year × Density × Lines				**n.s**			**n.s**
	Year × Density × TINs				**n.s**			**n.s**

Table A17 Effect of the interaction between tiller inhibition (TIN) gene and seed density on grains m^{-2} and TGW in some DH lines during 08/09, 09/10 seasons at CIMMYT experimental station in Ciudad Obregon, North West Mexico

Tin1A allele	Seed density m^{-2}	Line	Grains m^{-2}			TGW (g)		
			08/09	09/10	Mean	08/09	09/10	Mean
No	50	36	8274.3	15045.5	**11659.9**	36.0	38.6	**37.3**
		51	10533.0	14879.5	**12706.3**	39.6	42.9	**41.2**
		87	7967.1	16540.2	**12253.7**	27.3	29.3	**28.3**
		93	10484.6	15755.0	**13119.8**	41.5	42.0	**41.7**
	Mean		**9314.8**	**15555.1**	**12434.9**	**36.1**	**38.2**	**37.1**
	150	36	10491.3	16130.6	**13311.0**	36.7	39.3	**38.0**
		51	10871.2	14739.2	**12805.2**	41.2	43.1	**42.1**
		87	8491.8	17885.7	**13188.7**	27.3	30.5	**28.9**
		93	11494.0	14837.1	**13165.6**	40.2	44.4	**42.3**
	Mean		**10337.1**	**15898.2**	**13117.6**	**36.3**	**39.3**	**37.8**
	450	36	10097.2	15794.2	**12945.7**	37.2	38.7	**37.9**
		51	9890.9	13945.2	**11918.0**	41.0	43.1	**42.0**
		87	8007.1	16650.6	**12328.8**	27.6	29.4	**28.5**
		93	11244.5	16270.8	**13757.6**	41.1	43.8	**42.4**
	Mean		**9809.9**	**15665.2**	**12737.6**	**36.7**	**38.7**	**37.7**
Mean of non tin lines			**9820.6**	**15706.2**	**12763.4**	**36.4**	**38.7**	**37.6**
Yes	50	1	11430.2	21844.1	**16637.2**	22.3	25.6	**23.9**
		61	12320.7	18127.9	**15224.3**	32.7	34.3	**33.5**
		90	10684.5	16250.5	**13467.5**	36.5	37.3	**36.9**
		124	8509.8	15688.5	**12099.1**	29.1	28.6	**28.8**
	Mean		**10736.3**	**17977.7**	**14357.0**	**30.2**	**31.4**	**30.8**
	150	1	11331.3	23162.6	**17246.9**	23.8	26.4	**25.1**
		61	13301.7	19576.1	**16438.9**	31.0	34.9	**33.0**
		90	11147.9	17347.3	**14247.6**	34.5	35.0	**34.7**
		124	8588.2	17957.6	**13272.9**	29.4	28.2	**28.8**
	Mean		**11092.3**	**19510.9**	**15301.6**	**29.7**	**31.1**	**30.4**
	450	1	11984.4	24820.6	**18402.5**	25.0	25.5	**25.3**
		61	13728.7	19510.3	**16619.5**	32.2	35.0	**33.6**
		90	11362.2	16028.6	**13695.4**	36.2	35.7	**36.0**
		124	8449.3	17940.3	**13194.8**	30.5	26.2	**28.4**
	Mean		**11381.1**	**19574.9**	**15478.0**	**31.0**	**30.6**	**30.8**
Mean of tin lines			**11069.9**	**19021.2**	**15045.6**	**30.3**	**31.0**	**30.7**
Mean of 50			**10025.5**	**16766.4**	**13396.0**	**33.1**	**34.8**	**34.0**
Mean of 150			**10714.7**	**17704.5**	**14209.6**	**33.0**	**35.2**	**34.1**
Mean of 450			**10595.5**	**17620.1**	**14107.8**	**33.9**	**34.7**	**34.3**
General mean			**10445.2**	**17363.7**	**13904.5**	**33.3**	**34.9**	**34.1**
C.V%					**10.0**			**4.1**
LSD	**Year**				**989.94****			**n.s**
	Density				**n.s**			**n.s**
	Year × Density				**n.s**			**n.s**
	Lines				**1226.65****			**1.21****
	TINs				******			******
	Year × Lines				**1642.98****			**2.04****
	Year × TINs				******			******
	Density × Lines				**n.s**			**n.s**
	Density × TINs				**n.s**			**n.s**
	Year × Density × Lines				**n.s**			**n.s**
	Year × Density × TINs				**n.s**			**n.s**

Table A18 Effect of the interaction between tiller inhibition (TIN) gene and seed density on spikes DM m^{-2} and flag leaves DM m^{-2} at GS61 in some DH lines during 08/09, 09/10 seasons at CIMMYT experimental station in Ciudad Obregon, North West Mexico

Tin1A allele	Seed density m^{-2}	Line	Ears DM (g m^{-2})			Flag leaves (g m^{-2})		
			08/09	09/10	Mean	08/09	09/10	Mean
No	50	36	209.4	406.8	**308.1**	56.5	83.0	**69.7**
		51	241.4	370.5	**305.9**	52.0	60.6	**56.3**
		87	315.6	575.1	**445.3**	46.3	71.5	**58.9**
		93	210.4	453.6	**332.0**	45.0	61.5	**53.3**
	Mean		**244.2**	**451.5**	**347.8**	**49.9**	**69.2**	**59.5**
	150	36	340.9	448.3	**394.6**	81.8	92.9	**87.3**
		51	313.8	488.2	**401.0**	66.3	71.7	**69.0**
		87	435.2	600.1	**517.6**	57.2	69.4	**63.3**
		93	243.6	491.4	**367.5**	57.0	62.9	**59.9**
	Mean		**333.4**	**507.0**	**420.2**	**65.6**	**74.2**	**69.9**
	450	36	361.7	445.1	**403.4**	64.5	84.1	**74.3**
		51	310.9	499.7	**405.3**	60.4	76.3	**68.3**
		87	443.7	750.3	**597.0**	66.5	77.7	**72.1**
		93	295.1	599.8	**447.4**	71.8	78.8	**75.3**
	Mean		**352.8**	**573.7**	**463.3**	**65.8**	**79.2**	**72.5**
Mean of non tin lines			**310.1**	**510.7**	**410.4**	**60.4**	**74.2**	**67.3**
Yes	50	1	338.2	469.2	**403.7**	64.4	90.3	**77.4**
		61	204.2	281.4	**242.8**	57.6	64.5	**61.0**
		90	205.7	330.9	**268.3**	50.5	50.6	**50.6**
		124	222.9	409.1	**316.0**	58.1	83.5	**70.8**
	Mean		**242.7**	**372.6**	**307.7**	**57.7**	**72.2**	**65.0**
	150	1	364.1	511.1	**437.6**	58.5	93.7	**76.1**
		61	208.2	304.8	**256.5**	63.4	71.2	**67.3**
		90	247.6	425.9	**336.8**	58.2	70.2	**64.2**
		124	304.3	431.0	**367.7**	65.7	83.5	**74.6**
	Mean		**281.0**	**418.2**	**349.6**	**61.5**	**79.6**	**70.5**
	450	1	385.7	639.0	**512.3**	62.8	107.2	**85.0**
		61	261.6	338.5	**300.1**	72.9	77.9	**75.4**
		90	322.4	418.5	**370.5**	67.6	73.1	**70.4**
		124	309.7	428.7	**369.2**	61.6	89.9	**75.8**
	Mean		**319.9**	**456.2**	**388.0**	**66.2**	**87.0**	**76.6**
Mean of tin lines			**281.2**	**415.7**	**348.5**	**61.8**	**79.6**	**70.7**
Mean of 50			**243.5**	**412.1**	**327.8**	**53.8**	**70.7**	**62.3**
Mean of 150			**307.2**	**462.6**	**384.9**	**63.5**	**76.9**	**70.2**
Mean of 450			**336.4**	**514.9**	**425.7**	**66.0**	**83.1**	**74.6**
General mean			**295.7**	**463.2**	**379.4**	**61.1**	**76.9**	**69.0**
C.V%					**18.3**			**16.6**
LSD	**Year**				**61.99****			**7.20***
	Density				**40.41****			**8.45****
	Year × Density				**n.s**			**n.s**
	Lines				**60.93****			**10.08****
	TINs				******			**n.s**
	Year × Lines				**82.24****			**14.11****
	Year × TINs				******			**n.s**
	Density × Lines				**n.s**			**n.s**
	Density × TINs				**n.s**			**n.s**
	Year × Density × Lines				**n.s**			**n.s**
	Year × Density × TINs				**n.s**			**n.s**

Table A19 Effect of the interaction between tiller inhibition (TIN) gene and seed density on lamina DM m^{-2} and stems DM m^{-2} at GS61 in some DH lines during 08/09, 09/10 seasons at CIMMYT experimental station in Ciudad Obregon, North West Mexico

Tin1A allele	Seed density m^{-2}	Line	Lamina DM (g m^{-2})			Stems DM (g m^{-2})		
			08/09	09/10	Mean	08/09	09/10	Mean
No	50	36	67.6	160.9	**114.2**	199.4	490.9	**345.2**
		51	111.2	155.3	**133.2**	451.4	690.7	**571.0**
		87	44.5	128.5	**86.5**	197.2	467.5	**332.3**
		93	103.3	167.3	**135.3**	416.4	784.4	**600.4**
	Mean		**81.6**	**153.0**	**117.3**	**316.1**	**608.4**	**462.2**
	150	36	70.8	161.1	**116.0**	286.5	531.0	**408.8**
		51	128.6	201.0	**164.8**	532.9	865.6	**699.2**
		87	49.6	125.1	**87.3**	240.1	482.0	**361.0**
		93	112.8	171.0	**141.9**	468.1	789.3	**628.7**
	Mean		**90.5**	**164.5**	**127.5**	**381.9**	**667.0**	**524.4**
	450	36	49.7	145.7	**97.7**	279.5	489.4	**384.4**
		51	121.9	195.7	**158.8**	515.8	861.9	**688.8**
		87	48.7	130.7	**89.7**	267.9	537.7	**402.8**
		93	128.7	198.7	**163.7**	538.7	939.4	**739.1**
	Mean		**87.2**	**167.7**	**127.5**	**400.5**	**707.1**	**553.8**
Mean of non tin lines			**86.4**	**161.7**	**124.1**	**366.2**	**660.8**	**513.5**
Yes	50	1	*	165.1	*	223.6	567.9	**395.8**
		61	111.0	211.0	**161.0**	408.7	717.6	**563.2**
		90	108.6	170.3	**139.4**	396.2	653.7	**525.0**
		124	93.0	165.6	**129.3**	233.5	494.9	**364.2**
	Mean		**104.2**	**178.0**	**143.2**	**315.5**	**608.5**	**462.0**
	150	1	*	181.8	*	194.3	623.1	**408.7**
		61	109.7	207.8	**158.8**	414.6	756.5	**585.5**
		90	93.4	188.1	**140.7**	408.4	780.1	**594.3**
		124	87.0	154.2	**120.6**	270.9	478.4	**374.7**
	Mean		**96.7**	**183.0**	**140.0**	**322.0**	**659.5**	**490.8**
	450	1	*	176.9	*	202.3	603.3	**402.8**
		61	107.8	227.9	**167.8**	480.4	809.9	**645.2**
		90	116.0	177.2	**146.6**	498.6	794.4	**646.5**
		124	71.1	143.7	**107.4**	243.9	477.0	**360.5**
	Mean		**98.3**	**181.4**	**140.6**	**356.3**	**671.2**	**513.8**
Mean of tin lines			**99.7**	**180.8**	**141.3**	**331.3**	**646.4**	**488.9**
Mean of 50			**91.2**	**165.5**	**128.4**	**315.8**	**608.5**	**462.1**
Mean of 150			**94.3**	**173.8**	**134.0**	**352.0**	**663.2**	**507.6**
Mean of 450			**92.3**	**174.6**	**133.4**	**378.4**	**689.1**	**533.8**
General mean			**92.6**	**171.3**	**131.9**	**348.7**	**653.6**	**501.2**
C.V%					**17.1**			**15.9**
LSD	**Year**				**15.35****			**165.35****
	Density				**n.s**			**41.84***
	Year × Density				**n.s**			**n.s**
	Lines				**19.87****			**70.22****
	TINs				******			**n.s**
	Year × Lines				**20.05***			**78.75***
	Year × TINs				**n.s**			**n.s**
	Density × Lines				**n.s**			**n.s**
	Density × TINs				**n.s**			**n.s**
	Year × Density × Lines				**n.s**			**n.s**
	Year × Density × TINs				**n.s**			**n.s**

Table A20 Effect of the interaction between tiller inhibition (TIN) gene and seed density on plant height and rachis length at GS61 in some DH lines during 08/09, 09/10 seasons at CIMMYT experimental station in Ciudad Obregon, North West Mexico

Tin1A allele	Seed density m^{-2}	Line	Plant height (cm)			Rachis length (cm)		
			08/09	09/10	Mean	08/09	09/10	Mean
No	50	36	68.8	69.9	**69.4**	12.8	16.3	14.5
		51	92.0	92.3	**92.2**	12.1	13.9	13.0
		87	64.6	66.9	**65.7**	12.7	15.3	14.0
		93	92.2	95.2	**93.7**	12.3	13.7	13.0
	Mean		**79.4**	**81.1**	**80.2**	**12.5**	**14.8**	**13.6**
	150	36	67.7	68.5	**68.1**	12.1	15.1	13.6
		51	93.6	97.0	**95.3**	11.1	13.4	12.3
		87	65.5	68.7	**67.1**	11.9	14.6	13.2
		93	90.9	97.3	**94.1**	11.6	13.2	12.4
	Mean		**79.4**	**82.9**	**81.2**	**11.7**	**14.1**	**12.9**
	450	36	67.9	68.0	**68.0**	11.3	13.9	12.6
		51	91.3	98.1	**94.7**	9.9	13.0	11.5
		87	63.8	66.9	**65.4**	11.2	13.7	12.5
		93	91.1	96.3	**93.7**	10.7	12.5	11.6
	Mean		**78.5**	**82.3**	**80.4**	**10.8**	**13.3**	**12.0**
Mean of non tin lines			**79.1**	**82.1**	**80.6**	**11.7**	**14.1**	**12.9**
Yes	50	1	73.3	65.7	**69.5**	13.3	16.3	14.8
		61	91.4	93.0	**92.2**	12.6	14.5	13.6
		90	89.2	89.2	**89.2**	13.2	15.0	14.1
		124	67.4	68.0	**67.7**	15.9	18.5	17.2
	Mean		**80.3**	**79.0**	**79.7**	**13.7**	**16.1**	**14.9**
	150	1	68.3	71.8	**70.0**	13.0	16.1	14.5
		61	91.8	94.8	**93.3**	11.8	13.1	12.4
		90	88.3	89.6	**89.0**	11.3	13.6	12.5
		124	68.2	70.4	**69.3**	14.5	17.4	16.0
	Mean		**79.1**	**81.6**	**80.4**	**12.7**	**15.1**	**13.9**
	450	1	68.1	70.5	**69.3**	11.3	15.3	13.3
		61	91.5	93.0	**92.3**	10.8	12.4	11.6
		90	87.9	87.7	**87.8**	11.1	12.8	12.0
		124	66.4	68.7	**67.6**	13.7	16.0	14.9
	Mean		**78.5**	**80.0**	**79.2**	**11.7**	**14.1**	**12.9**
Mean of tin lines			**79.3**	**80.2**	**79.8**	**12.7**	**15.1**	**13.9**
Mean of 50			**79.9**	**80.0**	**79.9**	**13.1**	**15.5**	**14.3**
Mean of 150			**79.3**	**82.3**	**80.8**	**12.2**	**14.6**	**13.4**
Mean of 450			**78.5**	**81.1**	**79.8**	**11.2**	**13.7**	**12.5**
General mean			**79.2**	**81.2**	**80.2**	**12.2**	**14.6**	**13.4**
C.V%					**2.8**			**3.1**
LSD	**Year**				**n.s**			**0.08****
	Density				**n.s**			**0.31****
	Year × Density				**n.s**			**n.s**
	Lines				**1.94****			**0.37****
	TINs				*****			**0.49****
	Year × Lines				**4.88****			******
	Year × TINs				******			**n.s**
	Density × Lines				**n.s**			**0.49***
	Density × TINs				**n.s**			**n.s**
	Year × Density × Lines				**n.s**			**n.s**
	Year × Density × TINs				**n.s**			**n.s**

Table A21 Effect of the interaction between tiller inhibition (TIN) gene and seed density on total and fertile spikelets spike^{-1} at GS61 in some DH lines during 08/09, 09/10 seasons at CIMMYT experimental station in Ciudad Obregon, North West Mexico.

Tin1A allele	Seed density m^{-2}	Line	Total spikelets spike^{-1}			Fertile spikelets spike^{-1}		
			08/09	09/10	Mean	08/09	09/10	Mean
No	50	36	26.6	29.9	28.2	24.4	28.8	26.6
		51	27.8	29.7	28.8	24.9	27.5	26.2
		87	30.3	32.6	31.5	28.6	31.0	29.8
		93	27.6	30.0	28.8	24.7	28.0	26.3
	Mean		**28.1**	**30.5**	**29.3**	**25.6**	**28.8**	**27.2**
	150	36	24.2	28.8	26.5	22.3	26.6	24.4
		51	26.1	28.8	27.4	22.5	26.3	24.4
		87	28.3	30.9	29.6	25.9	28.9	27.4
		93	26.7	28.8	27.8	23.4	26.1	24.8
	Mean		**26.3**	**29.3**	**27.8**	**23.5**	**27.0**	**25.2**
	450	36	22.3	24.3	23.3	20.0	22.4	21.2
		51	23.7	27.7	25.7	20.7	25.3	23.0
		87	26.8	28.2	27.5	24.2	25.9	25.1
		93	24.2	27.0	25.6	21.9	24.3	23.1
	Mean		**24.2**	**26.8**	**25.5**	**21.7**	**24.5**	**23.1**
Mean of non tin lines			**26.2**	**28.9**	**27.5**	**23.6**	**26.8**	**25.2**
Yes	50	1	32.7	34.7	33.7	31.2	34.3	32.8
		61	27.9	29.9	28.9	27.3	29.6	28.5
		90	29.5	30.2	29.8	29.2	29.9	29.6
		124	31.6	32.9	32.3	31.3	32.4	31.9
	Mean		**30.4**	**31.9**	**31.2**	**29.8**	**31.6**	**30.7**
	150	1	30.4	34.0	32.2	28.7	33.7	31.2
		61	25.6	27.2	26.4	25.0	26.3	25.6
		90	25.5	27.5	26.5	24.4	26.5	25.5
		124	29.8	30.9	30.3	29.3	30.3	29.8
	Mean		**27.8**	**29.9**	**28.9**	**26.9**	**29.2**	**28.0**
	450	1	28.1	30.2	29.2	25.4	29.8	27.6
		61	22.9	26.0	24.4	22.5	24.9	23.7
		90	23.5	25.5	24.5	22.8	24.8	23.8
		124	26.3	28.5	27.4	25.8	28.2	27.0
	Mean		**25.2**	**27.6**	**26.4**	**24.1**	**26.9**	**25.5**
Mean of tin lines			**27.8**	**29.8**	**28.8**	**26.9**	**29.2**	**28.1**
Mean of 50			**29.3**	**31.2**	**30.3**	**27.7**	**30.2**	**28.9**
Mean of 150			**27.1**	**29.6**	**28.3**	**25.2**	**28.1**	**26.6**
Mean of 450			**24.7**	**27.2**	**25.9**	**22.9**	**25.7**	**24.3**
General mean			**27.0**	**29.3**	**28.2**	**25.3**	**28.0**	**26.6**
C.V%					**2.8**			**3.8**
LSD	**Year**				**1.04****			**0.98****
	Density				**0.89****			**0.82****
	Year × Density				**n.s**			**n.s**
	Lines				**0.69****			**0.88****
	TINs				******			******
	Year × Lines				**0.72***			**1.19****
	Year × TINs				******			*****
	Density × Lines				**1.33****			**1.18***
	Density × TINs				******			**1.63***
	Year × Density × Lines				**n.s**			**n.s**
	Year × Density × TINs				**n.s**			**n.s**

10.4 Appendix IV GENSTAT program and output examples

10.4.1 GENSTAT outputs for CIMMYT wheat historic releases experiments 2008/09 and 2009/10

10.4.1.1 An example of ANOVA table for separate years

Analysis of variance

Variate: Yield_m2

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	3	12946.6	4315.5	6.72	
Rep.*Units* stratum					
Variety	11	140319.1	12756.3	19.86	<.001
Residual	33	21192.4	642.2		
Total 47	174458.1				

Standard errors of differences of means

Table	Variety
rep.	4
d.f.	33
s.e.d.	17.919

Least significant differences of means (5% level)

Table	Variety
rep.	4
d.f.	33
l.s.d. 36.457	

10.4.1.2 An example for ANOVA table for average of the two years

Analysis of variance

Variate: Yield_m2

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum					
Year	1	3162.	3162.	1.02	0.351
Residual	6	18580.	3097.	2.84	
Rep.*Units* stratum					
Variety	11	301484.	27408.	25.15	<.001
Year.Variety	11	15150.	1377.	1.26	0.265
Residual	66	71912.	1090.		
Total 95	410288.				

Standard errors of differences of means

Table	Year	Variety	Year Variety
rep.	48	8	4
s.e.d.	11.359	16.504	25.068
d.f.	6	66	60.26
Except when comparing means with the same level(s) of Year			23.341
d.f.			66

Least significant differences of means (5% level)

Table	Year	Variety	Year Variety
rep.	48	8	4
l.s.d.	27.794	32.952	50.139
d.f.	6	66	60.26
Except when comparing means with the same level(s) of Year			46.601
d.f.	66		

10.4.1.3 An example of the regression analysis

Regression analysis

Response variate: TGW_1 TGW
Fitted terms: Constant, Year_of_release

Summary of analysis

Source	d.f.	s.s.	m.s.	v.r.	F pr.
Regression	1	119.02	119.020	29.64	<.001
Residual	10	40.16	4.016		
Total	11	159.18	14.471		

Percentage variance accounted for 72.2
Standard error of observations is estimated to be 2.00.

Message: the following units have high leverage.

Unit	Response	Leverage
1	33.20	0.44

Estimates of parameters

Parameter	estimate	s.e.	t(10)	t pr.
Constant	-425.0	85.6	-4.97	<.001
Year_of_release	0.2336	0.0429	5.44	<.001

10.4.2 GENSTAT outputs for CIMMYT L14 x Rialto DH population (*Tin1A*) experiments 2008/09 and 2009/2010

10.4.2.1 An example of ANOVA table for separate years

Analysis of variance

Variate: AGDM_m2

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	9305.	4652.	0.90	
Rep.Density stratum					
Density	2	17227.	8614.	1.67	0.298
Residual	4	20686.	5172.	2.42	
Rep.Density.Tin stratum					
Tin	1	14936.	14936.	6.98	0.038
Density.Tin	2	12160.	6080.	2.84	0.135
Residual	6	12838.	2140.		
Total	17	87151.			

Standard errors of differences of means

Table	Density	Tin	Density Tin
rep.	6	9	3
s.e.d.	41.520	21.805	49.367
d.f.	4	6	7.18
Except when comparing means with the same level(s) of Density			37.768
d.f.			6

Least significant differences of means (5% level)

Table	Density	Tin	Density Tin
rep.	6	9	3
l.s.d.	115.273	53.355	116.157
d.f.	4	6	7.18
Except when comparing means with the same level(s) of Density			92.414
d.f.	6		

10.4.2.2 An example for ANOVA table for average of the two years

Analysis of variance

Variate: AGDM_m2

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum					
Year	1	1549598.	1549598.	587.15	<.001
Residual	4	10557.	2639.	0.27	
Rep.Density stratum					
Density	2	30883.	15441.	1.58	0.263
Density.Year	2	240.	120.	0.01	0.988
Residual	8	78024.	9753.	1.53	
Rep.Density.Tin stratum					
Tin	1	17155.	17155.	2.69	0.127
Density.Tin	2	4980.	2490.	0.39	0.685
Tin.Year	1	1752.	1752.	0.27	0.610
Density.Tin.Year	2	7563.	3781.	0.59	0.568
Residual	12	76484.	6374.		
Total	35	1777236.			

Standard errors of differences of means

Table	Density	Tin	Year	Density Tin
rep.	12	18	18	6
s.e.d.	40.32	26.61	17.12	51.84
d.f.	8	12	4	17.03
Except when comparing means with the same level(s) of				
Density				46.09
d.f.				12

Table	Density Year	Tin Year	Density Tin Year
rep.	6	9	3
s.e.d.	49.60	31.65	67.71
d.f.	9.95	15.85	21.35
Except when comparing means with the same level(s) of			
Year	57.02	37.63	73.32
d.f.	8	12	17.03
Density.Year			65.19
d.f.			12
Tin.Year			73.32
d.f.			17.03

Least significant differences of means (5% level)

Table	Density	Tin	Year	Density Tin
rep.	12	18	18	6
l.s.d.	92.97	57.98	47.54	109.37
d.f.	8	12	4	17.03
Except when comparing means with the same level(s) of				
Density				100.43
d.f.				12

Table	Density Year	Tin Year	Density Tin Year
rep.	6	9	3
l.s.d.	110.60	67.14	140.68
d.f.	9.95	15.85	21.35
Except when comparing means with the same level(s) of			
Year	131.48	82.00	154.67
d.f.	8	12	17.03
Density.Year			142.03
d.f.			12
Tin.Year			154.67
d.f.			17.03

10.4.3 GENSTAT outputs for Experiment at Thriplow, Hertfordshire UK 2008/09

Analysis of variance

Variate: AGDM_m2

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	130223.	65112.	8.04	
Rep.*Units* stratum					
Line	23	1770973.	76999.	9.51	<.001
Contrast 1	1	14854.	14854.	1.83	0.182
Residual	46	372437.	8096.		
Total 71	2273633.				

Standard errors of differences of means

Table	Line
rep.	3
d.f.	46
s.e.d.	73.47

Least significant differences of means (5% level)

Table	Line
rep.	3
d.f.	46
l.s.d. 147.88	

10.4.4 GENSTAT outputs for Experiment at Sutton Bonington, Leicestershire UK 2009/10

Analysis of variance

Variate: Grain_yield_m2

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
REP stratum	2	9225.8	4612.9	0.40	
REP.DENSITY stratum					
DENSITY	1	209145.8	209145.8	18.18	0.051
Residual	2	23008.2	11504.1	14.79	
REP.DENSITY.Tin_gene stratum					
Tin_gene	1	57.4	57.4	0.07	0.799
DENSITY.Tin_gene	1	7947.6	7947.6	10.22	0.033
Residual	4	3111.2	777.8		
Total	11	252496.0			

Standard errors of differences of means

Table	DENSITY	Tin_gene	DENSITY Tin_gene
rep.	6	6	3
s.e.d.	61.925	16.102	63.984
d.f.	2	4	2.27
Except when comparing means with the same level(s) of DENSITY			22.771
d.f.			4

Least significant differences of means (5% level)

Table	DENSITY	Tin_gene	DENSITY Tin_gene
rep.	6	6	3
l.s.d.	266.442	44.704	245.800
d.f.	2	4	2.27
Except when comparing means with the same level(s) of DENSITY			63.221
d.f.	4		