OPTIMISING ROOT GROWTH TO IMPROVE UPTAKE AND UTILIZATION OF WATER AND NITROGEN IN WHEAT AND BARLEY

by

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To Margarida

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ANOVA - Analysis of variance

A - CO_2 assimilated during photosynthesis

$Aest_{max}$ - Estimated maximum photosynthetic rate

AGDW - Above ground dry weight

AI - Aridity index

A_{max} - Maximum photosynthetic rate

AW_{FC} - Available water at field capacity

BD - Bulk density

C_a - Partial pressure of CO_2 in the atmosphere

C_i - Partial pressure of CO_2 in the inter-cellular spaces

C_{RLD} - Critical root length density

C_{RVD} - Critical root volume density

D - Diffusion coefficient of the resource ion in the soil

d - Depth

DAS - Days after sowing

DI - Deficit irrigation

DM - Dry mass

E - Transpiration

ET - Evapotranspiration

FC - Field capacity

GA - Green area per plant

g_c - Stomatal conductance for CO_2

GN - Total grain number per plant

GNE - Grains per ear for all shoots

GNS - Grain number per ear in the main shoot

GS - Growth stages

g_s - Stomatal conductance

g_w - Stomatal conductance for water

Y - Grain yield

HI - Harvest index

IGW - Individual grain weight assessed on all fertile shoots per plant

IGWS - Individual grain weight assessed on the main shoot

IS - Infertile tiller

k - Resource capture coefficient

k_{RVD} - Resource capture coefficient for root volume density

k_{RLD} - Resource capture coefficient for root length density

L - Irrigation

LAI - Leaf area per unit ground area

LCP - Light compensation point

LRWC - Leaf relative water content

LSP - Light saturation point

LWC - leaf water content

MS - Main shoot

NUE - Nitrogen-use efficiency

Nup - Nitrogen uptake

NupE - N-uptake efficiency

NutE - N-utilization efficiency

p - fraction of the root system accumulated to from the soil surface to a given depth

P- Proportion of weight in each soil-depth layer to the bottom of the root system

PAR - Photosynthetic active radiation

PWC - Plant water content

Q - Photon flux density

q' - apparent quantum yield

r - Root radius

R:S - Root shoot ratio

R_a - Molecular ratio $^{13}C/^{12}C$ in the air

Rd - Dark photorespiration

RD - Root diameter

RDI - Regulated deficit irrigation

rL:rV - Root fineness

RLD - Root length density

R_p - Molecular ratio $^{13}C/^{12}C$ in the plant

RVD - Root volume density

RW - Root dry weight

rW:rV - Root tissue density

RWC - Relative water content

RWD - Root weight density

SDI - Sustained deficit irrigation

SE - Standard error

SED - Standard error deviation

SLN - Specific leaf nitrogen

SRL - Specific root length

TRL - Total root length

TRV - Total root volume

TRW - Total root weight

TSW - Total straw weight

V_L - Volume at layer L

W_a - Difference of partial pressure of water in the atmosphere

WC - Water content

WU - Water-use

WUE - Water-use efficiency

WUE_{ph} - Water-use efficiency of photosynthesis

WUE_{grain} - WUE in respect to grain yield

Y - Grain yield

β - Shape of the cumulative distribution with depth

β_L - Shape of the cumulative distribution of length with depth

β_V - Shape of the cumulative distribution of volume with depth

β_W - Shape of the cumulative distribution of weight with depth

$\delta^{13}C$ - Carbon isotopic composition

$\Delta^{13}C$ - Carbon isotopic discrimination

δ_a - Deviation of the isotopic composition of the air in relation to a standard

δ_p - Deviation of the isotopic composition of the plant in relation to a standard

θ_{FC} - Volume basis water content at field capacity

θ_L - Volumetric soil moisture at layer L

θ_v - Volume basis water content

ν - Vapour pressure deficit

ϕ - Fraction of available resource

ϕ_c - Carbon lost by tissue respiration

ϕ_w - Water lost during the night if the stomata are not completely closed

Abstract

Durum wheat (*Triticum turgidum* L. var *durum*) and spring barley (*Hordeum vulgare* L.*)* are the most widely grown crop species in the semi-arid to arid areas of the Mediterranean region. However, their average on-farm yields are relatively low, 1.95 and 2.60 t ha^{-1}, respectively (FAO, 2007). Water is generally recognized as the most limiting factor for barley and durum wheat production in the Mediterranean, though it has been found, at least for some regions, that N fertilizer applications have been limiting (Passioura, 2002). Water in the Mediterranean is relatively scarce and predictions for 2025 show that water limitations for agricultural production in that region will intensify (IWMI, 2000). Nitrogen fertilizer represents a significant cost of production for the grower and may also have negative environmental impacts through nitrate leaching, use of fossil fuels for manufacture and application, and N_2O emissions associated with denitrification. Reducing excessive N fertilizer inputs and increasing water productivity, whilst maintaining acceptable yields, will be aided by increases in uptake efficiency.

To be in a position to manage irrigation and N inputs more effectively, an improved quantitative understanding of relationships between root traits and capture of water and nitrogen is required. The major phase of root growth in wheat and barley is during tillering and stem extension, and total length of the root system increases until about anthesis (Gregory *et al.*, 1978b; Barraclough & Leigh, 1984). A theoretical model (van Noordwijk, 1983) indicated that the rooting trait best related with water and N capture is the root length density (root length cm/ soil volume cm^3; RLD). Field data sets of barley grown on stored water in Syria indicated a RLD of about 1 cm cm^{-3} is required for extraction of ca. 90% of the available water, and it was defined as the critical root length density - C_{RLD} (Gregory & Brown, 1989). In field-grown durum wheat and barley, RLD usually exceeds C_{RLD} in the upper soil profile, while below 60 to 80 cm it is typically lower than 1 cm cm^{-3}. The relationship between RLD in cereal root systems and below-ground resource capture was recently described in a quantitative model (King *et al.*, 2003), linking the size (RLD) and cumulative distribution of the root system with depth (β) to the proportional capture of available water and nitrogen (ϕ) during grain filling (King *et al.*, 2003). β describes the shape of the cumulative

distribution with depth, according to: $p = 1 - \beta^d$; where p is the fraction of the root system accumulated from the soil surface to a given depth (d).

ϕ is calculated as: $\phi = 1 - e^{-k.RLD}$, where k is the resource capture coefficient (cm^2).

The overall aim of the present study was to: (i) identify root traits in barley and durum wheat for improved water and N capture under different intensities of water and/or N stresses, and (ii) quantify responses of root growth, root: shoot partitioning and water and N capture to simulated Mediterranean environments differing in water and N stresses, using controlled-environment experimental conditions.

The main hypotheses tested were:

1. Mediterranean barley and durum wheat have a similar root system morphology, and comparable cumulative distribution of RLD with depth (β_{RLD}).
2. Water and N deficits increase R:S, however total root weight and length will be reduced.
3. The proportion of roots deeper in the profile will increase with water and N deficits (higher β).
4. k can be defined from the relationship between RLD and ϕ, and hence a C_{RLD} can be calculated; k should not differ between genotypes and the C_{RLD} will be ca. 1 cm cm^{-3}.
5. The k value for root volume density (root volume / soil volume; RVD) can be calculated according to King *et al.* (2003), and critical root volumes (C_{RVD}) for a 90% water extraction can be calculated. However, RLD will explain a higher proportion of ϕ for water capture than RVD.
6. Aboveground dry weight (AGDW) and yield (Y) decrease with N and water deficits and there is an interaction between water availability and N fertilizer, such that responses to N are relatively greater under high than low water availability.
7. Water-use efficiency (AGDW / water use; WUE) increases with water stress and N availability, while grain $\Delta^{13}C$ decreases, and responses are similar for spring barley and durum wheat.
8. Nitrogen-use efficiency (grain DM / N available; NUE), N-uptake efficiency (above groung N / N available; NupE) and N-utilization efficiency (grain DM /

aboveground N; NutE) will decrease with increasing water deficits and increasing N supply and responses are similar for spring barley and durum wheat.

In each of 2006, 2007 and 2008 one glasshouse soil column (15 cm diameter x 150 cm length) experiment was conducted at the University of Nottingham, School of Biosciences, Sutton Bonington Campus, UK (52.5^{o} N, 1.3^{o} W). The responses of Jordanian spring barley cv. Rum (2006-2008) and durum wheat cvs Hourani (2006-2007) and Karim (2007) to two levels of irrigation (drought and fully irrigated) and up to three levels of N fertilizer (nil, 50 and 100 kg ha^{-1} N, equivalents) were examined. In 2006 and 2007 for each genotype there were six treatment combinations (2 irrigation treatments x 3 fertilizer N levels), in 2008 for barley there were two irrigation treatments at one level of N fertilizer (50 kg N ha^{-1}, equivalent). The experiments used a factorial randomised block design in three (2006) or five replicates (2007 and 2008). In each experiment, detailed analysis at sequential samplings through the season was carried out, including anthesis and harvest, of root growth and morphology (by root digital image analysis), as well as for the aboveground growth and dry matter partitioning. Water and N uptake were measured and their use-efficiencies evaluated. In 2006, water uptake was gravimetrically measured by weekly weighing a sub-set of soil columns for each treatment. While in 2007 and 2008, water content was weekly measured at different soil-depth intervals using a Theta-T probe (ML2x Delta T Devices, Cambridge, UK) via access apertures in columns for a sub-set of columns. WUE was calculated as the AGDW /total water use, from the date of transplantation to harvest and also by the slope of the linear regression of cumulative AGDW on cumulative water uptake through time.

This project attempted a comprehensive study of root (and shoot) responses of barley and durum wheat to water and/ or nitrogen stresses, to identify root characteristics for resource acquisition in Mediterranean type environments. However the conditions were atypical of Mediterranean ecosystems. High soil N available (at sowing + mineralization through the season) and/or leaching led to inconsistent and contradictory response to the ones usually found in the literature.

Excessive temperatures known to be inhibitory to plant growth and development were felt in the glasshouse, with peaks exceeding 50 ºC. In the field, roots usually experience much lower temperatures below ground. However in these experiments they were

subject to the same high temperatures as shoots, this would have had a major impact on the observed root distributions. Moreover, soil in the columns was found to have quite large bulk densities (1.61, 1.85 and 1.76 g cm^{-3} in 2006, 2007, and 2008, respectively), offering a quite high resistance to root growth and consequently shoot growth (Bowen, 1981). To avoid roots growing in the edges, only one plant per soil column was used. However when compared to field grown crops, it only represents an half to a fifth of the plant densities usually found in wheat and barley grown in the Mediterranean. Therefore the usual cropping inter-competition for soil resources was not accounted for. For this reasons the root densities presented in this work might not be representative of those found in the field grown crops, and hence its use has to be cautiously.

Due to the large amount of time needed to extract the root system from the soil, and posterior fine cleaning before scanning, only the top (0 – 20 m); mid (60 - 80 cm) and bottom (>125 cm) of the root system where possible to be analysed. Consequently the total root weight, length and volume, are not real totals but the sum of the layers analysed. Other root morphology parameters, like mean root diameter, specific root length (SRL) and root volume root weight ratio (rV:rW) where calculated in function of those layers. The calculation of the root parameters distribution with depth, using β coefficients (β_W - weight, β_L – length and β_V – volume), was also done taking in account those soil depth sections. This partial analysis can result in a different distribution with depth when compared with a full analysis. Moreover the root shoot ratio (R:S) was estimated using the β_W, hence those values may not be the same as if all root system was analysed.

Root growth of barley was generally representative of values reported in the literature in the present experiments, but root growth of durum wheat genotypes showed some signs of restriction in the soil columns, particularly in 2007, possibly in part due to the high soil bulk density (BD = 1.85 g cm^{-3}). The root to shoot dry weight ratio (R:S) increased with drought, but relatively more for wheat than for barley, so that total root weight (TRW) was actually higher under water limitations for durum wheat than under full irrigation. After anthesis for all genotypes under the droughted treatment, there was a consistent increase in the allocation of root biomass deeper in the soil profile (higher β_W). Total root weight (TRW), total root length (TRL) and total root volume (TRV) were well correlated; therefore RWD, RLD and RVD distribution with depth followed

similar patterns. Hence, an increase of β_L and β_V was also found under drought. Beta values for root length were (averaged across 2006, 2007 and 2008): 0.97, 0.97 and 0.96 for barley cv. Rum, wheat cv. Hourani and wheat cv. Karim under irrigation; and 0.98, 0.98 and 0.97 under drought, respectively. N was shown to occasionally reduce RLD, possibly associated with extreme and uniform N concentration in the soil (due to a high mineralization) causing lateral root formation to cease (Linkohr *et al.*, 2002).

The sub-traits most affecting TRL differed between genotypes. For durum wheat changes in length were mainly associated with increases in R:S and TRW, whilst for barley cv. Rum specific root length (SRL; root length cm / root weight g) was more important in determining TRL. Therefore SRL could be a promising trait to target in breeding, since it may be possible to increase RLD without increasing the allocation of biomass from the aboveground to the roots.

Overall water use (WU) was higher for barley than wheat cultivars associated with its more extensive root system and higher aboveground growth. However, differences between the WU of plants subjected to drought of wheat cultivars and barley were not large. As expected WU decreased with drought and WUE increased. For barley WUE was relatively higher than for wheat cv. Hourani, and wheat cv. Karim. However, $\Delta^{13}C$ in the grains, across years was similar between genotypes. Leaf SPAD values measured at anthesis were always higher for barley than wheat, possibly indicating higher specific leaf nitrogen (SLN) resulting in higher assimilation rate per unit leaf area (Cabrera-Bosquet *et al.*, 2009). N-use efficiency was higher for barley than for durum wheat cultivars and decreased with drought and N application for all genotypes. Differences in NUE were mainly explained by NupE.

Fitting the King *et al.* (2003) equation to the RLD and ϕ data for water, a k_{RLD} was found for barley cv. Rum of 2.4 cm^{-2} under drought (2007-08), resulting in a C_{RLD} of 0.97 cm cm^{-3}. This was similar to the value previously found by Gregory & Brown (1989); however no value could be fitted under irrigation. For wheat cv. Karim relatively higher values of k_{RLD} were found: 0.59 and 0.40 cm^{-2} under irrigation and drought, respectively, in 2007; corresponding to C_{RLD} values of 0.41 and 0.64 cm cm^{-3}, respectively. Overall results indicated that under drought C_{RLD} values were higher than under irrigation.

Fitting an adapted King *et al.* (2003) equation to RVD *vs* ϕ for water showed a more consistent relationship than was found for RLD. Similar values of k_{RVD} were observed for barley (5.13 and 4.45, under irrigation and drought, respectively) and wheat cv. Hourani (5.03 and 4.00, under irrigation and drought, respectively), though wheat cv. Karim had relatively higher values (10.04 and 5.86, under irrigation and drought, respectively). Therefore, C_{RVD} values for wheat cv. Karim were lower than for the other two genotypes. k_{RVD} values under drought were lower than those found under irrigation, resulting in higher C_{RVD} under drought.

AGDW and grain yield (Y) was relatively higher for barley than for both wheat varieties. Furthermore wheat cv. Karim showed the lowest values of Y. Those yield differences were mainly associated with a higher fertile shoot number per plant for barley. Indeed Y was strongly positively correlated with the fertile shoots and grain number per plant (R^2 = 0.76 and 0.97, respectively). Drought decreased AGDW, number of fertile shoots and therefore Y for all genotypes but more severely for barley than for the wheat genotypes.

N fertilizer effects were only consistent in 2006 where the N50 treatment increased fertile shoot number, AGDW and Y per plant, as well as WU, but only under irrigation, consistent with the literature (Ebrahim, 2008). Barley proved to have higher WUE associated with a higher SLN, and produced a higher Y. Water use and NupE were also higher under drought for barely than for wheat genotypes due to its more extensive root system. Therefore, it seems that on the basis of the present results under Mediterranean conditions, barley cv. Rum should be preferred when high rain or irrigation is available. When water is limited durum wheat varieties will probably maintain Y relatively better than barley. Nevertheless, these findings should be interpreted cautiously since wheat growth in this work was possibly limited more by the CE growing conditions in the UK than barley. Furthermore, the root growth of wheat cv. Karim was apparently susceptible to mechanical impedance that usually increases in drying soil.

Overall, root systems of barley and wheat and their distribution with depth were broadly similar. However, under drought durum wheat seemed more adapted, not only relatively increasing the biomass allocated to the roots (high R:S), but in fact absolutely increasing TRW when compared to the irrigated plants. Traits underlying variation in

total root length were different between genotypes; durum wheat was mainly dependent on the amount of biomass allocated to roots, while barley seems able to produce more root length by increasing SRL due to changes in tissue density. Therefore breeding programs should consider SRL a potential target trait. The relation between RLD and ϕ was verified resulting in a k value for RLD for barley of 2.4 cm^{-2}. A C_{RLD} of approximately 1cm cm^{-3} for barley was confirmed. However, results suggested that it might be lower under irrigation than under drought and lower for wheat than for barley. RVD was slightly better related to ϕ than RLD. Therefore more studies relating proportional resource capture and RVD are needed to confirm these findings and establish the basis of that relationship. β was confirmed by the present results to be a good trait to summarize the overall effects of changes of root distribution with depth and with drought.

A simple framework relating the biomass allocated to roots (R:S), the investment in length (SRL) and the cumulative distribution of roots with depth (β) to a potentially higher RLD at depth and water and N uptake is suggested. Finally, the implications of the current findings for establishing agronomic and breeding strategies to improve below-ground resource capture, utilization and yield production under water and/or N stresses are discussed.

1 INTRODUCTION

1.1 GLOBAL FOOD DEMAND IN A CHANGING CLIMATE

According to the most recent predictions, the world population is predicted to increase from the present 6.9 billion to more than 9.0 billion by 2050 (Lutz *et al.*, 2001; Hamilton, 2009), of which approximately 4.0 billion will be living in water-scarce or -stressed countries (Engelman, 2009). Today's crop land per capita is half of what it was in the 1960s (Engelman, 2009) and with rate of population growth more land has to be allocated to build infrastructures, urbanization, as well as the increasing demands for land for bio-energy production and biodiversity protection (Sands & Leimbach, 2003; Jordan *et al.*, 2007; Campbell *et al.*, 2008; Gahukar, 2009). Competition for land and water, and the increasing price of fertilizers (Raun *et al.*, 2002) may result in an increase of world food prices. The constant release of nitrous oxide (a greenhouse gas) to the atmosphere as a result of denitrification of nitrate fertilizers and consequent global warming impacts and the inevitable unpredictable weather events that might occur as a result will also be a challenge for global food security (Reynolds & Borlaug, 2006). Increasing crop yields while decreasing the use of fertilizers, water and fossil fuels is the challenge for plant and crop scientists for the next century (Hamilton, 2009).

In the 1960s with the introduction of wheat semi-dwarf varieties - with greater partitioning to ear, more grains m^{-2} and increased lodging resistance, so that higher amounts of N fertilizer could be used; - together with irrigation and pest management led to the 'Green Revolution' started at CIMMYT (International Maize and Wheat Improvement Center) in Mexico and many parts of Asia. This made it possible for the growth rate of food production to exceed that of population growth (Swaminathan, 2007), though it failed to arrive Africa (Azam-Ali, 2007; Rockstrom *et al.*, 2007; Blaustein, 2008), where the total cereal production is only 40% of the global food production (FAO, 2007). Furthermore, global yields for wheat and barley seem to be reaching a plateau (Figure 1.1), possibly due to economical reasons such as the reduction in use of expensive agro-chemicals as suggested by Calderini & Slafer (1998), or due to the fact that in some countries the harvest index (HI, proportion of grain biomass by total aboveground biomass) might be approaching the theoretical maximum value of 0.62 (Austin *et al.*, 1980).

To achieve long-term increases in cereal productivity without associated ecological harm, the so called 'Evergreen Revolution' has been proposed (Swaminathan, 2007). To achieve this goal, science and technology will play an important role; the solution will not be in one simple tool but will involve a combination of methods and techniques including further development of high-yielding and well-adapted genotypes with high resource-use efficiency through breeding (Reynolds & Borlaug, 2006; van Ginkel & Ogbonnaya, 2007; Reynolds *et al.*, 2009) and the use of crop management practices from a more efficient and precise irrigation and N fertilisation (Isherwood, 2000; Sandhu *et al.*, 2000; Rockstrom *et al.*, 2009) to the use of bio-pesticides, bio-fertilizers and reduced tillage (Swaminathan, 2007).

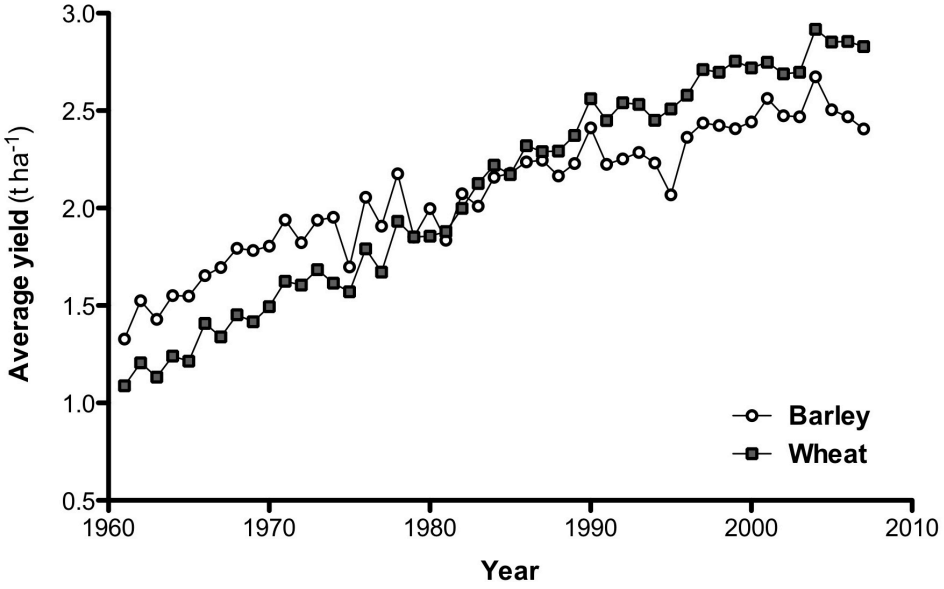

Figure 1.1 Total wheat and barley world average yields from 1961 and 2007 (FAO, 2007).

1.2 WHEAT AND BARLEY PRODUCTION IN THE MEDITERRANEAN

Wheat and barley are the two main arable crops in the Mediterranean Basin, constituting 80% (28% of barley and 52% of wheat) of the total cereal production area and contributing 61% (20% of barley and 41% of wheat) of its arable production (FAO, 2007). The land use for both wheat and barley between the North and South Mediterranean Basin (78% and 83%, respectively) is quite similar (FAO, 2007).

Though yields in the North Mediterranean countries average 2.8 t ha^{-1} for barley and 3.2 t ha^{-1} for wheat and in the South 1.1 and 2.0 t ha^{-1}, respectively (FAO, 2007).

The main reason for the differences in average on-farm yields is related to a lower aridity index (ratio of mean annual precipitation to mean annual potential evapotranspiration; Figure 1.3) in the South and therefore the crops are more affected by drought conditions. However, Egypt shows a different trend to the overall pattern where 100% of its cropland is irrigated (Yang & Zehnder, 2002) and wheat yields reach 6.5 t ha^{-1} more than any in the Northern Mediterranean country (FAO, 2007). Excluding Egypt, the difference between these two areas is even larger with on-farm wheat yields in the South being only 43% of those in the North (FAO, 2007).

1.2.1 Future perspectives on water demands

To sustain the growing population there is an increase in water demand not only for human consumption but for growing domestic and industrial needs, as well as for food (agricultural and industrial) production (IWMI, 2000). Water scarcity can be caused by the excessive exploitation of ground water for irrigating crops, as well as pollution of groundwater associated with excessive use of N fertilizers. Also domestic and industrial activities associated with water acidity caused by air pollutants, can all lead to water scarcity (Middleton & Saunders, 1997; Gleick, 1998; SIWI & IWMI, 2004).

Climate change is expected to have a direct effect on crop production due to changes in rainfall leading to more frequent drought or flooding and warmer or cooler temperatures responsible to changes in growing season (Gregory *et al.*, 2005). The consequences of climate change on food security will be different in different parts of the world, but with regard to water scarcity it is expected that the areas that are already suffering significant drought will be those more prejudiced in the future.

Plants use between 500 litres (in highly efficient irrigated areas) and 4000 litres of water (in low productivity rainfed systems) to produce one kilogram of staple food grains such as wheat (Rijsberman & Manning, 2006). Concerning water use, grain production is therefore quite an inefficient activity. Besides the water lost by the plant in its normal

physiological functions, some will runoff due to poor or inefficient root systems and/or other bad agronomical practices (e.g. too little or much water applied, time of the day for irrigation, and phasing of water supply in relation to crop demand).

In order to increase crop performance and yields under water-limited conditions it will be necessary to increase water uptake to improve season-long water use (WU), water-use efficiency (WUE) and harvest index (proportion of aboveground biomass as grain; HI) coupling together new genetic technologies (Araus *et al.*, 2002) with classic breeding techniques and better agronomic practices (Lægreid *et al.*, 1999; Gleick, 2003).

Water-use efficiency is usually determined as the total dry matter produced by water consumed (Larcher, 2003):

$$\text{WUE (g l}^{-1}) = \frac{\text{Dry matter produced}}{\text{WU}} \qquad \textbf{Equation 1.1}$$

Water-use efficiency is therefore the cumulative increase in dry matter and water used through the crop growing cycle. For water-limited environments grain yield is a function of water use (WU), water-use efficiency (WUE) and harvest index HI (Passioura, 1977):

$$\text{Grain Yield (Y)} = \text{WU} \times \text{WUE} \times \text{HI} \qquad \textbf{Equation 1.2}$$

Water use is equal to evapotranspiration (ET); this is the sum between the water transpired by the crop (T) and the water evaporated from the soil (E) (Fischer, 1981).

1.2.2 The Mediterranean ecosystem and water availability

Mediterranean ecosystems represent about 5% of the terrestrial ecosystems (Davis & Richardson, 1995; Vilà & Sardans, 1999); they occur between the 31° and 40° north and south of the equator on the western sides of continents (Nahal, 1981). These areas are: the Mediterranean Basin, California, Chile, South Africa and south-western Australia (Figure 1.2) (Castri, 1981). The Mediterranean climate is usually defined as a

transitional regime between temperate and dry tropical climates, characterised by a concentration of rainfall in winter, occurrence of a distinct summer drought of a variable length, high variability of precipitation from year to year, mild to warm or hot summers, and cool to cold winters, combined with high solar radiation especially in summer (Castri, 1981; Pereira & Chaves, 1993).

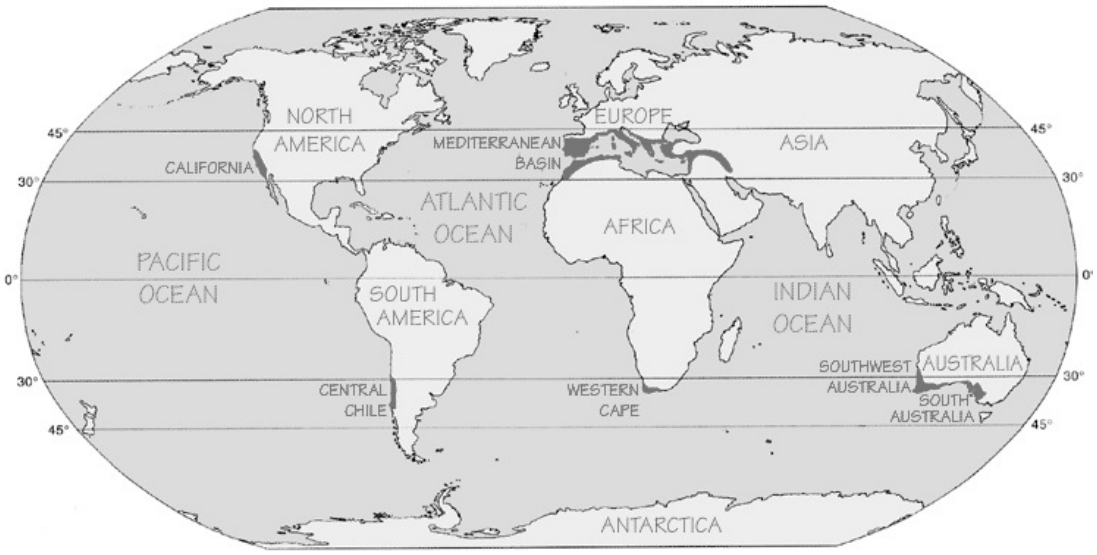

Figure 1.2 World map with Mediterranean climate areas in highlight (adapted from Castri, 1981).

The Mediterranean Basin comprises about 60% of all Mediterranean areas and, according to the aridity index, most of the Northern Mediterranean is considered humid (AI > 0.65) to sub-humid (0.5 < AI ≤ 0.65), reaching the semi-arid (0.05 < AI ≤ 0.2) to hyper-arid (0 ≤ AI ≤0.05) classification at the Southern Mediterranean basin (Figure 1.3). Furthermore in North Africa and the Middle East water has become an increasing constraint to food production and economical development (Yang & Zehnder, 2002), and predictions for 2025 (IWMI, 2000) are that all the Southern Mediterranean basin areas will suffer economical[1] or physical water scarcity[2] (Figure 1.4).

[1] **Economic water scarcity** – when lack of water infrastructure is more important then the lack of resources (Rijsberman & Manning 2006).
2 **Physical water scarcity** - lack of resources resources cannot satisfy the demands (Rijsberman & Manning 2006).

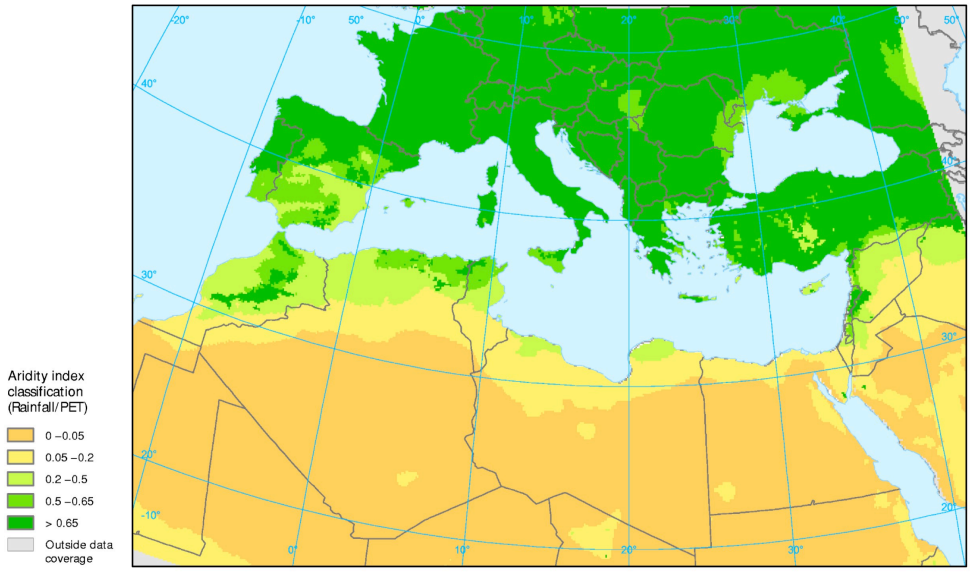

Figure 1.3 Aridity index in the Mediterranean basin calculated from 1961 to 1990 (source EEA, 2003).

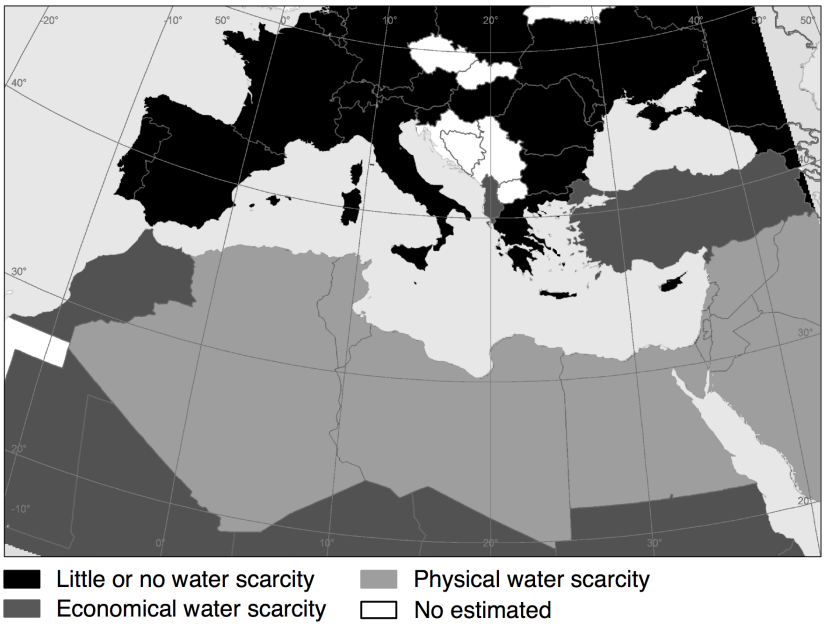

Figure 1.4 Water status projected to 2025 at Mediterranean area basin (adapted from IWMI, 2000).

1.2.3 Nitrogen in crop production and impacts to the environment

Despite the fact that Nitrogen (N) constitutes only 2 to 4% of the plant dry material it is the most important plant macro-nutrient (Mengel & Kirkby, 2001). Nitrogen constitutes part of essential plant cell compounds from proteins to chlorophyll and genes (Srivastava & Singh, 1999). Although being one of the most widely distributed elements in nature (80% of the Earth's atmosphere, Bidwell, 1974), N is often in deficit in plants. From the entire N in nature ca. 98% is in the primary rocks and ca. 2% in the atmosphere and only a small fraction will be available to the plants due to a series of complex microbiological processes (Bidwell, 1974; Mengel & Kirkby, 2001; Pask, 2009). Plant N uptake is mainly in two forms: nitrate (NO_3^-) and ammonium (NH_4^+); in arable crops the first is usually preferred, but in poor soils and acid or wet soils NH_4^+ is normally used instead (Mengel & Kirkby, 2001; Larcher, 2003).

N deficiency can decrease the carbohydrate source size, by decreasing leaf growth, area and duration; source activity by decreasing photosynthetic rate per leaf area; and source sink capacity by decreasing size of vegetative storage organs (Engels & Marschner, 1995), with negative consequences on crop yields. The impacts of N on overall crop growth and yields are described in 2.3.1 and 2.3.2.

The use of mineral fertilizers particularly N has proven to be indispensable for crop production. Indeed the two-fold increase in agricultural food production in the past forty years has been largely due to the increased use of N fertilizer (Lægreid *et al.*, 1999; Hirel *et al.*, 2007). The total N applied for global wheat production in 2007/08 is estimated at 17.4 Mt corresponding to 17.3% of the total N fertilisation in agriculture (Heffer, 2009); to ensure enough food to feed the expected population in 2050, N and phosphorous (P) fertilisation has to triple if we keep using the current agronomic practices (Tilman *et al.*, 2001). Worldwide production of N fertilizers is almost entirely based upon Haber-Bosch process that uses fossil fuels, consuming ca. 1.3% of the total world energy consumption (Gilland, 1993). Therefore, although the benefits of N fertilisation on crop production are unquestionable, the harm to the environment and populations of excessive use of N fertilizer must be considered.

Considering the life cycle of synthetic nitrogen fertilizer the potential environmental impacts of N fertilizers are (Khalil *et al.*, 2002; Blottnitz *et al.*, 2004; Ju *et al.*, 2009):

- ***Global Warming*** – caused by the use of fossil fuels and emission of green house gases (CO_2 and NO_x) during fertilizer production; and relative impacts on global warming due to the increase of nitrogenous gases (NO_x) released from denitrification of applied fertilizer by soil bacterial (e.g. NO2 is 200–300 times more potent than CO2 as a greenhouse gas, Khalil *et al.*, 2002);
- ***Air pollution*** – N fertilizer application can lead to ammonia (NH_3) release to the atmosphere, where it reacts with acidic compounds forming ammonium salts responsible for smog aerosols affecting atmosphere opacity and earth radiation budget (Renard *et al.*, 2004);
- ***Eutrophication and pollution of drinking water*** – due to its high mobility in the soil nitrate leaching is a major ecological problem.

Excessive use of N fertilizers also has a major environmental impact through pollution of ground water by NO_3^- leaching. This has led the EU to establish the nitrate directive: 91/676/CEE in order to minimize NO_3^- impacts. The most dangerous impact of Nitrate in ground water is to human health, as it can cause methemoglobinemia disorder in infants a serious and often fatal illness (Strebel *et al.*, 1989; Blottnitz *et al.*, 2004). NO_3^- leaching can also cause eutrophication of marine ecosystems stimulating algae blooms that block sunlight and cause aquatic grasses, that are food and shelter for aquatic creatures, to die (Blottnitz *et al.*, 2004). Furthermore, the respiration of the algae at night as well as decomposition of dead algae will decrease the oxygen dissolved in the water at around dawn that is essential for aquatic organisms (Blottnitz *et al.*, 2004; Giles, 2005). Besides the above-mentioned drivers to a more judicious use of N fertilizers, the constant rising of fossil fuel prices required to produce, transport and apply fertilizers costs to the grower are now also of concern (Hirel *et al.*, 2007; Hobbs, 2007). The negative environmental, health and economical impacts due to the use of N fertilizers stress the necessity to increase the nitrogen-use efficiency [NUE = grain dry weight / g N available (N applied + soil N – chapter 2.3] through agricultural management practices and breeding of more efficient crops (chapter 2.4.1).

1.2.3.1 Nitrogen use in the Mediterranean

Durum wheat and spring barley are the most widely grown crop species in the semi-arid to arid areas of the Mediterranean region. Barley is usually recognised as more adapted than wheat to low nutrients and drier conditions (Josephides, 1992; Cossani *et al.*, 2009). However recent field experiments in Spain seem to indicate that this is not universally true (Cossani *et al.*, 2009), where the response of both species to different combinations of N and irrigation treatments were similar.

Under Mediterranean conditions, water is usually recognized as the most limiting factor for crop production. For that reason, in the past little attention was given to N (Vlek *et al.*, 1981). In countries in the South Mediterranean region (Morocco, Jordan, Lebanon and Tunisia) growers are still somewhat resistant to the application of N fertilizers to wheat and barley (especially in rainfed conditions) and when N applications are carried out usually values for durum wheat do not exceed 100 kg N ha^{-1} and for spring barley 50 kg N ha^{-1} and they rarely take into account soil N analysis (Thabet *et al.*, 2009). The high cost of N fertilizers and the general assumption by farmers that N in Mediterranean conditions has small effects on yields is the main reason for the lack of adoption of N fertilisation (Thabet *et al.*, 2009). It has been suggested that for some Mediterranean areas poor or inadequate nitrogen supply has been as much responsible for cereal yield losses as water availability (Latiri-Souki *et al.*, 1998; Passioura, 2002; Ali *et al.*, 2006).

N fertilizer recovery in cereal crop production in the Mediterranean is a very inefficient process. Values of NUE as low as 15% and NupE of 49% have been reported for durum wheat growing in southern Spain (Lopez-Bellido *et al.*, 2008), and ca. 20% cf. to ca. 50%, respectively for spring barley in Jordan (Ebrahim, 2008). However those, values have been shown to be highly dependent on genotype, environmental conditions and N application (Lopez-Bellido *et al.*, 2008). The main causes for low N uptake efficiency (NupE) are: (i) poor synchrony between fertilizer N and crop demand, e.g. associated with large application of N fertilizer early in the season (Raun & Johnson, 1999; López-Bellido *et al.*, 2005); (ii) uniform field applications to spatially variable fields (Hurley *et al.*, 2004); (iii) use of 'yield-based' N recommendations assuming constant efficiency of

fertilizer recovery (Sylvester-Bradley *et al.*, 1990) and (iv) failure to take account of yearly weather variations, e.g. the amount of soil N mineralized in warm, wet years (Shanahan *et al.*, 2008).

1.3 ROOT CAPTURE

Although the influence of canopy characteristics on aboveground productivity of cereals is now relatively well understood, due to the difficulty of access and complexity of environment interactions, understanding the role of the root system is less complete and subject of discussion (Passioura, 1983; Gregory, 1994a; Hoad *et al.*, 2001). Though there is no doubt of their importance to water and N capture. Root system characteristics vary widely between and within species (Fitter, 1985; Hoad *et al.*, 2001; Dunbabin *et al.*, 2003), and root traits are a relatively new target in agronomic programmes aimed at improving WUE and NUE. For a long time, due to its high mobility (Dunbabin *et al.*, 2004), nitrogen supply was considered independent of the root system characteristics, assuming that only mass flow and diffusion were the relevant mechanisms for the uptake of N by the plant (Herrera *et al.*, 2005). However, some works showed that N capture depends on the ability of the root system to respond to spatial and temporal nitrogen supply (Fitter *et al.*, 1991). Furthermore, a positive correlation was found between nitrate and water uptake and root length density in maize (M.Cooper *et al.*, 1987; Wiesler & Horst, 1993; Wiesler & Horst, 1994) in several catch crop species (Thorup-Kristensen, 1993). Root traits were incorporated in the model developed by Dunbabin *et al.* (2003). These previous studies indicate that greater root length densities are more effective in resource acquisition. For cereals, theoretical calculations suggest the optimum value of RLD for water and N capture is about 1 cm cm^{-3}; above this value there is an excessive presence of roots and intra competition between roots of the same system may occur (van Noordwijk, 1983). Usually, below about 80 cm soil depth RLD values of cereals roots are less than 1 cm cm^{-3} (Barraclough & Leigh, 1984; Barraclough & Weir, 1988; Wahbi & Gregory, 1989) and so insufficient for effective nitrate and water capture. According to a sensitivity analysis of the model developed by King *et al.* (2003), the cumulative distribution of RLD with depth (described by a parameter β in the model) is an important trait and a more uniform distribution of roots

in the soil profile theoretically resulting in a greater economic return from water and nitrogen capture – better yield. A more uniform root system distribution with depth increases the effectiveness of the whole system; firstly it permits a more rapid access to resources deeper in the profile, secondly it delays the point where the intra-root competition occurs and the crop achieves greater RLD in the subsoil that is required for effective N and water uptake (King *et al.*, 2003). The particular properties of each nutrient in the soil imposes different RLD requirements for an effective uptake, e. g. due the low mobility of P (López-Bucio *et al.*, 2002; Poirier & Bucher, 2002) in the soil a relatively higher RLD is required for an effective uptake when compared to water and/ or nitrogen.

Differences in the distribution of RLD with depth may be associated with the velocity at which roots elongate to depth (*RFV* – root front velocity) and the proliferation rate at each soil layer (Thomas *et al.*, 1995). RFV is closely related with the water and N extracted by the crop (Monteith, 1986; Robertson *et al.*, 1993; Thomas *et al.*, 1995). Another important trait influencing the potential for water and nutrient acquisition by roots is the mean root diameter. According to Fitter (1987) thinner roots relate to greater below-ground resource capture per unit of investment in biomass, confirmed by King *et al.* (2003) where the model indicated greater uptake associated with a lower specific root weight (dry mass per unit root length). In contrast, Eissenstat and Yanai (1997) found that in citrus, non-mycorrhizal roots are thinner than mycorrhizal roots, and have about 6% higher construction cost and 9% higher maintenance respiration. Thinner roots may also have constrained axial water transport (McCully & Canny, 1998), low plant support and a weak resistance to herbivores and drought (Fitter, 1987; Fitter, 1996).

1.4 AIMS OF THE THESIS

High seasonal variability in rainfall, with soil characterised by low and variable N content and often prone to wind and water erosion due to irregular steep slopes (López-Bellido *et al.*, 2000), make agriculture in the Mediterranean a challenge. The stronger environmental limiting factors to crop growth and yields in those areas are soil moisture and nitrogen, the former of which depends on rainfall and its distribution during the

growing season (Slafer, 2003). All of that aggravated by alterations to rainfall patterns and temperature increase caused by climate change (Huntingford *et al.*, 2005) and population growth. Aims for new durum wheat and spring barley cultivars and better management tools, in order to improve NUE and WUE whilst maintaining and ideally increasing yields. Since roots are the main organs responsible for the uptake of N and water, understanding root growth, morphology and function is essential for breeding new cultivars.

The overall aims of this thesis are therefore to:

(i) Comparison of the responses of durum wheat and barley, roots and shoots growth to water and nitrogen deficits, using controlled environment conditions simulating Mediterranean environments;

(ii) Quantify responses of root growth (including distribution with depth), root: shoot partitioning and water and N capture to simulated Mediterranean environments differing in water and N stresses;

(iii) Identify best root system traits in barley and durum wheat for improved water and N capture under different intensities of water and/or N stresses;

(iv) Produce a framework for root growth and associated sub-traits that could contribute to the refinement of crop simulation models;

(v) Quantify responses of aboveground WUE and NUE of barley and durum wheat to different N and water deficits.

2 LITERATURE REVIEW

2.1 ROOT SYSTEM MORPHOLOGY AND DISTRIBUTION OF WHEAT AND BARLEY

Anchorage, support, and water and nutrient uptake are the main functions of the plant root system. Due to the difficult access and complexity of environmental interactions, roots are still one of the most challenging subjects in plant study, but the importance of the often entitled hidden half (Waisel *et al.*, 1996) is unquestionable.

Two types of roots constitute the wheat and barley root systems: the primary and the secondary roots (Hoad *et al.*, 2001). The primary roots (often called seminal roots), usually between three to eight axes, are the first to develop and they arise from the coleorhizae of the seed (Key, 1973; Gregory *et al.*, 1978b; Hoad *et al.*, 2001) being active throughout all the crop life (Gregory *et al.*, 1978b). Their growth is mainly downward occupying the deeper spaces of the soil profile (Key, 1973). They have a diameter between 0.2 to 0.4 mm, a branching order from one to three and in a fully developed crop they constitute 5 to 10% of the total root system (Hoad *et al.*, 2001).

The secondary (often called crown, nodal or adventitious roots) are the roots that grow from the nodes of the coleoptile, stem and tillers (Key, 1973; Gregory *et al.*, 1978b; Hoad *et al.*, 2001). The onset of tillering is the starting point of the growth of the secondary roots, and their formation is intimately related to tiller formation (Klepper *et al.*, 1984; Hoad *et al.*, 2001), so that factors favouring tillering will increase secondary root production. The diameter of secondary roots ranges from 0.3 to 0.7 mm and they form lateral branches to the fourth order with a diameter of 0.1-0.2 mm (Key, 1973; Hoad *et al.*, 2001).

Concerning the study of cereal root systems it is not uncommon to see the terms architecture and morphology being misused. Fitter (1985) and Lynch (1995) give some light on this subject, separating the study of the root system in four categories:

Root Morphology **-** refers to the surface features of a single root axes as an organ. It includes the characteristics of the epidermis such as root hairs, root cap, pattern of appearance of lateral roots, cortical senescence and diameter. Weight, volume, and area are also part of the morphology.

Topology **-** describes the branching pattern of the individual root axes.

Distribution **-** refers to the distribution of different root traits, often morphologic ones (e.g. biomass length, biomass, etc.), as a function of several factors, the most common being soil depth.

Architecture **-** studies the spatial configuration of the root system as a whole. Since it describes multiple root axes both topology and distribution are included in its study.

2.1.1 Rooting depth

Rooting depth (maximum depth reached by the roots) is a very important root trait since it determines the amount of the soil profile that a plant can explore. For UK field-grown winter wheat in non-stressed conditions roots were found from 140 to 200 cm soil depths (Gregory *et al.*, 1978b; Barraclough, 1989), a range of rooting depth from 73 to 96 cm soil depth was reported for barley under a wide variety of soils and years (Dwyer *et al.*, 1988). For different spring barley varieties growing in a Mediterranean type environment rooting depth below 80 cm was reported, while in the same conditions spring wheat roots were only found in the first 60 cm of the soil profile (Gregory *et al.*, 1992). Borg & Grimes (1986) compared using different data sets the maximum rooting depth for a broad number of species and reported the maximum rooting depth under favourable environmental conditions varied between 150 to 290 cm for barley and around 150 to 300 cm for wheat. But in field experiments in the Mediterranean type region of Australia spring wheat rooting depth was observed to be between 80 to 120 cm for 10 spring wheat varieties (Siddique *et al.*, 1990). Wheat and barley rooting depth depends not only on the variety but also strongly depends on the soil type and below ground resources availability, but generally the longer a crop grows the deeper the root system (Barraclough *et al.*, 1991).

2.1.2 Root shoot ratio (R:S), root dry weight and weight density

Anatomical differences between roots and shoots are such that though complementary they constitute two different systems within the plant (Brouwer, 1983). Shoots collect the resources associated with the energy and organic compounds, and roots are responsible for the uptake of the essential mineral nutrients, including nitrogen and water (Brouwer, 1983). In annual plants, after germination root growth is favoured, followed by a rapid increase in shoot growth after emergence. After flowering the aboveground growth (fruit and grain formation) is favoured whereas the root weight usually remains constant or decreases (Brouwer, 1983; Gregory *et al.*, 1997). For winter wheat, Hamblin et al. (1990) described a decrease of biomass allocated to the roots from 40% at 25 DAS to 15% at harvest in non-limiting conditions, and similarly Gregory (1978b) and Barraclough (1984) reported decreases from 34 - 40% during tillering to 7 - 10% at anthesis. Detailed experiments in wheat and barley using ^{14}C pulse-label techniques confirmed the different pattern of allocation of C to the roots, with 45% of the total C assimilated being transported to the roots during tillering decreasing to 30% at stem elongation and only 12-14% allocated to the roots after anthesis (Gregory & Atwell, 1991).

For winter and spring wheat total root dry weight (RW) was found to increase exponentially to anthesis where it reaches its maximum (Gregory *et al.*, 1978b; Barraclough & Leigh, 1984; Gregory *et al.*, 1992) with a small decrease at harvest (Gregory *et al.*, 1978b). The decrease at harvest is associated with root death in the top 50 cm depth, but a slight increase in weight was found in soil depths bellow 100 cm (Gregory *et al.*, 1978b) probably in response to water availability. But for different spring barley varieties the maximum total RW was reached shortly before anthesis (Gregory *et al.*, 1992). Total RW values for different spring wheat varieties, soil and climates of: 75, 77, 90, 95 and 107 g m^{-2} have been recorded; and for spring barley: 65, 80, 90, 126, 133 and 189 g m^{-2} (various authors in: Gregory *et al.*, 1978b; Gregory, 1994a; Hoad *et al.*, 2001). For winter wheat under field conditions RW decreases exponentially with depth and at anthesis 60 - 70% of the total root weight is in the upper 30 cm soil depth (Gregory *et al.*, 1978b; Barraclough & Weir, 1988).

Another important trait regarding weight is the root weight density (RWD):

$$RWD\ (g\ m^{-3}) = \frac{RW}{Soil\ volume}$$

Equation 2.1

RWD describes the RW per unit of soil volume, and its distribution through the soil profile also follows an exponential decrease. Under field conditions in Jordan Ebrahim (2008) found that durum wheat had significantly higher RWD in the first 80 cm of the soil profile than spring barley, but deeper in the profile the opposite was true. In soil column experiments with 3 plants per column Baburai Nagesh (2006) found large differences between the RWD at anthesis amongst four winter wheat genotypes, in the range 488 - 800 g m^{-3} in the top 20 cm, 163 - 416 g m^{-3} from 40 to 60 cm and 94 - 375 g m^{-3} from 80 to 100 cm. Utilising a similar system as Baburai Nagesh (2006) but with 2 plants per column, Ebrahim (2008) found that at anthesis not only durum wheat had an higher RWD throughout all the soil profile but also its distribution was more uniform when compared to spring barley. For durum wheat RW was 300 g m^{-3} in the top 20 cm and 170 g m^{-3} in the 80 - 100 cm soil layer compared to 205 g m^{-3} and 25 g m^{-3}, respectively, in spring barley.

2.1.3 Root length density and resource capture

Directly measuring root length is an extremely difficult and time consuming task. So RW was for a long time the preferred trait to be assessed. The first “quick” and widely used method to calculate the root length was the line intersection method (Newman, 1966). This was further developed by Marsh (1971) and both methods were described by Tennant (1975). In the 1990’s with the evolution of computers new methods of automatically analysing plant root systems were introduced (Collins *et al.*, 1987; Chikushi *et al.*, 1990) and presently a range of software packages is available not only to measure length but also the areas, volume and diameter of a root system (Arsenault *et al.*, 1995; Kaspar & Ewing, 1997; Kimura & Yamasaki, 2001).

Root length density (RLD) is the root length (cm) per unit of soil volume (cm^{-3}), and is currently the most used trait to describe root quantity and is also considered the most reliable trait describing soil exploitation (van Noordwijk, 1983; Kramer & Boyer, 1995; Atkinson, 2000):

$$\text{RLD (cm cm}^{-3}) = \frac{\text{Root Length}}{\text{Soil Volume}} \qquad \textbf{Equation 2.2}$$

For wheat and barley growing in the field, RLD exponentially decreases with depth and generally the highest values are found at anthesis slightly decreasing at harvest (Gregory *et al.*, 1978b; Thomas *et al.*, 1995). However, root growth after anthesis is not uncommon, especially deeper in the profile, and is not only related with genotype but with the physical properties of the soil, as well as water and nutrient availability (Dwyer *et al.*, 1988; Thomas *et al.*, 1995).

For a long time, plant and crop physiologists have tried to answer the question: "How many roots does a plant need?" (van Noordwijk, 1983). Defining a critical RLD value below which there is an insufficient amount of roots to uptake the available resources in the soil has been the objective of several studies (van Noordwijk, 1983; Barraclough *et al.*, 1989), but that value depends not only on type and structure of the soil but also of the resource under consideration (water and mobile or immobile nutrients) and its availability. Using a theoretical model, van Noordwijk (1983) concluded that the required RLD to extract all the available water in the soil would be in the range of 1 to 5 cm cm^{-3}, and similarly 0.1 to 1 cm cm^{-3} and 1 to 10 cm cm^{-3} to extract all the available nitrate and phosphate, respectively. In field experiments in the UK investigating winter wheat it was found that below 1 cm cm^{-3} RLD there was a marked decrease in water uptake (Barraclough *et al.*, 1989). Furthermore, it was found that for barley growing in Mediterranean conditions a RLD of 1 cm cm^{-3} would extract all the available water in the soil and that above this value the extraction rate did also not increase (Gregory & Brown, 1989).

King *et al.* (2003) developed a quantitative model for UK winter wheat where the root distribution with depth is given by:

$$p = 1 - \beta^d \qquad \textbf{Equation 2.3}$$

where p is the fraction of the root system accumulated from the soil surface to a given depth (d) and β a parameter that describes the shape of the cumulative distribution with depth. As β approaches 1 a higher fraction of roots is distributed deeper in the profile (King *et al.*, 2003; Abad *et al.*, 2004). The parameter β is predicted to increase with time, since with prolonged crop growth a larger proportion of roots will be presented deeper in the soil profile. This equation was found to be robust enough to describe the root weight and length distribution with depth (Jackson *et al.*, 1996). Since both water and nitrogen are mainly transported by mass flow of soil solution to the roots (Tinker and Nye, 2000 in King *et al.*, 2003; Bingham & McCabe, 2004) one equation was used to describe their uptake:

$$\phi = 1 - e^{-k\,RLD} \qquad \textbf{Equation 2.4}$$

where ϕ is the fraction of available resource and k is the resource capture coefficient (cm^2). Fitting Equation 2.4 to spring barley field experiments in dry Mediterranean conditions Bingham and McCabe (2004) found a k value of 2 cm^2 for water and nitrogen, equating to a RLD of 1 cm cm^{-3} extracting 86% of the available resources and 2 cm cm^{-3} 98%.

For spring barley and durum wheat in Mediterranean field conditions, RLD of 1 to 2 cm cm^{-3} is usually found in the upper 20 cm of the soil profile, but below 40 cm values are usually lower than 1 cm cm^{-3}; below ca. 100 cm values of 0.38 cm cm^{-3} have been recorded for wheat and 0.14 - 0.17 cm cm^{-3} for barley (Gregory *et al.*, 1978b; Ebrahim, 2008). In controlled environment conditions using soil columns, Ebrahim (2008) found that under well watered conditions durum wheat had a significantly higher RLD when compared to spring barley in all soil profile layers to 100 cm, with values from 2.28 to 0.77 cm cm^{-3} and 1.22 to 0.076 cm cm^{-3}, respectively. For both field and CE conditions below 40 cm soil depth there was insufficient roots to extract all the available nutrients in the soil.

As seen from different field experiments roots are often in "excess" in the top layers of the soil profile for water and N uptake but are limited in the bottom layers. So one could conclude from Equation 2.3 that increasing β, representing a more uniform RLD distribution in the soil profile, would increase uptake deeper in the profile and also delay the point where inter-root competition begins hence increases the effectiveness of the root system with consequent increases in yield and economical return for water and N capture (King *et al.*, 2003). However, some caution is required since decreasing RLD in the top of the soil profile could reduce the anchorage of the root system with negative consequences for lodging resistance (Waisel *et al.*, 2002).

2.1.3.1 Specific root length (SRL) and root weight: root volume ratio (rW:rV)

If RLD is found to describe the potential resource uptake of a root system, specific root length (SRL) then describes the economy of root length production in relation to the ratio of biomass investment (mass allocated to the root) to return in root length (Ryser, 2006):

$$\text{SRL (m g}^{-1}) = \frac{\text{Root Length (m)}}{\text{Root Dry Weight (g)}} \qquad \textbf{Equation 2.5}$$

According to Ryser (1998) in closely related genotypes or species SRL correlates with nutrient acquisition capacity. Theoretically a high SRL (thinner roots) would be beneficial especially in resource-deficit situations. However, experimental results are not so clear and often contradicting effects of responses of SRL to low resource availability are found in the literature (Ryser, 1998).

For different spring barley and wheat varieties Løes and Gahoonia (2004) recorded SRL values from 182 to 243 m g^{-1} in barley and 173 to 197 m g^{-1} in wheat, and a good correlation between root weight and root length probably due to a reasonably uniform root system diameter. Furthermore root systems of young barley and wheat plants in the field were found to have relatively high SRL values decreasing through time as thickening of roots occur (Wilhelm *et al.*, 1982; Fitter, 1985).

SRL is a complex trait depending not only on root fineness but also on the tissue density. Root fineness is the ratio of root length by root volume (Ryser & Lambers, 1995):

$$rL:rV\ (mm\ mm^{-3}) = \frac{\text{Root Length}}{\text{Root Volume}} \qquad \textbf{Equation 2.6}$$

where rL:rV is the root fineness. Since mean root diameter is extremely well correlated with rL:Vr (Ryser & Lambers, 1995) the former is often use instead of rL:Vr.

Root tissue density (rW:rV) expresses the dry matter content of the root and is calculated (Ryser & Lambers, 1995) as:

$$rW:rV\ (mg\ mm^{-3}) = \frac{\text{Root Weight}}{\text{Root Volume}} \qquad \textbf{Equation 2.7}$$

The parameter rW:rV it is a very important ecological trait found to be well correlated with the life span and growth rate in grass root systems (Ryser & Lambers, 1995; Ryser, 1996; Wahl & Ryser, 2000). The relationship between the above-mentioned parameters can be summarized as:

$$SRL = \frac{rL:rV}{rW:rV} \qquad \textbf{Equation 2.8}$$

SRL is highly correlated with growth rate, so plants with high values of SRL generally produce root length more rapidly, obtaining greater RLD and hence resource capture (Eissenstat, 1992). The parameter rW:rV is inversely correlated with root growth rate (RGR) but well correlated with life span and low nutrient loss rates, particularly under low nutrient supply (Ryser, 1998). Root diameter can be related to the soil volume explored by the depletion zone radius (*rdz*) (Nye & Tinker 1977 in Fitter, 1987) calculated according to the following equation:

$$rdz = r + 2\sqrt{Dt} \qquad \textbf{Equation 2.9}$$

where *r* is the root radius (cm), *D* the diffusion coefficient of the resource ion in the soil ($cm^2\ s^{-1}$) and *t* the time (s). According to this equation, the volume of soil explored given, by *rdz,* increases with root diameter, though higher root diameter also increases the assimilate costs of root production due to higher rW:rV (Fitter *et al.*, 1991). The

relationship between volume of soil explored and costs in terms of investment of assimilate in roots can be estimated by (Fitter, 1987):

$$\frac{r + 2\sqrt{Dt}}{r^2}$$ **Equation 2.10**

From Equation 2.10 one can therefore conclude that finer roots are more efficient per unit investment in assimilate. Consequently thinner root systems would potentially confer an advantage to the plant in resource-uptake efficiency (Ryser, 1998), though these roots may have limited transport (McCully & Canny, 1998), storage, and support capacity (Fitter, 1996).

2.2 WATER USE AND USE EFFICIENCY

For water-limited environments grain yield is a function of water use (WU), water use efficiency (WUE) and harvest index (HI, proportion of grain biomass by total aboveground biomass) (Passioura, 1977):

$$\text{Grain Yield (Y)} = \text{WU} \times \text{WUE} \times \text{HI}$$ **Equation 2.11**

Water use is equal to evapotranspiration (ET), and is the sum of the water transpired by the crop (T) and the water evaporated from the soil (E) (Fischer, 1981). In agronomy WUE is usually determined as the total aboveground dry matter produced per unit water consumed (Larcher, 2003):

$$\text{WUE (g l}^{-1}) = \frac{\text{Dry matter produced}}{\text{WU}}$$ **Equation 2.12**

WUE is therefore the cumulative increase in dry matter and water used thought the crop growing cycle. Usually in the calculation of WUE the dry matter does not include the root weight. For cereal crops a more economical WUE is the often considered (Bolton, 1981; Katerji *et al.*, 2008):

$$\text{WUE}_{\text{grain}} \text{ (g l}^{-1}) = \frac{\text{Grain dry weight}}{\text{WU}}$$ **Equation 2.13**

were WUE_{grain} is the WUE in respect to grain yield.

In physiology water-use efficiency is often expressed at the leaf level as the ratio between the carbon assimilated and water evaporated through transpiration by the leaf during photosynthesis, this 'instantaneous WUE' is the water-use efficiency of photosynthesis (WUE_{ph}) (Kramer & Boyer, 1995; Larcher, 2003):

$$WUE_{ph}\ (\mu mol\ CO_2\ m^{-2}\ s^{-1}/\ mmol\ H_2O\ m^{-2}\ s^{-1}) = \frac{A}{E} \qquad \textbf{Equation 2.14}$$

where A is the CO_2 assimilated during photosynthesis and E is the water transpired by the leaf. A and E can be described by two simple equations relating them to the stomatal conductance (g_s) for either CO_2 (g_c) or water (g_w) and the difference of partial pressure of CO_2 (C_a) and water in the atmosphere (W_a) and in the inter-cellular spaces (C_i and W_i, respectively), respectively (Condon *et al.*, 2002):

$$\text{a)} \quad A = g_c(C_a - C_i)$$

$$\text{b)} \quad E = g_w(W_i - W_a) \qquad \textbf{Equation 2.15}$$

From the Equation 2.15 a and b, the WUE_{ph} can be estimated by (Farquhar *et al.*, 1989; Condon *et al.*, 2002):

$$WUE_{ph} = \frac{C_a\left(1 - \frac{C_i}{C_a}\right)}{1.6\nu} \qquad \textbf{Equation 2.16}$$

where 1.6 is a correction factor for the relative diffusion of CO_2 and water in the air, and ν *is* the vapour pressure deficit. The WUE_{ph} can also be calculated for whole the crop cycle (Farquhar *et al.*, 1989; Máguas & Griffiths, 2003):

$$WUE_{ph} = \frac{C_a\left(1 - \frac{C_i}{C_a}\right)\left(1 - \phi_c\right)}{1.6\nu\left(1 + \phi_w\right)} \qquad \textbf{Equation 2.17}$$

where ϕ_c is the carbon lost by tissue respiration and ϕ_w is the water lost during the night if the stomata are not completely closed.

WUE_{ph} can be indirectly estimated by carbon isotopic discrimination analysis of plant material. In nature two carbon stable isotopes ^{12}C (98.9 %) and ^{13}C (1.1 %) occur, and one radioactive isotope ^{14}C (10^{-12} ‰) (Smith, 1972; O'Leary, 1981; Farquhar *et al.*, 1989). These isotopes differ slightly in their chemical reactivity, determining their distribution in nature (Máguas, 1997). During CO_2 incorporation by photosynthesis a discrimination occurs against ^{13}C, reflecting the plant metabolism and the environmental conditions (O'Leary, 1981). In C3 plants the discrimination occurs due to the difference in the diffusion rates of ^{12}C and ^{13}C through the stomata and to discrimination by the Rubisco (Ribulose-1,5-bisphosphate carboxylase/ oxygenase) enzyme (Farquhar *et al.*, 1989). The carbon isotopic composition of plants ($\delta^{13}C$) is usually expressed in terms of carbon isotopic discrimination ($\Delta^{13}C$) relating the $^{13}C/^{12}C$ from plant tissues to that in the air (Farquhar & Richards, 1984):

$$\Delta^{13}C\ (\ddot{a}) \quad = \quad \frac{R_a}{R_p} - 1 \qquad \textbf{Equation 2.18}$$

where R_a and R_p are the molecular ratios $^{13}C/^{12}C$ in the air and in the plant, respectively. The practical measurement is done by comparing $\delta^{13}C$ of the plant material to that from analysis of a reference material:

$$\text{a)} \quad \delta_p = \frac{R_p}{R_s} - 1$$

$$\text{b)} \quad \delta_a = \frac{R_a}{R_s} - 1 \qquad \textbf{Equation 2.19}$$

where δ_a and δ_p are the deviation of the isotopic composition of the plant and the air in relation to a standard, usually Pee Dee Belemite PDB (R_s = 0.01124) (Farquhar *et al.*, 1989; Brugnoli, 1990), and so the isotopic discrimination of the plant can be obtained by:

$$\Delta^{13}C = \frac{\delta_a - \delta_p}{1 - \delta_p} \qquad \textbf{Equation 2.20}$$

The atmospheric CO_2 has a $\delta_a \approx$ -8‰ (Farquhar *et al.*, 1989) and in C3 plants the δ_p value varies between -21 ‰ e -37 ‰, resulting in a $\Delta^{13}C$ within 13 ‰ and 28 ‰ (Jones, 1993).

Assuming that the diffusion in and out of the stomata is proportional to the partial pressure of CO_2 in the atmosphere (C_a) and in the inter-cellular spaces (C_i), Farquhar et al (1982) developed the following equation for $\Delta^{13}C$:

$$\Delta^{13}C = a\frac{C_a - C_i}{C_a} + b\frac{C_i}{C_a} = a + (b - a)\frac{C_i}{C_a} \qquad \textbf{Equation 2.21}$$

where a is the C fractionation that occurs due to diffusion in the air (4.4 ‰; Craig, 1954), and b the fractionation during carboxylation mainly due to Rubisco but also caused by phosphoenolpyruvate carboxylase – PEPc (29‰; Roeske & Oleary, 1984). Combining Equation 2.21 and 2.17 it is possible to demonstrate that the $\Delta^{13}C$ in plant tissues and WUE_{ph} are negatively correlated (Farquhar *et al.*, 1989; Máguas & Griffiths, 2003):

$$WUE_{ph} = \frac{C_a\left(b - \Delta^{13}C\right)\left(1 - \phi_c\right)}{1.6\nu\,(b - a)\left(1 + \phi_w\right)} \qquad \textbf{Equation 2.22}$$

Using carbon isotope discrimination through the $^{13}C/^{12}C$ ratio, which is inversely related with WUE_{ph} it is possible to assess the effects of water deficits on the instantaneous WUE. Using $\Delta^{13}C$, compared with gas exchange methods, has the advantage of being an integrative measurement giving information on WUE_{ph} during all the lifespan of the plant material analysed.

For different Mediterranean varieties of durum wheat $\Delta^{13}C$ in the grain was found to be well correlated with grain yield (Y), though $\Delta^{13}C$ in leaves was only correlated with Y under extreme drought conditions and with biomass production under favourable conditions (Merah *et al.*, 1999).

2.2.1 Plant growth responses to water deficits

The importance of water for plants is undoubted; it performs a varied number of physiological and structural functions. Water constitutes on average 80 to 90% of the fresh weight of herbaceous plants providing a continuous liquid phase in which gases, minerals and other solutes enter the cells and move from one cell to another and within the different plant organs. Water is a reactant or substrate in most of the plant's vital reactions (e.g. photosynthesis) and it maintains the plant turgor essential for cell growth, enlargement, form and movement of various plant structures, like the stomata opening (Kramer & Boyer, 1995).

Water deficits occur when the rate of transpiration surpasses the rate of water absorption by the roots (Kramer & Boyer, 1995). This shortage of water can take place when there is a very high evaporative demand (high vapour pressure deficit; v), or by soil dryness, osmotic binding of water in saline soil or even in frozen soils; it is a slow process that increases in intensity the longer it lasts (Larcher, 2003). A deficit of water does not immediately imply water stress, it will depend on the time-scale of the shortage and the ability of the plant to suppress or avoid it. Here water stress will be defined as situations where the plant water potential and turgor are reduced enough to interfere with the normal plant function (Kramer & Boyer, 1995).

The first and most sensible response to water deficiency is a decrease in turgor, followed by a decrease in plant growth rate (van den Boogaard *et al.*, 1996; Larcher, 2003). The most common and described effects of water stress are therefore a reduction in dry matter production, leaf area and crop yield (Kramer, 1983). Gupta *et al.* (2001) showed that not only did drought decrease the aerial biomass and yield of wheat plants, but also that the effect was higher when the stress was imposed at anthesis when compared to the booting stage. They also showed that those effects were less pronounced in a drought-tolerant wheat cultivar that was able to maintain a cooler canopy, a higher turgor pressure at booting stage, higher leaf osmotic pressure and cooler leaves. In cereals the decrease in yield under drought conditions is associated with a decrease in tiller number and in spikelets production with a obvious negative effect in grain number (Giunta *et al.*, 1995; Gupta *et al.*, 2001). Foulkes *et al.* (2002)

showed for winter wheat that drought significantly decreased not only the number of ears/m^2 but also grains/ear and grain weight with a consequent decrease in grain yield.

2.2.1.1 Leaf expansion and senescence

Leaf expansion and senescence are particularly susceptible to water deficiency (Turner & Begg, 1981). The causes for restricted leaf expansion with drought have been discussed extensively and there are mainly two views on this question; some authors attribute the cause to water relations (water potential and cell turgor) in the leaf (Kramer, 1988; Hsiao *et al.*, 1998), while others indicate the role of root signals (such as abscisic acid; ABA) to the leaves, in response to water depletion in the soil as the main cause (Passioura, 1988a; Passioura, 1988b; Gowing *et al.*, 1990).

Evidence for water relations as the main cause of the decrease in leaf expansion were described by Boedt & Hensley (1987 in Kramer, 1988) where leaves of field-grown maize in South Africa showed visual symptoms of water stress in soil near field capacity. Tazaki et al. (1980 in Kramer, 1988) in Japan reported similar effects for rice leaves, even though plants were rooted in wet soil. Furthermore, seedling experiments in maize plants using the pressure-pump technique (Hsiao *et al.*, 1998) showed that an increase in the water pressure in the roots was quickly and fully transmitted to the base of the leaf increasing the leaf elongation. Contrasting with these findings, Passioura (1988b) growing wheat seedlings in drying soil but maintaining leaf turgidity using the pressure-chamber method, showed a decrease in the relative expansion rate of leaves. Additional evidence for the root chemical signal was given by Gollan *et al.* (1986) where wheat and sunflower plants showed a decrease in stomatal conductance with an increase of water deficits while the pressure in the plant was maintained. Using partial root-zone drying (PRD) techniques where half of the root system is droughted whilst the other half is irrigated, to maintain the same leaf water status as control plants (full irrigation), results showed a decrease of 65% of leaf area and 70% of water loss in apple plant seedlings subjected to PRD. Moreover, cutting the roots that were in contact with the dried soil leaf growth equalised the level of the control plants (Gowing *et al.*, 1990).

ABA concentration increases in shoots, leaves and roots on plants growing under water deficits and its exogenous application on well watered plants mimics many of the drought effects on the plant (Davies *et al.*, 1994; Taylor *et al.*, 2000). The chemical mechanism involves the synthesis of ABA by the plant root system when sensing the drying of the soil, transfer in the xylem to shoots and leaves inducing stomatal closure, water uptake and a reduction in shoot and leaf growth (Zhang & Davies, 1990; Davies & Zhang, 1991; Davies *et al.*, 1994; Hartung & Jeschke, 1999). A more recent hypothesis is that both hydraulic and chemical signals interact and that the importance of one or the other will depend on the timescale considered (Aphale, 2004). Experiments in maize and barley showed that sudden changes in leaf water status by light, humidity or salinity greatly affect leaf-elongation rate, and that those effects vanished when their roots were placed in a pressure chamber to maintain the xylem and air pressures in equilibrium, showing that hydraulic relations dominate in this response (Munns *et al.*, 2000). If the saline or water stress is prolonged, root signals override water relations and pressurization fails to maintain leaf elongation rates (Munns *et al.*, 2000). The combination of hydraulic and chemical factors was also demonstrated by differences in the sensitivity of different maize lines under drought to xylem ABA (Stikić & Davies, 2000).

Senescence is the last phase of plant development; it is genetically controlled occurring even when conditions are favourable, and comprises a series of biochemical processes that culminate with cell death (Smart, 1994; Masclaux *et al.*, 2000). Leaf senescence rate is known to increase due to water deficiencies, though proportionally less than leaf elongation rate (Ludlow 1975 in Turner & Begg, 1981). Many field experiments have shown that winter wheat plants subjected to drought senesce earlier than plants under irrigation, e.g. (Barraclough *et al.*, 1989; Foulkes *et al.*, 2001). In Mediterranean-type climates wheat yields growing in dry conditions were found to be inversely related with leaf duration after anthesis (Fischer and Kohn 1966 in Turner & Begg, 1981). For spring barley plants Legg *et al.* (1979) found a decrease in yields from 30 to 40% when water limited from emergence and between 10 to 20% when water stressed from approximately stem elongation, due to decrease of leaf area (smaller leaves and fewer tillers) and premature senescence. Furthermore the reestablishment of irrigation near anthesis delayed plant senescence by about 10 days but they still senesced earlier than the plants that were continuously irrigated (Legg *et al.*, 1979).

2.2.1.2 Photosynthesis

Water deficiency can reduce plant photosynthesis by decreasing leaf area, but also by decreasing the efficiency of carbon fixation efficiency as well as by promoting stomata closure (Kramer, 1983). The loss of leaf area and hence intercepted radiation is the main cause of the overall decrease in plant photosynthesis and hence growth for spring barley, but at the leaf level stomatal closure was found to be responsible to decrease up to 11% of daily photosynthesis but only 6% over the whole season (Legg *et al.*, 1979).

Photosynthesis involves the diffusion of CO_2 to the leaf and carboxylation. Since C_a surrounding the leaf is relatively stable, the CO_2 gradient will be mainly a function of the biological processes that affect C_i (Baburai Nagesh, 2006). Changes in C_i in the leaves are mainly determined by diffusion limitations through the stomata and the mesophyll and alterations in photosynthetic metabolism (Ribulose-1,5-bisposhpate carboxylase oxygenase (Rubisco) activity) (Chaves *et al.*, 2009). The inflow of CO_2 to the leaf and exit of water are both mediated through the stomata therefore the crucial factors affecting one will also affect the other. Both stomatal closure and increase of Rubisco concentration decrease C_i leading to an increase in leaf WUE_{ph}.

Siddique (1999), for winter wheat growing under drought conditions in the field, found a decreased with g_s but the weak relationship between them revealed that non-stomatal factors were also involved. Under moderate water stress, the decline in photosynthetic rate with the decrease in relative water content (RWC) was found to be mainly related with g_s, but at severe water deficits metabolism factors in the mesophyll play the major role in cereals (Chaves, 1991; Shangguan *et al.*, 1999; Lawlor, 2002; Tang *et al.*, 2002). So at moderate water stress there is an initial decrease in C_i due mainly to a decrease in g_s, as the stress level increases C_i levels raise indicating a predominance of non-stomatal processes, this point is called the C_i inflexion point (Lawlor, 1995; Flexas & Medrano, 2002). When the water deficits are slowly imposed the C_i inflexion point seems to be reached at higher levels of stress (Chaves, 1991; Shangguan *et al.*, 1999).

Rubisco content is generally not affected by moderate and/ or severe water stress (Flexas & Medrano, 2002), but its activity is induced by it (Flexas *et al.*, 2006).

Experiments of Flexas *et al.* (2006) with tobacco and soybean plants revealed that the down regulation of Rubisco was related with g_s and not RWC and Parry *et al.* (2002) found that decreases of RWC in wheat had little effect on Rubisco activity. Furthermore, the stomatal closure threshold for the down-regulation of Rubisco was species dependent; and g_s was observed to be a good indicator of the Rubisco activity under water stress conditions (Flexas *et al.*, 2004; Flexas *et al.*, 2006). Bota *et al.* (2004) confirmed for different species the main role of g_s in down regulating photosynthesis and that Rubisco activity would only become relevant under severe drought.

Nevertheless, the decrease of Rubisco activity with water deficits is still a matter of discussion (Lawlor, 2009). For wheat it seems associated with a decrease of soluble protein and chlorophyll (Holaday *et al.*, 1992) and impairment regeneration of Ribulose - 1, 5- biphosphate (RuBP) (Lawlor, 2002; Parry *et al.*, 2002; Bota *et al.*, 2004). More recently, Chaves *et al.* (2009) asserted that plants perceive and respond to water deficits not only by physiological and biochemical modifications, but by in parallel quickly altering gene expression (down-regulation of key photosynthetic genes).

2.2.1.3 Drought and root development

As previously mentioned, water deficits decrease carbon assimilation by the plant due to a reduction of green leaf area but also due to a decline in photosynthetic rate leading to an overall decrease in plant dry matter growth.

Under drought, plants tend to increase the proportion of total carbon allocated to the roots (Gregory *et al.*, 1997). For example, Hamblin *et al.* (1990) in wheat reported an increase in biomass allocated to the roots from 15% in a wet year to a 30% in a dry year and Gregory *et al.* (1997) in wheat reported a similar pattern of R:S ratio decreasing with time where the value was almost constantly ca. 8% higher when plants were submitted to drought (1997). Barraclough *et al.* (1989) also found a decrease in R:S with prolonged drought for field grown winter wheat.

Though R:S increases with drought the absolute weight of both roots and shoots decrease. However, shoots are generally more affected by drought than roots probably

due to the fact that more severe water deficits develop and persist longer in the transpiring shoots (Kramer, 1983; Karrou & Maranville, 1994a; Palta & Gregory, 1997). From the functional standpoint it makes sense that roots would be prioritised during drought, since maintaining root growth enables the plant to more quickly access water whilst decreasing transpiration. The relationship between these two systems is often described as a competition where both compete for carbohydrates, minerals and water, the most successful being the one nearer the source (Brouwer, 1983). The growth of the root and shoot systems is an integrative process working in a functional equilibrium described by Davidson as (1969; Gregory, 1994a):

$$\text{root mass} \times \frac{\text{specific root activity}}{\text{(absorption)}} = \text{shoot mass} \times \frac{\text{specific shoot activity}}{\text{(photosynthesis)}} \qquad \textbf{Equation2.23}$$

So when light is limited roots will be more prejudiced than shoots and the opposite when soil resources are in deficit, this functional balance hypothesis is elegantly explained by Brouwer (1983). Under water-limiting conditions solutes accumulate in the root tip attracting the movement of water by diffusion, allowing the cells in the root tip to maintain their turgor and growth (Sharp & Davies, 1979). Experiments using pulse-labelled ^{13}C confirmed that water deficits increased the allocation of assimilated C to the roots due to a higher reduction of growth to the above ground than below-ground plant components (Palta & Gregory, 1997).

Although water deficits usually increase the percentage of carbon allocated to the roots (Hamblin *et al.*, 1990), wheat greenhouse experiments of Karrou & Maranville (1994a) found that R:S decreased, increased or was not affected by drought depending on the variety considered. However Li *et al.* (Li *et al.*, 2001) found no significant differences on R:S for different types of water stresses applied to winter wheat in China.

As described above for R:S, the root growth dynamic under drought is not simple, since drought not only affects plant and root growth but also the soil structure and N availability (Robinson, 1994) which in turn affects root growth. These different feedback cycles will be related to the genotype, soil type, nutrient and water availability and distribution in the soil profile. Thus, a general description of drought effects on root growth is not easy, especially when observations from different experiments are often contradictory. For example, Hamblin *et al.* (1990) describe an increase in RLD for winter wheat in the top 10 cm of the soil profile with drought, but not deeper in the

profile where plants were unable to grow roots below 90 cm depth; whilst in well watered conditions roots were found below 150 cm depth. In contrast to these observations, a field investigation of Barraclough *et al.* (1989) on winter wheat in the UK revealed that though water deficits had a small effect on plant root weight they had a larger effect on root length and its distribution with depth. Total root length and RLD in the top layers of the soil profile to 10 cm depth decreased, while compensatory growth occurred deeper in the soil where roots were found 20 cm deeper under drought.

Drought was also reported to increase the extension of thin roots with a consequent decrease in mean root diameter in winter wheat in glasshouse conditions (Li *et al.*, 2001; Baburai Nagesh, 2006). For winter wheat growing in soil columns, Baburai Nagesh (2006) observed an increase of SRL with drought, and Ebrahim (2008) observed the same for field-grown durum wheat and spring barley under Mediterranean conditions, where barley SRL values were generally higher than for wheat. Specific root length is positively correlated with root extension rate (Eissenstat, 1991). Maximizing SRL seems to be an advantage particularly in water- and nutrient-limited conditions, since more root length is produced for the biomass invested (Eissenstat, 1992; Wahl & Ryser, 2000) and consequently higher RLD. Intuitively thinner roots would be advantageous for acquiring soil resources, though there may be trade-offs with other root functions such as anchorage, support and transport (Fitter, 1996). Furthermore, thinner roots are particularly vulnerable to drought (Fitter, 1987; Ryser, 1998). Root diameter was shown to be highly correlated with plant dry mass (Hetrick *et al.* 1988 in Ryser, 1998) and the diameter of conducting vessels. Therefore the relatively high diameters reported for irrigated compared to droughted plants (Li *et al.*, 2001; Baburai Nagesh, 2006) might relate to the necessity of the root system to support a larger plant and facilitate faster and greater water uptake and transport.

Root tissue density (rW:rV) is highly correlated with root life span but inversely correlated with root expansion (Ryser, 1996; Wahl & Ryser, 2000). So low rW:rV will make possible to the plant to increase SRL (Valenzuela-Estrada *et al.*, 2008) and possibly resource acquisition but it will compromise root longevity.

2.3 NITROGEN USE AND USE EFFICIENCY

Before considering increasing NUE through breeding and/ or management strategies it is essential to understand the complexity of this parameter. Nitrogen-use efficiency (NUE) is defined as grain dry matter yield (Y) per unit of N available (from the soil and/or fertilizer) (Moll *et al.*, 1982; López-Bellido *et al.*, 2005):

$$NUE(g\ g^{-1}) = \frac{Y}{N\ available} = NupE \times NutE \qquad \textbf{Equation 2.24}$$

where NupE (N-uptake efficiency) is the efficiency with which the nitrogen available to the plant was absorbed, and NutE (N-utilization efficiency) is the efficiency with which the N acquired by the crop is used to produce grain yield:

$$\text{a)} \quad NupE\ (g\ g^{-1}) = \frac{Total\ plant\ N\ uptake}{N\ available}$$

$$\text{b)} \quad NutE\ (g\ g^{-1}) = \frac{Y}{Total\ plant\ N\ uptake} \qquad \textbf{Equation 2.25}$$

According to Equation 2.25 an improvement in either NupE or NutE would improve NUE. NUE is usually reported to decrease with N application (Sieling *et al.*, 1998), due to bad application practices (timing and/or amounts) leading a decrease in NupE . Thus, if high amounts of N are applied the plant might not uptake all N available (NupE) and even if so the N absorbed may be utilized less efficiently (NutE). Bad timing, this is applying N out of synchrony with the relevant phases of crop growth and N demand might also lead to low uptake or utilization and hence NUE. Low water availability can also decrease NupE due to N becoming less available with drought. High amounts of rainfall or irrigation can also decrease NupE, since this will increase leaching, and once again the N available will not be used.

2.3.1 Nitrogen and plant growth

In cereals increases of total biomass, yield and yield components (tillers, ears and grain number) caused by nitrogen application are well known and widely reported (Krentos & Orphanos, 1979; Greenwood, 1982; Barraclough *et al.*, 1989; Latiri-Souki *et al.*, 1998; Mengel & Kirkby, 2001; Jiang *et al.*, 2004; Cossani *et al.*, 2009). N fertilizer increases plant N uptake and the leaf cell number and volume and it may also increase photosynthetic rate and efficiency (Lawlor *et al.*, 1988). The increase in crop growth rate is mainly associated with an increase in canopy green area and hence radiation interception. Radiation-use efficiency (RUE, biomass production per unit incident radiation) usually responds initially from nil to low-to-moderate N fertilizer applications, but not for further N applications above this level (Lawlor, 1995). For spring barley and durum wheat growing in the Mediterranean conditions, N application increased the aboveground biomass and LAI at anthesis that led to an increase in grain yield, resultant from a higher number of ears per plant with larger grain number while HI remained unchanged (Cabrera-Bosquet *et al.*, 2009; Cossani *et al.*, 2009; Fois *et al.*, 2009). Effects of N fertilisation on individual grain weight are not always consistent and no effects (Barraclough *et al.*, 1989; Cabrera-Bosquet *et al.*, 2009) or slight decreases have been reported (Cossani *et al.*, 2009; Fois *et al.*, 2009).

Senescence in cereals usually starts just before grain filling, where the proteins in the vegetative organs are degraded in order to supply N to the grain (Hörtensteiner & Feller, 2002). Senescence in cereals first starts in the older leaves where proteolysis of stromal enzymes (e.g. Rubisco, glutamine syntethase and glutamate synthase) occurs (Hörtensteiner & Feller, 2002) marked by a progressive yellowing of the leaves (Masclaux *et al.*, 2000). Numerous studies reported that N deficiency leads to an early onset and faster rate of leaf senescence (Barraclough *et al.*, 1989; Dreccer *et al.*, 2000) due to a source-sink imbalance. In crops supplied with ample N leaf senescence is delayed prolonging photosynthetic activity and hence carbon and N use for biomass production and yield.

One of the first detectable signs of N deficits is the yellowing of older leaves due to a decrease in chlorophyll content resultant from chloroplast proteolysis into amino acids and movement to the younger leaves (Marschner & Marschner, 1995; Mengel & Kirkby, 2001). Specific leaf nitrogen (leaf N content per unit area; SLN) increases with N application (Cabrera-Bosquet *et al.*, 2009), increasing the number of chloroplasts in the mesophyll and chlorophyll, Rubisco and ATP synthase protein concentration in the leaves (Cabrera-Bosquet *et al.*, 2009). These lead to an increase in the leaf photosynthetic activity and consequently plant net photosynthesis (Jiang *et al.*, 2004; Cabrera-Bosquet *et al.*, 2009). The increase in CO_2 assimilation was shown to be non-stomatal related (since both stomatal conductance (g_s) and stomatal limitation were unrelated with SLN) but a result of carboxylation efficiency by Rubisco and RuBP regeneration ability (Cabrera-Bosquet *et al.*, 2009).

The combination of the fact that N application improves plant biomass and LAI, causing less soil to be prone to evaporation, associated with the increase in photosynthesis by non-stomatal factors (Cabrera-Bosquet *et al.*, 2009) and higher RLD (Barraclough *et al.*, 1989) leads to an higher WUE (Cabrera-Bosquet *et al.*, 2007).

In simple terms beneficial effects of N on crops can therefore be explained by an increase in GAI and aboveground biomass, in plants that stay green for longer and that are photosynthetically more efficient, increasing RUE and carbon assimilation and leading to higher yield.

2.4 NITROGEN AND ROOT GROWTH

It is well established that plants respond to N deficiencies by increasing R:S (or root weight to total plant weight ratio) due to the functional equilibrium between the growth of the root and shoot systems (Novoa & Loomis, 1981; Brouwer, 1983; Dreccer *et al.*, 2000; Mengel & Kirkby, 2001; Reich, 2002), described previously in section 2.2.1.3. Herrera *et al.* (2005) showed that high N supply increased the number of roots, and when N was limited root formation ceased earlier. Furthermore, localised N application on barley seminal root systems was found to promote the number and extension rate of both first- and second-order lateral roots (Drew *et al.*, 1973). For two

barley varieties growing in the Mediterranean under field conditions the root to total plant ratio increased when N + P fertilizer was not applied with the treatment difference diminishing from beginning of stem elongation, to anthesis and maturity; the difference was only significant for one variety (Brown *et al.*, 1987b). Barraclough *et al.* (1989) in N x drought field experiments in winter wheat in the UK found an increase in R:S and a slight decrease in total root dry weight with low N supply, but only significantly so under drought. At anthesis N fertilizer increased RLD in both irrigated and drought conditions, to 80 and 120 cm soil depth, respectively (Barraclough *et al.*, 1989). Water uptake also increased with N due to a higher RLD and higher ground cover reducing soil evaporation. The fact that N fertilizer had no effect on total root weight but increased total root length by 32% indicated the importance of effects on SRL. For different spring barley varieties grown at two sites in Syria the R:S decreased with N + P fertilizer and irrigation although total root length increased (Brown *et al.*, 1987b). Average RLD between anthesis to maturity was found to increase with N +P application to a depth of 60 to 75 cm in the site with higher water availability, but only to 60 cm soil depth at the drier site, where the RLD under low N conditions was slightly higher (Cooper *et al.*, 1987). Varietal differences in RLD and distribution with depth were observed and an interaction between N and genotype on water uptake deeper in the profile (Cooper *et al.*, 1987). N + P supply increased ground cover causing a decrease in soil evaporation, associated with higher evapotranspiration and transpiration, hence higher WUE (Cooper *et al.*, 1987). Finally N supply not only increased in RLD at anthesis but also prolonged root growth during grain filling and slightly higher values of RLD were found deeper in the soil profile (75 to 120 cm) (Gregory & Brown, 1989).

N application has been observed to increase mean root diameter in graminoids but decreased rW:rV (Ryser & Lambers, 1995; Ryser, 1998). N application effects on SRL are inconsistent and increases, decreases or neutral effects have been reported for different species (Ryser & Lambers, 1995; Ryser, 1998). Field experiments with spring barley and durum wheat in Jordan showed no consistent response for SRL at different soil layer depths for three different levels of N fertilizer (Ebrahim, 2008). However, the average SRL increased with N application under rainfed conditions for durum wheat, with a neutral effect under irrigation, but the opposite was found for spring barley. There is a gap in the literature regarding the effects of N fertilisation on SRL and its components in cereals in field conditions. SRL is a complex parameter that is

determined by root length, tissue density and diameter (Equation 2.8) It provides a measure of plant investment in potential resource acquisition (RLD) but also reflects root longevity and RGR, and therefore it might be an interesting trait in phenotyping to be used in breeding programs for optimized root systems.

Roots are responsible for the uptake of N by the plant so improvements at its level would be responsible for an increase of NUE by increasing NupE (Equation 2.4 and 2.5 - a). For a long time, due to its high mobility (Dunbabin *et al.*, 2004), nitrogen supply was considered independent of the root system characteristics, assuming that only mass flow (ions carried along in the transpiration stream) and diffusion (ions moving down a concentration gradient, either through bulk soil water or along water films surrounding particles) were the relevant mechanisms for N uptake by the plant (Karrou & Maranville, 1994b; Herrera *et al.*, 2005). Nowadays it is believed that N capture also depends on the ability of the root system to respond to spatial and temporal nitrogen supply (Fitter *et al.*, 1991). Furthermore, a positive correlation was found between nitrogen capture and RLD in maize (Wiesler & Horst, 1993; Wiesler & Horst, 1994) and also durum wheat and barley (Ebrahim, 2008). As described previously N supply generally increases RLD increasing therefore the N uptake by the crop but not necessarily increase NupE or NUE, and what is generally more common is a decrease of those efficiencies (Cabrera-Bosquet *et al.*, 2007; Pask, 2009) due to losses to the environment (*vide* chapter 1.1.3). Ebrahim (2008) in soil columns and field experiments in spring barley and durum wheat found a decrease in both NUE and NutE with N application, while NupE was unaltered. Though a model exercise suggested that higher RLD and deeper rooting depths would reduce residual nitrate in high leaching soils (Dunbabin *et al.*, 2003).

2.5 Strategies to increase nitrogen- and water-use efficiency of wheat and barley

As described in previous sections (section 1.1.2.1 and 1.1.3) the production of durum wheat and barley in the Mediterranean is predominantly limited by availability of water and/or N. For the economic and environmental reasons previously discussed N

deficiencies cannot be solved by simply increased use of N fertilizers. Though part of the solution lies in the use of N fertilization and irrigation, their application has to be done with suitable agronomic practices.

Nitrogen becomes less available to the plant as the soil dries. Consequently water availability and N application should in fact be considered together (Hoad *et al.*, 2001). For winter wheat in the UK N and water deficits were together found to reduce yield by 61%, while individually they reduced the crop yield by 56 and 19%, respectively (Barraclough *et al.*, 1989). Moreover, experiments with spring wheat under semi-arid conditions in Sudan showed an increase in yield with progressive increases of N under irrigation. While under drought initially there was a slight increase in yields with N application after which higher N levels had a negative effect on yield (Ali *et al.*, 2006).

Cereal production is generally characterized by low Nitrogen Use Efficiency (Shanahan *et al.*, 2008). In fact only 33% of the total N applied in the world is used by the plants; the rest is lost in the system (*vide* chapter 1.1.3) representing a loss of £9.7 billion per annum (Raun *et al.*, 2002). In Mediterranean rain-fed conditions less than 50% of N applied is recovered. Only with a combination of management and breeding strategies will it be possible to improve NUE and WUE in the South Mediterranean.

2.5.1 Agronomical strategies for higher NUE and WUE

Increasing NUE and WUE through management strategies has most potential to increase water uptake (WU) and NupE. To improve NUE and WUE farmers should consider the soil type and N availability, climate, previous cropping and animal manures when establishing the N fertilisation and irrigation regimes together with soil management practices (tillage and organic matter) (Raun & Johnson, 1999). A simple measure to decrease loss of N through immobilization is the application of fertilizer below the soil surface (Sharpe *et al.*, 1988).

In harsh Mediterranean type environments characterized by erratic rainfall, like in Southern Spain, supplemental irrigation was proven to increase durum wheat and barley yields and slightly decrease the risk of crop failure (Abeledo *et al.*, 2003). Furthermore,

when N was applied in similar region both barley and wheat showed an increase in both yields, under rainfed and irrigated conditions (Cossani *et al.*, 2009). Different types of irrigation systems can be used to improve crop yields in the Mediterranean. However in the poor areas of the Southern Mediterranean, trickle irrigation seems the most appropriate, at least when compared with the more traditional and inefficient surface irrigation, or the more expensive linear boom system. However, greater attention has been diverted not to the irrigation equipment, but to the timing. Deficit irrigation (DI) has been shown as a promising technique to improve yields under drought environment, while using less water and saving money. It can be applied in two forms: (i) regulated deficit irrigation (RDI); that implies irrigation with frequent but small amounts of water in proper growth stages (Zhang *et al.*, 2006) and (ii) sustained deficit irrigation (SDI) where the water deficit increases progressively as the season advances due to a combination of uniform application of a reduced amount of water and the depletion of the soil water reserve (Fereres & Soriano, 2007).

For both wheat and barley the N requirement depends on the crop growth stage. N uptake before onset of stem extension represents only 25% of the total N uptake. This is followed by a rapid increase of N uptake to flag leaf representing 40% of total uptake, and a further 20% will be acquired from flag leaf to anthesis, with the remainder taken up post anthesis to harvest (HGCA, 1998; HGCA, 2006). Splitting N applications in order to achieve a better synchronization between supply and demand has been suggested (Shanahan *et al.*, 2008). Split N applications in two or three timings (Karam *et al.*, 2009) taking in account crop development has proven to be an efficient way to increase yields and decrease N losses and thus NUE. Typically N is applied early in the season to encourage tiller formation, with a second application from onset to mid stem elongation and a further application possibly at booting to ensure rapid canopy expansion through tiller survival and sufficient grains per ear (HGCA, 1998). Though in temperate climates split timings of N fertilisation has been proved to increase NUE, it is still matter of discussion in the arid Mediterranean areas (Garrido-Lestache *et al.*, 2005; Arregui & Quemada, 2008). When it is not possible to split N applications due to labour and fuel costs, the best time to apply N as a top-dressing would between tillering and stem elongation (López-Bellido *et al.*, 2005; Lopez-Bellido *et al.*, 2006). N applications should always take in account rainfall forecast and if necessary use supplementary irrigation (when available) to avoid limiting fertilizer N recovery due to water deficits

(Lopez-Bellido *et al.*, 2006). N fertilizer tended to increase WUE in durum wheat grown in Tunisia under dry conditions. Such effects are mainly due to less soil evaporation caused by a higher ground cover, higher LAI (leaf area per unit ground area) (Latiri-Souki *et al.*, 1998), but also due to a more extensive root system and hence higher water uptake (Cooper *et al.*, 1987).

Canopy and leaves are known to serve as indicators of the crop N status (Shanahan *et al.*, 2008). Agronomic options for raising NupE include in-season crop monitoring using high precision ground-based sensors including those based on measuring spectral reflectance, chlorophyll content and leaf photosynthetic activity (Foulkes *et al.*, 2009).

Spectral reflectance is a remote-sensing technique that measures the canopy light reflectance properties based on the absorption of light at specific wavelengths. The reflectance in the visible (VIS) wavelengths (400–700 nm) is lower than in the NIR (near infrared) wavelengths (700–1300 nm) because of the high absorption of light energy by leaf pigments. Spectral characteristics are affected by canopy size, crop N status and senescence. Spectral reflectance indices, e.g. NDVI (normalized difference vegetation index) = (NIR - VIS)/(NIR + VIS), have proved useful in the assessment of early biomass of different wheat genotypes (Elliott & Regan, 1993; Bellairs *et al.*, 1996; Babar *et al.*, 2006). NDVI has been correlated with senescence in cereals (Idso *et al.*, 1980; Adamsen *et al.*, 1999). Gupta *et al.* (2001) suggested that comparison of wavelengths at which chlorophyll-beta (640nm) and chlorophyll-alpha (673nm) have maximum absorbance may give good sensitivity to maturity.

Plants with greater leaf N concentrations typically have more chlorophyll. Chlorophyll in leaves absorbs most strongly in the blue (around 450 nm) and red (around 670 nm) light, and reflects in the green (around 550 nm) region of the light spectrum. The Minolta SPAD 502 CM measures light transmission in the red (650 nm) and near-infrared (940 nm) parts of the spectrum and has been used to estimate leaf chlorophyll content in maize (Blackmer *et al.*, 1994) and to predict grain N requirements in wheat (López-Bellido *et al.*, 2004).

Though new techniques exist for a more efficient and precise crop monitoring at the spatial level they will probably not be available soon to the farmers in the field, so generally the agricultural recommendation should be simple and cost effective to the end user.

2.5.2 Breeding for more water and N efficient crops

Regardless of the importance of "new" improved agronomic intervention strategies to enhance WUE and NUE, breeding modern cultivars better adapted to the particular conditions of the Mediterranean ecosystem will play a major role for the future of crop production. The complete set of interactions will then be: breeding x management x environment. Breeding for high WUE and NUE while maintaining or increasing yields is a difficult task. Most efficient systems will combine optimized agronomy and new N-efficient cultivars.

2.6 OBJECTIVES AND HYPOTHESIS

The present study aims to identify and quantify root traits responsible for improved uptake of water and N under supply-limited conditions as well as traits associated with improved utilization of water and N hence aboveground growth. Therefore the optimization of roots through judicious amounts of N fertilizer and applied water to improve nitrogen-use efficiency (NUE) and water-use efficiency (WUE) was investigated in the present study in CE conditions simulating water and N stresses in Mediterranean type conditions. The overall objectives of this work were to:

1. Compare the response of durum wheat and barley roots and shoots growth, to water and/ or N deficits, under controlled environment conditions;
2. Identify root traits for improved below-ground resource capture under different intensity of water and/ or N stress in spring barley and durum wheat;
3. Quantify responses of root growth, root: shoot partitioning and water and N capture to simulated water and/or N stressed typical of Mediterranean environments, using controlled environment conditions on spring barley and durum wheat.

The specific hypotheses to be tested in this study are:

1. Mediterranean barley and durum wheat have similar root system morphology, in terms of weight, length, diameter and volume;

2. Comparable distribution of root morphological traits density (RWD, RLD, RVD and diameter) with depth between barley and durum wheat is observed;

3. Root weight and size (measured as volume and length) decrease with water application and increase with N availability, and spring barley and durum wheat responses should be broadly similar;

4. N fertilizer application effects on root DM growth are significantly larger under full irrigation than under drought;

5. Water and N deficits increase the biomass allocated to the roots, i.e. higher R:S;

6. Drought decreases mean root diameter (RD) favouring root expansion, whereas N application increases both;

7. Both specific root length (SRL) and root weight to volume ratio (rV:rW) will increase with drought and with N stress;

8. More uniform root system distribution, and a relatively higher proportion of roots deeper in the soil profile, occurs with water and N deficits (higher β: weight – β_W, length – β_L and volume – β_V);

9. The percentage of cumulative water use extracted from deeper in the profile increases with drought;

10. Increasing water availability increases seasonal water uptake (WU) and nitrogen uptake (Nup), in similar proportion for barley and wheat;

11. N application increases seasonal water use, and in the same proportion for barley and wheat;

12. A resource capture coefficient (k) can be defined from the relationship between RLD and ϕ (proportional resource capture) for water and N in barley and durum wheat, and its value does not differ significantly between these species, hence Critical RLD does not differ;

13. Aboveground dry weight (AGDW) and grain yield (Y) for barley and durum wheat are similar, and will decrease with N and water deficits and there will be an interaction between water and N availability, such that responses to fertilizer N are relatively greater under high than low water availability;

14. WUE_{grain} and WUE (measured as AGDW at harvest per WU or as cumulative AGDW per cumulative water use through the season) will increase with drought and N application; and these responses are similar for barley and durum wheat;

15. Grain $\Delta^{13}C$ will increase with water and decrease with N availability;

16. NUE, NupE and NutE will decrease with increasing water deficits and increasing N supply and responses to N are similar for barley and durum wheat.

3 MATERIALS AND METHODS

3.1 EXPERIMENTAL DESIGN AND TREATMENTS

In each of 2006, 2007 and 2008 one glasshouse experiment was conducted at the University of Nottingham, School of Biosciences, Sutton Bonington Campus, UK (52.5º N, 1.3º W). This chapter describes the details of each experiment regarding the experimental design, microclimate measurements, soil characteristics and plant measurements. A summary of the treatments applied in each of the experiments is presented in the Table 3.1.

Table 3.1 Experimental treatments (species, irrigation, nitrogen fertilizer) number of replicates and destructive sampling points (Sampling points) for the experiments carried in 2006, 2007 and 2008. AW_{FC} – available water at field capacity.

Experiments Year	Species	Treatments		Reps.	Sampling points
		Irrigation	Nitrogen		
2006	Barley cv. Rum Wheat cv. Hourani	**Irrigated** (90% AW_{FC}) **Droughted** (50% to 25% AW_{FC})	**0 Kg ha^{-1}** **50 Kg ha^{-1}** **100 Kg ha^{-1}**	3	5
2007	Barley cv. Rum Wheat cv. Karim Wheat cv. Hourani	**Irrigated** (90% AW_{FC}) **Droughted** (50% to 25% AW_{FC})	**0 Kg ha^{-1}** **50 Kg ha^{-1}** **100 Kg ha^{-1}**	5	3 *(1 for wheat cv Hourani)*
2008	Barley cv. Rum	**Irrigated** (90% AW_{FC}) **Droughted** (50% to 25% AW_{FC})	**50 Kg ha^{-1}**	5	3

The 2006 and 2007 experiments used a factorial randomised block design and the 2008 experiment used a completely randomized block design.

The Mediterranean Sea with its 2.500.000 Km^2 comprises more than half of the Mediterranean climate areas of the world, with an annual rainfall ranging between 200 to 900 mm and a relatively wide range of temperatures, depending on the altitude, proximity and natural barriers (López-Bellido, 1992). This work pretended, to some extent, to mimic the conditions found in the semi-arid to arid regions of South

Mediterranean basis, particularly those found in Jordan, Morocco and Tunisia. In the Table 3.2 is the set of conditions likely to be encountered in those regions, alongside with the temperatures found in the glasshouse during the 3 years of experiment.

The Mediterranean growing conditions are characterized by an adequate amount of rainfall during winter, while water deficit emerges in spring, resulting in a moderate stress for rainfed wheat around anthesis, which increases in severity throughout grain filling (Thabet *et al.*, 2009). The irrigation treatment in the Table 3.2, referrers to the droughted treatment used in this work, and it tries to mimic a Mediterranean rainfed cropping system.

Table 3.2 Average minimum and maximum temperatures, rainfall for the last 30 years (World Meteorological Organization, 2010) and soil characteristics (López-Bellido, 1992) likely to occur in the Mediterranean region of Jordan (Amman), Morocco (Marrakesh) Tunisia (Tunis), and soil details for Ebrahim (2008) experiments in Jordan (. Are also included the set of target conditions for the glasshouse experiments, the average temperatures were the measured temperatures, the irrigation treatment here presented pretends to mimic a Mediterranean rainfed cropping system.

			Mediterranean			Glasshouse experiments		
			Jordan	**Morocco**	**Tunisia**	**2006**	**2007**	**2008**
Average Temperatures (ºC)	**Winter**	**Minimum**	4.6	8.7	7.6	Vernalization in a growth room at 6ºC		Glasshouse with no heating 7.7 ºC
	Summer	**Minimum**	17.6	19.8	19.3	18.2	15.4	14.9
		Maximum	31.5	36.0	31.0	39.6	36.8	33.9
Rainfall (mm)	**Winter + Autumn**		208.9	68.7	304.6	Irrigation to 90% AW_{FC}		
	Spring		60.1	44.9	107.8	Irrigation to 50% AW_{FC}		
	Summer		0.3	7.1	53.1	Irrigation to 25% AW_{FC}		
Soils			Sandy loam soil with low organic (1.9 %) mater and N content (58.2 Kg N ha^{-1})			Sandy loam soil with low organic matter and N content	20% sandy loam soil and 80% washed sand	40% sandy loam soil and 60% of washed sand

3.1.1 Genotype treatment

In this study three South Mediterranean cereals genotypes were used: one spring barley (*Hordeum vulgare* L.) variety, cv. Rum (in 2006, 2007 and 2008), and two durum wheat (*Triticum durum* L.) varieties, cvs Hourani (in 2006 and 2007) and Karim (in 2007).

Both barley cv. Rum and wheat cv. Hourani are commonly grown in Jordan, and seed was supplied by Dr Jamal Ayad from the University of Jordan. The durum wheat cv. Karim is a modern variety currently grown in Tunisia and Morocco, and seed was supplied by Dr Dahan Rachid from INRA, Morocco.

3.1.2 Irrigation treatment

3.1.2.1 2006

There were two irrigation treatment levels ("fully irrigated" and "droughted"). The irrigation treatment was initiated 15 days after transplanting plants into the soil columns. Prior to imposing the irrigation treatment, all columns received a weekly irrigation based on estimated evapotranspiration (gravimetric analysis) in one set of 36 columns (3 replicates for each irrigation x N x genotype treatment combination). In the fully irrigated treatment level, soil water content was maintained to 90% of available water at field capacity (AW_{FC}). In the droughted treatment level, water was restricted in two stages. From GS23/24 (Zadoks *et al.*, 1974)**,** water was applied to maintain 50% of AW_{FC}, and after GS61 (for barley cv. Rum) water applied to maintain only 25% AW_{FC}. In the fully irrigated treatment, columns were irrigated approximately every 7 days. Water applied to each treatment level is presented in Table 3.3. The soil surface of each column was filled with vermiculite to a depth of 2 cm to ensure the minimum surface evaporation losses (Figure 3.3 b). Irrigation treatments were applied in the basis of the water available in the whole column.

To avoid any micro- or macronutrients deficiencies besides N, on the 16 March (55 DAS) the plants where supplied with a 1 l of N-free nutrient solution (Table 3.4) (Broadley *et al.*, 2000; Broadley *et al.*, 2003).

Table 3.3 Irrigations (l) applied for the different irrigation treatment levels in 2006.

Species	Irrigation	Fertilizer N (kg N ha^{-1})	Irrigation in l for 2006 (DAS*): 75	83	91	102	111	122	137	143	151	157	163	Total
Barle cv. Rum	**Irrigated**	**0**	1.53	0.55	1.32	1.02	0.95	2.48	3.38	1.35	1.80	1.35	1.35	17.1
		50	1.09	0.60	0.90	2.01	1.64	4.04	5.51	2.20	2.94	2.20	2.20	25.4
		100	1.01	0.62	0.93	2.39	1.96	3.69	5.03	2.01	2.69	2.01	2.01	24.4
	Droughted	**0**	1.04	0.00	0.64	0.41	0.00	2.01	0.00	0.00	0.00	0.00	0.00	4.1
		50	0.96	0.00	0.56	0.74	0.00	1.78	0.00	0.00	0.00	0.00	0.00	4.0
		100	0.97	0.00	0.41	1.68	0.00	2.42	0.00	0.00	0.00	0.00	0.00	5.5
Wheat cv. Hourani	**Irrigated**	**0**	1.12	0.59	0.89	1.28	1.46	1.53	2.09	0.83	1.11	0.83	0.83	12.6
		50	1.00	0.50	0.75	0.91	1.47	1.95	2.66	1.07	1.42	1.07	1.07	13.9
		100	0.93	0.48	0.71	1.29	1.44	1.12	1.53	0.61	0.82	0.61	0.61	10.1
	Droughted	**0**	1.11	0.00	0.10	0.00	0.00	0.56	0.00	0.00	0.00	0.00	0.00	1.8
		50	1.04	0.00	0.26	0.32	0.00	0.81	0.00	0.00	0.00	0.00	0.00	2.4
		100	1.02	0.00	0.12	0.09	0.00	2.68	0.00	0.00	0.00	0.00	0.00	3.9

*DAS - days after sowing.

Table 3.4 Composition of the N-free complete nutrient solution.

Macronutrients	mM	Micronutrients	mM
KH_2PO_4	0.25	H_3BO_3	30.0
KOH	0.50	$MnSO_4.4H_2O$	10.0
$MgSO_4.7H_2O$	0.75	$ZnSO_4.7H_2O$	1.0
$CaCl_2.2H_2O$	0.03	$CuSO_4.5H_2O$	3.0
FeNaEDTAer	0.10	$Na_2MoO_4.2H_2O$	0.5
$CaSO_4.H_2O$	4.00		

3.1.2.2 2007

Similarly to the 2006 experiment, the irrigation treatment was initiated 15 days after transplanting (72 DAS) the seedlings to soil columns (ca. GS39 for wheat cv. Karim and Hourani and GS55 for barley cv. Rum on the main tiller). Prior to this, all columns received a weekly irrigation with nitrogen-free macro- and micronutrient solution (Table 3.4) based on estimated transpiration to maintain the water content to 90% AW_{FC}.

To periodically quantify the soil water content and guide irrigation scheduling, a set of 90 columns covering 5 replicates of all treatment combinations was used for soil water measurements at 20/25 cm soil depth intervals using a Theta-T probe (ML2x Delta T Devices, Cambridge, UK) connected to a Moisture Meter (HH2 Delta T Devices, Cambridge, UK) via access apertures cut in the side of PVC columns (Figure 3.1). To

measure the soil moisture, the ThetaProbe MLX2 (Delta-T Devices Ltd., Cambridge, UK) was gravimetrically calibrated (*vide* section 3.5). To avoid any other nutrient deficits, a N-free nutrient solution supplying all other plant macro- and micronutrients (Table 3.4) was added to columns of all treatments each time the drought treatment needed irrigation; otherwise tap water was used for irrigation. The soil surface of each column covered with a 'weed control fabric' – a very fine mesh that permits the rapid drainage and avoids the rapid water evaporation after irrigation and the growth of weeds (Figure 3.4 a). As in 2006 the irrigation treatments were applied in the basis of the available water in the whole column. Irrigation information for the 2007 experiment is presented in Table 3.5.

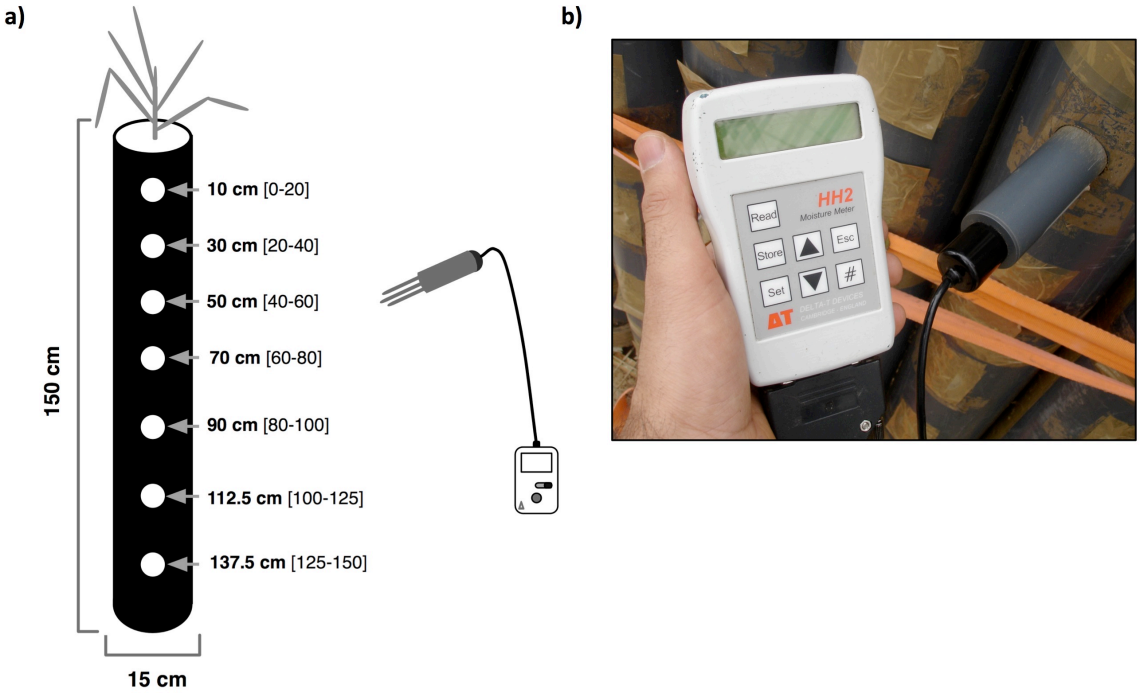

Figure 3.1 Scheme of the columns used to periodically measure the water moisture at different depths (**a**) and detail of soil moisture content measurement on soil columns using ThetaProbe ML2x coupled to a HH2 moisture meter (**b**).

Table 3.5 Irrigations (l) applied for the different treatment levels in the 2007 experiment.

Species	Irrigation	Fertilizer N (kg N ha^{-1})	Irrigation in l for 2007 (DAS*):												Total
			69	79	86	97	104	110	118	124	132	138	146	153	
Barley cv. Rum	**Irrigated**	**0**	0.20	0.47	0.63	0.78	0.26	0.51	0.63	0.45	0.39	0.31	0.66	0.32	5.61
		50	0.20	0.51	0.49	0.65	0.41	0.51	0.67	0.31	0.58	0.40	0.50	0.27	5.50
		100	0.20	0.61	0.47	0.78	0.37	0.51	0.55	0.43	0.39	0.43	0.53	0.20	5.47
	Droughted	**0**	0.20	0.00	0.22	0.28	0.00	0.00	0.00	0.48	0.30	0.00	0.00	0.00	1.48
		50	0.20	0.00	0.32	0.44	0.00	0.00	0.00	0.35	0.20	0.00	0.00	0.00	1.51
		100	0.20	0.00	0.20	0.42	0.00	0.00	0.00	0.15	0.22	0.00	0.00	0.00	1.19
Wheat cv. Karim	**Irrigated**	**0**	0.20	0.55	0.38	0.44	0.40	0.27	0.52	0.39	0.26	—	—	—	3.41
		50	0.20	0.56	0.37	0.47	0.26	0.29	0.43	0.36	0.20	—	—	—	3.14
		100	0.20	0.26	0.16	0.66	0.26	0.17	0.55	0.28	0.24	—	—	—	2.78
	Droughted	**0**	0.20	0.00	0.10	0.26	0.00	0.00	0.00	0.16	0.00	—	—	—	0.72
		50	0.20	0.00	0.10	0.25	0.00	0.00	0.00	0.06	0.00	—	—	—	0.61
		100	0.20	0.00	0.17	0.33	0.00	0.00	0.00	0.04	0.00	—	—	—	0.74
Wheat cv. Hourani	**Irrigated**	**0**	0.20	0.57	0.39	0.46	0.26	0.44	0.78	0.53	0.65	0.27	0.54	0.30	5.40
		50	0.20	0.44	0.14	0.75	0.16	0.36	0.58	0.36	0.40	0.20	0.41	0.32	4.09
		100	0.20	0.40	0.36	0.52	0.18	0.31	0.63	0.32	0.40	0.23	0.54	0.40	4.49
	Droughted	**0**	0.20	0.00	0.10	0.29	0.00	0.00	0.00	0.37	0.28	0.00	0.00	0.00	1.24
		50	0.20	0.00	0.10	0.25	0.00	0.00	0.00	0.16	0.22	0.00	0.00	0.00	0.93
		100	0.20	0.00	0.16	0.39	0.00	0.00	0.00	0.33	0.18	0.00	0.00	0.00	1.26

*DAS - days after sowing

3.1.2.3 2008

As previously described, the irrigation treatment was applied in the basis of whole the column and was initiated 15 days after transplanting. Prior to this all columns received a weekly irrigation with VITAX complete nutrient solution on estimated transpiration to maintain the available water to 90% of that at field capacity. The irrigation was done once a week. For the irrigated plants soil moisture content was maintained to 90% AW_{FC}, and for the droughted plants the soil moisture content was maintained to 50% AW_{FC} before anthesis and 25% AW_{FC} after anthesis (Table 3.6). All the plants were supplied with 50 kg N ha^{-1} after transplantation; and the irrigations were made with N-

free nutrient solution when both treatments required water. Otherwise the plants were irrigated with tap water.

Table 3.6 Irrigations (l) applied for the different treatment levels during the course of the 2008 experiment.

Species	Irrigation	Fertilize N (kg N ha^{-1})	Irrigation in l for 2008 (DAS*):													Total
			41	52	58	66	72	79	86	93	100	107	114	121	128	135	
Barley cv. Rum	**Irrigated**	**50**	0.15	0.28	1.50	1.20	1.08	1.38	1.22	1.53	1.75	1.67	1.52	1.53	1.47	1.25	17.5
	Droughted	**50**	0.11	0.00	0.34	0.38	0.38	0.54	0.00	0.06	0.24	0.42	0.00	0.00	0.00	—	2.5

*DAS - days after sowing

3.1.3 Nitrogen treatment

3.1.3.1 2006

According to personal communication of Dr Jamal Ayad of the University of Jordan, the typical N fertilization applications for durum wheat and barley in Jordan were 110 kg N ha^{-1} and 50 kg N ha^{-1}, respectively. In order to evaluate the response of the different genotypes to N fertilization, three levels of N fertilizer were imposed in 2006: at an equivalent rate of nil N (N0), 50 kg N ha^{-1} (N50) and 100 kg N ha^{-1} (N100). Ammonium nitrate prill was applied to columns in nil, one or two applications of equivalents to 50 kg N ha^{-1} (N0, N50 and N100 respectively), the first on 27 March (66 DAS – GS23/24) and the second on 5 April (75 DAS, GS41 for barley and GS30 for wheat cv. Hourani).

3.1.3.2 2007

The nitrogen treatments in 2007 were similar to those applied in 2006, but both N50 and N100 were supplied with one application of ammonium nitrate prill on the 11 of May 2007 (72 DAS).

3.1.3.3 2008

No N treatments were imposed in the experiment in 2008. However, 50 kg N ha^{-1} was applied to all the plants after transplantation to avoid any N deficiency.

3.2 PLANT ESTABLISHMENT, TRANSPLANTATION AND GROWING CONDITIONS IN SOIL COLUMNS

3.2.1 2006

Single seeds of barley cv. Rum and wheat cv. Hourani were sown on 20 January 2006 in plastic pots with 7 cm diameter, 8.5 cm depth (Figure 3.2 a), at a depth of 2 cm. The soil used was sandy loam of low N availability; the full soil characteristics are presented in Table 3.7. Previous experiments (2005, unpublished data) showed that wheat cv. Hourani requires some vernalization. So plants were subjected to a vernalization period of 52 days in a growth room at 6 ºC and a 12 hours photoperiod (Figure 3.3 a). The photosynthetic active radiation (PAR) in the growth room was measured using a PAR 'Special' sensor (SKP 210, Skye Instrument LTD, UK) coupled to a SKP200 meter (Skye Instrument LTD, UK) and averaged 170.6 μmol m^{-2} s^{-1} (n = 20). During vernalization the plants were irrigated every two days with tap water.

After vernalization (13 March 2006), the plants were transplanted into PVC columns (one plant per column), 15 cm diameter, filled to a depth of 100 cm (Figure 3.2 c) or 150 cm (Figure 3.2 d) using the same source of soil used to fill the sowing pots and placed in a glasshouse with frost protection (minimum temperature 10ºC, Figure 3.3 b). The 100 cm columns were used on the first two samplings and the 150 cm columns for the final sampling. The columns were longitudinally split into two halves, which were then taped together with parcel tape and the bottom was closed with a polythene sheet, perforated with 5 drainage holes with 5 mm diameter to allow drainage (Figure 3.2 b).

During 24-25 of June 2006 some of the plants lodged (Figure 3.3 c) but only severely in a few plants that then were discarded from the growth analysis. To avoid further and/or more severe lodging, plant supports were co-located in the soil columns (Figure 3.3 d).

Table 3.7 Characteristics of the soil used in the 2006 experiment. Bulk density referrers to the bulk density measured in the soil column, and available N is the soil N at the start of the experiment.

Bulk density ($g\ cm^{-3}$)	**Field Capacity** ($m^{-3}\ m^{-3}$)	**Available N** ($Kg\ N\ ha^{-1}$ in 150 cm soil depth)	**pH**
1.61	0.395	98.5	7.6
Organic matter (%)	**Sand (%)**	**Silt (%)**	**Clay (%)**
1.7	48.0	20.4	31.6

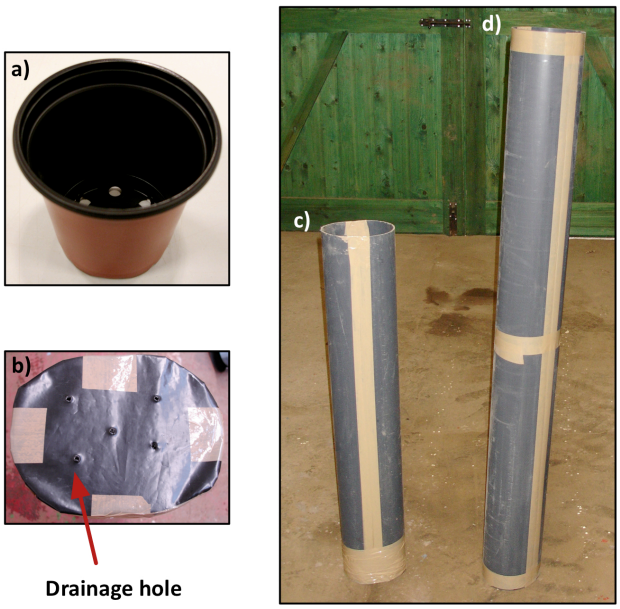

Figure 3.2 Seed sowing pots (**a**), detail of the columns bottom showing the 5 mm diameter drainage holes (**b**) and taped soil columns with 15 cm diameter and 100 or 150 cm height (**c** and **d** respectively).

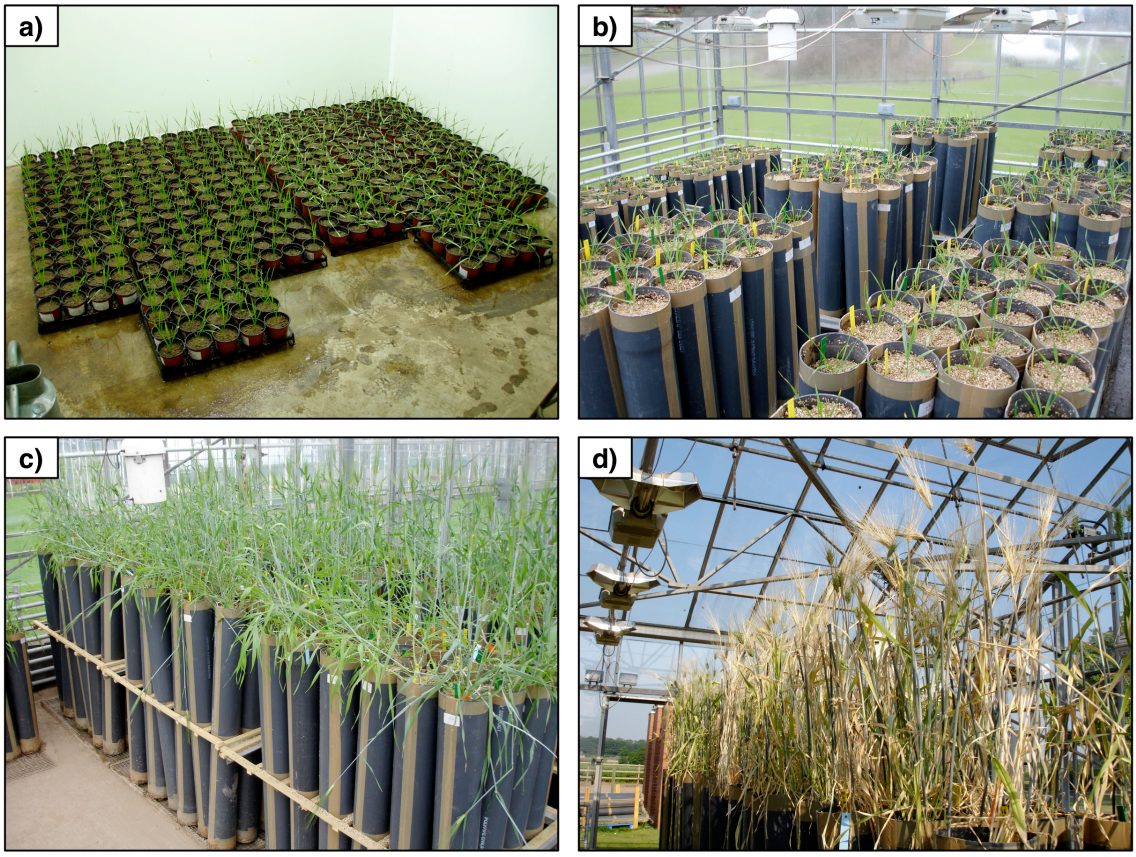

Figure 3.3 Pictures of the 2006 experiment: **a**) wheat cv. Hourani and barley cv. Rum in growth room during vernalization, **b**) after transplantation into soil columns, **c**) general view of the plants on the lodging episode and **d**) plants near to maturity after collocation of plant supports to avoid further lodging.

3.2.2 2007

When comparing the growth of wheat cv. Hourani in the 2006 experiment to that under Mediterranean field conditions (Ebrahim, 2008), it appeared to be growing relatively weakly in the glasshouse conditions. Therefore a more modern variety of durum wheat, cv. Karim, was included in the 2007 experiment. Wheat cv. Hourani was also included but only assessed at harvest.

Attempting to achieve the required low N in the soil medium and also to reduce the time required for root washing and preparation of samples prior to root scanning, the soil medium was changed to a mixture of 80% commercial washed sand and 20% of sandy loam soil (from the same source as the one used in 2006). The details of the soil + sand mixture are presented in Table 3.8. On 28 February 2007, seeds of durum wheat cv. Hourani, cv. Karim and spring barley cv. Rum were sown in small pots (Figure 3.2 a)

and subjected to 47 days of vernalization as previously described. The day/night temperature in the growth room was then raised to 15/10 °C for the final 8 days to avoid a temperature shock after transplantation to the soil columns in the glasshouse. During vernalization the plants were irrigated every two days with VITAX complete nutrient solution (N:P:K at 2:1:4; Vitax LTD, UK) at a ratio of 1:200. The average PAR measured in the growth room was 188.7 μmol m^{-2} s^{-1}.

When transplanted to the soil columns in the glasshouse (24 April 2007) the majority of plants had only one shoot. To avoid lodging plant supports were placed immediately after transplantation (Figure 3.4 a).

Table 3.8 Characteristics of the mixture of 20% of sandy loam soil and 80% of commercial washed sand used in the 2007 experiment. Bulk density referrers to the bulk density measured in the soil column, and available N is the soil N at the start of the experiment.

Bulk density (g cm^{-3})	**Field Capacity** (m^{-3} m^{-3})	**Available N** (Kg N ha^{-1} in 150 cm soil depth)	**PH**
1.85	0.193	244.5	7.4
Organic matter (%)	**Sand** (%)	**Silt** (%)	**Clay** (%)
0.3	89.6	4.1	6.3

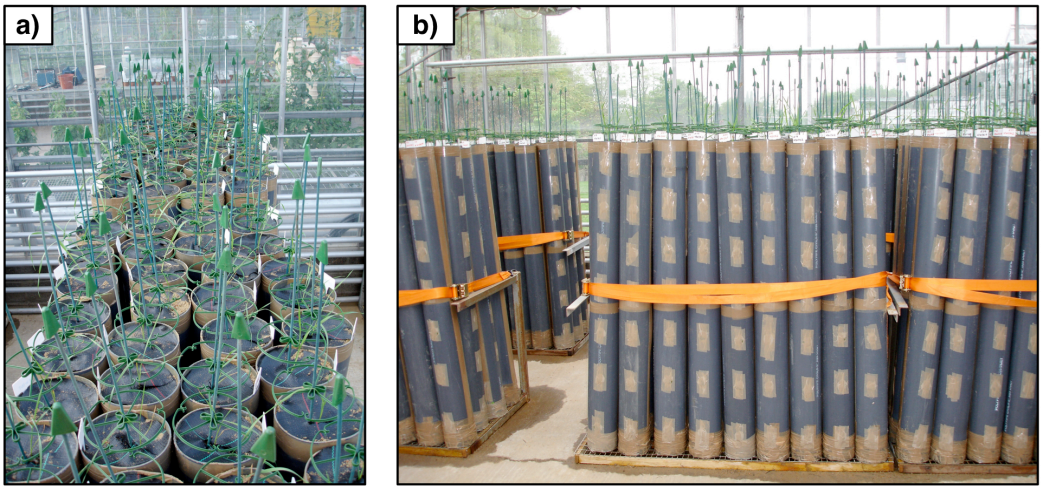

Figure 3.4 a) The plant supports used in 2007 and 2008 to avoid lodging and the 'weed control fabric' used to avoid rapid water evaporation after irrigation. **b**) Column experiment setup for the 2007 experiment.

3.2.3 2008

In 2008 only barley cv. Rum and the irrigation treatment were applied. Since only barley was used the plants were not subjected to vernalization. The plants were sown in plastic pots (Figure 3.2 a) on 4 February 2008 in a glasshouse. The soil used was a mixture of 40% field sandy loam soil and 60% commercial washed sand (soil details in Table 3.9). During the nursery phase the plants were irrigated every other day with VITAX complete nutrient solution (N:P:K at 2:1:4; Vitax LTD, UK) diluted at a ratio of 1:200. On the 3 March (28 DAS) the plants were transplanted to soil columns with access holes to measure the soil moisture throughout the soil depth (Figure 3.1 a). Plant supports and weed control fabric were applied as in 2007 (Figure 3.4).

Table 3.9 Characteristics of the mixture of 40% of sandy loam soil and 60% of commercial washed sand used in the 2008 experiment. Bulk density refers to the bulk density measured in the soil column, and available N is the soil N at the start of the experiment.

Bulk density ($g\ cm^{-3}$)	**Field Capacity** ($m^{-3}\ m^{-3}$)	**Available N** ($Kg\ N\ ha^{-1}$ in 150 cm soil depth)	**PH**
1.76	0.242	226.0	7.4
Organic matter (%)	**Sand** (%)	**Silt** (%)	**Clay** (%)
0.8	79.2	8.2	12.6

3.3 SOIL COLUMN FILLING

The filling of the soil columns (Figure 3.2 c and d) was done in several steps of filling, compaction and refilling. Firstly, the columns were filled to the top and irrigated to saturation. The next day the soil had sunk about 40 cm, and the columns were refilled and irrigated to saturation again, repeating the process to the point that there was no more soil consolidation; the process was repeated three times. Using this method a more "natural" compaction of the soil was achieved.

3.4 BULK DENSITY AND WATER CONTENT AT FIELD CAPACITY (FC) DETERMINATION

Each year after completion of column filling three columns (only two for 2007) were irrigated to saturation and the top closed with a plastic bag covered with kitchen foil to avoid evaporation (Figure 3.5). After 48 hours of drainage the soil was assumed to be at field capacity (FC, Dani & Wraith, 2000; Scott, 2000). The columns were then transversally opened and the soil extracted in 20 or 25 cm layers (Figure 3.6). The wet soil was weighed, before and after drying for 24 hours at 115 ºC. The bulk density (BD) and the volume basis water content (θ_v) at field capacity (θ_{FC}) for the different layers (Figure 3.6 a and b) was determined by Equation 3.1 and Equation 3.2, respectively (Rowell, 1994):

$$BD\ (g\ cm^{-3}) = \frac{\text{Mass of oven dried soil (g)}}{\text{Soil column layer volume } (cm^3)} \qquad \textbf{Equation 3.1}$$

$$\theta_v\ (m^3\ m^{-3}) = \frac{\text{Volume of water } (m^3)}{\text{Bulk volume of soil } (m^3)} \qquad \textbf{Equation 3.2}$$

with: $\text{Volume of water } (m^3) = \frac{\text{Mass of water (kg)}}{\text{Density of water } (kg\ m^{-3})}$

and $\text{Mass of water (kg)} = \text{Mass of wet soil} - \text{Mass of oven dried soil.}$

The available water at field capacity (AW_{FC}) is defined as the θ_{FC} minus the water at the permanent wilting point (θ_{PWP}). In this work θ_{PWP} was considered to be $\theta_{FC}/2$ (Dani & Wraith, 2000) so the water available at FC (AW_{FC}) would then be:

$$AW_{FC} = \theta_{FC} - \theta_{PWP} = \theta_{FC} - \frac{\theta_{FC}}{2} \qquad \textbf{Equation 3.3}$$

Forty-eight hours before transplantation the columns were irrigated to saturation and left to drain to ensure that at transplantation the soil was at FC.

Figure 3.5 Procedures to achieve the field capacity (FC) in soil columns: irrigation to saturation (**a**) and closure of the top with plastic bag (**b**) and kitchen foil (**c**).

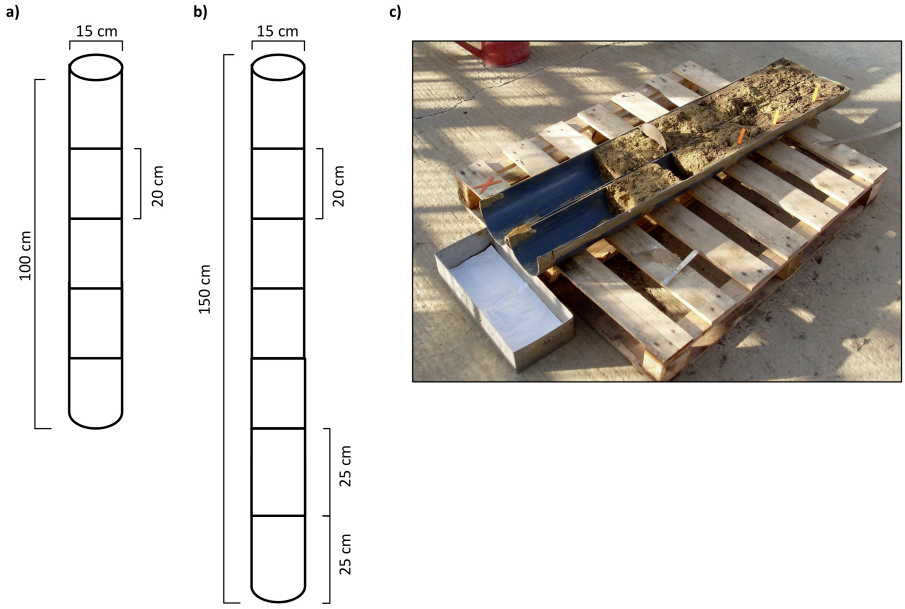

Figure 3.6 Scheme of the soil depth layers to be analysed for the different types of soil columns (**a** and **b**), and open column being sampled for FC and bulk density determination (**c**).

3.5 THETAPROBE ML2X CALIBRATION

To measure the soil moisture using the ThetaProbe MLX2 (Delta-T Devices Ltd., Cambridge, UK), it needed to be calibrated to the specific soil used (Kaleita *et al.*, 2005). The ThetaPobe ML2x calibration was carried out on a subset of four columns (Figure 3.1 a) in 2007 and five columns in 2008. The columns were irrigated to saturation and left to drain for different times in order to obtain different soil moisture contents. Two columns in 2007 and three in 2008 were allowed to drain for 48 h (*vide* section 3.4). One column was allowed to drain for one week and another for two weeks, after which the voltage (mV) for each soil-depth layer was measured. The columns were

then opened and the soil extracted in seven soil-depth layers (Figure 3.6). The soil was weighed and left to dry for 24h at 115 ºC after which the soil dry weight was measured. The θ_v was then calculated using equations 3.1 and 3.2. The resultant linear regression between the values of θ_v measured gravimetrically and Theta Probe mV values observed was use to estimate θ_v.

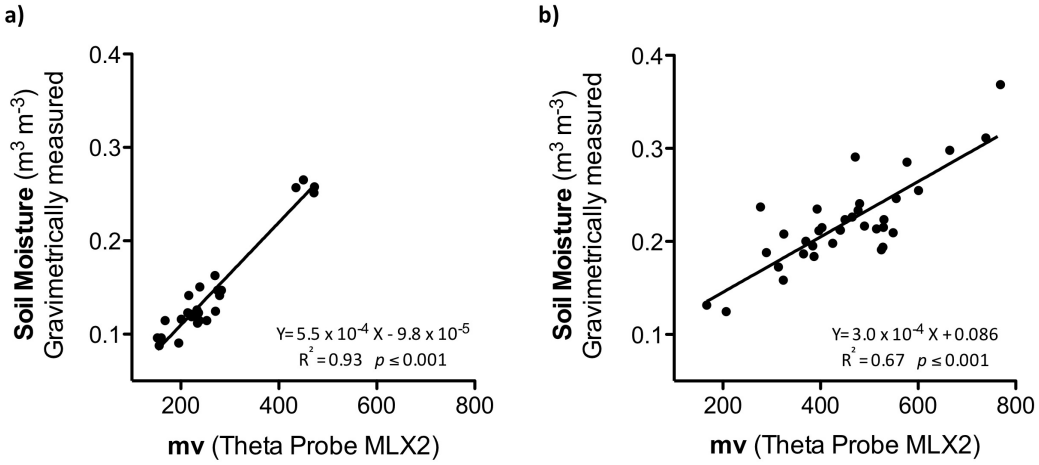

Figure 3.7 ThetaProbe MLX2 (Delta-T Devices Ltd., Cambridge, UK) calibration line for the soil used in the **a**) 2007 and **b**) 2008 experiments.

3.6 PLANT MEASUREMENTS

3.6.1 Timing of growth analysis samplings

In 2006, there were five destructive sampling points based on calendar date, starting 15 days after transplanting (GS23/24), with an interval of 15-20 days (Table 3.10).

Table 3.10 2006 experiment sampling points, respective days after sowing (DAS) and growth stages growth stages (GS; Tottman, 1987).

Sampling point	Date	DAS	GS	
			Barley cv. Rum	Wheat cv. Hourani
1st	28/03	67	31	23
2nd	13/04	83	51	31
3rd	02/05	102	61	55
4th	22/05	122	71	61
5th	11/06	142	92	92

In 2007, three destructive samplings were carried out for barley cv. Rum and wheat cv. Karim and one for wheat cv. Hourani (Table 3.11).

Table 3.11 2007 experiment sampling points, respective days after sowing (DAS) and growth stages (GS; Tottman, 1987).

Species	Irrigation	Sampling points Date/ *DAS*/ *GS*		
		1st	2nd	3rd
Barley cv. Rum	**Irrigated**	15/05 *76 DAS* **GS51**	26/06/2007 *118 DAS* **GS61**	23/08 *176 DAS* **GS92**
	Drought			16/08/2007 *169 DAS* **GS92**
Wheat cv. Karim	**Irrigated**	15/05 *75 DAS* **GS39**	09/07/2007 *131 DAS* **GS61**	26/07 *148 DAS* **GS92**
	Drought			13/07 *135 DAS* **GS92**
Wheat cv. Hourani	**Irrigated**	—	—	13/08 *166 DAS* **GS92**
	Drought			01/08 *154 DAS* **GS92**

In 2008, three destructive samplings were carried out on five plants per treatment (Table 3.12). This smaller experiment provided important additional data to (i) determine the critical root length density (C_{RLD}) and/ or root volume density (C_{RLD}) required to extract at least 90% of the water available in the soil, and (ii) describe the RLD and RVD distribution with depth.

Table 3.12 Sampling points, calendar date, respective days after sowing (DAS), growth stages (GS; Tottman, 1987) and measurements performed in the 2008 experiment for barley cv. Rum.

Sampling point Date/ *DAS*/ GS	Measurements
03/03 *28 DAS* **GS13/14**	Growth and root analysis, SPAD, WC and RWC
29/04 *85 DAS* **GS31**	Growth analysis, SPAD, WC and RWC
12/06 – Drought; *129 DAS* 15/07 – Irrigated; *162 DAS* **GS92**	Growth, root analysis and yield analysis

3.6.2 Developmental stages and growth analysis

For all the sampling points in each year the developmental stage accordingly to the Zadoks' scale was recorded (Zadoks *et al.*, 1974; Tottman, 1987), according to the stage on the main stem. The date when each plant reached GS31 and GS61, was also recorded. Date of maturity was assumed to be reach when ca. 100% of green leaf lamina area had senesced.

After the plant was sampled, the plant height of the main stem to the tip of the ear and the fresh weight of the aboveground plant was measured, after which the shoots were separated into four categories: main stem, fertile tiller 1-3 (T1-3), fertile tiller 4+ (T4+), and infertile shoots (IS). Each of the categories was separately analysed. For the fertile shoot categories, the number of shoots/ears as well as: (i) flag-leaf green and dead areas, (ii) remaining leaf lamina green and dead areas, (iii) stem plus sheath green and non-green areas, and (iv) green ear area was recorded using a leaf area meter (Licor 3100, Lexicon instruments, Lincoln, Nebraska). The dry weight of all green and non-green plant components was recorded after drying for 48 h at 80ºC. The aboveground dry weight of the infertile shoots was also recorded (those with no green area prior to GS61 and those without an ear from GS61 onwards). At the final harvest, the ears of each shoot category were hand threshed and the chaff and grain weighed separately. The grain number was measured using a seed counter (CONTADOR, Hoffman Manufacturing, Inc, Jefferson, USA) and the dry weight was measured after drying for 48 h at 80°C.

3.6.3 Plant water status

Plant water content (PWC) was measured at each sampling point as described by (Beadle *et al.*, 1985):

$$\text{PWC (\%)} = \frac{\text{Plant fresh weight} - \text{Plant dry weight}}{\text{Plant dry weight}} \times 100 \qquad \textbf{Equation 3.4}$$

Relative water content (RWC) is a widely used method of assessing the plant water status (Equiza *et al.*, 2001; Mwale, 2005); and, at least for bread wheat and barley, is considered to be a better indication of plant water status than leaf water potential (Merah, 2001). Relative water content is closely related with cell volume and so may reflect the balance between water supply to leaf and transpiration rate (Winter *et al.*, 1988a). In each experiment at each sampling point prior to harvest, five segments of 5 cm diameter were excised from the middle of well-developed leaves of the harvested plants and their fresh weight (Wf) was recorded (Equiza *et al.*, 2001). The segments were then placed for six hours in petri dishes filled with distilled water, under illumination in order to avoid loss of dry weight arising from respiration during hydration (Mwale, 2005), after which the turgid weight (Wt) was measured. The dry weight (Wd) of the leaf segments was measured after 48 h at 80ºC. The leaf water content (LWC) and RWC were then measured as in equations 3.5 and 3.6 (Beadle *et al.*, 1985; Larcher, 2003):

$$\text{LWC}\ (\%) = \frac{\text{Wf} - \text{Wd}}{\text{Wf}} \times 100 \qquad \textbf{Equation 3.5}$$

$$\text{RWC}\ (\%) = \frac{\text{Wf} - \text{Wd}}{\text{Wt} - \text{Wd}} \times 100 \qquad \textbf{Equation 3.6}$$

3.6.4 Chlorophyll concentration (SPAD)

The chlorophyll concentration was indirectly measured in 5 leaves (flag leaf and 4 well-developed leaves of the main shoot) in all sampling points (with exception of harvest in all experiments and sampling points 1 and 2 in 2006) with a chlorophyll meter - SPAD-502 (Minolta, Osaka, Japan). Leaf veins can affect SPAD readings due to their thickness and paleness (Baburai Nagesh, 2006), so they were avoided. The SPAD chlorophyll meter measures the absorbance in two wavelength regions, the red and infrared regions. Using these transmittances a numerical value that is proportional to the chlorophyll concentration present in the leaf is calculated (Konica Minolta 2003).

3.6.5 Root morphology

3.6.5.1 Root washing

At each sampling, after sampling plants, the roots were extracted for assessment of root morphology traits. The soil columns were separated in two halves by cutting the parcel tape and soil samples were then taken relating to 20 cm and 25 cm depth horizons as shown in Figure 3.6. The soil samples were placed in plastic bags and stored in a cold room (4 °C) for not more than 3 weeks prior to root extraction. Plant roots were then extracted from the soil using a Delta-T root washer (RWC-UM-2, Delta-T Devices LTD, Cambridge, UK; Figure 3.8). The Delta-T root washer consists of four buckets with a central overflow downpipe and two nozzle jets. The system is connected to a pump that supplies the ideal pressure for root extraction (0.34 to 0.48 KPa, Delta-T Devices LTD, 2001). The jet nozzles inside the buckets create a strong vortex breaking the soil, causing the roots to float to the overflow downpipe being collected by a 550 μm sieve. Due to the large volume of the soil samples, it was found that for an optimum extraction a soil sample should be divided into two buckets and run for 20 min in the root washer. The Delta-T root washer separates the roots from the soil by weight and size. Heavy soil particles remain in the bucket after extraction while fine and light particles pass through the filter, though organic matter particles and other soil debris are caught in the sieve. After extracting the samples were stored in a freezer (-20 °C), the fine cleaning was performed after leaving the sample to thaw over night. The unfrozen sample of roots and debris were spread in an acrylic box with water, and the live roots (white to light brown colour) were then manually selected using fine forceps.

3.6.5.2 Root scanning and image analysis

Cleaned roots samples were spread in an acrylic box (size A4) with tap water to minimize the number of overlaps, and were digitalized at 400 dpi resolution and 256 greys contrast (Tiff file format) with a scanner with a transparency adapter (WinRHIZO STD 1600+, Regent Instruments Inc., Quebec, Canada; Figure 3.9 a). When the root sample was too large to complete in one scan, two or more scans were performed. On the scanned images of the root systems (Figure 3.9 b) the total length, mean diameter, total area and volume were measured, using the WinRHIZO regular V.2002c software (Regent Instruments Inc., Quebec, Canada). Subsequent to scanning the root system, dry weight was recorded after drying for 48 h at 80ºC. Due to the time taken to extract and properly clean the root samples (> 2 h per sample) to be digitalized, it was only possible to analyse the soil depths corresponding to the top, mid and bottom layers of the root system distribution in the soil column. The specific soil layers sampled and analysed for the different years and genotypes are presented in Table 3.13. For this reason, the root morphology parameters were calculated for only these layers. Furthermore, the parameters: total root weight, length and volume presented are the sum of the values for those specific soil-depth layers, and not the “true” totals.

Table 3.13 Soil-depth layers analysed for root morphology traits at different growth stages during the experiments conducted in 2006, 2007 and 2008.

Year	Genotype	Growth Stage	Soil Layers Analysed
2006	**Barley cv. Rum** **Wheat cv. Hourani**	67 DAS	0 - 20, 20 - 40 and 40 - 60 cm
		Anthesis	0 - 20, 60 - 80 and > 125 cm
		Harvest	0 - 20, 60 - 80 and > 125 cm
2007	**Barley cv. Rum** **Wheat cv. Karim**	75 DAS	0 - 20, 40 - 60 and 60 - 80 cm
		Anthesis	0 - 20, 60 - 80 and > 125 cm
		Harvest	0 - 20, 60 - 80 and > 125 cm
	Wheat cv. Hourani	Harvest	0 - 20, 60 - 80 and > 125 cm
2008	**Barley cv. Rum**	28 DAS	0 - 20 cm
		Harvest	0 - 20, 60 - 80 and > 125 cm

Figure 3.8 Root washer - Delta-T devices LTD, Cambridge, UK.

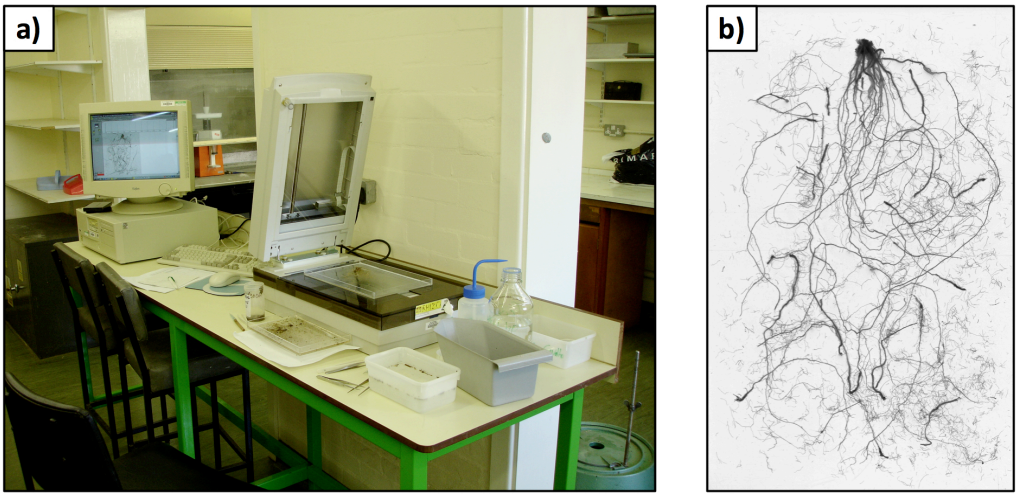

Figure 3.9 Root scanner (WinRHIZO STD 1600+, Regent Instruments Inc., Quebec, Canada) (**a**) and barley cv. Rum under irrigation and 100 Kg N ha-1 fertilizer root scan (**b**).

3.6.5.3 Root weight, length and volume distribution with depth (β) calculation

The β parameter describing the shape of the proportional distribution of root weight (β_W), length (β_L) and volume (β_V) with soil depth was calculated fitting the equation 2.3 ($p = 1 - \beta_w^d$) to the cumulative fractional distribution of the relevant traits (p) with soil depth (d) in the 20 cm soil layers analysed for each treatment replicate.

3.6.5.4 Total root weight estimation and R:S calculation

The R:S ratio is usually calculated as the ratio between the aboveground dry mass (AGDM; g) and the total root dry mass (g). But, since in these experiments the complete root system was not analysed (Table 3.13), the total root weight was first estimated by interpolation between soil layers and used to calculate R:S. Using equation 2.3 and the calculated β_W (*vide* section 4.2.1), the cumulative fraction (p) of the root system to the maximum depth of each successive soil-depth layer (d) was calculated, and with that the proportion (P) of weight in each soil-depth layer to the bottom of the root system. Knowing the total root weight measured ($TRW_{measured}$) and the estimated proportion of the total root system in the measured soil layers ($P_{measured}$), the total root weight was calculated (TRW_{est}; Equation 4.1):

$$TRW_{est} = \frac{TRW_{measured}}{P_{measured}} \qquad \textbf{Equation 4.1}$$

The R:S was then calculated as:

$$R:S = \frac{AGDM\ (g)}{TRW_{est}\ (g)} \qquad \textbf{Equation 4.2}$$

3.6.6 Plant water use and water use efficiency (WUE)

Plant water use (WU) in 2006 was gravimetrically measured weekly as:

$$\text{WU (l)} = \text{Column Weight}_{T1}\text{ (kg)} + \text{Irrigation (l)} - \text{Column Weight}_{T2}\text{ (kg)} \quad \textbf{Equation 3.7}$$

In 2007 and 2008 the WU was calculated weekly using the soil moisture per layer data measured with the ThetaProbe MLX2:

$$\text{WU (l)} = \left[\sum_{L=1}^{7}(\theta_L \times V_L)\right]_{T1} + \text{Irrigation} - \left[\sum_{L=1}^{7}(\theta_L \times V_L)\right]_{T2} \quad \textbf{Equation 3.8}$$

with: θ_L as the volumetric soil moisture ($m^3\ m^{-3}$) at layer L and V_L the volume at layer L (dm^{-3}).

Water-use efficiency (WUE; g l^{-1}) and WUE_{grain} (g l^{-1}) at harvest were measured as the aboveground biomass, or grain dry weight, respectively, divided by WU per plant. Water-use efficiency ($WUE_{cumulative}$; g l^{-1}) was also measured as the slope of the linear regression (forced through origin) of the cumulative aboveground dry matter (g) on cumulative WU for relevant samplings. In this calculation of cumulative WU estimation losses to soil evaporation and drainage were assumed to be zero.

3.6.7 Plant water uptake per soil depth

Using the measurements of soil moisture for the different soil depth layers in the 2007 and 2008 experiments, the water uptake for each soil layer was measured. For this the θ_L measured before irrigation (I) was converted into water content (WC_{T1}) by multiplying its value by the respective soil layer volume (V_L): $WC = \theta_L \times V_L$). The water content after irrigation (WC_{T2}) for the first layer (L1) was calculated as the $WC_{T2} = WC_{T1} + I$. If this sum was higher than the water content at FC (WC_{FC}) the excess water was assumed to drain to L2. This procedure was repeated from layer to layer to estimate the water draining from layer to layer and the water content for each layer after

irrigation. The water uptake for a specific layer was then calculated as the difference between the WC for that layer on respective dates.

3.6.7.1 RLD and RVD and water uptake

In 2007 and 2008, the RLD and RVD at harvest were analysed for three soil-depths: 0 – 20, 60 – 80 and > 125 cm. The proportional resource (water) capture (ϕ), was calculated as the percentage of available water (water available = water in the soil – water at permanent wilting point) captured from: i) anthesis to harvest for the droughted treatment and ii) during the last 3 weeks of grain growth for the irrigated treatment for each soil-depth. This was then used to estimate a resource capture coefficient (k) from the RLD and RVD data according to the equations 5.1 and 5.2 (King *et al.*, 2003):

$$\phi_{RLD} = 1 - e^{-k_{RLD} \times RLD}, \text{ for RLD} \qquad \textbf{Equation 5.1}$$

$$\phi_{RVD} = 1 - e^{-k_{RVD} \times RVD}, \text{ for RVD} \qquad \textbf{Equation 5.2}$$

Where: k_{RLD} (cm^2) is the resource capture coefficient for RLD and k_{RVD} (dimensionless) for RVD.

Critical RLD (C_{RLD}) and critical RVD (C_{RVD}) in the present study are defined as the values of RLD and RVD required for the plants to extract 90% (ϕ_{RLD} and ϕ_{RVD} = 0.9) of the water available in the soil. The 90% uptake was empirically assumed as the 'easily available' water (King *et al.*, 2003). Calculations of C_{RLD} and C_{RVD} were made solving equations 5.1 and 5.2 for RLD and RVD, respectively (see Equation 5.3) for a ϕ = 0.9. This way C_{RLD} and C_{RVD} were calculated by substituting the calculated k_{RLD} and k_{RVD} in the Equation 5.4 a and b.

$$\text{RLD (or RVD)} = \frac{\ln(1-\phi)}{-k_{RLD}(\text{or } k_{RVD})} \qquad \textbf{Equation 5.3}$$

$$\textbf{a)}\ C_{RLD} = \frac{2.3}{k_{RLD}} \quad \text{and} \quad \textbf{b)}\ C_{RVD} = \frac{2.3}{k_{RVD}} \qquad \textbf{Equation 5.4}$$

3.6.8 Carbon isotope discrimination

Dried grain samples for the various treatments were ground to a fine powder (< 200 μm) using an IKA A10 mill (IKA® Werke GmbH & Co. KG, Staufen, Germany) and sent to be analysed at the Stable Isotopes and Instrumental Analysis Facility (SIIAF), Universidade de Lisboa, Lisbon, Portugal. Approximately 0.2 mg of ground grain samples were encapsulated in tin capsules. After which, the carbon stable isotope ratio C^{13}/C^{12} was determined, using a stable isotope ratio mass spectrometer (Sira II – VG ISOGAS, UK) coupled via an open-split to a elemental analyser (EuroEA – EuroVector, Italy), for sample preparation by combustion-reduction. $\delta^{13}C$ values were calculated with reference to the Vienna Pee Dee belemnite (VPDB) scale, using within-run laboratory standards of sorghum and wheat calibrated against international standards (IAEA CH6 and IAEA CH7). Laboratory standards were inserted between samples to check for stability and to allow drift correction when necessary. Precision of the carbon isotope analysis was 0.06‰.

3.6.9 Photosynthesis light response curves

In 2007 for barley cv. Rum at 119 DAS (17 days after GS61), leaf gas exchange was measured in green flag leaves using a Walz portable gas exchange fluorescence system (GFS-3000, Walz, Effeltrich, Germany; Figure 3.10 b). The system was connected to a leaf chamber Measuring Head 3010-S (Walz, Effeltrich, Germany; Figure 3.10 a) with 4 cm^{-2} leaf surface. Conditions in the leaf chamber were set up as: 80% relative humidity, temperature 25 ºC, 380 ppm of CO_2 concentration and artificial light supply of 2000 μmol m^{-2} s^{-2} (LED-Array/ PAM-Fluorometer 3055-FL Walz, Effeltrich, Germany). After photosynthetic rate (A - μmol m^{-2} s^{-1}) signal stabilisation (1 – 3 minutes) the value was registered and assumed to be the maximum photosynthetic rate (A_{max}). Stomatal conductance (g_s – mmol m^{-2} s^{-1}), sub-stomatal CO_2 concentration (C_i - mmol CO_2 mol^{-1} s^{-2}) and transpiration rate (E – mmol m^{-2} s^{-1}) were also measured during the A_{max}

determination. The WUE_{ph} during A_{max} was calculated as: WUE_{ph} (mmol CO_2 mol^{-1} H_2O) = A_{max}/E.

At 134 DAS for barley cv. Rum plants the photosynthetic response to photon flux density (Q) – light response curves (LRC) – were performed on the leaf below the flag leaf using a Walz portable gas exchange fluorescence system (GFS-3000, Walz, Effeltrich, Germany). Relative humidity in the leaf chamber was set up to 80%, the CO_2 concentration to 380 ppm and the temperature to 25 ºC.

Light response curves were performed against a PAR of: 100, 200, 300, 600, 900, 1200 and 2000 μmol m^{-2} s^{-2}; the change in PAR and respective A were automatically recorded. The LRC started at a PAR of 600 μmol m^{-2} s^{-1} for a period of 5 minutes, then decreasing in 3 minutes intervals to 300, 200 and 100 μmol m^{-2} s^{-1}, after which the light increased in similar steps from 100, 200, 300 and 600 μmol m^{-2} s^{-1}. The subsequent increases from 900, 1200 and 2000 μmol m^{-2} s^{-1} were done for a period of 5 minutes. The option to start the LRC at 600 μmol m^{-2} s^{-1} for 5 minutes was done to initiate a plant response to light while avoid light saturation. During the course of the experiment, it was found that the stabilization time for high PAR levels was higher than for the low levels, and so the time of exposure to was increased to 5 minutes for PAR levels above 600 μmol m^{-2} s^{-1}. The shape of the light response curve was modelled by fitting the Prioul & Chartier (1977) nonrectangular hyperbola equation by the least square fit using the Prism 5.0b software package (GraphPad Software, Inc. San Diego, California, USA):

$$A = \frac{q'\times Q + A_{max} - \sqrt{\left(q'\times Q + A_{max}\right)^2 - 4k\, q'\times Q \times A_{max}}}{2k} + Rd \qquad \textbf{Equation 3.8}$$

where q' = apparent quantum yield, Q = photon flux density, Rd = the dark photorespiration and k = the curve convexity. This modelled A was then used to calculate the A_{max}, ϕ, light compensation point (LCP) and light saturation point (LSP).

The actual A_{max} was considered to be the value of A at 2000 μmol m^{-2} s^{-1}. The WUE at A_{max} was measured and the A_{max}/g_s was also calculated.

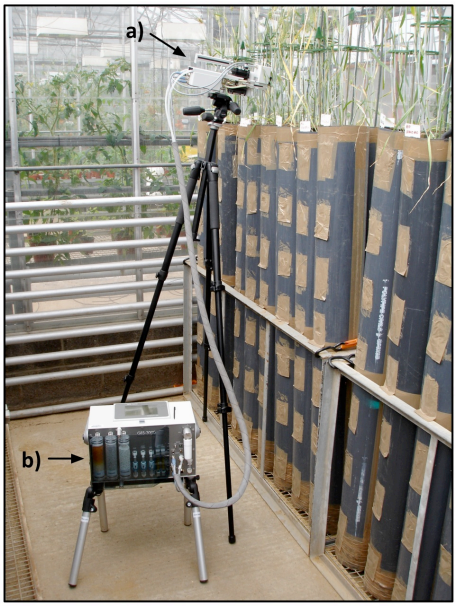

Figure 3.10 Leaf chamber Measuring Head 3010-S (Walz, Effeltrich, Germany; **a**) and portable gas exchange fluorescence system, GFS-3000 (Walz, Effeltrich, Germany; **b**).

3.6.10 Plant nitrogen content

For all years the aboveground oven-dried plant material was, depending on plant development, combined into: i) straw (leaves, stems and, at harvest, chaff), ii) ears (at anthesis) and iii) grain (at harvest), and then milled to a particle size of < 200 µm. 50 to 75 mg of sample were then weighed and encapsulated in tin capsules. The encapsulated samples were then analysed for N% according to the Dumas method using the Fisons NA-2000 elemental analyzer (Fisons, Ipswich, UK) calibrated against an atropine standard (N content = 4.8%). The Dumas N method consists of: (i) converting all N forms in the sample into gaseous nitrogen oxides by complete combustion at pure oxygen, (ii) further reducing to N_2 (in a hot copper catalyst) and (iii) N_2 quantification by comparing the change in thermal conductivity with a reference cell (Simonne *et al.*, 1997; Pask, 2009).

The total N in grams can therefore be calculated by multiplying the N% with the dry weight of the plant component, and the total N uptake as the sum of the amounts of N in all aboveground plant components.

3.7 SOIL MINERAL N ANALYSIS

Soil available mineral N (amonium and nitrate) before the start of the experiments was determined in accordance with Defra approved procedures (RB427) by the NRM laboratories (Bracknell, UK). Due to the cost of soil N analysis, it was not possible to analyse the soil N content intensively. Therefore the soil N content was only analysed at harvest in 2007 and 2008. In 2007, soil mineral N content was measured for all N and irrigation treatments but only for barley cv. Rum and wheat cv. Karim; and as a bulk sample of 5 replicates for each of the 0 – 20, 60 – 80 and > 125 cm soil layer depths. In the 2008 experiment, the soil mineral N content was analysed for each irrigation treatment and replicates for the same soil depth layers that were analyzed in 2007.

The soil N analysis was performed as described by Grindlay (1995): 40 g of soil sample was mixed and sieved, after which the exchangeable mineral N was extracted in a solution of potassium chloride. The solid particles were then filtered out and the filtrate automatically analysed for ammonium and nitrate. The ammonium was determined by heating with salicylate and hypochlorite using an alkaline phosphate buffer, forming a green colour proportional to the ammonia concentration in the sample. Whereas the nitrate was reduced to nitrite by passing the filtrate to a copperised cadmium column, and then diazotised with sulphanilamide followed by coupling with N-(1-napthyl) ethylenediamine dihydrochloride. The concentration was determined by reading the resulting magenta dye in a spectrophotometer at λ = 520 nm. The results are then expressed on a dry matter basis and also converted to a 30 cm soil depth basis.

3.8 GLASSHOUSE MICROCLIMATE CONDITIONS

Experiments were carried out in a glasshouse without supplementary light. For the first 30 days after seedling transplantation to soil columns in the glasshouse (2006 and 2007), the minimum temperature was set up to 10 ºC to avoid any frost damage early in the season. When the temperature was above 20 °C the glasshouse vents were

programmed to automatically open. For the 2006 and 2007 experiments, air temperature in the glasshouse was measured using a thermocouple sensor, and the solar radiation using four tube solarimeters placed in the top of the glasshouse. Light and temperature were measured every 10 minutes and the hourly average was automatically recorded by a data logger (CR10, Campbell Scientific, Inc., Utah, USA). For the 2008 experiment the light data were acquired as previously described, and the air temperature was recorded using a TinyTag Ultra 2 data logger (TGU-4500, Gemini Data Loggers (UK) Ltd. Chichester, UK). To measure occurately the air temperature inside the glasshouse a thermocouple (2006 and 2007) or a Tiny Tag logger (2008) was placed inside a card box with vents and a fan to allow for ventilation.

3.9 STATISTICAL ANALYSIS

Data were entered into Microsoft Excel 2008 for Mac (Microsoft Corporation, Washington, USA) spreadsheets and the comparison of means performed using the GenStat statistical package 12th edition (Lawes Agricultural Trust, Rothamsted Experimental Station, UK).

For the 2006 experiment the comparison of means was carried out using a standard three-way analysis of variance (ANOVA) [Species (2 levels) x Irrigation (2 levels) x N (3 levels)] applied to a randomized block design (3 blocks). Though in the 2006 experiment it was found that the relative faster growth of barley cv. Rum might have caused some shading to wheat cv. Hourani. Because of this it was decided that in the 2007 experiment, spring barley and durum wheat genotypes should be allocated to separate experimental areas in the glasshouse to avoid any effects of shading between barley and wheat plants. For this reason in 2007 the comparison of means was performed separately for each genotype by a two-way ANOVA procedure [irrigation (2 levels) x N (3 levels)] applied to a randomized block design. When the ANOVA result showed significant differences between treatments the least significant difference (LSD) test was used to compare the means between specific treatments. In 2008 only the irrigation treatment (2 levels) was imposed for barley cv. Rum in a completely randomized block design. Therefore a one-way ANOVA was used. Means standard

error (SE) and standard error of the difference of means (SED) were calculated using GenStat 12th edition.

Non-linear curve fitting for estimation of root morphology (β_W, β_L, β_V), water uptake (k_{RLD}, and k_{RVD}) and LRC parameters, as well as the calculation of its standard errors was performed using the Prism 5.0b software package.

Linear regression curve fitting was used to estimate WUE and calculate relationships between: root morphology parameters, yield vs yield components, and NUE vs NutE /NupE, and associated standard errors in each case, utilizing Prism 5.0b software package. Parallel regression analysis (simple linear regression with groups) was used to compare the difference between treatments in parameters estimated by linear regression using GenStat 12th edition.

4 ABOVEGROUND DRY MATTER GROWTH, WATER- AND NITROGEN-USE EFFICIENCY

4.1 INTRODUCTION

This chapter describes the shoot production, green area, aboveground dry matter growth and partitioning through the season, as well as yield and yield components of durum wheat and barley as affected by water deficits and nitrogen fertilization. It then quantifies the water- and nitrogen-use efficiencies of durum wheat and barley as affected by water and N availability. The development and growth of the plants in the respective experiments are related to the glasshouse microclimate conditions (irradiance and air temperature) and a detailed analysis of the yield, its components and partitioning between tiller orders is also set out in this chapter.

The effects of water deficits and N fertilization on NupE (N-uptake / N available), NutE (grain DM / aboveground N) and consequently NUE are examined.

Passioura (1977; 1996), considering water as the most limiting factor for crop production, developed the following equation:

$$Y = WU \times WUE \times HI \qquad \textbf{Equation 6.1}$$

According to this simple model, Y can be increased by increasing:

WU – water uptake (linked to rooting traits)

WUE – water-use efficiency (linked to stomatal conductance traits)

HI – harvest index (linked to changes in DM partitioning) (Araus *et al.*, 2002).

Though this model is simple, since its factors are not totally independent, its analysis can be complicated. Increasing WUE might be achieved by decreasing WU and therefore growth and Y under drought (Tambussi *et al.*, 2007). Increases in HI in wheat modern cultivars were mainly achieved by decreasing stem height, with the introduction

of semi-dwarf genes (Slafer & Araus, 2007). However under drought this trait can have a negative impact on yield since grains are often sustained by the assimilates accumulated in the stem internodes before anthesis (Loss & Siddique, 1994 in Araus *et al.*, 2002). WU is closely related with RLD (King *et al.*, 2003) or RVD. Therefore, increasing the biomass allocated to the roots (R:S) in order to increase density of roots in the soil, and specially deeper in the profile, seems sensible though less biomass will be allocated to the grain. ^{13}C isotope discrimination ($\Delta^{13}C$) is genetically correlated with Y (Slafer & Araus, 2007) and was found to be inversely correlated with WUEph [Assimilation (μmol CO_2 m^{-2} s^{-1}) / Evaporation (mmol H_2O m^{-2} s^{-1})] (Farquhar & Richards, 1984). Genetic gains in Y may therefore be achieved by selecting for lower $\Delta^{13}C$ and so higher WUE (Rebetzke *et al.*, 2002). However in various studies in drought environments $\Delta^{13}C$ and Y are positively correlated (Condon *et al.*, 2004; Slafer & Araus, 2007). Explanations for that fact were extensively explained by Condon *et al.* (2004) and Slafer and Araus (2007) but in summary breeding for higher $\Delta^{13}C$ seems adequate for situations were Y is in part determined by season rainfall, while when all the stored soil moisture is exhausted during crop cycle, breeding for lower $\Delta^{13}C$ seems more appropriate (Araus *et al.*, 2002).

Katerji *et al.* (2008) compiled the WUE for different crop species growing in the Mediterranean, and found that values for wheat varied from 0.5 to 2.5 g l^{-1} and for barley between 1.46 and 2.78 g l^{-1}. Furthermore for field grown barley cv. Rum and durum wheat cv. Hourani in Jordan, Ebrahim (2008) found a WUE 70% higher for barley than for durum wheat. N application was reported to increase WUE in spring wheat growing in controlled-environment conditions by that author. In this chapter the WUE for biomass and yield (WUE_{grain}) for the three years of experiment are presented as well as the HI. $\Delta^{13}C$ of grain samples at harvest was also analysed in the experiments.

In this work, nitrogen-use efficiency (NUE) follows the definition by Moll *et al.* (1982): NUE is the grain yield per unit of N available (soil and/or fertilizer). NUE is then divided into two components: i) N-uptake efficiency (NupE) = (crop N-uptake (Nup) / N available) and ii) N-utilization efficiency (NutE) = (grain yield / Nup). According to Ortiz-Monasterio *et al.* (1997) working in Mexico with 10 spring wheat cultivars increases in NUE resulted in an improvement of both NupE and NutE, though the

importance of the first relative to the second increased with N application, and the opposite was found for low N. However Muurinen *et al.* (2006) growing spring wheat and barley in Finland found a high correlation between NupE and NUE. Furthermore both barley and wheat had a similar NUE. For winter wheat and barley grown in Italy Delogu *et al.* (1998) found a higher NUE for the latter, due to a higher NupE and NutE. Furthermore, N application decreased NutE but increased NupE proportionally more hence increased NUE.

The specific hypotheses tested in this chapter are:

1. Aboveground dry weight (AGDW) and grain yield (Y) for barley and durum wheat are similar, and will decrease with N and water deficits and there will be an interaction between water and N availability, such that responses to fertilizer N are relatively greater under high than low water availability;

2. WUE_{grain} and WUE (measured as AGDW at harvest per WU or as cumulative AGDW per cumulative water use through the season) will increase with drought and N application; and these responses are similar for barley and durum wheat;

3. Grain $\Delta^{13}C$ will increase with water and decrease with N availability;

4. NUE, NupE and NutE will decrease with increasing water deficits and increasing N supply and responses to N are similar for barley and durum wheat.

4.2 RESULTS

4.2.1 Glasshouse microclimate conditions

The total daily irradiance and minimum and maximum temperature in the glasshouse during the 2006, 2007 and 2008 experiments are presented in Figure 4.1. As mentioned in Chapter 3 (3.1.2 and 3.1.3) in 2006 and 2007 due to the vernalization requirements of the durum wheat genotypes the plants were initially sown in a growth room at 6 – 8 ºC (for 52 and 55 days respectively) after which they were transplanted into the soil columns and placed in a glasshouse with frost protection (minimum temperature 10 ºC). In 2008 the plants were sown in the glasshouse (without frost protection) and at 28 DAS (Julian day 62) transplanted into the soil columns. So data in Figure 4.1 are presented for the glasshouse microclimate conditions after transplantation for 2006 and 2007, and from sowing onwards for 2008.

Glasshouse temperatures 15 days after transplantation to the soil columns were particularly high in 2007 with an average maximum temperature of 33.9 ºC, compared to 27.3 ºC in 2006 and 21.5 ºC in 2008 (Figure 4.1). The overall average temperatures in the glasshouse (after transplantation) were 25.8 ºC, 25.0 ºC and 20.3 ºC in 2006, 2007 and 2008, respectively (Figure 4.1). Averaging across genotypes and treatments, pre-anthesis temperature (after transplantation) varied from 22.7 ºC in 2006 to 23.6 ºC in 2007 and 15.3 ºC in 2008. On the other hand, post-anthesis average temperatures varied from 28.7 ºC in 2006 to 25.7 ºC in 2007 and 22.9 ºC in 2008 (Figure 4.1). The temperatures in the glasshouse occasionally reached extremely high values with temperature peaks of 52.6 ºC in 2006, 56.9 ºC in 2007 and 44.9 ºC in 2008. In 2006 averaging across treatments and genotypes in 23% of days before anthesis maximum temperatures exceeded 35 ºC, and after anthesis that temperature was reached on 78% of days (Figure 4.1 d). These were likely harmful for wheat cv. Hourani in 2006 where during booting there were 6 days of temperatures between 35 and 40.1 ºC, while for barley cv. Rum only 3 days of near 35 ºC temperatures occurred during booting (Figure 4.1 d). In 2007, averaging across treatments, high temperatures (≥ 35 ºC) were reached in 45% of the days before anthesis and in 60% of the days thereafter (Figure 4.1 e). For

wheat cv. Karim and cv. Hourani, 3 days of peaks temperatures between 39.7 and 48.9 ºC occurred during booting. While for barley cv. Rum, due to its faster growth, there was only one day with a maximum temperature ≥ 35 ºC during booting (Figure 4.1 e), However an extremely high temperature of 53.1 °C occurred just 8 days before anthesis. 2008 was a milder year with no temperatures above 35 ºC during the pre-anthesis period and only 36% of the days post-anthesis exceed that value (Figure 4.1 f).

The total irradiance during the 2006 experiment was 290 x 10^3 W m^{-2}, 353 x 10^3 W m^{-2} in 2007 and 322 x 10^3 W m^{-2} in 2008 (Figure 4.1).

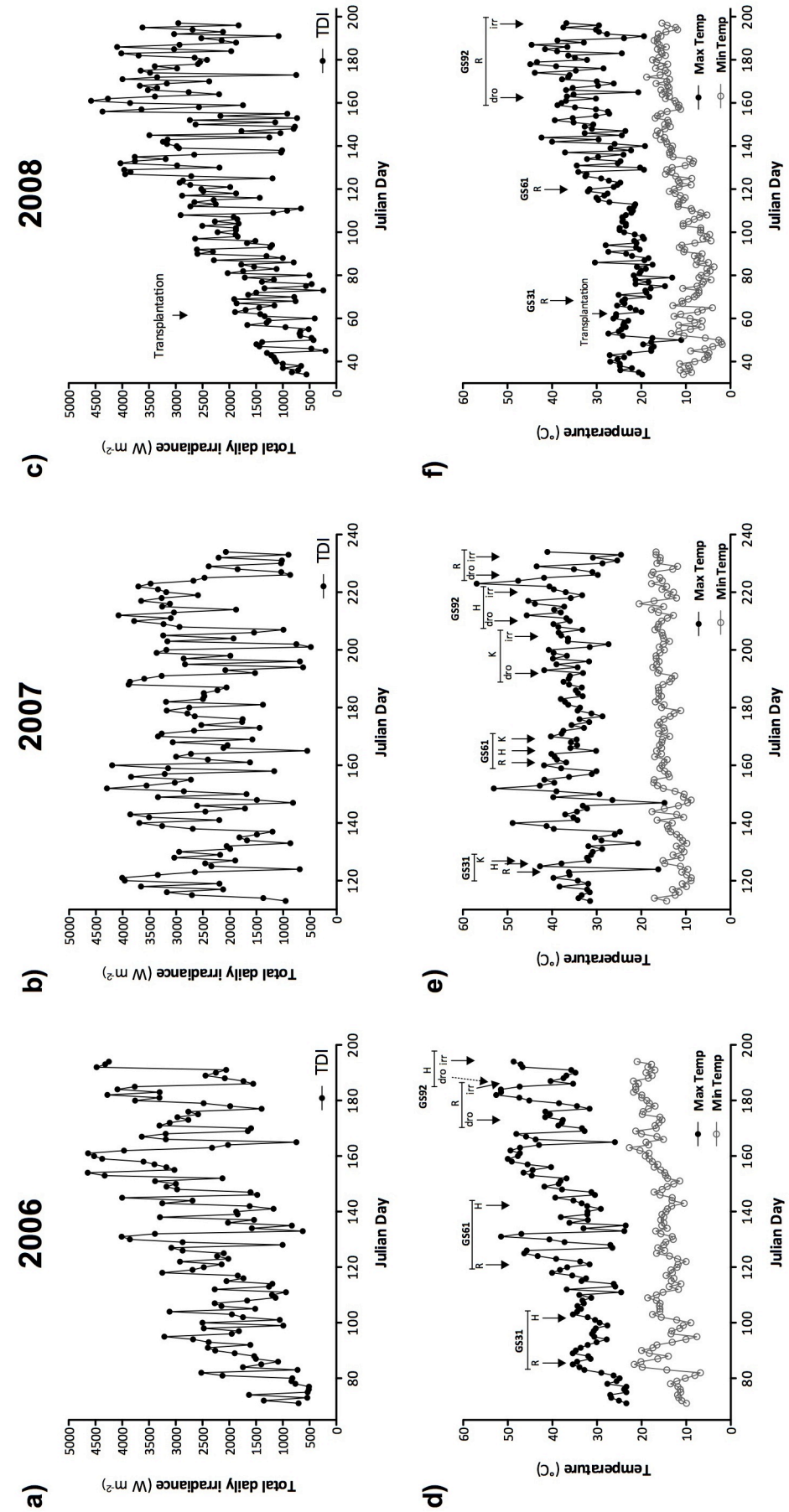

Figure 4.1 Total daily irradiance (TDI), maximum and minimum air temperature (Max Temp and Min Temp, respectively) collected from the glasshouse in the 2006 (**a**, **d**), 2007 (**b**, **e**) and 2008 (**c**, **f**) experiments. In grey are indicated the most relevant growth stages in the Zadoks scale (1974) for barley cv. Rum (R), and wheat cv. Hourani (H) and Karim (K), under two irrigation treatments (dro – drought and irr – irrigated).

4.2.2 Plant development

In the three years of experiments (2006, 2007 and 2008) N application did not affect the dates when the plants reached the growth stages (GS): 31, 61 and 92 (maturity). So in Table 4.1 only the data for genotypes and irrigation treatments are presented. Across N and irrigation treatments barley cv. Rum reached GS31 at Julian day 85 in 2006, 123 in 2007 and 69 in 2008. Barley cv. Rum reached GS31 sooner than both spring durum wheat varieties though more so in 2006: 17 days compared to ca. 4 days in 2007 (Table 4.1). This may have been partly associated with the high air temperatures 15 days after transplantation in 2007 reducing the tillering period for durum wheat. The drought treatment did not affect the date of reaching GS61 averaging across N application, genotypes and experiments, though water-limited plants matured faster than the irrigated plants, by an average of 18 days for barley cv. Rum, 13 days for wheat cv. Karim and 9 days for wheat cv. Hourani (Table 4.1). In 2006 the drought treatment was imposed 19 days before GS61 for barley cv. Rum and 40 days before GS61 for wheat cv. Hourani. In 2007 the drought treatment started 24, 32 or 28 days before GS61, for barley cv. Rum, wheat cv. Karim and wheat cv. Hourani, respectively. For barley cv. Rum in 2008 drought was imposed 33 days before anthesis. The duration of the phase from GS31 to GS61 was similar for all genotypes, averaging across experiments: 41 days for barley cv. Rum, 40 for days for wheat cv. Hourani and 42 days for wheat cv. Karim (Table 4.1).

In 2006, barley cv. Rum had a faster development than wheat cv. Hourani reaching maturity, averaging across irrigation treatments, 11 days sooner. However, in 2007 the inverse was observed with barley cv. Rum achieving maturity 14 days later than wheat cv. Hourani (Table 4.1). This might be associated with higher photoperiod sensitivity for wheat cv. Hourani when compared to barley cv. Rum, since in 2006 when the plants were transplanted the photoperiod was around 7.5 hours and in 2007 it was approximately 13 hours.

Wheat cv. Karim had a shorter growth period compared to the other genotypes investigated, with only ca., 141 days compared to 158 and 172 days for wheat cv. Hourani and barley cv. Rum, respectively, in 2007 (Table 4.1).

Table 4.1 Julian days (JD) for transplantation of seedlings into the soil columns (Transpl.) and different plant growth stages (GS; Tottman, 1987), for spring barley cv. Rum and durum wheat cvs Karim and Hourani under different irrigation treatments in the 2006, 2007 and 2008 experiments.

Year	Species	Irrigation	Sown	Transpl.		JD		
						GS31	GS61	GS92
			JD	JD	GS			
2006	Barley cv. Rum	Irrigated	19	71	22/23	85	121	186
		Droughted						173
	Wheat cv. Hourani	Irrigated			22/23	102	142	194
		Droughted						187
2007	Barley cv. Rum	Irrigated	58	113	15/21	123	161	233
		Droughted						226
	Wheat cv. Karim	Irrigated			14/15	127	169	205
		Droughted						192
	Wheat cv. Hourani	Irrigated			15/21	126	165	221
		Droughted						210
2008	Barley cv. Rum	Irrigated	34	62	13/14	69	119	196
		Droughted						163

A summary of the key results found for the different experiments can be found in the Tables 4.2 to 4.6. When averaged across irrigation and nitrogen treatments the aboveground weight (AGDW) decreased by 71% for barley cv. Rum and 50% for wheat cv. Hourani from 2006 to 2007. Furthermore, the yields decreased by 76% for barley cv. Rum and 40% for wheat cv. Hourani (Table 4.2, Table 4.3 and Table 4.5), probably associated with the high bulk density values in the 2007 experiment (1.85 g cm^{-3}, Figure 5.1), that might have limited the root expansion and hence shoot growth (Table 4.2, Table 4.3 and Table 4.5). Overall AGDW and yields, were higher for barley than for durum wheat, possibly due to its higher root growth, measured as total root weight and length (TRW and TRL, respectively), providing a higher water use (WU) and nitrogen uptake (Nup; Table 4.2, Table 4.3, Table 4.4 and Table 4.5). Furthermore water use

efficiency (WUE) and nitrogen use efficiency (NUE) was higher for barley than for wheat (Table 4.2, Table 4.3, Table 4.4 and Table 4.5).

Overall drought decreased AGDW and Y for both genotypes, however to a higher extent for barley (Table 4.2 to 4.6).

Responses of root growth to drought differ between genotypes. For barley water deficits decreased TRW and TRL, while increasing for wheat (Table 4.2 to 4.6).

As expected WU and Nup increased with irrigation for all genotypes, WUE, however decreased (Table 4.2 to 4.6). Overall NUE increased with water application for all genotypes, though it decreased with N application (Table 4.2 to 4.6).

Nitrogen application had generally no significant effects on the variable in study (Table 4.2 to 4.6). Nevertheless in 2006, there was a trend (p = 0.075) for an increase in AGDW with N50, but only under irrigation and for barley (Table 4.2). Furthermore, in 2006 under irrigation N50 increased Y for both genotypes however increased (Table 4.2).

A detailed description and discussion of the shoots, roots and resource capture responses to N application and water deficits, is presented in the next sections 4.x, 5 and 6 respectively.

Table 4.2 Aboveground dry weight (AGDW), grain yield (Y), total root dry weight (TRW, sum of the weight at 0 – 20, 60 – 80 and > 125 cm soil depth layers), total root length (TRL, sum of the length at 0 – 20, 60 – 80 and > 125 cm soil depth layers), plant water used (WU, from transplantation to harvest), water use efficiency (WUE), nitrogen uptake (Nup) and nitrogen use efficiency (NUE) at harvest, for barley cv. Rum and durum wheat cv. Hourani subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) for the 2006 experiment.

Species	Irrigation	Fertilizer N (kg N ha^{-1})	AGDW (g)	Y (g)	TRW (g)	TRL (m)	WU (l)	Nup (g)	WUE (g l^{-1})	NUE (g g^{-1})
Barley cv. Rum	**Irrigated**	**0**	35.1	17.5	0.570	93.3	20.0	0.788	1.74	100.3
		50	48.1	25.7	0.404	79.8	28.5	1.048	1.72	97.8
		100	27.7	15.3	0.319	38.8	24.4	0.618	1.12	43.7
		Mean	*36.9*	*19.5*	*0.431*	*70.6*	*24.3*	*0.818*	*1.53*	*80.6*
	Droughted	**0**	23.7	13.5	0.549	43.3	6.0	0.462	3.96	77.7
		50	24.0	12.0	0.417	46.8	5.3	0.458	4.52	45.6
		100	24.0	10.3	0.341	47.2	6.2	0.362	3.03	29.3
		Mean	*23.9*	*11.9*	*0.436*	*45.8*	*5.8*	*0.427*	*3.84*	*50.9*
Wheat cv. Hourani	**Irrigated**	**0**	12.2	5.0	0.184	28.3	14.9	0.267	0.83	28.6
		50	17.0	6.9	0.154	34.4	17.6	0.380	0.97	26.4
		100	13.5	6.6	0.138	23.0	14.1	0.308	1.08	18.2
		Mean	*14.2*	*6.2*	*0.159*	*28.6*	*15.5*	*0.318*	*0.96*	*24.4*
	Droughted	**0**	13.4	5.5	0.329	55.4	4.0	0.297	3.34	31.4
		50	11.3	3.8	0.373	56.0	5.2	0.240	2.23	14.6
		100	11.8	4.1	0.324	49.2	7.0	0.258	1.71	15.8
		Mean	*12.2*	*4.5*	*0.342*	*53.5*	*5.4*	*0.265*	*2.43*	*20.6*
		SED (df)								
		Species (22)	2.15^{***}	0.99^{***}	0.041^{***}	6.9^{*}	0.69^{***}	0.048^{***}	0.150^{***}	3.95^{***}
		Irrigation (22)	2.15^{***}	0.99^{***}	0.041^{*}	69^{ns}	0.69^{***}	0.048^{***}	0.150^{***}	3.95^{***}
		Nitrogen (22)	2.64^{ns}	1.21^{ns}	0.050^{ns}	8.4^{ns}	0.84^{**}	0.058^{ns}	0.184^{**}	4.84^{***}
		*Species*Irrigation (22)*	3.05^{**}	1.40^{**}	0.059^{*}	9.7^{***}	0.97^{***}	0.067^{**}	0.212^{*}	5.59^{**}
		*Species*Nitrogen (22)*	3.73^{ns}	1.71^{ns}	0.071^{ns}	11.9^{ns}	1.19^{ns}	0.083^{ns}	0.260^{ns}	6.58^{**}
		*Irrigation*Nitrogen (22)*	3.73^{ns}	1.71^{*}	0.071^{ns}	11.9^{ns}	1.19^{**}	0.083^{ns}	0.260^{*}	6.58^{*}
		*Species * Irrigation * Nitrogen (22)*	5.27^{ns}	2.42^{ns}	0.100^{ns}	16.8^{ns}	1.69^{*}	0.117^{ns}	0.368^{*}	9.69^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 4.3 Aboveground dry weight (AGDW), grain yield (Y), total root dry weight (TRW, sum of the weight at 0 – 20, 60 – 80 and > 125 cm soil depth layers), total root length (TRL, sum of the length at 0 – 20, 60 – 80 and > 125 cm soil depth layers), plant water used (WU, from transplantation to harvest), water use efficiency (WUE), nitrogen uptake (Nup) and nitrogen use efficiency (NUE) at harvest, for barley cv. Rum subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) for the 2007 experiment.

Irrigation	Fertilizer N (kg N ha^{-1})	AGDW (g)	Y (g)	TRW (g)	TRL (m)	WU (l)	Nup (g)	WUE (g l^{-1})	NUE (g g^{-1})
Irrigated	**0**	11.2	4.28	0.207	27.8	9.38	0.29	1.20	9.91
	50	10.2	4.25	0.225	29.5	9.26	0.26	1.10	8.17
	100	10.1	4.36	0.176	24.6	9.80	0.26	1.04	7.17
	Mean	*10.5*	*4.30*	*0.202*	*27.3*	*9.48*	*0.27*	*1.11*	*8.42*
Drought	**0**	7.6	3.74	0.168	25.9	5.21	0.16	1.49	8.66
	50	6.9	3.32	0.150	18.2	4.93	0.16	1.40	6.39
	100	6.6	2.81	0.147	23.7	4.96	0.14	1.32	4.61
	Mean	*7.0*	*3.29*	*0.155*	*22.6*	*5.03*	*0.153*	*1.40*	*6.55*
	SED (df)								
	Irrigation (20)	*0.58****	*0.437**	*0.017***	*2.8*^{ns}	*0.237****	*0.013****	*0.090***	*0.822**
	Nitrogen (20)	*0.71*^{ns}	*0.535*^{ns}	*0.020*^{ns}	*3.4*^{ns}	*0.290*^{ns}	*0.015*^{ns}	*0.110*^{ns}	*1.007***
	*Irrigation*Nitrogen (20)*	*1.00*^{ns}	*0.757*^{ns}	*0.029*^{ns}	*4.9*^{ns}	*0.410*^{ns}	*0.022*^{ns}	*0.155*^{ns}	*1.424*^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 4.4 Aboveground dry weight (AGDW), grain yield (Y), total root dry weight (TRW, sum of the weight at 0 – 20, 60 – 80 and > 125 cm soil depth layers), total root length (TRL, sum of the length at 0 – 20, 60 – 80 and > 125 cm soil depth layers), plant water used (WU, from transplantation to harvest), water use efficiency (WUE), nitrogen uptake (Nup) and nitrogen use efficiency (NUE) at harvest, for durum wheat cv. Karim subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) for the 2007 experiment.

Irrigation	Fertilizer N (kg N ha^{-1})	AGDW (g)	Y (g)	TRW (g)	TRL (m)	WU (l)	Nup (g)	WUE (g l^{-1})	NUE (g g^{-1})
Irrigated	**0**	5.22	2.97	0.103	7.0	6.14	0.09	0.86	6.87
	50	3.84	2.14	0.066	5.8	5.90	0.07	0.65	4.11
	100	4.75	2.68	0.082	7.0	5.79	0.08	0.82	4.40
	Mean	*4.60*	*2.60*	*0.083*	*6.6*	*5.94*	*0.080*	*0.78*	*5.13*
Drought	**0**	3.98	2.16	0.151	12.4	3.78	0.07	1.10	5.00
	50	3.80	2.11	0.084	10.7	3.36	0.07	1.13	4.06
	100	4.43	2.34	0.151	15.8	3.80	0.08	1.14	3.84
	Mean	*4.07*	*2.20*	*0.129*	*13.0*	*3.65*	*0.073*	*1.12*	*4.30*
	SED (df)								
	Irrigation (20)	*0.007*^{ns}	*0.298*^{ns}	*0.017**	*1.4****	*0.155****	*0.008*^{ns}	*0.112***	*0.552*^{ns}
	Nitrogen (20)	*0.008*^{ns}	*0.365*^{ns}	*0.021*^{ns}	*17*^{ns}	*0.189*^{ns}	*0.010*^{ns}	*0.138*^{ns}	*0.677**
	*Irrigation*Nitrogen (20)*	*0.011*^{ns}	*0.516*^{ns}	*0.030*^{ns}	*2.4*^{ns}	*0.268*^{ns}	*0.014*^{ns}	*0.195*^{ns}	*0.957*^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 4.5 Aboveground dry weight (AGDW), grain yield (Y), total root dry weight (TRW, sum of the weight at 0 – 20, 60 – 80 and > 125 cm soil depth layers), total root length (TRL, sum of the length at 0 – 20, 60 – 80 and > 125 cm soil depth layers), plant water used (WU, from transplantation to harvest), water use efficiency (WUE), nitrogen uptake (Nup) and nitrogen use efficiency (NUE) at harvest, for durum wheat cv. Hourani subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) for the 2007 experiment.

Irrigation	Fertilizer N (kg N ha^{-1})	AGDW (g)	Y (g)	TRW (g)	TRL (m)	WU (l)	Nup (g)	WUE (g l^{-1})	NUE (g g^{-1})
Irrigated	**0**	8.97	4.24	0.193	31.8	8.54	0.18	1.05	9.81
	50	6.84	3.28	0.131	20.5	7.28	0.14	0.94	6.31
	100	5.62	2.63	0.133	21.2	7.69	0.11	0.73	4.32
	Mean	*7.14*	*3.38*	*0.152*	*24.5*	*7.84*	*0.143*	*0.91*	*6.81*
Drought	**0**	7.02	3.46	0.209	33.3	4.82	0.13	1.47	8.01
	50	5.77	2.89	0.155	27.8	4.44	0.11	1.32	5.56
	100	5.61	2.78	0.141	18.8	4.42	0.11	1.26	4.56
	Mean	*6.13*	*3.04*	*0.168*	*26.6*	*4.56*	*0.117*	*1.35*	*6.04*
	SED (df)								
	Irrigation (20)	0.531^{ns}	0.286^{ns}	0.015^{ns}	2.6^{ns}	0.198^{***}	0.010^{**}	0.098^{***}	0.576^{ns}
	Nitrogen (20)	0.651^{**}	0.350^{**}	0.018^{**}	3.2^{**}	0.242^{**}	0.013^{**}	0.120^{ns}	0.706^{***}
	*Irrigation*Nitrogen (20)*	0.920^{ns}	0.495^{ns}	0.026^{ns}	4.6^{ns}	0.342^{ns}	0.018^{ns}	0.170^{ns}	0.998^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 4.6 Aboveground dry weight (AGDW), grain yield (Y), total root dry weight (TRW, sum of the weight at 0 – 20, 60 – 80 and > 125 cm soil depth layers), total root length (TRL, sum of the length at 0 – 20, 60 – 80 and > 125 cm soil depth layers), plant water used (WU, from transplantation to harvest), water use efficiency (WUE), nitrogen uptake (Nup) and nitrogen use efficiency (NUE) at harvest, for barley cv. Rum subjected to full irrigated and droughted treatments for the 2008 experiment.

Irrigation	AGDW (g)	Y (g)	TRW (g)	TRL (m)	WU (l)	Nup (g)	WUE (g l^{-1})	NUE (g g^{-1})
Irrigated	16.3	8.25	0.604	166.4	19.96	0.440	0.81	16.9
Drought	10.4	5.79	0.465	121.7	5.83	0.210	1.81	11.9
SED (df)								
Irrigation (6)	1.21^{**}	0.692^{*}	0.075^{ns}	15.42^{*}	0.637^{***}	0.044^{**}	0.376^{*}	1.42^{*}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

4.2.3 Fertile shoot number per plant

4.2.3.1 2006

At 67 DAS both barley cv. Rum (GS31) and wheat cv. Hourani (GS23) had three fertile shoots plant^{-1} (Figure 4.2 a, d). Whereas at 83 DAS, barley cv. Rum (GS51) had more fertile shoots plant^{-1} ($p \leq 0.001$) than wheat cv. Hourani (GS31), 8.4 cf. 5.2. This difference was maintained ($p \leq 0.001$) to 102 and 123 DAS, with barley cv. Rum (GS61/71) having approximately 40% and 64% more fertile shoots than wheat cv. Hourani (GS55/61), respectively (Figure 4.2 a, d). Drought decreased by two the number of fertile shoots plant^{-1} at 102 DAS ($p \leq 0.01$) for both genotypes (Figure 4.2 a, d). At 123 DAS drought decreased fertile shoots plant^{-1} ($p \leq 0.05$) by 14% for barley cv. Rum though only by 6% for wheat cv. Hourani ($p \leq 0.067$ for species x irrigation).

From anthesis to harvest for barley cv. Rum under irrigation the fertile shoot number increased by 75%, although under drought it did not change (Figure 4.2 a). For wheat cv. Hourani there was a slight decrease in the fertile shoot number per plant under drought from anthesis to harvest. At harvest for barley cv. Rum fertile shoots plant^{-1} was 106% higher than for wheat cv. Hourani (Figure 4.2 a, d). At harvest there was an interaction between species and irrigation ($p \leq 0.05$), with irrigation increasing fertile shoots by 109% for barley cv. Rum but not for wheat cv. Hourani (Figure 4.2 a, d).

N fertilization had no statistically significant effect on the fertile shoots plant^{-1} in the experiment. For barley cv. Rum the number of fertile shoots for N0 and N50 continued to increase from anthesis to harvest, with N50 having 13% more shoots than N0. While for N100 the number of fertile shoots per plant did not increase from 123 DAS (≈ GS83) onwards (Figure 4.2 a).

4.2.3.2 2007

In 2007, Barley cv. Rum at 76 DAS (GS51) had fewer fertile shoots plant^{-1} than in 2006 and 2008, 2.6 and 8.3 respectively (Figure 4.2 a and Figure 4.3 a). At anthesis the fertile shoot number for barley cv. Rum increased to 5.4 (Figure 4.3 a); there was an interaction between irrigation and N ($p \leq 0.05$), with N100 increasing shoot number by 28% under irrigation though decreasing it by 32% under drought (Figure 4.3 a). At harvest total shoots plant^{-1} was 7.1 averaging across all treatments contrasting with 11.9 in 2008 (Figure 4.2 a). Overall the number of fertile shoots plant^{-1} at harvest was slightly higher for the irrigated treatment (7.7 cf. 6.6 under drought) though not significantly so ($p = 0.18$; Figure 4.3 a).

For durum wheat cv. Karim in 2007 after 76 DAS (GS39) most of the plants did not produce any more tillers, resulting in a fertile shoots plant^{-1} of only 3.4 at anthesis (Figure 4.3 d). At anthesis neither irrigation nor nitrogen had a statistically significant effect on the fertile shoot number (Figure 4.3 d). From anthesis to harvest the fertile shoot number under drought decreased by 35% (Figure 4.3 d) resulting in an effect of irrigation ($p \leq 0.05$) at harvest, with water deficits decreasing fertile shoots by 27%. Throughout the season N application had no significant effect on the fertile shoot number (Figure 4.3 d).

In 2007 durum wheat cv. Hourani was only sampled at harvest, where the fertile shoot number was 5.5 plant^{-1} averaged across treatments, contrasting with 7.8 cf. in 2006 (Figure 4.2 d and Figure 4.4 a). Neither water nor N had a significant effect on the fertile shoot number, though there was a tendency for N application ($p \leq 0.15$) to decrease the tiller number by 26%, N100 cf. N0 (Figure 4.4 a).

4.2.3.3 2008

In 2008 the barley cv. Rum plants were transplanted to the columns at GS13/14, at which point no tillers were produced (Figure 4.5 a). At anthesis fertile shoots plants^{-1}

increased to 7, with a tendency ($p \leq 0.13$) for the irrigated plants to have a slightly higher number (8 cf. 6 under drought) (Figure 4.5 a). From anthesis to harvest the number of fertile shoots remained constant under full irrigation while decreasing under drought. This caused a 38% decrease ($p \leq 0.001$) in fertile shoots plant^{-1} under drought at harvest (Figure 4.5 a).

4.2.4 Green Area per plant

4.2.4.1 2006

Barley cv. Rum (GS31) green area per plant (GA) at 67 DAS was 83.2 cm^2 while for wheat cv. Hourani (GS23) it was 66.5 cm^2 ($p \leq 0.001$, Figure 4.2 c, f). The difference between genotypes was maintained until 83 DAS ($p \leq 0.001$), with barley cv. Rum having 49% higher GA at this stage (Figure 4.2 c, f). At 102 DAS, although GA was not significantly different between genotypes, drought overall decreased green area ($p \leq 0.001$) by 26% for barley cv. Rum (GS61) and 28% for wheat cv. Hourani (GS55) (Figure 4.2 c, f). At 123 DAS, both species started to senesce, but for barley cv. Rum (GS71) only under drought and low N, though GA did not differ between genotypes (Figure 4.2 c, f). There was an interaction between species and irrigation treatments ($p \leq 0.001$), with drought reducing GA by 69% for barley cv. Rum (Figure 4.2 c, f), but no effect for wheat cv. Hourani. There was also a trend for an increase in GA with N application but only under irrigation and for barley cv. Rum ($p = 0.06$, Figure 4.2 c, f).

4.2.4.2 2007

For barley cv. Rum in 2007, GA increased by 40.9 cm^2 from 76 DAS (GS51) to anthesis (Figure 4.3 c). Drought decreased ($p \leq 0.05$) GA by 12% at anthesis, though its value averaged across treatments was more than 50% lower than in 2006 at the corresponding stage (Figure 4.2 c, Figure 4.3 c). N application had no significant effect on GA for barley cv. Rum (Figure 4.3 c).

For wheat cv. Karim GA slightly increased from 53.6 to 60.2 cm^2 from 76 DAS (GS39) to anthesis under irrigation, though under drought it decreased from 56.4 to 25.7 cm^2 ($p \leq 0.001$, Figure 4.3 f). Green area $plant^{-1}$ was not statistically affected by N fertilization (Figure 4.3 f).

4.2.4.3 2008

Average GA values for 2008 at anthesis were 55% of those in 2006, 296.2 cf. 654 cm^2 $plant^{-1}$, respectively (Figure 4.2 c and Figure 4.5 c). At GS61 drought decreased GA 20% but not significantly so ($p = 0.18$; Figure 4.2 c and Figure 4.5 c).

4.2.5 Aboveground dry weight per plant

4.2.5.1 2006

The aboveground dry weight per plant (AGDW) generally followed similar patterns of increase with time as the shoot number (Figure 4.2 a, b, d, f). At 67 DAS, barley cv. Rum (GS31) plants were 26% heavier ($p \leq 0.01$) than those of wheat cv. Hourani (GS23; Figure 4.2 b, d). The difference between the two species continued to increase until 102 DAS ($p \leq 0.001$), where AGDW of wheat cv. Hourani (GS55) was only 35% of that of barley cv. Rum (GS61; Figure 4.2 b, d). At this stage drought decreased plant AGDW ($p \leq 0.01$) by 2.04 g for barley cv. Rum and 0.74 g for wheat cv. Hourani (Figure 4.2 b, d). Aboveground DW $plant^{-1}$ for wheat cv. Hourani (GS61) at 123 DAS was 15.4 g lower than for barley cv. Rum (GS71). At this stage, drought decreased AGDW by 27% for barley ($p \leq 0.01$; Figure 4.2 b, d), but the decrease for durum wheat was not statistically significant. At harvest the AGDW for barley cv. Rum was 230% higher than for wheat cv. Hourani. Drought decreased AGDW ($p \leq 0.001$) for both genotypes, but more severely for barley cv. Rum ($p \leq 0.05$), with water deficits decreasing AGDW by 40% compared to 20% for wheat cv. Hourani (Figure 4.2 b, d).

There was a trend for N50 to increase AGDW by 6.6 g compared to N0 for barley cv. Rum ($p = 0.075$; Figure 4.2 b, d), but not for durum wheat.

4.2.5.2 2007

In 2007 for barley cv. Rum the AGDW increased from 0.86 g plant^{-1} at 76 DAS (GS51) to 4.78 g at anthesis (Figure 4.3 b). Drought decreased AGDW ($p \leq 0.05$) by 12% at anthesis and 33% at harvest ($p \leq 0.001$), though nitrogen had no significant effect on the AGDW (Figure 4.3 b). For barley cv. Rum, AGDW at anthesis was 56% lower than in 2006, and at harvest 40% lower (Figure 4.2 b and Figure 4.3 b).

Averaging across N and irrigation treatments, for wheat cv. Karim AGDW at 76 DAS (GS39) was 0.44 g, increasing to 4.49 g at anthesis and slightly decreasing to 4.34 g at harvest (Figure 4.3 e). None of the treatments applied significantly affected the AGDW for wheat cv. Karim (Figure 4.3 e).

The plant AGDW at harvest for wheat cv. Hourani in 2007 was 6.64 g representing only 48% of the value in 2006 (Figure 4.2 d and Figure 4.4 b). At harvest there was a tendency ($p = 0.069$) for drought to decrease AGDW by 1.0 g plant^{-1} (Figure 4.4 b). N application had a negative impact on plant growth, decreasing AGDW ($p \leq 0.01$) across irrigation treatments by 1.7 g plant^{-1} with N50 and by 2.38 g plant^{-1} with N100 (Figure 4.4 b). The overall difference in AGDW in 2007 compared to 2006 is related to a decrease in fertile shoot number. Four main reasons might be appointed to that difference: (i) poor light conditions observed in the growth room during vernalization in 2007 (*vide* section 3.2.1), (ii) high temperatures registered (average of 33.9 ºC) 15 days after transplantation in 2007; (iii) due to the different FC inherent to the different soil types used (0.395 and 0.193 m^3 m^{-3} in 2006 and 2007 respectively), the actual amount of water available to the plants differed between years. The decision only to irrigate to 90% of WA_{FC} was made to avoid water and N runoff. Increasing the number of weekly irrigations would have been another option but due to the number of treatments that was not feasible; (iv) high bulk densities in the soil columns in 2007 (Figure 5.1).

4.2.5.3 2008

Averaged across irrigation treatments, AGDW of Barley cv. Rum at anthesis in 2008 was 55% of that in 2006, and 45% at harvest, possibly due to the lower FC of the soil used in 2008 (0.242 compared to 0.395 m^3 m^{-3}; Figure 4.5 b). For barley cv. Rum there was a trend ($p = 0.07$) for restricted water availability to decrease AGDW at anthesis by 19% (Figure 4.5 b). At harvest drought decreased AGDW ($p \leq 0.001$) by 40% (Figure 4.5 b).

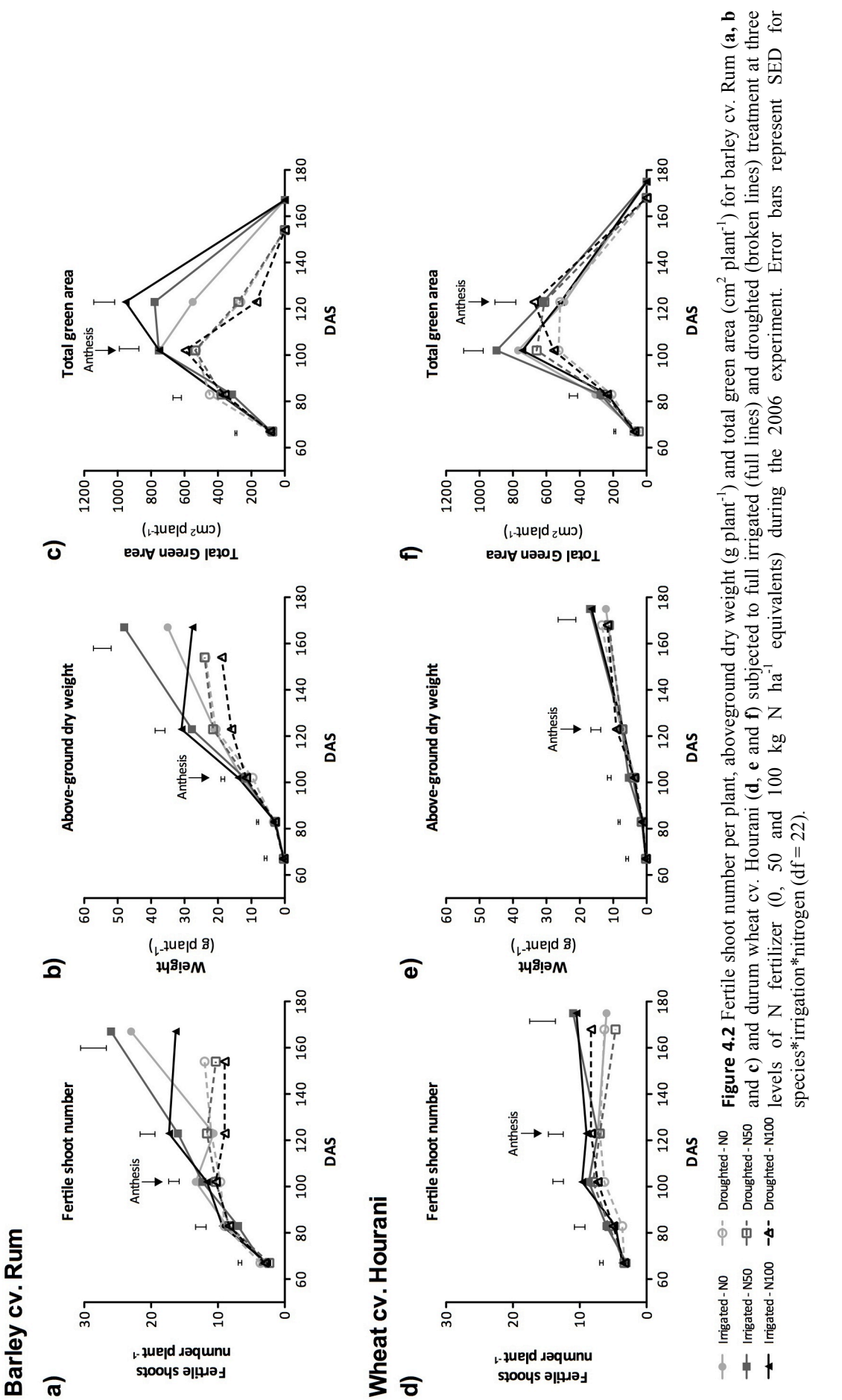

Figure 4.2 Fertile shoot number per plant, aboveground dry weight (g plant^{-1}) and total green area (cm^2 plant^{-1}) for barley cv. Rum (**a**, **b** and **c**) and durum wheat cv. Hourani (**d**, **e** and **f**) subjected to full irrigated (full lines) and droughted (broken lines) treatment at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1} equivalents) during the 2006 experiment. Error bars represent SED for species*irrigation*nitrogen (df = 22).

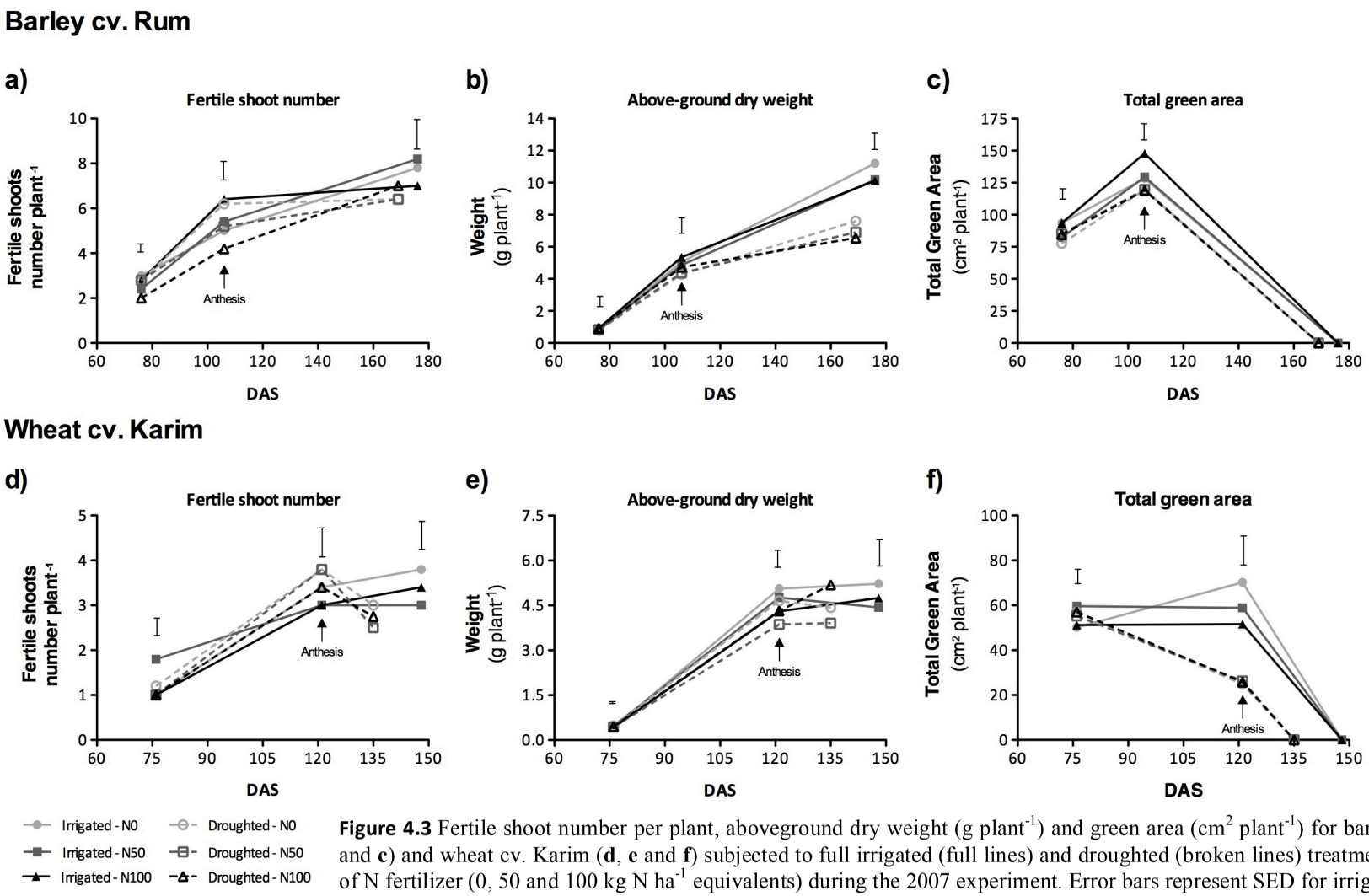

Figure 4.3 Fertile shoot number per plant, aboveground dry weight (g plant^{-1}) and green area (cm^2 plant^{-1}) for barley cv. Rum (**a**, **b** and **c**) and wheat cv. Karim (**d**, **e** and **f**) subjected to full irrigated (full lines) and droughted (broken lines) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1} equivalents) during the 2007 experiment. Error bars represent SED for irrigation*nitrogen (df = 20).

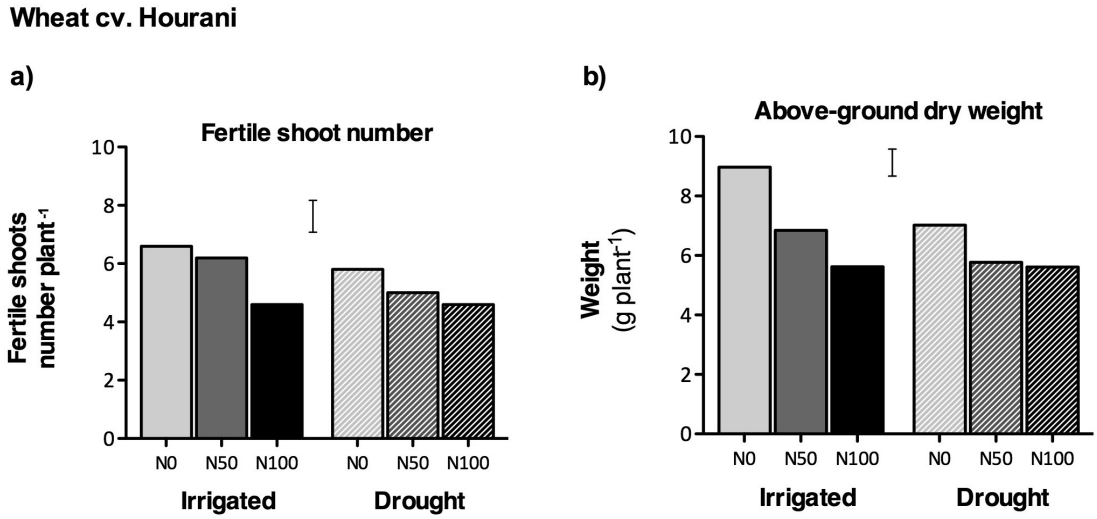

Figure 4.4 Fertile shoot number per plant (**a**) and aboveground dry weight (**b**, g plant^{-1}) for wheat cv. Hourani subjected to full irrigated (full bars) and droughted (striated bars) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1} equivalents) at harvest for the 2007 experiment. Error bars represent SED for irrigation*nitrogen (df = 20).

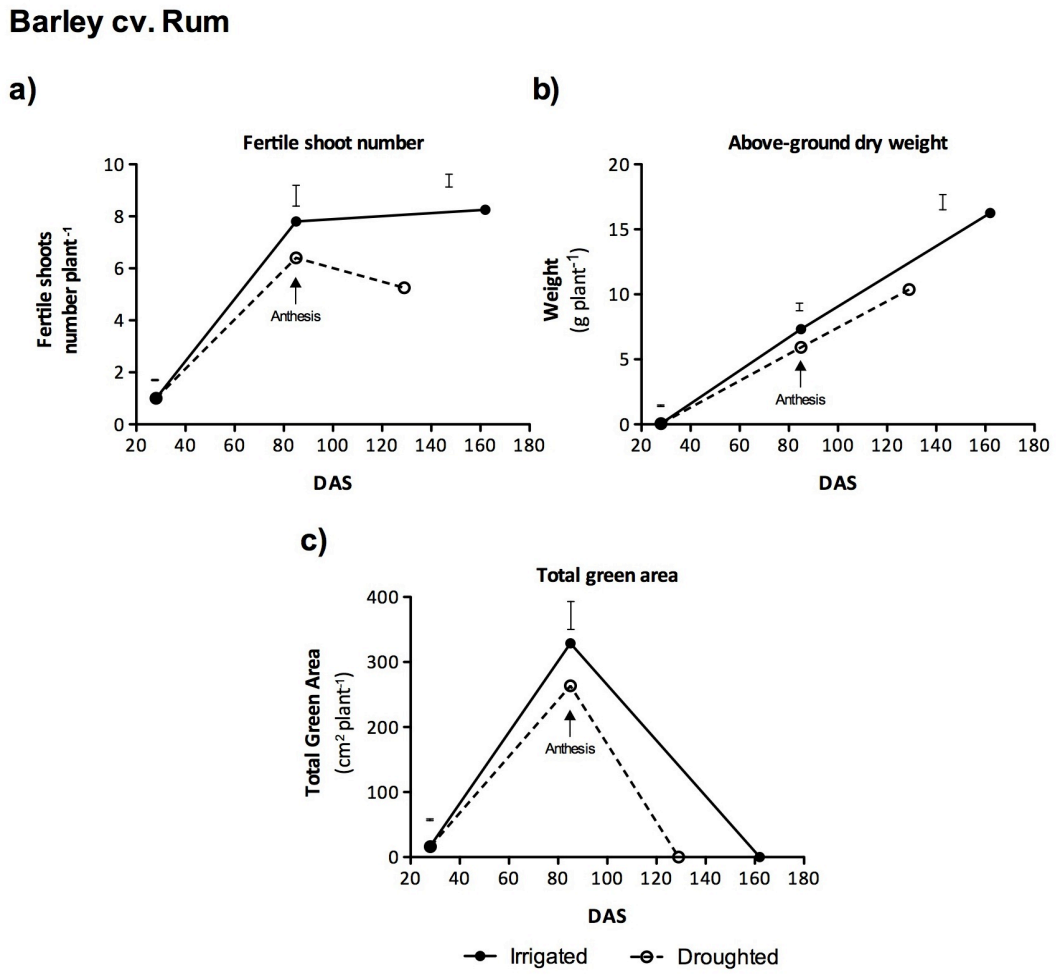

Figure 4.5 Fertile shoot number, aboveground dry weight (g plant^{-1}) and total green area (cm^2 plant^{-1}) for barley cv. Rum (**a**, **b** and **c**) subjected to full irrigated (full lines) and droughted (broken lines) treatments during the 2008 experiment. Error bars represent SED for irrigation (df = 6).

4.2.6 Dry matter partitioning

4.2.6.1 2006

At 102 DAS averaging across irrigation and N treatments, for wheat cv. Hourani (GS55) leaf weight (green + dead leaves) was 0.43 g (33%) higher ($p \leq 0.01$) than for barley cv. Rum (GS61; Figure 4.6 and Figure 4.7). At this stage drought decreased leaf partitioning ($p \leq 0.05$) by 12% for both genotypes when averaged across N treatments (Figure 4.6 and Figure 4.7). Biomass allocated to stems did not differ between genotypes (49%); however, stem weight averaging across N and irrigation treatments was 5.91 g for barley cv. Rum and only 2.05 for wheat cv. Hourani ($p \leq 0.001$, Figure 4.6 and Figure 4.7). At this stage overall barley cv. Rum (GS61) allocated 38% (4.53 g) of its biomass to ears compared to only 3% (0.14 g; $p \leq 0.001$) for wheat cv. Hourani, furthermore drought increased the biomass allocated to ears by 4.6% and 3.2% for barley cv. Rum and wheat cv. Hourani, respectively ($p \leq 0.05$) N application had no effect on the biomass partitioning at this stage.

At 123 DAS averaging across irrigation and N treatments AGDW allocated to leaves was 76% lower ($p \leq 0.001$; Figure 4.6 and Figure 4.7) for barley cv. Rum (GS71; 2.12 g) than wheat cv. Hourani (GS6; 11.58 g). Although stem weight was 2.65 g higher for barley cv. Rum than wheat cv. Hourani, it corresponded to a 21.1% higher percentage of biomass in stems ($p \leq 0.001$) for wheat cv. Hourani (Figure 4.6 and Figure 4.7). N application had a similar effect for both species ($p \leq 0.001$), with N50 increasing the biomass allocated to stems by 5% and N100 by 6%, when averaged across genotypes and irrigation treatments. The percentage of biomass allocated by barley cv. Rum to ears was 65% (15g) while for wheat cv. Hourani was only 22% (1.7 g; $p \leq 0.001$), when averaged across N and irrigation treatments. Neither N applications nor irrigation treatments had a significant effect on the biomass allocated to ears.

At harvest, partitioning did not respond differently to N application or drought and irrigation treatments, although differences between genotypes were observed (Figure 4.6 and Figure 4.7). Averaging across N and irrigation treatments wheat cv. Hourani invested 10.3% more of its AGDW (2.45 g) in leaves when compared to barley cv. Rum

(2.28 g; Figure 4.6 and Figure 4.7). Wheat cv. Hourani allocated 27% (3.71 g) of its AGDW to stems compared to 25% (7.51 g) for barley cv. Rum ($p = 0.08$; Figure 4.6 and Figure 4.7). The percentage of biomass allocated to infertile shoots was 3.5% (0.45 g) for wheat cv. Hourani but only 0.9% (0.28 g) for barley cv. Rum ($p \leq 0.01$; Figure 4.6 and Figure 4.7). Averaging across N and irrigation treatments, the percentage of AGDW partitioning to the grains was 40% higher ($p \leq 0.001$) for barley cv. Rum (15.7 g) when compared to wheat cv. Hourani (8.2 g; Figure 4.6 and Figure 4.7). Chaff weight as percentage of AGDW did not differ between genotypes and treatments applied, representing overall 12.8 % of the total AGDW (Figure 4.6 and Figure 4.7).

4.2.6.2 2007

In 2007, for barley cv. Rum at anthesis, drought did not affect the percentage of biomass allocated to leaves (6%) and stems (32%), although overall AGDW across N treatments was reduced by 12% ($p \leq 0.05$; Figure 4.8). The percentage of biomass allocated to ears also did not change between irrigation and drought plants (57.6%), though the total ear weight was 14% higher ($p \leq 0.05$) for the irrigated plants. N had no significant effect on dry matter partitioning on the plant components in 2007 (Figure 4.8). At harvest the percentage of biomass allocated by barley cv. Rum to leaves was not significantly affected by irrigation treatments: averaging across N treatments partitioning to leaves was 5.8% for the full irrigated plants (0.60 g) and 5.6% for the plants under drought (0.38 g). When averaged across irrigation treatments, there was a trend ($p = 0.10$) for an increase of AGDW allocated to the leaves with N application, by 17 and 29% with N50 and N100 respectively (Figure 4.8). Drought decreased by 4% ($p \leq 0.05$) the biomass allocated to the shoots, corresponding to a decrease of 0.60 g in the actual shoot weight ($p \leq 0.001$). At harvest, the biomass allocated to infertile shoots was 3% to the plants under drought (0.21 g) contrasting with 14% (1.51 g) under full irrigation ($p \leq 0.01$; Figure 4.8). Drought increased the relative allocation of AGDW to chaff ($p = 0.07$) and grain ($p \leq 0.01$) by 14% (Figure 4.8).

For wheat cv. Karim in 2007 at anthesis, drought increased ($p \leq 0.05$) the percentage of AGDW allocated to leaves, from 7.0% (0.31 g) to 7.5% (0.32 g; Figure 4.9). The percentage of biomass allocated to stem did not differ between full irrigated and drought treatments, or N application, corresponding to an overall average of 25% (1.13 g; Figure 4.9). No significant differences between N and irrigation treatments were found for the percentage of biomass allocated to ears, averaging 67% across treatments (3 g).

At harvest, neither leaf dry weight nor the percentage of biomass allocated to leaves differed between treatments. Overall the dry weight of leaves corresponded to 7% (0.30 g) of the plant AGDW (Figure 4.9). Wheat cv. Karim allocated relatively more biomass to shoots under drought, 23% (0.92 g) compared to 22% (0.99 g) when full irrigated ($p \leq 0.05$; Figure 4.9). Under full irrigation plants allocated 2% ($p \leq 0.05$) more of its AGDW to grain when compared to the droughted plants, corresponding to 2.6 g cf. and 2.2 g respectively.

For wheat cv. Hourani in 2007 at harvest, drought decreased the biomass allocated to leaves ($p \leq 0.01$) by 15%. However, N application had no significant effect on the biomass partitioned to the leaves (Figure 4.10). The overall percentage of biomass allocated to stems was 28%, and it did not significantly change with the N or irrigation treatments. Overall chaff weight corresponded to 14% of the AGDW and was not significantly affected by N or irrigation treatments (Figure 4.10). Drought plants allocated 2% more of their AGDW in grain when compared to the plants under full irrigation ($p \leq 0.05$).

4.2.6.3 2008

For barley cv. Rum in 2008 at anthesis, partitioning of AGDW to leaves was not significantly affected by the irrigation treatments, averaging 13% for the plants under full irrigation (0.95 g) and 12% for the droughted plants (0.72%; Figure 4.11). There was a trend ($p = 0.11$) for a higher allocation of AGDW to shoots under irrigation, 52% (3.84 g) cf. compared to 48% (2.90 g) under drought (Figure 4.11). At anthesis the

biomass allocated to ears was not statistically different between irrigation treatments, constituting 37% (2.42 g) of the total AGDW (Figure 4.11).

At harvest, plants subjected to water limitation allocated 4% (0.46 g) of AGDW to leaves, contrasting ($p \leq 0.001$) with the 6% (0.98 g) allocated under full irrigation. However, both full irrigation and drought treatments allocated a similar proportion of their AGDW to stems, 26% (4.20 g) cf. and 25% (2.58 g), respectively (Figure 4.11). Drought did not significantly affect the biomass allocated to infertile shoots, averaging 2.3% across irrigation treatments (Figure 4.11). Irrigation increased the percentage of AGDW allocated to the chaff (2.43 g) by 17% compared to the drought treatment (1.34 g; $p \leq 0.05$). Although the grain weight decreased by 30% under drought ($p \leq 0.05$), the percentage of biomass in grains did not significantly differ between irrigated (56%) and droughted treatments (51%, Figure 4.11).

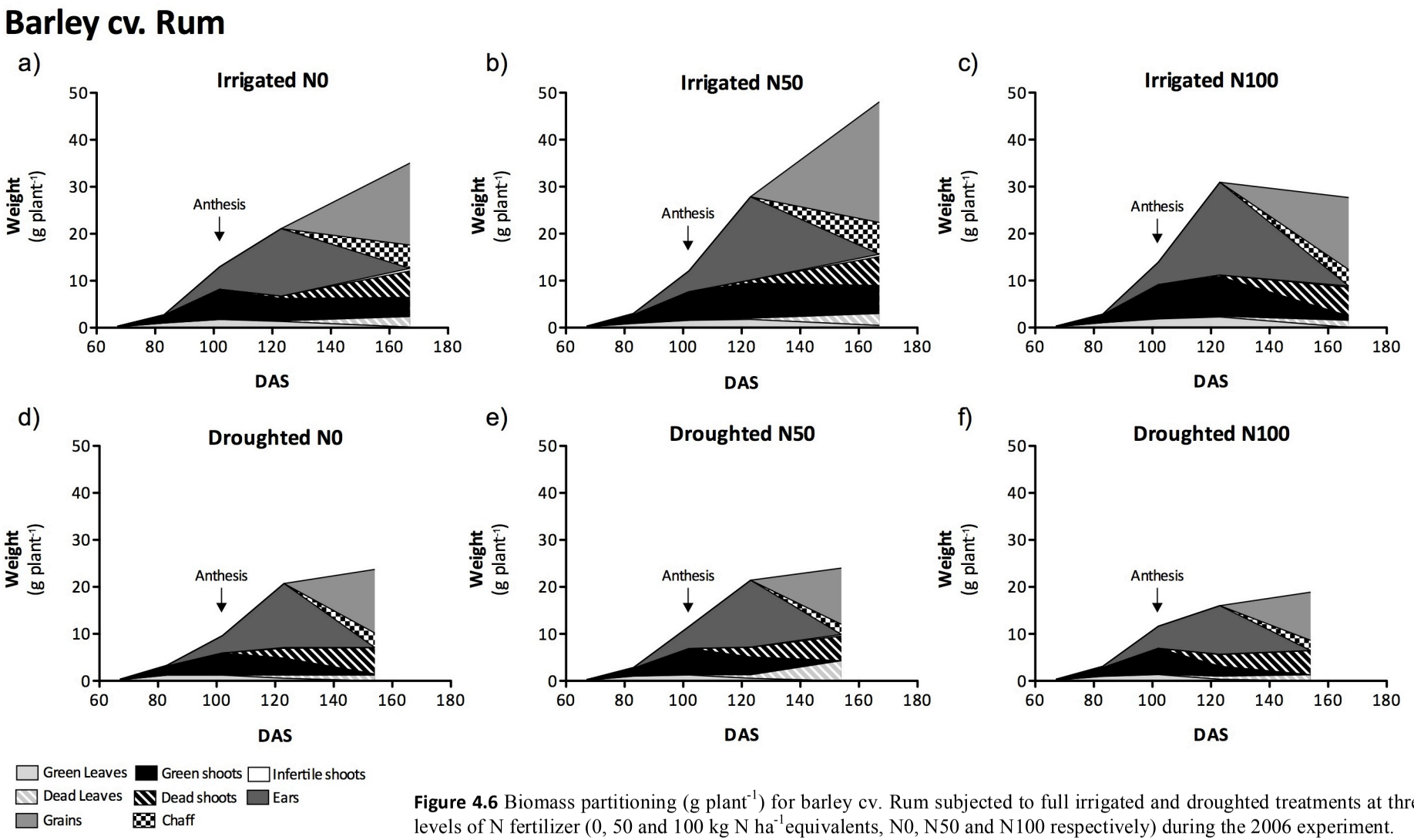

Figure 4.6 Biomass partitioning (g plant^{-1}) for barley cv. Rum subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}equivalents, N0, N50 and N100 respectively) during the 2006 experiment.

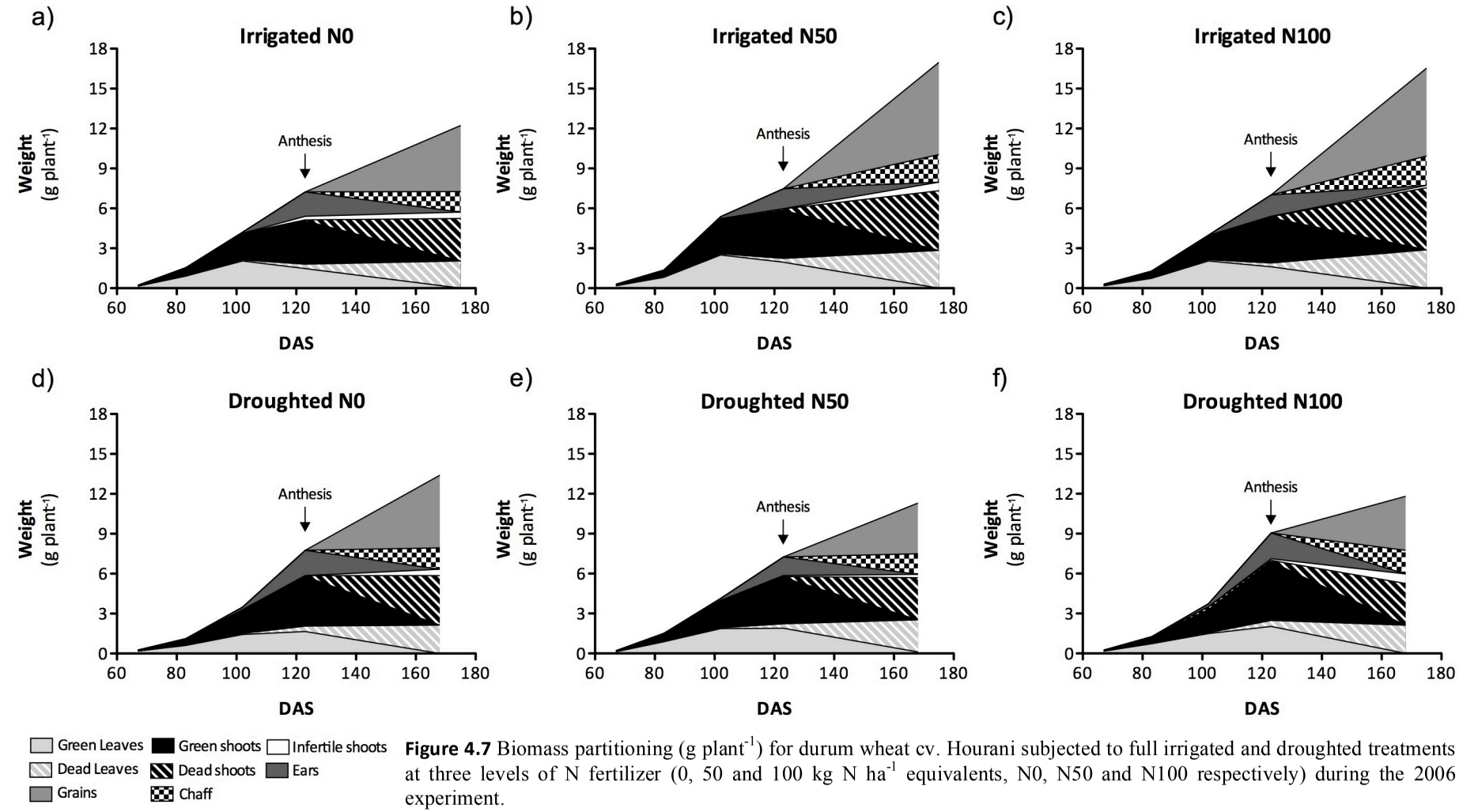

Figure 4.7 Biomass partitioning (g plant^{-1}) for durum wheat cv. Hourani subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1} equivalents, N0, N50 and N100 respectively) during the 2006 experiment.

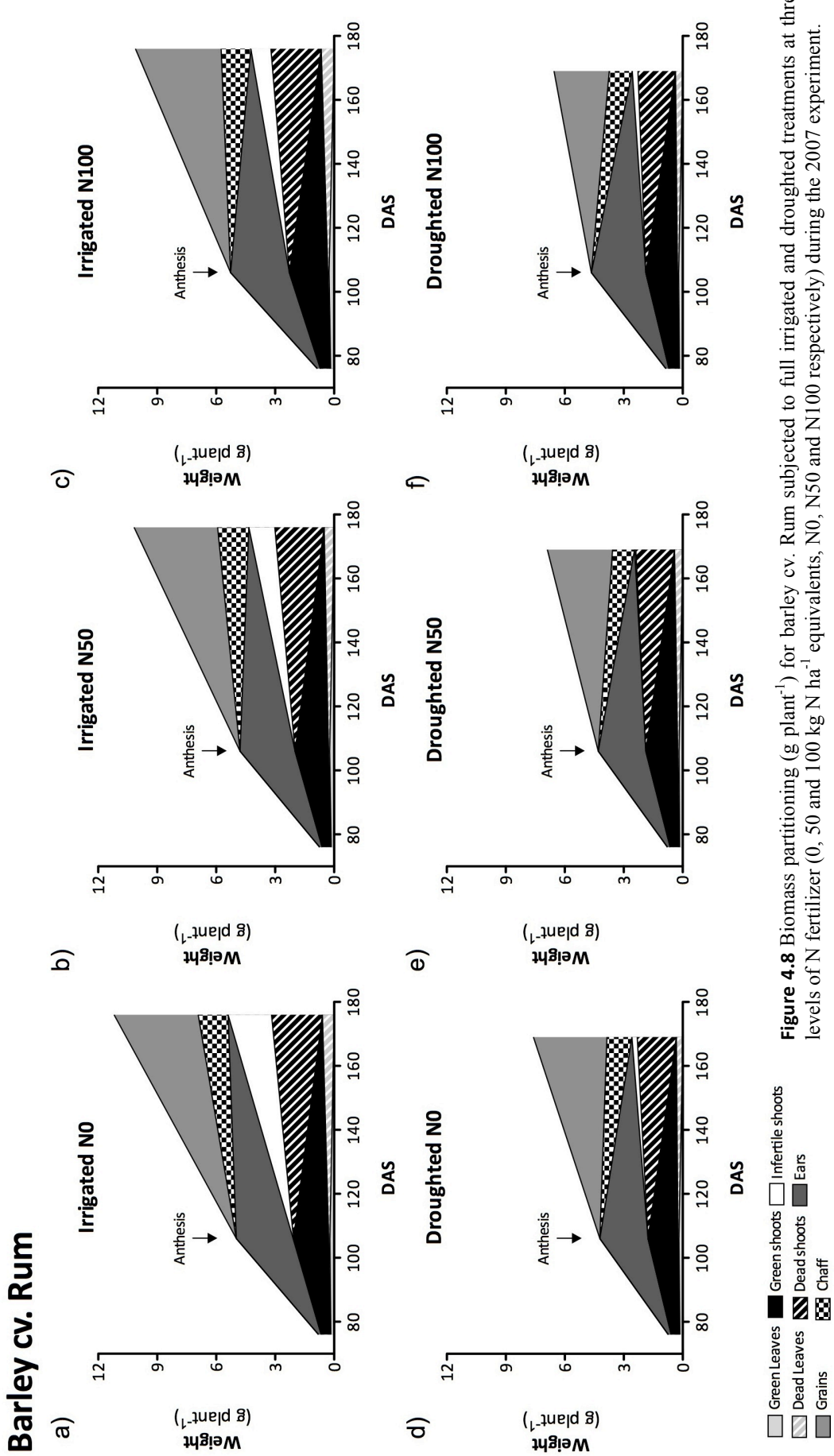

Figure 4.8 Biomass partitioning (g plant^{-1}) for barley cv. Rum subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1} equivalents, N0, N50 and N100 respectively) during the 2007 experiment.

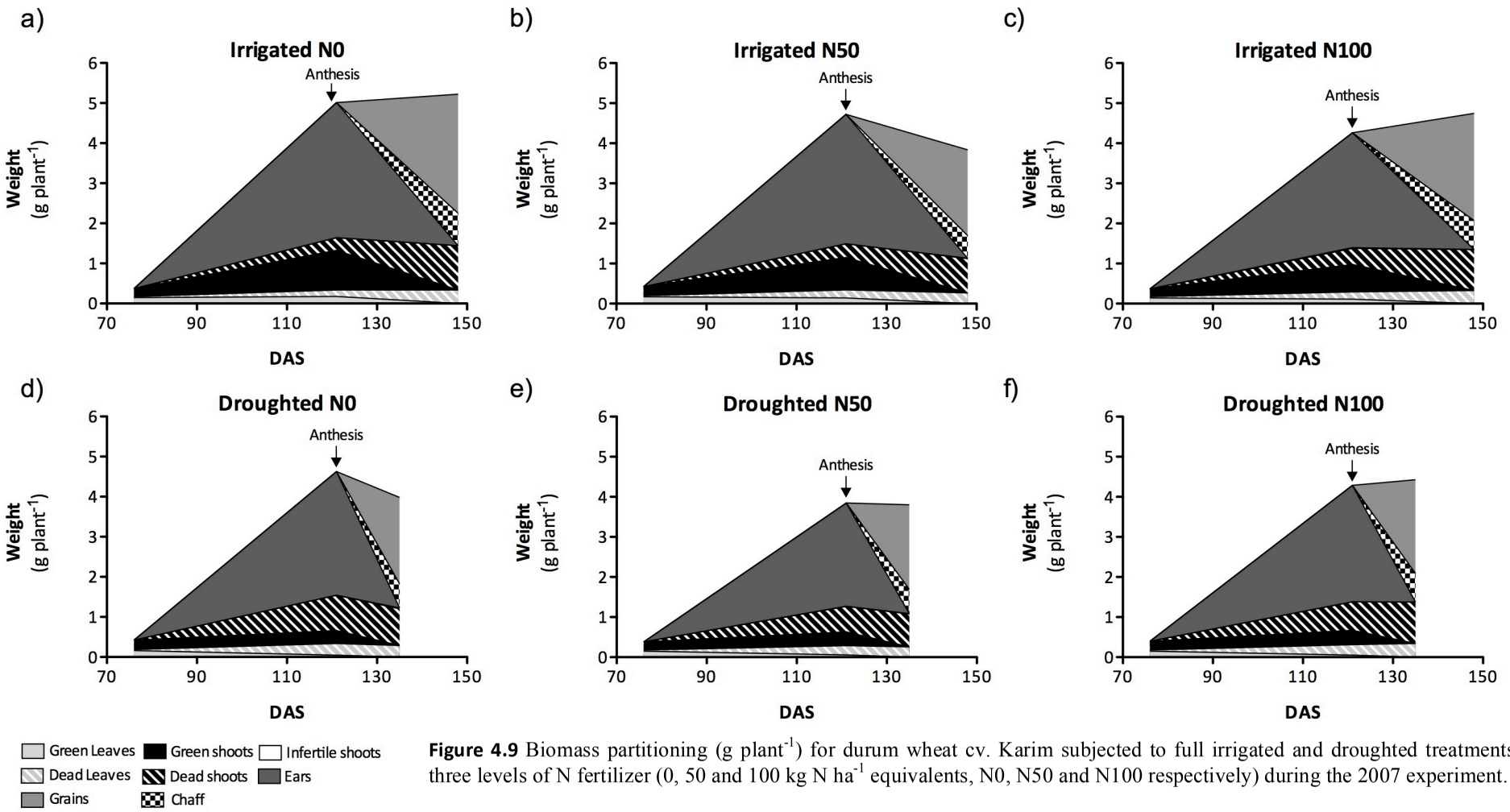

Figure 4.9 Biomass partitioning (g plant^{-1}) for durum wheat cv. Karim subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1} equivalents, N0, N50 and N100 respectively) during the 2007 experiment.

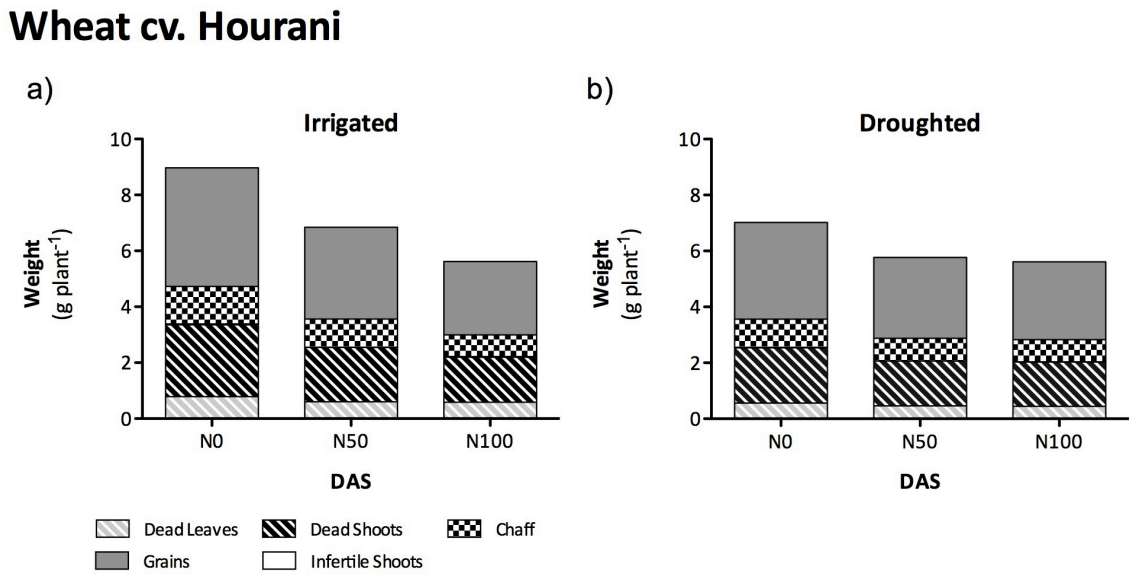

Figure 4.10 Biomass partitioning (g plant^{-1}) for wheat cv. Hourani subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1} equivalents, N0, N50 and N100 respectively) at harvest for the 2007 experiment.

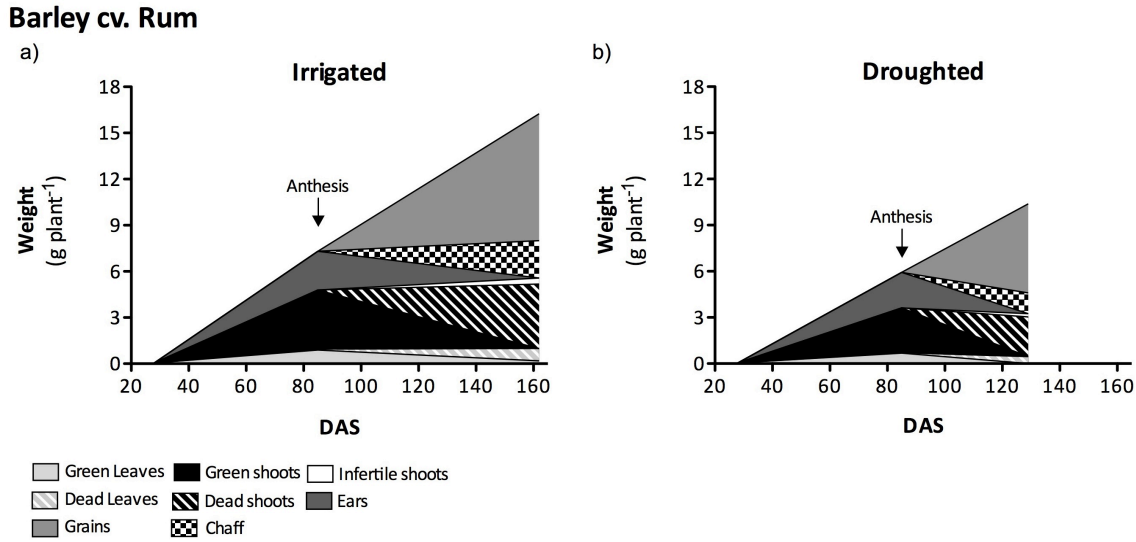

Figure 4.11 Biomass partitioning (g plant^{-1}) for barley cv. Rum subjected to full irrigated and droughted treatments for the 2008 experiment.

4.3 YIELD AND YIELD COMPONENTS

4.3.1 2006

Averaging across N and irrigation treatments, grain yield on the main shoot (YS) was slightly higher ($p \leq 0.05$) for barley cv. Rum than wheat cv. Hourani, 1.6 and 1.2 g ear^{-1}, respectively. When averaged across species and irrigation treatments, N50 increased YS ($p \leq 0.05$) by 26% while N100 had no significant effect (Table 4.7).

Overall grain yield (Y) per plant was 196% higher for barley cv. Rum than for wheat cv. Hourani ($p \leq 0.001$). Drought decreased the Y ($p \leq 0.001$) but to a greater extent for barley cv. Rum (38%) than wheat cv. Hourani (34%) ($p \leq 0.01$; Table 4.7). There was an interaction between irrigation and nitrogen ($p \leq 0.05$), with N50 increasing Y by 5.1 g plant^{-1} under irrigation, when averaged across genotypes, though N100 had no effect. There was a trend for an interaction between species and nitrogen ($p = 0.068$), with an increase in Y by 21% with N50 but only for barley cv. Rum when averaged across irrigation treatments (Table 4.7).

In 2006, averaged across N treatments, barley cv. Rum had 8.3 more ears plant^{-1} than wheat cv. Hourani ($p \leq 0.001$; Table 4.7). Drought decreased ears plant^{-1} ($p \leq 0.001$) but to a greater extent ($p \leq 0.05$) for barley cv. Rum (52%) than wheat cv. Hourani (29%; Table 4.7).

Grain number per ear on the main shoot (GNS) was not significantly affected by N or irrigation treatments (Table 4.7). Grains per ear for all shoots (GNE), when averaging across genotypes N and irrigation treatments, was 31% lower than for the main shoot alone; N application had no significant effect on GNE. However it tended to increase GNE by 31% with water deficits but only for barley cv. Rum ($p = 0.076$; Table 4.7).

The total grain number per plant (GN) was 56% lower for wheat cv. Hourani than barley cv. Rum (Table 4.7; $p \leq 0.001$). There was an interaction for species x irrigation x nitrogen ($p \leq 0.05$), with N50 increasing GN by 48% but only under irrigation and for barley cv. Rum. Drought decreased ($p \leq 0.001$) GN by 35% for barley cv. Rum and 37% wheat cv. Hourani, when averaged across N application treatments.

Overall individual grain weight assessed on the main shoot (IGWS) and on all fertile shoots per plant (IGW) was 19 and 17%, respectively, higher for barley cv. Rum than durum wheat cv. Hourani ($p \leq 0.05$ and 0.001, respectively; Table 4.7). Averaging across genotypes and irrigation treatments N100 decreased the IGWS by 11.4 mg when compared to N50 (Table 4.7; $p \leq 0.05$). Drought decreased IGW by 7% for barley cv. Rum and increased by 13% wheat cv. Hourani (Table 4.7; $p \leq 0.05$). N100 decreased IGW compared to N0 by 16% for barley cv. Rum under drought; whereas N100 decreased IGW by 21% for wheat cv. Hourani under irrigation ($p \leq 0.05$; Table 4.7).

Averaging across irrigation and N treatments, HI for barley cv. Rum was 0.54 while for wheat cv. Hourani was 0.38 ($p \leq 0.001$); and neither water nor nitrogen had a significant effect on HI (Table 4.7).

Table 4.7 Number of ears per plant, grain number per ear for the main shoot (GNS) and for all ears (GNE) per plant, total grain number per plant (GN), individual grain weight for the main shoot ear (IGWS) and for all ears per plant (IGW), grain DM yield for the main shoot ear (YS) and for all ears per plant (Y) and harvest index (HI) for the plant for barley cv. Rum and durum wheat cv. Hourani subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) for the 2006 experiment.

Species	Irrigation	Fertilizer N (kg N ha^{-1})	Ears $plant^{-1}$	Grain number			Individual grain weight (mg)		Yield (g)		HI
				GNS	GNE	TGN	IGWS	IGW	YS	Y	
Barley cv. Rum	**Irrigated**	**0**	23.0	30.0	17.6	373	49.3	46.8	1.47	17.5	0.504
		50	26.0	42.7	21.8	552	51.2	46.7	2.18	25.7	0.540
		100	16.3	32.7	21.2	330	47.1	46.7	1.53	15.3	0.557
		Mean	*21.8*	*35.1*	*20.2*	*418*	*49.2*	*46.7*	*1.73*	*19.5*	*0.534*
	Droughted	**0**	12.0	36.7	25.3	295	48.3	46.0	1.77	13.5	0.574
		50	10.3	33.0	25.8	267	55.7	45.3	1.74	12.0	0.510
		100	9.0	27.7	28.4	255	24.2	38.8	0.79	10.3	0.534
		Mean	*10.4*	*32.5*	*26.5*	*272*	*42.7*	*43.3*	*1.43*	*11.9*	*0.539*
Wheat cv. Hourani	**Irrigated**	**0**	6.0	31.0	23.8	136	38.2	36.9	1.19	5.0	0.410
		50	11.0	34.0	17.8	194	37.5	35.9	1.28	6.9	0.408
		100	10.3	30.9	22.2	226	31.5	29.2	0.96	6.6	0.404
		Mean	*9.1*	*32.0*	*21.3*	*185*	*35.7*	*34.0*	*1.14*	*6.2*	*0.407*
	Droughted	**0**	6.3	31.0	24.8	157	38.4	35.1	1.21	5.5	0.408
		50	4.7	29.3	21.9	97	44.6	39.5	1.31	3.8	0.342
		100	8.3	27.0	15.0	94	40.8	40.7	1.14	4.1	0.321
		Mean	*6.4*	*29.1*	*20.6*	*116*	*41.3*	*38.4*	*1.22*	*4.5*	*0.357*
		SED (df)									
		Species (22)	*1.63****	*2.41*^{ns}	*1.88*^{ns}	*19.3****	*3.43**	*1.49****	*0.152**	*0.99****	*0.025****
		Irrigation (22)	*1.63****	*2.41*^{ns}	*1.88*^{ns}	*19.3****	*3.43*^{ns}	*1.49*^{ns}	*0.152*^{ns}	*0.99****	*0.025*^{ns}
		Nitrogen (22)	*2.00*^{ns}	*2.96*^{ns}	*2.31*^{ns}	*23.6*^{ns}	*4.20**	*1.82*^{ns}	*0.186**	*1.21*^{ns}	*0.031*^{ns}
		*Species*Irrigation (22)*	*2.31**	*3.41*^{ns}	*2.66*^{ns}	*27.3*^{ns}	*4.85*^{ns}	*2.11**	*0.215*^{ns}	*1.40***	*0.036*^{ns}
		*Species*Nitrogen (22)*	*2.83*^{ns}	*4.18*^{ns}	*3.26*^{ns}	*33.4**	*5.94*^{ns}	*2.58*^{ns}	*0.264*^{ns}	*1.71*^{ns}	*0.044*^{ns}
		*Irrigation*Nitrogen (22)*	*2.83*^{ns}	*4.18*^{ns}	*3.26*^{ns}	*33.4***	*5.94*^{ns}	*2.58*^{ns}	*0.264*^{ns}	*1.71**	*0.044*^{ns}
		*Species*Irrigation*Nitrogen (22)*	*4.00*^{ns}	*5.91*^{ns}	*4.62*^{ns}	*47.2**	*8.40*^{ns}	*3.65**	*0.373*^{ns}	*2.42*^{ns}	*0.062*^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

4.3.2 2007

For barley cv. Rum in 2007, irrigation treatments or N fertilizer did not significantly affect YS. However, overall Y was 31% higher ($p \leq 0.05$) under irrigation (Table 4.8). Averaging across N and irrigation treatments, Y for barley cv. Rum was only 3.8 g contrasting 15.7 g in 2006 (Table 4.7 and Table 4.8). Averaged across N and irrigation treatments, ears plant^{-1} was 42% of that in 2006 (6.8 cf. 16.1, respectively). Drought did not significantly decrease the number of ears per plant (Table 4.7 and Table 4.8). When averaged across N treatments, drought showed a trend to decrease GNS ($p = 0.06$) and GNE ($p = 0.08$) by 24 and 20%, respectively, decreasing the GN per plant by 30% ($p \leq 0.01$; Table 4.8). In 2007, for barley cv. Rum, drought increased ($p \leq 0.01$) IGWS and IGW by 14 and 7%, respectively, when averaged across N treatments (Table 4.7 and Table 4.8). Averaging across irrigation treatments, there was a trend for N50 to decrease IGN ($p \leq 0.06$) by 2.7 mg. Overall HI increased ($p \leq 0.05$) from 0.41 to 0.46 under drought, while N fertilizer did not significantly affect HI (Table 4.8).

For wheat cv. Karim the average yield across N and irrigation treatments was 1.5 g on the main shoot increasing to 2.4 g per plant, and the average between treatments did not significantly change. Drought tended to decrease Y by 15% ($p = 0.20$; Table 4.9). The number of ears plant^{-1} decreased under drought ($p \leq 0.05$) by 27% when averaged across N treatments (Table 4.9). Neither restricted water availability nor N fertilization significantly affected the GNS, though there was a trend for GNE when averaged across N treatments to increase by 4.5 with drought ($p = 0.09$; Table 4.9). GN for wheat cv. Karim was not significantly affected by the treatments applied (Table 4.9). Neither did irrigation and N fertilization affect the IGWS and IGW. Overall the IGW measured 4.1 mg lower than IGWS (Table 4.9). For wheat cv. Karim, the HI slightly decreased by 3% ($p \leq 0.05$) under drought (Table 4.9).

Turning to the second wheat cultivar grown in 2007 (wheat cv. Hourani), effects of N application and drought on the YS were not significant. However, when averaged across

irrigation treatments, N application decreased Y by 0.77 g with N50 and 1.15 g with N100 compared to N0 (Table 4.10). Averaged across N application treatments, Y was 10% lower under drought though the difference was not statistically different ($p = 0.27$; (Table 4.10). For cv. Hourani the ears plant^{-1} across N and irrigation treatments was 5.5 (Table 4.7 and Table 4.10). Effects of irrigation and N applications on GNS and GNE were not significant. The average GNS (32.2) was approximately twice the GNE (15.9; Table 4.10). GN was not significantly affected by restricted water availability. However, N application decreased the GN ($p \leq 0.05$) by 20% with N50 and 27% with N100 (Table 4.10). IGWS averaged across N treatments decreased from 42.4 mg under restricted water availability to 38.9 mg with irrigation ($p \leq 0.05$). However IGW was not significantly affected by the treatments applied (Table 4.10). HI was positively affected by restricted water availability ($p \leq 0.05$) increasing by 4% under the drought treatment (Table 4.10).

In 2007, overall Y for barley cv. Rum was 3.8 g, for wheat cv. Karim was 2.4 g and for wheat cv. Hourani was 3.21 g (Table 4.8, Table 4.9 and Table 4.10). When averaged across treatments, the lower Y in 2007 than in 2006 seemed mainly associated with a decrease in the number of ears per plant, by 56% for barley cv. Rum and 30% for wheat cv. Hourani. Besides that in 2006 both wheat cv. Hourani and barley cv. Rum had a similar GNS and GNE, ca, 30 and 20 respectively (Table 4.7). The GNS for wheat cv. Hourani remained roughly constant between years and GNE decreased by 38%; while for barley cv. Rum these parameters decreased by 80 and 76%, respectively (Table 4.8). Overall, both durum wheat varieties in 2007 had higher GNE and HI than barley, and IGW was roughly similar between genotypes. Therefore the differences in Y between genotypes in 2007 were mainly a result of differences in GN associated with differences in ears plant^{-1}.

Table 4.8 Number of ears per plant, grain number per ear for the main shoot (GNS) and for all ears (GNE) per plant, total grain number per plant (GN), individual grain weight for the main shoot ear (IGWS) and for all ears per plant (IGW), grain DM yield for the main shoot ear (YS) and for all ears per plant (Y) and harvest index (HI) for the plant for barley cv. Rum subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) for the 2007 experiment.

		Barley cv. Rum								
Irrigation	**Fertilizer N** (kg N ha^{-1})	**Ears** $plant^{-1}$	**Grain number**			**Individual grain weight** (mg)		**Yield** (g)		**HI**
			GNS	**GNE**	**GN**	**IGWS**	**IGW**	**YS**	**Y**	
Irrigated	**0**	7.8	23.6	15.6	101	40.1	42.3	0.935	4.28	0.383
	50	8.2	17.2	13.0	107	42.0	39.6	0.700	4.25	0.415
	100	7.0	23.0	15.5	108	41.4	40.5	0.884	4.36	0.421
	Mean	*7.7*	*21.3*	*14.7*	*105*	*41.1*	*40.8*	*0.840*	*4.30*	*0.406*
Droughted	**0**	6.4	18.2	13.4	83	48.1	45.3	0.872	3.74	0.494
	50	*6.4*	16.8	12.4	77	45.7	42.5	0.773	3.32	0.472
	100	7.0	13.8	9.6	65	46.8	43.1	0.641	2.81	0.426
	Mean	*6.6*	*16.3*	*11.8*	*75*	*46.8*	*43.6*	*0.762*	*3.29*	*0.464*
	SED (df)									
	Irrigation (20)	0.77^{ns}	2.53^{ns}	1.57^{ns}	9.4^{**}	1.74^{**}	0.92^{**}	0.092^{ns}	0.437^{*}	0.028^{*}
	Nitrogen (20)	0.94^{ns}	3.10^{ns}	1.92^{ns}	11.5^{ns}	2.13^{ns}	1.13^{ns}	0.113^{ns}	0.535^{ns}	0.035^{ns}
	*Irrigation*Nitrogen (20)*	1.33^{ns}	4.39^{ns}	2.72^{ns}	16.3^{ns}	3.01^{ns}	1.60^{ns}	0.159^{ns}	0.757^{ns}	0.049^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 4.9 Number of ears per plant, grain number per ear for the main shoot (GNS) and for all ears (GNE) per plant, total grain number per plant (GN), individual grain weight for the main shoot ear (IGWS) and for all ears per plant (IGW), grain DM yield for the main shoot ear (YS) and for all ears per plant (Y) and harvest index (HI) for the plant for wheat cv. Karim subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) for the 2007 experiment.

		Wheat cv. Karim								
Irrigation	**Fertilizer** (kg N ha^{-1})	**Ears plant^{-1}**	**Grain number**			**Individual grain weight** (mg)		**Yield** (g)		**HI**
			GNS	**GNE**	**GN**	**IGWS**	**IGW**	**YS**	**Y**	
Irrigated	**0**	3.8	36.4	20.8	74	44.1	40.3	1.61	2.97	0.568
	50	2.6	31.0	19.6	53	45.4	42.1	1.38	2.14	0.546
	100	3.4	34.4	22.1	70	43.7	38.4	1.54	2.68	0.561
	Mean	*3.3*	*33.9*	*20.8*	*65*	*44.4*	*40.3*	*1.51*	*2.60*	*0.559*
Droughted	**0**	2.6	40.4	24.4	61	40.6	36.2	1.64	2.16	0.537
	50	*2.2*	36.8	26.6	53	44.8	40.5	1.65	2.11	0.553
	100	2.4	34.4	25.0	62	42.7	39.1	1.45	2.34	0.528
	Mean	*2.4*	*37.2*	*25.3*	*59*	*42.7*	*38.6*	*1.58*	*2.20*	*0.539*
	SED (df)									
	Irrigation (20)	0.37^{*}	3.23^{ns}	2.59^{ns}	8.0^{ns}	1.53^{ns}	1.96^{ns}	0.153^{ns}	0.298^{ns}	0.009^{*}
	Nitrogen (20)	0.45^{ns}	3.96^{ns}	3.17^{ns}	9.8^{ns}	1.87^{ns}	2.40^{ns}	0.187^{ns}	0.365^{ns}	0.011^{ns}
	*Irrigation*Nitrogen (20)*	0.64^{ns}	5.60^{ns}	4.49^{ns}	13.8^{ns}	2.64^{ns}	3.40^{ns}	0.265^{ns}	0.516^{ns}	0.015^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 4.10 Number of ears per plant, grain number per ear for the main shoot (GNS) and for all ears (GNE) per plant, total grain number per plant (GN), individual grain weight for the main shoot ear (IGWS) and for all ears per plant (IGW), grain DM yield for the main shoot ear (YS) and for all ears per plant (Y) and harvest index (HI) for the plant for wheat cv. Hourani subjected to full irrigated and droughted treatments and three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) for the 2007 experiment.

Irrigation	Fertilizer N (kg N ha^{-1})	Wheat cv. Hourani								
		Ears $plant^{-1}$	Grain number			Individual grain weight (mg)		Yield (g)		HI
			GNS	GNE	GN	IGWS	IWG	YS	Y	
Irrigated	**0**	6.6	30.8	14.9	98	41.7	43.5	1.28	4.24	0.473
	50	6.2	35.0	13.5	78	38.4	42.2	1.34	3.28	0.479
	100	4.6	33.2	19.3	66	36.7	39.5	1.23	2.63	0.461
	Mean	*5.8*	*33.0*	*15.9*	*81*	*38.9*	*41.7*	*1.28*	*3.38*	*0.471*
Droughted	**0**	5.8	31.0	14.8	83	42.6	42.2	1.32	3.46	0.489
	50	*5.0*	29.8	13.6	67	42.4	43.2	1.26	2.89	0.499
	100	4.6	33.0	14.7	66	42.2	42.8	1.38	2.78	0.496
	Mean	*5.1*	*31.3*	*14.4*	*72*	*42.4*	*42.7*	*1.32*	*3.04*	*0.495*
	SED (df)									
	Irrigation (20)	0.65^{ns}	1.55^{ns}	2.28^{ns}	7.2^{ns}	1.40^{*}	1.12^{ns}	0.071^{ns}	0.286^{ns}	0.009^{*}
	Nitrogen (20)	0.79^{ns}	1.89^{ns}	2.79^{ns}	8.9^{*}	1.72^{ns}	1.37^{ns}	0.087^{ns}	0.350^{**}	0.011^{ns}
	*Irrigation*Nitrogen (20)*	1.12^{ns}	2.68^{ns}	3.95^{ns}	12.6^{ns}	2.43^{ns}	1.94^{ns}	0.123^{ns}	0.495^{ns}	0.015^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

4.3.3 2008

In 2008 for barley, drought decreased ears $plant^{-1}$ (Table 4.11). The GNS was not affected by the irrigation treatments, but drought increased ($p \leq 0.05$) by 19% GNE. Plants under full irrigation produced more ($p \leq 0.05$) grains (176) than under drought (136; Table 4.11). IGWS and IGW were not significantly affected by drought, averaging across irrigation treatments 41.9 mg cf. and 44.3 mg, respectively (Table 4.11). YS did not differ between treatments, though the Y was 42% higher under full irrigation than under drought, mainly associated with differences in ears per plant (Table 4.11). The differences in HI between irrigation treatments were not significant (Table 4.11).

Table 4.11 Number of ears per plant, grain number per ear for the main shoot (GNS) and for all ears (GNE) per plant, total grain number per plant (GN), individual grain weight for the main shoot ear (IGWS) and for all ears per plant (IGW), grain DM yield for the main shoot ear (YS) and for all ears per plant (Y) and harvest index (HI) for the plant for barley cv. Rum subjected to full irrigated and droughted treatments for the 2008 experiment.

Irrigation	**Barley cv. Rum**								
	Ears plant^{-1}	**Grain number**			**Individual grain weight** (mg)		**Yield** (g)		**HI**
		GNS	**GNE**	**GN**	**IGWS**	**IGW**	**YS**	**Y**	
Irrigated	8.0	22.0	21.8	179	44.6	46.1	1.00	8.25	0.508
Droughted	5.0	26.0	25.9	136	39.1	42.4	1.01	5.79	0.559
SED (df)									
Irrigation (6)	*0.50****	*2.7^{ns}*	*1.25**	*14.1**	*5.37^{ns}*	*2.06^{ns}*	*0.161^{ns}*	*0.692**	*0.028^{ns}*

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Figure 4.12 presents the regression between yield and: i) ear number, ii) grain number, iii) grain number ear^{-1} and iv) individual grain weight across years for barley cv. Rum, wheat cv. Hourani and wheat cv. Karim. A strong relationship between ear number and yield (R^2 = 0.76) and between grain number and yield (R^2 = 0.97; Figure 4.12) was found. However regressions between grain number per ear as well as individual grain weight were not significant. Consequently one can therefore conclude that differences in yield between treatments were mainly a result of differences in the number of grains per plant, in turn, related to differences in the number of ears per plant and hence tiller production and survival.

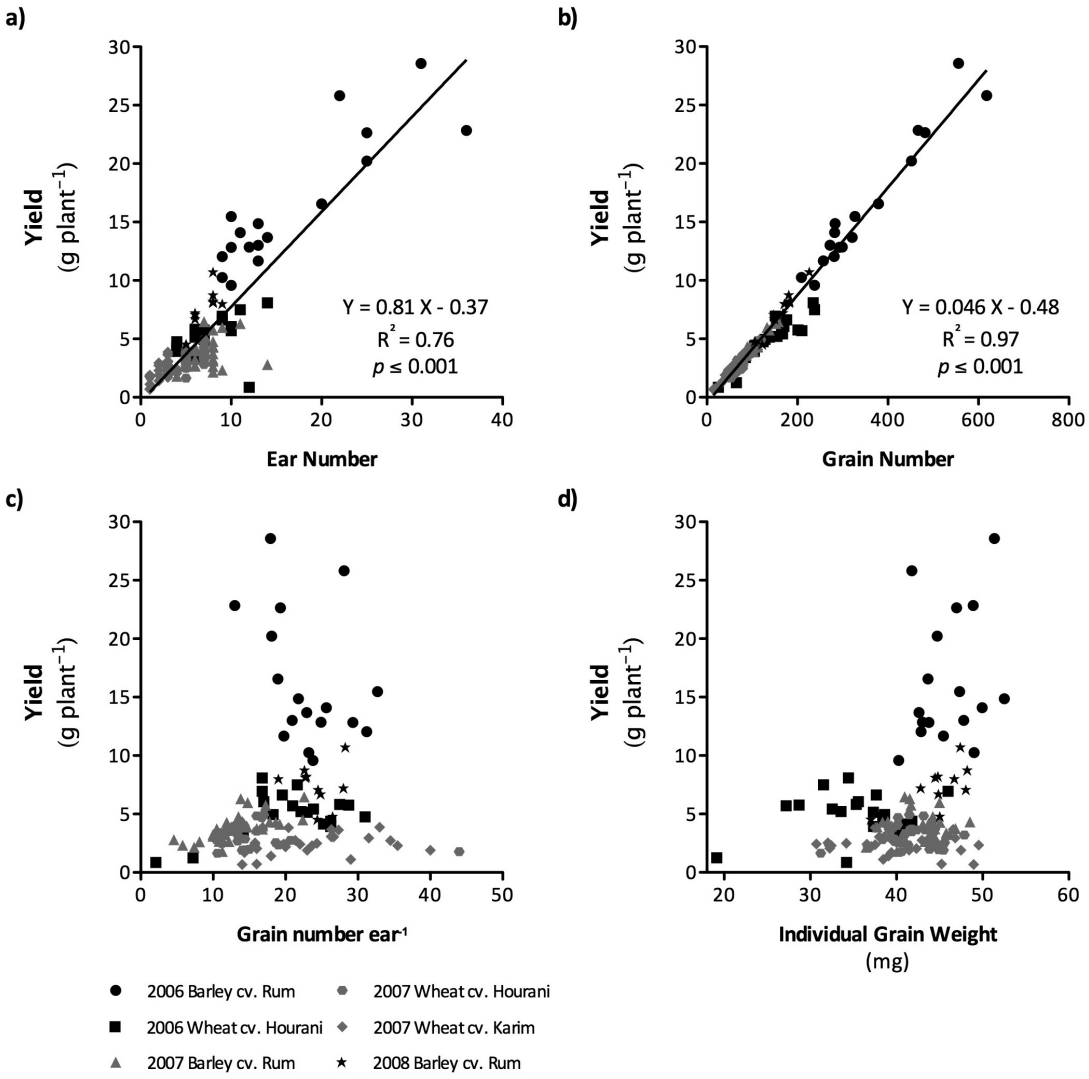

Figure 4.12 Linear regression of grain yield per plant versus ear number (**a**), grain number (**b**), grain number ear^{-1} (**c**) and individual grain weight (**d**). For barley cv. Rum, wheat cv. Hourani and wheat cv. Karim, subjected to full irrigated and droughted treatments (2006/07/08) at three levels of N fertilizer (2006/07 - 0, 50 and 100 kg N ha^{-1} equivalents). For yield versus grain number ear^{-1} and individual grain weight, regressions were not significant and are therefore not shown. Points on figures represent for each genotype include all irrigation x N treatment combinations,

4.3.4 Straw and grain partitioning per tiller category

4.3.4.1 2006

In Figure 4.13 and Figure 4.14 the detailed dry weight partitioning of straw and grain according to tiller category is shown: main shoot (MS), fertile shoots from tiller 1 to 3 (T1-3), from tiller 4 onwards (T4+) and infertile tillers (IS), for the 2006 experiment.

Total straw weight (TSW) was overall much higher ($p \leq 0.001$) for barley cv. Rum than wheat cv. Hourani, 13.6 g cf. and 7.7 g respectively (Figure 4.13). Drought decreased

TSW ($p \leq 0.001$) for barley cv. Rum and wheat cv. Hourani by 40 and 12%, respectively ($p \leq 0.05$; Figure 4.13). There was a trend for an increase in TSW with N application ($p = 0.10$) with N50 increasing it by 21% when averaged across genotypes and irrigation treatments (Figure 4.13). Regarding the tiller cohorts, the percentage of TSW in the MS was higher under drought than under the full irrigation treatment ($p \leq 0.01$), for both barley cv. Rum and wheat cv. Hourani, 60% and 12% higher respectively (Figure 4.13). The T1-3 cohort straw weight overall corresponded to 43% TSW for wheat cv. Hourani (3.2 g) and 27% barley cv. Rum (3.5 g; ($p \leq 0.001$), and overall increasing by 12% for wheat and 56% for barely under drought ($p \leq 0.05$). Overall for barley cv. Rum, straw weight on the T4+ category contributes with 58% (8.8 g) of the TSW, contrasting with only 24% (2.3 g) for wheat cv. Hourani ($p \leq 0.001$). Straw dry weight in the T4+ category decreased by 25% for barley cv. Rum and 37% for wheat cv. Hourani under drought ($p \leq 0.01$; Figure 4.13).

Grain weight (GW) on the main shoot overall represented only 10.3% (1.6 g) of the total Y for barley cv. Rum but 24.7% for wheat cv. Hourani (1.2 g, $p \leq 0.001$; Figure 4.14). There was an interaction between species and irrigation ($p \leq 0.001$) with GW in the MS contributing 11% more for the plant yield under drought than under full irrigation but only for wheat cv. Hourani (Figure 4.14). Though the percentage GW in the T1-3 category was higher for wheat cv. Hourani than barley cv. Rum, 54.9% and 34.5% respectively ($p \leq 0.001$), the absolute T1-3 grain weight was 2.1 g higher for barley cv. Rum ($p \leq 0.001$; Figure 4.14). Grain weight on T4+ was the major contributing tiller cohort for barley cv. Rum plant yield, corresponding to 55% of yield averaged across N and irrigation treatments, while for wheat cv. Hourani it was only 20% of the yield ($p \leq 0.001$). Drought decreased the grain weight on T4+ ($p \leq 0.001$) by 54% for barley cv. Rum and 69% for wheat cv. Hourani (Figure 4.14).

Overall effects in TSW and Y between treatments were mainly associated with differences in the T4+ cohort weight. Therefore it seems that increasing tillering was the main determinant in increasing both plant growth and Y (Figure 4.13 and Figure 4.14). Although regarding genotype differences not only overall reflected plant growth but also HI (Table 4.7), barley cv. Rum allocating relative more of its dry weight in Y than wheat cv. Hourani.

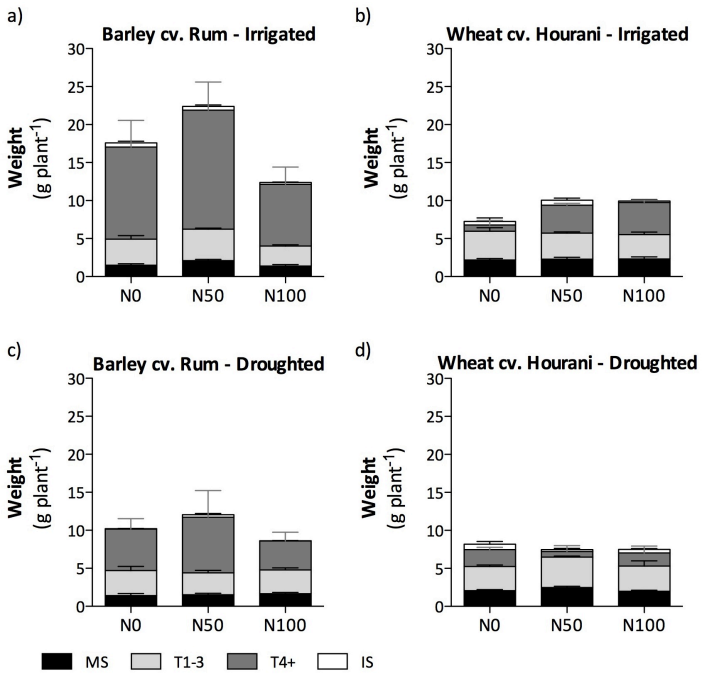

Figure 4.13 Straw weight (g plant^{-1}) partitioning per tiller category (main shoot - MS, fertile shoots from tiller 1 to 3 – T1-3, from tiller 4 onwards – T4+ and infertile shoots - IS) at harvest for barley cv. Rum and durum wheat cv. Hourani with full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1} equivalents, N0, N50 and N100 respectively) during the 2006 experiment. Error bars represent SE of the mean, df = 22.

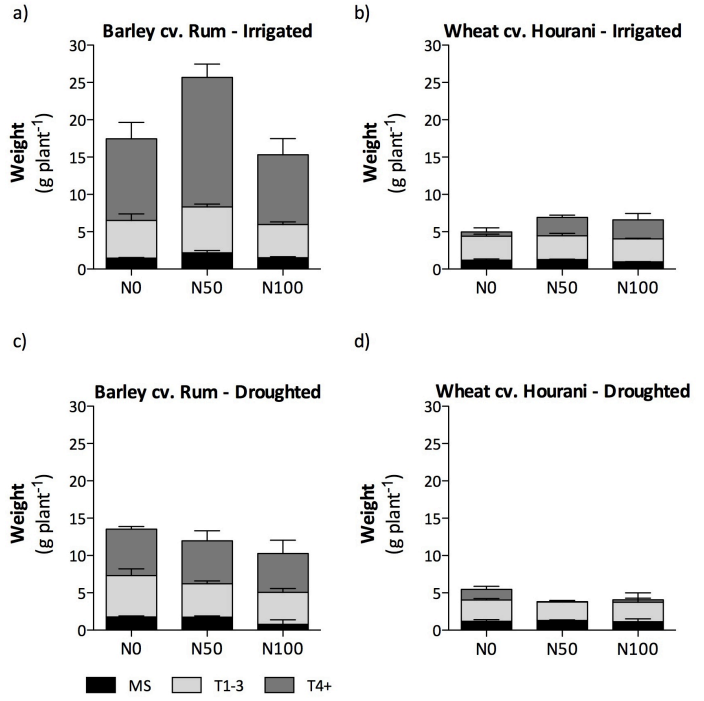

Figure 4.14 Grain weight (g plant^{-1}) per tiller category (main shoot - MS, fertile shoots from tiller 1 to 3 – T1-3 and from tiller 4 onwards – T4+) for barley cv. Rum and wheat cv. Hourani with full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1} equivalents, N0, N50 and N100 respectively) during the 2006 experiment. Error bars represent SE of the mean, df = 22.

4.3.4.2 2007

In 2007, for barley cv. Rum averaging across treatments, drought decreased TSW by 40%, though no significant effect was found for N application (Figure 4.15).

For barley cv. Rum averaging across N treatments, drought decreased the straw weight in all the shoot categories by: 15% for MS and T1-3 ($p \leq 0.05$), 45% for T4+ ($p \leq 0.05$), and 86% for IS ($p \leq 0.01$; Figure 4.15 a, d). Furthermore, when averaging across N treatments irrigated barley cv. Rum plants had an extremely large proportion of straw biomass allocated to IS, 22.3% compared to only 5.4% under drought ($p \leq 0.01$; Figure 4.15 a, d). N did not have a statistically significant effect on the straw weight or proportion of straw weight for the different shoot categories analysed.

For barley cv. Rum MS GW contributed 23.6 % (0.76 g) of the plant grain yield under drought but only 19.4% (0.84 g) under irrigation ($p \leq 0.01$; Figure 4.16 a, d). Also grain weight tended to be higher under irrigation than under drought in both the T1-3 ($p = 0.055$) and T4+ categories ($p = 0.065$) respectively (Figure 4.16 a, d).

For wheat cv. Karim TSW did not differ between N application and irrigation treatments, overall averaging 1.9 g (Figure 4.15 b, e). Averaging across N treatments, the proportion of straw biomass in the MS was 72.0% (1.3 g) under drought and 59.8% (1.2 g) under irrigation ($p \leq 0.05$); and 27.0 (0.6 g) and 38.7% (0.8 g), respectively, for T1-T3 ($p \leq 0.05$). Percentage of TSW in T4+ cohort was negligible (Figure 4.15 b, e).

Y for wheat cv. Karim was mainly contributed by the MS and T1-3 cohorts (Figure 4.16 b, e). Under drought MS was responsible for 76% (1.6 g) of Y and 61% (1.5) when irrigated ($p \leq 0.01$; Figure 4.16 b, e). In contrast the relative percentage of Y on T1-3 cohort was 63% higher ($p \leq 0.01$) under irrigation (1.1 g) when compared to drought treatment (0.6 g; Figure 4.16 b, e).

The TSW for wheat cv. Hourani was 23% higher under irrigation (3.8 g) than under drought (3.1 g; $p \leq 0.05$), and decreased by 22% with N50 and 30% for N100 ($p \leq 0.01$; Figure 4.15 c, f). Straw weight on the MS for wheat cv. Hourani was not affected by the treatments applied (Figure 4.15 c, f). Straw weight on the T1-3 shoot category was lower under drought than irrigation ($p \leq 0.05$), 2.1 g and 1.5 g, respectively, when averaged across N treatments (Figure 4.15 c, f). N fertilizer application, however, had a negative effect on straw weight on T1-3 ($p \leq 0.05$), in both irrigated and drought treatments. Averaging across irrigated treatments, N50 decreased grain weight by 27% and N100 by 43% compared to N0 (Figure 4.15 c, f). T4+ straw weight for N0 across irrigation treatments was 4.2% (0.20 g) of the TSW (Figure 4.15 c, f). Overall average IS weight for wheat cv. Hourani was only 0.4 % (0.01 g; Figure 4.15 c, f).

Restricted water availability did not significantly affect grain weight on the different shoot categories for wheat cv. Hourani (Figure 4.15 c, f). When averaged across irrigation treatments, N application decreased grain weight ($p \leq 0.05$) in the T1-3 category by 23 and 39% for the N50 and N100 applications, respectively (Figure 4.15 c, f). The percentage of total yield on the T4+ category was 5.4% for N0 under irrigation and 4.6% under drought; for N50 and N100 there were no fertile shoots on the T4+ cohort (Figure 4.15 c, f).

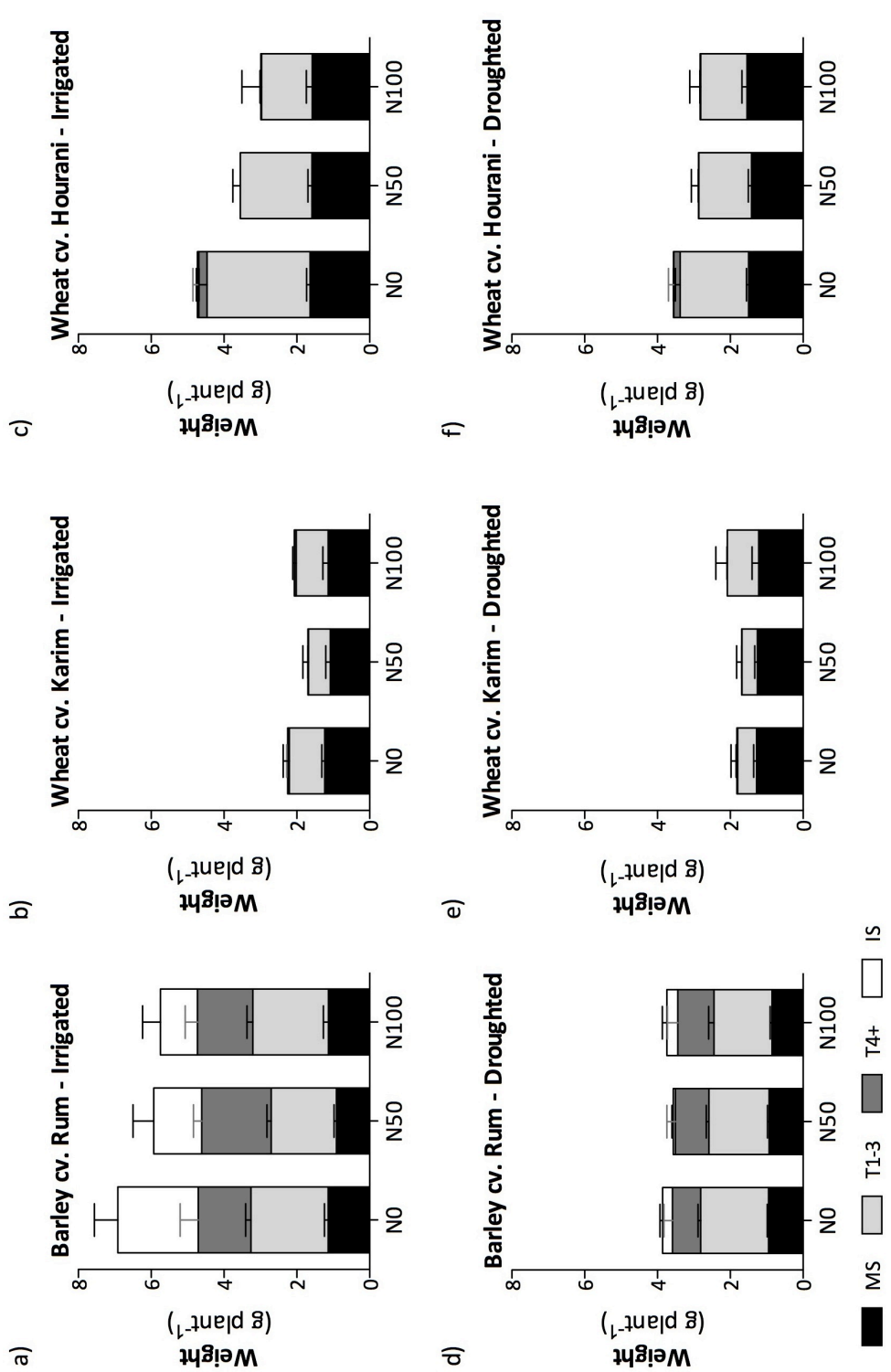

Figure 4.15 Straw dry weight (g plant^{-1}) per shoot category (main shoot - MS, fertile shoots from tiller 1 to 3 – T1-3, from tiller 4 onwards – T4+ and infertile shoots - IS) at harvest for barley cv. Rum (a and d), durum wheat cv. Kariml (b and e) and durum wheat cv. Hourani (c and f) with full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1} equivalents, N0, N50 and N100 respectively) during the 2007 experiment. Error bars represent SE of the mean, df = 22.

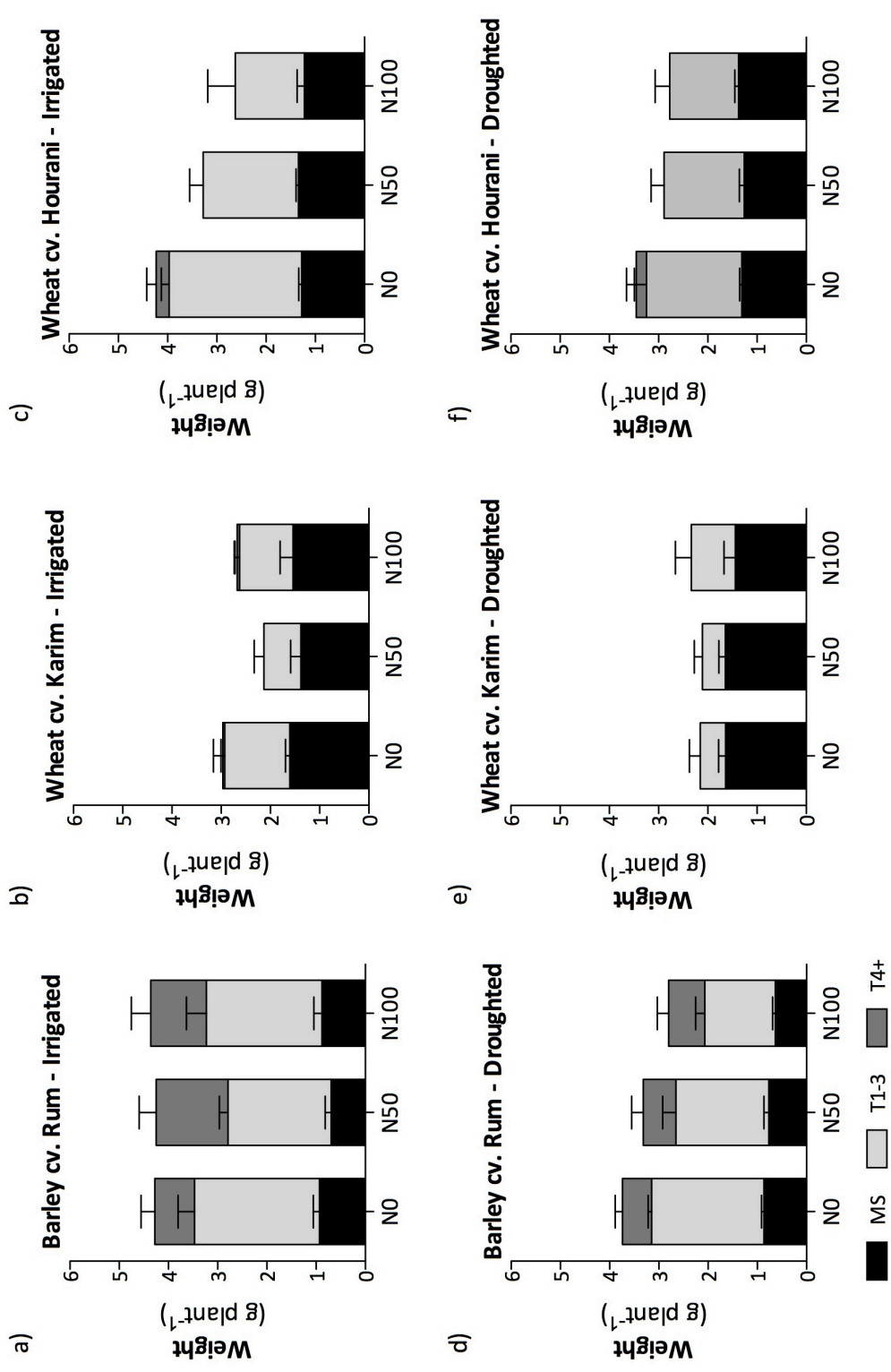

Figure 4.16 Grain dry weight (g plant^{-1}) per shoot category (main shoot - MS, fertile shoots from tiller 1 to 3 – T1-3 and from tiller 4 onwards – T4+ for barley cv. Rum (a and d), wheat cv. Karim (b and e) and wheat cv. Hourani (c and f) with full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1} equivalents, N0, N50 and N100 respectively) during the 2007 experiment. Error bars represent SE of the mean, df = 22.

4.3.4.3 2008

The TSW for barley cv. Rum in 2008 decreased ($p \leq 0.01$) by 43% under drought (4.3 g) compared to under full irrigation (8.0 g; Figure 4.17 a). The percentage of TSW in the MS under drought was 23% (1.0 g) while under full irrigation it was only 12% (1.0 g; $p \leq 0.01$). The proportion of TSW in the T1-3 cohort did not differ significantly between irrigation treatments, whereas 20% more of TSW ($p \leq 0.05$) was present in the T4+ category for the irrigated than the droughted treatment (Figure 4.17 a). TSW in IS did not significantly differ between treatments.

The proportion of Y on the MS did not significantly differ between full irrigation and water limitation (Figure 4.17 b), whereas that on the T1-3 was 25% higher under drought (3.6 g) when compared to the irrigated treatment (4.1 g). For the full irrigation treatment, the proportion of Y in the T4+ (3.1 g) was approximately double ($p \leq 0.05$) of that for the droughted plants (1.2 g; Figure 4.17 b), accounting for 38% of Y.

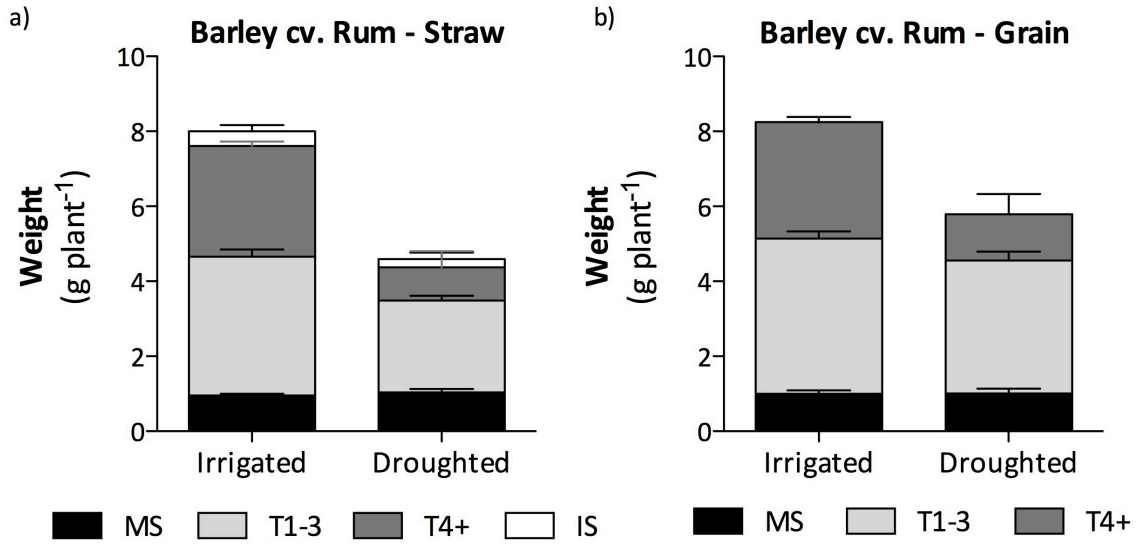

Figure 4.17 Straw (**a**) and grain (**b**) dry weight (g plant^{-1}) per shoot category (main shoot - MS, fertile shoots from tiller 1 to 3 – T1-3 and from tiller 4 onwards – T4+ and infertile shoots for barley cv. Rum, under full irrigated and droughted treatments, during the 2008 experiment. Error bars represent SE of the mean, df = 6.

4.4 PLANT WATER STATUS AND SPAD ASSESSMENT

The water content (WC) of the plant was assessed in three different ways: plant water content (PWC), leaf water content (LWC) and leaf relative water content (LRWC). PWC and LWC are an indication of the WC in the plant and leaf, respectively. The LRWC gives the WC in relation to the maximum WC (turgid WC) that a leaf can contain; it is associated with leaf anatomy and can indicate possible adaptation of the plant to stresses. SPAD provides a measurement of the greenness of the leaf, and is strongly correlated with nitrate content and chlorophyll concentration in the leaf (Montemurro *et al.*, 2006).

4.4.1 2006

At 67 DAS, when averaged across N and irrigation treatments, barley cv. Rum (GS31) had 4% higher PWC ($p \leq 0.001$) than wheat cv. Hourani (GS23). Although LWC and LRWC did not significantly differ between species, averaging overall 85% cf. and 80%, respectively (Table 4.12).

At 102 DAS overall PWC was 8% higher ($p \leq 0.001$) for wheat cv. Hourani (GS55) than barley cv. Rum (Table 4.12). Drought decreased PWC by 10% for barley cv. Rum, but not for wheat cv. Hourani ($p \leq 0.001$). N application did not significantly affect PWC (Table 4.12). Averaging across N and irrigation treatments, LWC for barley cv. Rum at 123 DAS was 82% compared with 83% for wheat cv. Hourani ($p \leq 0.01$). There was a trend ($p \leq 0.08$) for a decrease of LWC with drought by 1.5% for barley cv. Rum and 1.1% for wheat cv. Hourani, when averaged across N treatments (Table 4.12). LRWC did not statistically differ between barley and durum wheat, though when averaged across species and irrigation treatments it tended ($p \leq 0.08$) to decrease by 1% with N50 and 4% with N100 (Table 4.12).

Overall PWC of wheat cv. Hourani at 123 DAS was 19% higher ($p \leq 0.001$) than for barley cv. Rum (Table 4.12). Drought had a negative effect on PWC decreasing it by

10% but only for barley cv. Rum ($p \leq 0.001$; Table 4.12). There was a species x irrigation interaction on LWC ($p \leq 0.001$), with drought decreasing LWC by 3% when averaged across N treatments for barley cv. Rum but not wheat cv. Hourani (Table 4.12). Drought also had a negative impact on LRWC but only for barley cv. Rum, decreasing it by 14% ($p \leq 0.01$), when averaged across N treatments. Neither differences between species nor N application treatments were statistically different (Table 4.12).

Overall SPAD values were higher for barley cv. Rum when compared to wheat cv. Hourani for both 102 DAS and 123 DAS, 64% and 28% higher respectively (Table 4.12; $p \leq 0.001$). There was an interaction of species x irrigation x nitrogen ($p \leq 0.05$) at 102 DAS with N50 decreasing SPAD by 10% but only for barley cv. Rum and under irrigation (Table 4.12). Averaging across N treatments SPAD values at 123 DAS decreased by 11% with drought but only for barley cv. Rum ($p \leq 0.01$; Table 4.12). At 123 DAS, there was an overall trend ($p \leq 0.07$) for an increase in SPAD with N50 under irrigation when compared to N0 and N100 (Table 4.12).

Table 4.12 Plant water content (PWC), leaf water content (LWC), leaf relative water content (LRWC) and SPAD assessment for barley cv. Rum and durum wheat cv. Hourani under full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents N0, N50 and N100 respectively) at 67, 102 and 120 DAS during the 2006 experiment.

Species	Irrigation	Fertilizer N (kg N ha^{-1})	PWC (%)			LWC (%)			LRWC (%)			SPAD	
			67 DAS	102 DAS	123 DAS	67 DAS	102 DAS	123 DAS	67 DAS	102 DAS	123 DAS	102 DAS	123 DAS
Barley cv. Rum	**Irrigated**	**0**	85.4	82.8	69.2	84.9	82.7	83.2	82.0	82.4	81.9	49.8	38.0
		50	83.6	82.2	72.1	83.9	83.5	82.4	77.3	84.0	80.7	45.0	41.2
		100	85.0	80.0	73.1	85.8	83.0	83.7	82.5	83.7	83.3	49.5	38.8
		Mean	*84.7*	*81.7*	*71.5*	*84.9*	*83.1*	*83.1*	*80.6*	*83.4*	*82.0*	*48.1*	*39.3*
	Droughted	**0**	84.3	78.9	65.4	84.9	83.0	81.1	82.6	84.4	74.7	49.8	35.3
		50	84.9	79.7	63.5	86.5	81.9	80.3	84.3	83.8	69.5	51.1	34.0
		100	84.5	79.4	64.2	83.3	80.6	80.1	77.5	81.3	68.2	50.2	36.1
		Mean	*84.6*	*79.3*	*64.4*	*84.9*	*81.8*	*80.5*	*81.4*	*83.2*	*70.8*	*50.4*	*35.2*
Wheat cv. Hourani	**Irrigated**	**0**	81.6	88.4	80.9	83.7	86.2	82.9	75.8	88.5	75.2	29.7	27.7
		50	80.9	88.2	82.3	85.1	87.0	84.6	82.0	85.5	80.4	31.6	30.7
		100	81.5	86.2	80.8	82.8	86.7	81.8	73.4	84.4	76.9	28.6	29.0
		Mean	*81.3*	*87.6*	*81.3*	*83.9*	*86.6*	*83.1*	*77.0*	*86.1*	*77.5*	*29.9*	*29.1*
	Droughted	**0**	81.8	86.4	78.7	86.2	84.7	83.0	81.0	87.0	78.1	30.5	29.0
		50	80.3	87.6	82.0	86.6	85.8	83.9	79.6	85.3	79.4	30.2	29.2
		100	81.1	86.7	81.3	85.3	86.5	84.4	78.7	79.7	79.7	29.2	29.5
		Mean	*81.1*	*86.9*	*80.7*	*86.0*	*85.7*	*83.8*	*79.7*	*84.0*	*79.1*	*30.0*	*29.2*
		SED (df)											
		Species (22)	0.55^{***}	0.73^{***}	1.77^{***}	0.74^{ns}	0.59^{***}	0.52^{**}	1.95^{ns}	1.19^{ns}	2.01^{ns}	0.74^{***}	0.69^{***}
		Irrigation (22)	0.55^{ns}	0.73^{*}	1.77^{***}	0.74^{ns}	0.59^{ns}	0.52^{ns}	1.95^{ns}	1.19^{ns}	2.01^{*}	0.74^{ns}	0.69^{**}
		Nitrogen (22)	0.68^{ns}	0.89^{ns}	2.17^{ns}	0.91^{ns}	0.72^{ns}	0.63^{ns}	2.39^{ns}	1.45^{ns}	2.46^{ns}	0.90^{ns}	0.84^{ns}
		*Species*Irrigation (22)*	0.78^{ns}	1.03^{ns}	2.50^{***}	1.05^{ns}	0.84^{ns}	0.73^{**}	2.76^{ns}	1.68^{ns}	2.84^{**}	1.04^{ns}	0.97^{**}
		*Species*Nitrogen (22)*	0.96^{ns}	1.26^{ns}	3.07^{ns}	1.29^{ns}	1.02^{ns}	0.90^{ns}	3.38^{ns}	2.05^{ns}	3.48^{ns}	1.27^{ns}	1.19^{ns}
		*Irrigation*Nitrogen (22)*	0.96^{ns}	1.26^{ns}	3.07^{ns}	1.29^{ns}	1.02^{ns}	0.90^{ns}	3.38^{ns}	2.05^{ns}	3.48^{ns}	1.27^{ns}	1.19^{ns}
		*Species * Irrigation * Nitrogen (22)*	1.35^{ns}	1.78^{ns}	4.34^{ns}	1.82^{ns}	1.45^{ns}	1.27^{ns}	4.78^{ns}	2.90^{ns}	4.92^{ns}	1.80^{*}	1.68^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and *ns* for a non significant result for the ANOVA test.

4.4.2 2007

In 2007 for barley cv. Rum at 75 DAS (GS51) overall PWC, LWC and LRWC were respectively, 83, 84 and 89% (Table 4.13). At anthesis none of the plant water status parameters was significantly affected by the treatments applied being: 70, 80 and 81% for PWC, LWC and LRWC, respectively when averaged across treatments (Table 4.13).

SPAD at anthesis for barley cv. Rum in 2007, when averaged across N treatments, decreased by 4% with restricted water availability. However N fertilizer had no significant effect on SPAD values (Table 4.13).

Table 4.13 Plant water content (PWC), leaf water content (LWC), leaf relative water content (LRWC) and SPAD assessment for barley cv. Rum in full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}equivalents, N0, N50 and N100, respectively) at 75 DAS and anthesis (GS61) during the 2007 experiment.

		Barley cv. Rum						
Irrigation	**Fertilizer N** (kg N ha^{-1})	**PWC (%)**		**LWC (%)**		**LRWC (%)**		**SPAD**
		75 DAS	**GS61**	**75 DAS**	**GS61**	**75 DAS**	**GS61**	**GS61**
Irrigated	**0**	83.6	69.3	83.5	79.9	89.6	77.8	51.8
	50	83.4	70.1	84.2	80.6	89.0	80.5	51.2
	100	82.0	71.6	85.2	79.7	88.2	83.2	50.7
	Mean	*83.0*	*70.3*	*84.3*	*80.1*	*88.9*	*80.5*	*51.2*
Droughted	**0**	83.0	69.5	83.7	80.7	89.3	81.6	47.6
	50	83.4	70.1	84.4	80.4	86.6	80.6	49.2
	100	83.7	69.3	83.4	80.5	89.8	80.8	50.6
	Mean	*83.4*	*69.6*	*83.8*	*80.5*	*88.6*	*81.0*	*49.1*
	SED (df)							
	Irrigation (20)	0.53^{ns}	0.51^{ns}	0.50^{ns}	0.38^{ns}	1.08^{ns}	1.22^{ns}	0.86^{*}
	Nitrogen (20)	0.65^{ns}	0.62^{ns}	0.68^{ns}	0.46^{ns}	1.33^{ns}	1.49^{ns}	1.06^{ns}
	*Irrigation*Nitrogen (20)*	0.92^{ns}	0.88^{ns}	0.97^{ns}	0.65^{ns}	1.87^{ns}	2.11^{ns}	1.50^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

In 2007, the overall PWC at 75 DAS for wheat cv. Karim (GS39) was 82%, and 81% for both LWC and LRWC (Table 4.14). Averaging across N treatments, drought had a negative effect on all the plant water status parameters considered, decreasing PWC by 6% ($p \leq 0.05$), LWC by 3% ($p \leq 0.05$) and trended ($p = 0.15$) to decrease LRWC by 7% (Table 4.14).

N application did not significantly affect SPAD measurements. However SPAD values when averaged across N treatments, were 20% higher under irrigation (Table 4.14).

Table 4.14 Plant water content (PWC), leaf water content (LWC), leaf relative water content (LRWC) and SPAD assessment for durum wheat cv. Karim in full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}equivalents, N0, N50 and N100 respectively) at 75 DAS and anthesis (GS61) during the 2007 experiment.

		Wheat cv. Karim						
Irrigation	**Fertilizer N** (kg N ha^{-1})	**PWC (%)**		**LWC (%)**		**LRWC (%)**		**SPAD**
		75 DAS	**GS61**	**75 DAS**	**GS61**	**75 DAS**	**GS61**	**GS61**
Irrigated	**0**	82.3	61.2	82.4	72.1	81.2	69.3	39.1
	50	82.6	61.2	83.2	75.5	81.9	76.9	34.0
	100	81.4	57.3	80.2	73.4	79.1	75.4	36.0
	Mean	*82.1*	*59.9*	*81.9*	*73.6*	*80.7*	*73.9*	*36.3*
Droughted	**0**	82.2	57.0	80.3	71.2	79.0	66.5	30.1
	50	83.0	55.7	81.7	72.1	82.9	70.0	28.9
	100	81.6	57.0	81.1	70.6	81.4	69.8	29.3
	Mean	*82.2*	*56.6*	*81.0*	*71.3*	*81.1*	*68.8*	*29.4*
	SED (df)							
	Irrigation (20)	0.44^{ns}	1.07^{*}	0.85^{ns}	1.55^{*}	2.16^{ns}	3.38^{ns}	1.98^{**}
	Nitrogen (20)	0.54^{ns}	1.31^{ns}	1.04^{ns}	1.90^{ns}	2.64^{ns}	4.14^{ns}	2.43^{ns}
	*Irrigation*Nitrogen (20)*	0.76^{ns}	1.85^{ns}	1.47^{ns}	2.68^{ns}	3.74^{ns}	5.85^{ns}	3.44^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

4.4.3 2008

Plant water status values for barley cv. Rum at 28 DAS in 2008 were the highest over the three experiments (Table 4.12, Table 4.13 and Table 4.15). From 28 DAS to anthesis PWC and LRWC decreased by 13% and LWC by 18%. However, irrigation treatments did not significantly affect plant water status (Table 4.15). SPAD values for irrigated and droughted plants were 49.9 and 46.0, respectively, though that difference was not significant ($p = 0.11$; Table 4.15).

Table 4.15 Plant water content (PWC), leaf water content (LWC), leaf relative water content (LRWC) and SPAD assessment for barley cv. Rum in full irrigated and droughted treatments at 28 DAS and anthesis during the 2008 experiment.

	Barley cv. Rum						
Irrigation	**PWC (%)**		**LWC (%)**		**LRWC (%)**		**SPAD**
	28 DAS	**GS61**	**28 DAS**	**GS61**	**28 DAS**	**GS61**	**GS61**
Irrigated	89.8	78.3	93.5	76.9	89.3	77.9	49.9
Droughted	89.7	77.2	91.5	77.7	89.0	80.3	46.0
SED (df)							
Irrigation (6)	0.28^{ns}	3.60^{ns}	1.04^{ns}	1.50^{ns}	0.38^{ns}	2.40^{ns}	2.17^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

In summary, spring barley compared to both durum wheat genotypes overall had a slightly higher PWC initially in the season. Though at anthesis, wheat cv. Hourani registered the highest values of PWC and LWC of the three genotypes. LRWC for barley cv. Rum at anthesis was generally higher when compared to both spring wheat varieties, possibly associated with reaching anthesis sooner, under relatively more "moderate" temperatures and lower water deficits. For wheat cv. Hourani plant water status measured at anthesis, as PWC, LWC and LRWC, seemed largely unaffected by water deficits, in contrast for wheat cv. Karim, all these parameters were negatively affected by drought. For barley cv. Rum at anthesis, drought decreased PWC, LWC and LRWC in 2006 though no effect was found in 2007 and 2008. N effects on plant water status were generally not significant.

SPAD values at anthesis for barley cv. Rum were respectively 68 and 53% higher than wheat cv. Hourani (2006) and wheat cv. Karim (2007). Drought decreased or tended to decrease SPAD values at anthesis for both barley cv. Rum and wheat cv. Karim, but SPAD for wheat cv. Hourani seems unaffected by water deficits. Generally no effects were found for N application treatment on SPAD assessments, with only a small increase with N50 for barley cv. Rum and Wheat cv. Hourani but only under irrigation.

4.5 WATER-USE EFFICIENCY

In this work WUE was assessed in four different ways: (i) as the AGDW (g) at harvest divided by the actual water used (l) by the plant from transplantation to harvest (WUE); (ii) the slope of the linear regression forced through the origin of the cumulative AGDW and the cumulative water used with time; (iii) the grain yield (Y, g) at harvest divided by the actual water used by the plant (l) from transplantation to harvest (WUE_{grain}); and (iv) by the $\Delta^{13}C$ in the grain at harvest.

4.5.1 2006

In 2006 averaging across N and irrigation treatments, WUE measured at harvest and WUE_{grain} was 58 and 125%, respectively, higher for barley cv. Rum when compared to wheat cv. Hourani ($p \leq 0.001$; Table 4.16). Averaging across N treatments drought increased WUE by 151% for barley cv. Rum and 153% for wheat cv. Hourani ($p \leq 0.001$; Table 4.16). For WUE, interactions for species x irrigation ($p \leq 0.001$), Irrigation x nitrogen ($p \leq 0.05$) and species x irrigation x nitrogen ($p \leq 0.005$) were found (Table 4.16). Thus for barley, cv. Rum N100 decreased WUE when compared with N0 and N50 for both irrigated and drought treatments. While N50 for barley cv. Rum did not significantly affect WUE under irrigation, it increased it under drought. For wheat cv. Hourani both N50 and N100 increased WUE under irrigation but in contrast decreased WUE under drought (Table 4.16). WUE_{grain} increased with drought ($p \leq 0.001$) but relatively more for barley cv. Rum (158%) compared to wheat cv. Hourani (128%)

(Table 4.16). There was an effect of N application ($p \leq 0.01$) and N application x irrigation ($p \leq 0.05$) on WUE_{grain}. With N50 and N100 applications overall decreasing WUE by 16 and 41%, respectively, under water limitations but not when full irrigated (Table 4.16). The $\Delta^{13}C$ of grain was not significantly affected by genotypes or N application. While irrigation increased $\Delta^{13}C$ by 7.6% for barley cv. Rum and by 5.6% for wheat cv. Hourani (Table 4.16).

Table 4.16 Total water-use efficiency (WUE) calculated from 52DAS (transplantation) to harvest, grain water-use efficiency (WUE_{grain}) and $\Delta^{13}C$ of grain for barley cv. Rum and durum wheat cv. Hourani in full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1} equivalents, N0, N50 and N100 respectively) for the 2006 experiment.

Species	Irrigation	Fertilizer N (kg N ha^{-1})	WUE (g l^{-1})	WUE_{grain} (g l^{-1})	$\Delta^{13}C$ of grain (‰)
Barley cv. Rum	**Irrigated**	**0**	1.74	0.87	21.4
		50	1.72	0.92	21.3
		100	1.12	0.62	21.1
		Mean	*1.53*	*0.80*	*21.3*
	Droughted	**0**	3.96	2.28	19.8
		50	4.52	2.28	19.8
		100	3.03	1.65	19.3
		Mean	*3.84*	*2.07*	*19.6*
Wheat cv. Hourani	**Irrigated**	**0**	0.83	0.34	20.7
		50	0.97	0.40	21.6
		100	1.08	0.43	21.5
		Mean	*0.96*	*0.39*	*21.3*
	Droughted	**0**	3.34	1.36	20.1
		50	2.23	0.78	19.6
		100	1.71	0.52	20.5
		Mean	*2.43*	*0.89*	*20.1*
		SED (df)			
		Species (22)	*0.150****	*0.097****	*0.207*^{ns}
		Irrigation (22)	*0.150****	*0.097****	*0.207****
		Nitrogen (22)	*0.184***	*0.119***	*0.254*^{ns}
		*Species*Irrigation (22)*	*0.212**	*0.138****	*0.293*^{ns}
		*Species*Nitrogen (22)*	*0.260*^{ns}	*0.168*^{ns}	*0.359*^{ns}
		*Irrigation*Nitrogen (22)*	*0.260**	*0.168**	*0.359*^{ns}
		*Species*Irrigation*Nitrogen (22)*	*0.368**	*0.238*^{ns}	*0.508*^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

4.5.2 2007

In 2007, drought significantly increased WUE, by 26, 45 and 49% respectively for barley cv. Rum, wheat cv. Karim and wheat cv. Hourani, when averaged across N treatments (Table 4.17). Also WUE_{grain} was positively affected by water deficits, by 45% for barley cv. Rum ($p \leq 0.01$), 39% for wheat cv. Karim ($p \leq 0.05$) and 57% for wheat cv. Hourani, when averaged across N treatments ($p \leq 0.001$; Table 4.17). The $\Delta^{13}C$ for grain for barley cv. Rum and wheat cv. Hourani was not affected by irrigation treatments; in contrast, drought decreased $\Delta^{13}C$ for wheat cv. Karim ($p \leq 0.001$; Table 4.17). N application generally did not significantly affect WUE, WUE_{grain} or $\Delta^{13}C$.

4.5.3 2008

Barley cv. rum WUE and WUE_{grain} increased by 123 and 146%, respectively, with water deficits ($p \leq 0.001$). While $\Delta^{13}C$ decreased by 5% with drought ($p \leq 0.05$; Table 4.18).

Table 4.17 Water-use efficiency (WUE), from 55DAS (transplantation) to harvest, grain water-use efficiency (WUE_{grain}) and $\Delta^{13}C$ of grain for barley cv. Rum, wheat cv. Karim and wheat cv. Hourani with full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents, N0, N50 and N100 respectively) for the 2007 experiment.

Irrigation	Fertilizer N (kg N ha^{-1})	Barley cv. Rum			Wheat cv. Karim			Wheat cv. Hourani		
		WUE ($g\ l^{-1}$)	WUE_{grain} ($g\ l^{-1}$)	$\Delta^{13}C$ of Grain (‰)	WUE ($g\ l^{-1}$)	WUE_{grain} ($g\ l^{-1}$)	$\Delta^{13}C$ of Grain (‰)	WUE ($g\ l^{-1}$)	WUE_{grain} ($g\ l^{-1}$)	$\Delta^{13}C$ of Grain (‰)
Irrigated	**0**	1.20	0.46	21.9	0.86	0.49	22.7	1.05	0.50	22.2
	50	1.10	0.46	21.9	0.65	0.36	22.7	0.94	0.45	22.2
	100	1.04	0.45	22.0	0.82	0.46	22.8	0.73	0.34	21.8
	Mean	*1.11*	*0.45*	*22.0*	*0.78*	*0.44*	*22.7*	*0.91*	*0.43*	*22.1*
Droughted	**0**	1.49	0.73	22.0	1.10	0.59	22.1	1.47	0.73	21.9
	50	1.40	0.67	21.8	1.13	0.63	22.3	1.32	0.66	22.8
	100	1.32	0.57	21.7	1.14	0.60	22.1	1.26	0.63	21.5
	Mean	*1.40*	*0.66*	*21.8*	*1.12*	*0.61*	*22.2*	*1.35*	*0.67*	*22.0*
	SED (df)									
	Irrigation (20)	0.090^{**}	0.061^{**}	0.15^{ns}	0.112^{**}	0.064^{*}	0.147^{***}	0.098^{***}	0.054^{***}	0.37^{ns}
	Nitrogen (20)	0.110^{ns}	0.074^{ns}	0.19^{ns}	0.138^{ns}	0.078^{ns}	0.180^{ns}	0.120^{ns}	0.067^{ns}	0.45^{ns}
	*Irrigation*Nitrogen (20)*	0.155^{ns}	0.105^{ns}	0.26^{ns}	0.195^{ns}	0.111^{ns}	0.255^{ns}	0.170^{ns}	0.094^{ns}	0.63^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ns for a non significant result for the ANOVA test.

Table 4.18 Water use efficiency (WUE) from 28DAS to harvest, grain water-use efficiency (WUE_{grain}) and $\Delta^{13}C$ of grain for barley cv. Rum in full irrigated and droughted treatments for the 2008 experiment.

Irrigation	Barley cv. Rum		
	WUE (g l^{-1})	**WUE_{grain}** (g l^{-1})	**$\Delta^{13}C$ of grain** (‰)
Irrigated	0.81	0.41	21.0
Droughted	1.81	1.01	19.9
SED (df)			
Irrigation (6)	*0.376**	*0.203**	*0.482**

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

4.5.4 Season-long water-use efficiency

The season-long WUE was also calculated as the slope of the simple linear regression (forced through the origin) between cumulative WU and AGDM produced from the first sampling point to harvest, and is presented in Figure 4.18 to Figure 4.20. A summary table with estimated WUE, WUE 95% *CI*, and R^2 and significance (*p*) of the fitted regressions is presented in Table 4.19. Parallel regression analysis by groups was performed using GenStat 12th edition in order to compare treatments (slope of linear regressions).

4.5.4.1 2006

For both barley cv. Rum and wheat cv. Karim in 2006 WUE, measured as the slope of the linear regression of ABGW by WU, was generally higher under drought than full irrigation (Figure 4.18 and Table 4.19). For barley cv. Rum under irrigation N100 application decreased WUE, for both irrigated and drought treatments when compared with N0 and N50 (Figure 4.18 a and Table 4.19). Furthermore, N application had a negative impact on WUE under water limitations for wheat cv. Hourani, though under irrigation the opposite was observed (Figure 4.18 b and Table 4.19).

Analysing overall effects of species, irrigation and N application treatments using parallel linear regression analysis, WUE was higher ($p \leq 0.001$) for barley cv. Rum (1.90 g l^{-1}, R^2 = 0.60) than wheat cv. Hourani (1.16 g l^{-1}, R^2 = 0.64); and WUE increased ($p \leq 0.001$) with drought (3.19 g l^{-1}, R^2 = 89) when compared to full irrigation (1.52 g l^{-1}, R^2 = 88). Comparison of N treatments, revealed no differences in WUE.

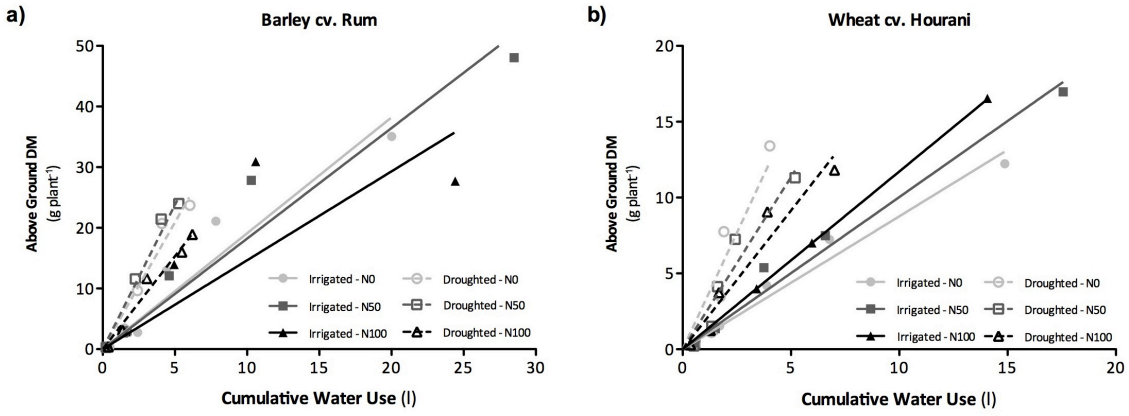

Figure 4.18 Linear regression forced through the origin (Y = slope * X) of the cumulative aboveground dry matter (g plant $^{-1}$) on cumulative water use (l) from 52DAS to harvest for barley cv. Rum (a) and durum wheat cv. Hourani (b) under full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1} equivalents, N0, N50 and N100 respectively) for the 2006 experiment. For further details of the linear regressions *vide* Table 4.19.

4.5.4.2 2007

In 2007, for barley cv. Rum WUE values were relatively lower than in 2006, particularly for the plants submitted to water limitations (Figure 4.18 a, Figure 4.19 a and Table 4.19). Values of WUE for wheat cv. Karim were generally lower than for barley cv. Rum. Furthermore, drought generally increased WUE for genotypes but to a higher extent for barley cv. Rum than for wheat cv. Karim (Figure 4.19 and Table 4.19).

For barley cv. Rum, drought overall increased WUE ($p \leq 0.001$) from 1.12 g l^{-1} when irrigated to 1.36 g l^{-1}. In contrast WUE averaged across irrigation treatments was not affected by N application; furthermore by parallel regression analysis a common curve was defined for all N fertilizer levels, constituting a WUE value of 1.19 g l^{-1} (R^2 = 0.89).

When analysed through parallel regression analysis, wheat cv. Karim had higher WUE under drought (0.59 g l^{-1}, R = 0.48) than under full irrigation (0.93 g l^{-1}; R^2 = 0.36). There were no significant differences between N treatments.

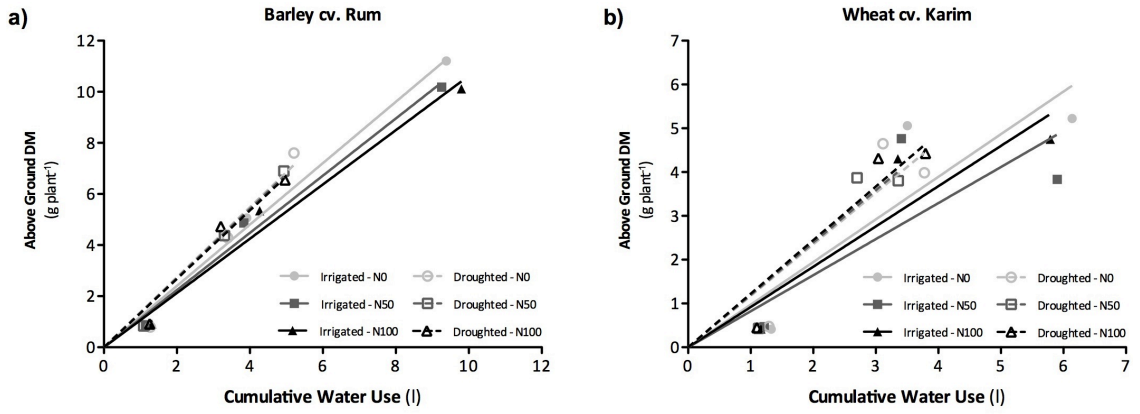

Figure 4.19 Linear regression forced through the origin (Y = slope * X) of the aboveground dry matter (g plant $^{-1}$) on cumulative water use (l) from 55DAS to harvest for barley cv. Rum and durum wheat cv. Karim under full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1} equivalents, N0, N50 and N100 respectively) for the 2007 experiment. For further details of the linear regression *vide* Table 4.19.

4.5.4.3 2008

As reported in previous years, plants subjected to drought (1.67 g l^{-1}) had higher WUE than under full irrigation (0.83 g l^{-1}) (Figure 4.20).

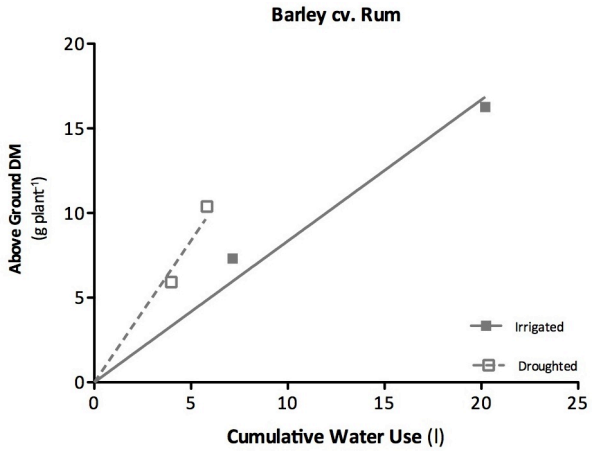

Figure 4.20 Linear regression forced through the origin (Y = slope * X) of the aboveground dry matter (g plant $^{-1}$) on cumulative water use (l) from 28DAS to harvest for barley cv. Rum under full irrigated and droughted treatments for the 2007 experiment. For details of the linear regression *vide* Table 4.19.

Table 4.19 Water-use efficiency (g l^{-1}) measured as the slope of the regression between cumulative AGDW on cumulative water used (for fitted regressions see Figures 4.18, 4.19 and 4.20), WUE 95% confidence interval (CI), and R^2 and probability of significance (*p*) for barley cv. Rum, durum wheat cv. Hourani and durum wheat cv. Karim under full irrigated and/ or droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) for the 2006 (df = 14), 2007 (df = 14) and 2008 experiments (df = 8).

Species	Irrigation	Fertilizer N (kg N ha^{-1})	WUE (g l^{-1})	*WUE 95% CI*	R^2	*p*
				2006		
	Irrigated	**0**	1.91	1.56 to 2.26	0.80	***
		50	1.82	1.58 to 2.07	0.89	***
		100	1.47	1.02 to 1.91	0.50	***
	Drought	**0**	4.18	3.61 to 4.75	0.87	***
		50	4.76	4.20 to 5.31	0.90	***
		100	3.07	2.56 to 3.57	0.80	***
				2007		
Barley cv. Rum	**Irrigated**	**0**	1.20	1.11 to 1.30	0.95	***
		50	1.12	1.01 to 1.23	0.92	***
		100	1.06	0.95 to 1.18	0.90	***
	Drought	**0**	1.37	1.22 to 1.52	0.89	***
		50	1.36	1.19 to 1.52	0.85	***
		100	1.34	1.21 to 1.47	0.89	***
				2008		
	Irrigated	**50**	0.83	0.76 to 0.91	0.92	***
	Drought	**50**	1.67	1.38 to 1.96	0.60	***
				2006		
	Irrigated	**0**	0.88	0.79 to 0.97	0.93	***
		50	1.00	0.91 to 1.10	0.95	***
Wheat cv. Hourani		**100**	1.17	1.08 to 1.26	0.97	***
	Drought	**0**	3.07	2.55 to 3.58	0.83	***
		50	2.27	1.99 to 2.55	0.89	***
		100	1.83	1.54 to 2.11	0.85	***
				2007		
	Irrigated	**0**	0.97	0.78 to 1.17	0.64	***
		50	0.82	0.60 to 1.05	0.41	***
Wheat cv. Karim		**100**	0.92	0.76 to 1.08	0.73	***
	Drought	**0**	1.18	0.93 to 1.42	0.63	***
		50	1.19	0.99 to 1.40	0.71	***
		100	1.22	0.93 to 1.52	0.58	***

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non Significant result for the ANOVA test.

4.6 LIGHT RESPONSE CURVES (LRC)

Gas exchange measurements were performed at 119 and 134 DAS (17 and 32 days after GS61, respectively) for barley cv. Rum. At 119 DAS the maximum photosynthetic rate (A_{max}), transpiration (E) and stomatal conductance (g_s) were measured at a PAR of 2000 μmol m^{-2} s^{-2} and the WUE_{ph} (A_{max}/ E) calculated (Table 4.20). At 134 DAS LRC were performed using photosynthetic rate (A) measurements at a PAR of 100, 200, 300, 600, 900, 1200 and 2000 μmol m^{-2} s^{-2}. The A value measured at 2000 μmol m^{-2} s^{-2} was considered as A_{max}, and at this PAR the E and g_s were recorded and the WUE_{ph} calculated (Table 4.21). Fitting the Prioul & Chartier (1977) equation to the LRC the A_{max} was estimated ($Aest_{max}$) as well as the apparent quantum yield (q'), light compensation point (LCP) and light saturation point (LSP).

As expected when averaged across N treatments A_{max} and E measured at 119 DAS were higher under full irrigation (Table 6.15). There was also a trend (p = 0.11) for a reduction in g_s with drought by 30% when averaging across N treatments. Regarding the WUE_{ph}, N applications decreased WUE_{ph} by 20 and 18% under irrigation with N50 and N100, respectively, while under drought N50 increased WUE_{ph} 34% (Table 6.15).

At 134 DAS, A_{max} measured at 2000 μmol m^{-2} s^{-2} and $Aest_{max}$ from the LRC decreased with drought under N0 and N50 applications ($p \leq 0.05$; Table 4.21). E, g_s, WUE_{ph} were not statistically affected by the treatments applied, while ϕ increased with drought ($p \leq$ 0.05) by 50% and LCP by 183% ($p \leq 0.05$; Table 4.21). There was an effect of irrigation ($p \leq 0.001$) and irrigation x nitrogen on LSP, such that drought decreased LSP under N0 and N50 applications but not under N100 (Table 4.21).

Table 4.20 Maximum photosynthetic rate (A_{max}) rate, transpiration (E), stomatal conductance (g_s), and WUE measured at 2000 (µmol m^{-2} s^{-1}) for barley cv. Rum in full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) at 119 DAS for the 2007 experiment.

Irrigation	Fertililizer (kg N ha^{-1})	Barley cv. Rum			
		A_{max} (µmol m^{-2} s^{-1})	E (mol m^{-2} s^{-1})	g_s (mmol m^{-2} s^{-1})	WUE_{ph} (mmol CO_2 mol^{-1} H_20)
Irrigated	**0**	12.19	2.13	203	5.73
	50	14.23	3.06	299	4.57
	100	12.72	2.66	323	4.72
	Mean	*13.05*	*2.62*	*275*	*5.01*
Droughted	**0**	10.84	2.28	255	4.71
	50	7.27	1.25	124	6.31
	100	9.08	2.11	201	4.22
	Mean	*9.06*	*1.88*	*194*	*5.08*
	SED (df)				
	Irrigation (15)	1.84^{*}	0.34^{*}	47.5^{ns}	0.25^{ns}
	Nitrogen (15)	2.25^{ns}	0.42^{ns}	58.2^{ns}	0.31^{*}
	*Irrigation*Nitrogen (15)*	3.18^{ns}	0.59^{ns}	82.3^{ns}	0.44^{***}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

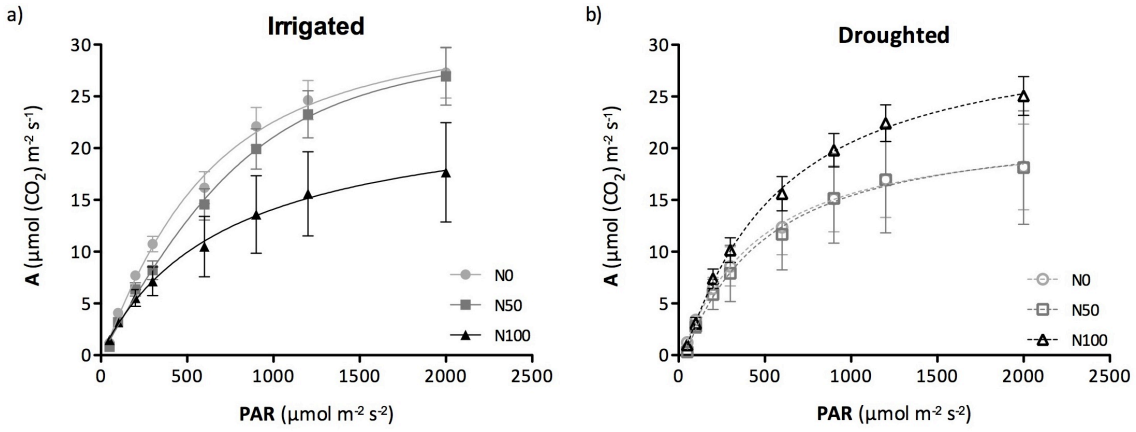

Figure 4.21 Light response curves (LRC) fitted with the Prioul & Chartier equation (1977) for barley cv. Rum in full irrigated (**a**) and droughted (**b**) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1} equivalents, N0, N50 and N100 respectively) at 134 DAS for the 2007 experiment (details for the curves parameters in Table 4.14.

Table 4.21 Maximum photosynthetic (A_{max}) rate measured at a PAR of 2000 (μmol m^{-2} s^{-1}) and estimated from the light response curve fitting (Figure 6.21), transpiration (E), stomatal conductance (g_s), WUE_{ph} measured at 2000 (mmol m^{-2} s^{-1}); and parameters estimated by fitting the Prioul & Chartier equation (1977) to light response curves: estimated Amax, apparent quantum yield (q') light compensation point (LCP) and light saturation point (LSP) for barley cv. Rum in full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) at 134 DAS for the 2007 experiment.

		Barley cv. Rum							
Irrigation	**Fertililizer** (kg N ha^{-1})	**A_{max}** (μmol m^{-2} s^{-1})	**$Aest_{max}$** (μmol m^{-2} s^{-1})	**E** (mol m^{-2} s^{-1})	**g_s** (mmol m^{-2} s^{-1})	**WUE_{ph}** (mmol CO_2 $mol^{-1}H_20$)	**q'**	**LCP** (μmolm^{-2} s^{-1})	**LSP** (μmol m^{-2} s^{-1})
Irrigated	**0**	27.3	33.4	6.0	667	5.80	0.046	10.3	781
	50	26.9	33.8	4.9	701	5.50	0.034	12.1	1024
	100	17.7	22.6	3.4	419	5.20	0.032	8.2	718
	Mean	*24.0*	*29.9*	*4.8*	*595*	*5.50*	*0.037*	*10.2*	*841*
Droughted	**0**	18.2	23.0	3.8	517	5.00	0.049	15.4	503
	50	18.2	25.3	3.4	452	5.60	0.057	35.6	481
	100	24.8	33.1	5.0	706	5.10	0.055	28.9	669
	Mean	*20.4*	*27.1*	*4.1*	*558*	*5.23*	*0.054*	*26.6*	*551*
	SED (df)								
	Irrigation (15)	2.41^{ns}	3.13^{ns}	0.79^{ns}	96.8^{ns}	0.58^{ns}	0.0062^{*}	3.72^{***}	69.1^{***}
	Nitrogen (15)	2.95^{ns}	3.84^{ns}	0.97^{ns}	118.6^{ns}	0.71^{ns}	0.0076^{ns}	4.56^{ns}	84.6^{ns}
*Irrigation*Nitrogen (15)*		4.17^{*}	5.43^{*}	1.37^{ns}	167.7^{ns}	1.00^{ns}	0.0107^{ns}	6.45^{ns}	119.7^{*}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

4.7 NUE

For all three experiments the N concentration in the plant material was analysed and the data used to calculate the NUE = Grain yield/N available (soil N+ fertilizer N). The NUE (NupE x NutE) can then be separated into NupE (Total plant N-uptake/ N available), and NutE (Grain yield/ Total plant N-uptake).

4.7.1 2006

In 2006, the NUE for barley cv. Rum overall was 2.9 times higher ($p \leq 0.001$) than for wheat cv. Hourani (Table 4.22). Averaging across N applications, drought decreased NUE ($p \leq 0.001$), but to a higher extent for ($p \leq 0.01$) barley cv. Rum (37%) than wheat cv. Hourani (16%; Table 4.22). There was an interaction between species x nitrogen ($p \leq 0.01$), with N50 and N100 decreasing NUE by 19 and 59%, respectively, for barley cv. Rum when averaged across irrigation treatments. In contrast, differences between means were not statistically different for wheat cv. Hourani (Table 4.22). Irrigation and N treatments interacted ($p \leq 0.05$), with N100 decreasing NUE under irrigation but not under N50. For wheat cv. Hourani increasing N fertilizer application decreased NUE by 45 and 25% with N50 and N100, respectively (Table 4.22).

Results of NupE in 2006 were extremely high, demonstrating that there was a high mineralization in the soil columns. NupE was 53% higher for barley cv. Rum than wheat cv. Hourani ($p \leq 0.001$). Full irrigation increased the NupE ($p \leq 0.001$), but only significantly for barley cv. Rum ($p \leq 0.01$; Table 4.22). NupE decreased with N application ($p \leq 0.001$) for both barley cv. Rum and wheat cv. Hourani ($p \leq 0.05$; Table 4.22). There was also an interaction between irrigation and N application, with a higher decrease on NupE with N fertilizer application under irrigation than under drought ($p \leq 0.05$; Table 4.22).

NutE for barley cv. Rum was 44% higher than for wheat cv. Hourani (Table 4.22). N application did not statistically affect NutE (Table 4.22). There was a trend ($p = 0.08$) for an interaction between species x irrigation, with drought increasing NutE by 17% for barley cv. Rum but no increase for wheat cv. Hourani (Table 4.22).

Table 4.22 N uptake efficiency (NupE), N utilization efficiency (NutE) and N use efficiency (NUE), for barley cv. Rum and wheat cv. Hourani with full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1} equivalents, N0, N50 and N100 respectively) for the 2006 experiment.

Species	Irrigation	Fertilizer N (kg N ha^{-1})	NupE (g g^{-1})	NutE (g g^{-1})	NUE (g g^{-1})
Barley cv. Rum	**Irrigated**	**0**	4.53	22.3	100.3
		50	3.99	25.1	97.8
		100	1.76	25.2	43.7
		Mean	*3.43*	*24.2*	*80.6*
	Droughted	**0**	2.65	30.4	77.7
		50	1.75	26.4	45.6
		100	1.03	27.8	29.3
		Mean	*1.81*	*28.2*	*50.9*
Wheat cv. Hourani	**Irrigated**	**0**	1.53	18.8	28.6
		50	1.45	18.3	26.4
		100	1.04	17.8	18.2
		Mean	*1.34*	*18.3*	*24.4*
	Droughted	**0**	1.71	18.4	31.4
		50	0.91	16.1	14.6
		100	0.80	20.0	15.8
		Mean	*1.14*	*18.2*	*20.6*
		SED (df)			
		Species (22)	0.207^{***}	1.13^{***}	3.95^{***}
		Irrigation (22)	0.207^{***}	1.13^{ns}	3.95^{***}
		Nitrogen (22)	0.254^{***}	1.39^{ns}	4.84^{***}
		*Species*Irrigation (22)*	0.293^{**}	1.60^{ns}	5.59^{**}
		*Species*Nitrogen (22)*	0.359^{*}	1.96^{ns}	6.58^{**}
		*Irrigation*Nitrogen (22)*	0.359^{*}	1.96^{ns}	6.58^{*}
		*Species*Irrigation*Nitrogen (22)*	0.508^{ns}	2.77^{ns}	9.69^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

4.7.2 2007

For barley cv. Rum in 2007, NUE was 28% higher under full irrigation than under water limitation ($p \leq 0.05$; Table 4.23), when averaged across N treatments. Averaging across irrigation treatments, N50 decreased NUE by 22% and N100 by 37% (Table 4.23) compared to N0.

NupE decreased from 0.541 g g^{-1} under irrigation to 0.302 g g^{-1} under drought ($p \leq 0.001$; Table 4.23). Furthermore NupE, decreased with N application ($p \leq 0.01$) by 23 and 37% with N50 and N100, respectively.

Averaging across N treatments NutE increased by 6.0 g g^{-1} ($p \leq 0.01$) under drought Table 4.23).

For durum wheat cv. Karim drought had no statistically significant effect on NUE, though N decreased it by 31% for both N50 and N100 applications compared to N0 ($p \leq 0.05$), when averaged across irrigation treatments (Table 4.23). NupE decreased with N application, with values of 0.132 g g^{-1} with N50 and 0.129 g g^{-1} with N100 compared to 0.183 g g^{-1} at N0, when averaged across irrigation treatments ($p \leq 0.05$; Table 4.23). Neither irrigation nor N had a significant effect on NutE (Table 4.23).

Irrigation did not statistically change NUE for wheat cv. Hourani. However, N application decreased NUE by 33 and 50% with N50 and N100, respectively (Table 4.23). NupE significantly decreased by 21% with drought ($p \leq 0.01$); and by 33 and 50% with N application of N50 and N100 application ($p \leq 0.01$) when averaged across N and irrigation treatments, respectively (Table 4.23).

Table 4.23 N-uptake efficiency (NupE), N-utilization efficiency (NutE) and N-use efficiency (NUE), for barley cv. Rum, wheat cv. karim and wheat cv. Hourani with full irrigated and droughted treatments and three levels of N fertilizer (0, 50 and 100 kg N ha^{-1} equivalents, N0, N50 and N100 respectively) for the 2007 experiment.

Irrigation	Fertilizer N (kg N ha^{-1})	Barley cv. Rum			Wheat cv. Karim			Wheat cv. Hourani		
		NupE (g g^{-1})	NutE (g g^{-1})	NUE (g g^{-1})	NupE (g g^{-1})	NutE (g g^{-1})	NUE (g g^{-1})	NupE (g g^{-1})	NutE (g g^{-1})	NUE (g g^{-1})
Irrigated	**0**	0.682	14.5	9.91	0.210	32.8	6.87	0.409	24.3	9.81
	50	0.508	16.0	8.17	0.132	30.2	4.11	0.264	23.9	6.31
	100	0.433	16.0	7.17	0.134	32.8	4.40	0.182	23.5	4.32
	Mean	*0.541*	*15.5*	*8.42*	*0.159*	*31.9*	*5.13*	*0.285*	*23.9*	*6.81*
Droughted	**0**	0.371	23.6	8.66	0.155	31.8	5.00	0.291	27.3	8.01
	50	0.301	21.1	6.39	0.131	30.8	4.06	0.209	26.3	5.56
	100	0.235	19.7	4.61	0.124	30.1	3.84	0.179	25.3	4.56
	Mean	*0.302*	*21.5*	*6.55*	*0.136*	*30.9*	*4.30*	*0.226*	*26.3*	*6.04*
	SED (df)									
	Irrigation (20)	0.0240^{***}	1.68^{**}	0.822^{*}	0.0153^{ns}	1.07^{ns}	0.552^{ns}	0.0203^{**}	0.88^{*}	0.576^{ns}
	Nitrogen (20)	0.0249^{**}	2.06^{ns}	1.007^{**}	0.0187^{*}	1.32^{ns}	0.677^{*}	0.0248^{***}	1.07^{ns}	0.706^{***}
	*Irrigation*Nitrogen (20)*	0.0416^{ns}	2.91^{ns}	1.424^{ns}	0.026^{ns}	1.86^{ns}	0.957^{ns}	0.0351^{ns}	1.52^{ns}	0.998^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

4.7.3 2008

In the 2008 experiment, NUE and NupE decreased by 30 ($p \leq 0.01$) and 53% ($p \leq 0.05$) with drought when averaged across N treatments, respectively (Table 4.24). Contrarily NutE increased by 46% with drought ($p \leq 0.05$; Table 4.24).

Table 4.24 N-uptake efficiency (NupE), N-utilization efficiency (NutE) and N-use efficiency (NUE) for barley cv. Rum with full irrigated and droughted treatments for the 2008 experiment.

Irrigation	**NupE** (g g^{-1})	**NutE** (g g^{-1})	**NUE** (g g^{-1})
Irrigated	0.91	19.0	16.9
Droughted	0.44	27.8	11.9
SED (df)			
Irrigation (6)	*0.100***	*2.69**	*1.42**

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a significant result for the ANOVA test.

In summary, treatment effects on NUE and its components (NupE and NutE) were variable between years. For barley cv. Rum, drought consistently decreased the NUE and NupE, while increasing NutE. NutE increased with drought for barley cv. Rum in all years, and for wheat cv. Hourani in 2007. Generally NUE decreased with N application and water deficits. NupE was also negatively affected by drought and N applications, and it was the main contributor to the differences in NUE observed between the treatments in the experiments (Figure 4.22).

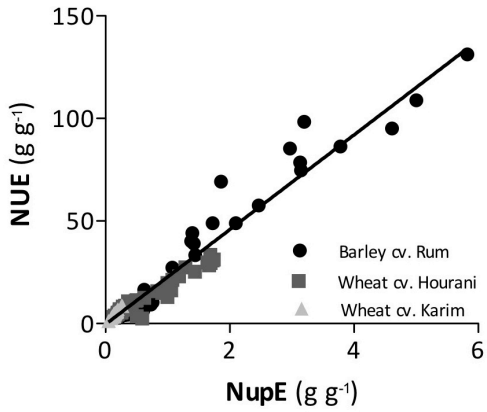

Figure 4.22 Linear regression of NupE on NUE (y = 23.08x – 0.35; $R^2 = 0.95$; $p \leq 0.001$) at harvest for all the plants analysed in the 2006, 2007 and 2008 experiments. Data include full irrigated and droughted treatments, as well as N application treatments (0, 50 and 100 kg N ha^{-1}, equivalents).

4.8 DISCUSSION

The aboveground responses for the three experiments are presently discussed. First the general plant development and growth are discussed after which a detailed analysis of the AGDW partitioning through the different plant components is set out (4.8.1 Plant development). The yield results as well as a thorough analysis of the distribution of yield per tiller cohort, and plant water status are also included. This discussion finishes with a detailed analysis of the experimental differences in WUE (section 4.8.4 Water-use efficiency) and NUE (section 4.8.5 NUE) and their components.

4.8.1 Plant development, shoot production and biomass growth

The 50% AW_{FC} drought treatment was imposed 15 days after transplantation, and increased to 25% AW_{FC} after barley cv. Rum reached anthesis, thus simulating the drought that is usually incurred in the South Mediterranean. Due to the difference in plant development between barley cv. Rum and the two durum wheat varieties, the more intense drought occurred for the wheat varieties relatively earlier in their development.

Barley cv. Rum reached GS31 sooner than both durum wheat varieties (cv. Hourani and Karim) by 17 days in 2007 and 3/4 days in 2008. The differences between 2007 and 2008 are associated with the high temperatures in 2008 after transplantation, where the growth of all durum wheat genotypes was accelerated and the development differences between durum wheat and barley diminished. GS61 was reached 4-21 days sooner for barley cv. Rum than wheat varieties. However, physiological maturity of the plant was generally reached later for barley cv. Rum than wheat cvs Hourani and Karim associated with an extended phase of tiller production for barley. For all genotypes plants submitted to water limitations reached maturity sooner than the irrigated plants. Evidence for more rapid development of barley than durum wheat was demonstrated by previous glasshouse and field experiments in Jordan by Ebrahim (2008), where barley cv. Rum reached GS31, GS61 and GS91, 12, 8 and 14 days sooner than wheat cv. Hourani. Similar differences were also found by Cossani *et al.* (2009) in field-grown barley (cv. Sunrise) and durum wheat (cv. Claudio) in NW Spain, with the former reaching G31 6 days and GS61 6/ 7 days before than the latter. Cossani *et al.* (2009) found durum wheat to reach maturity earlier under rain-fed than under irrigated conditions in dry years.

When grown in the field in Jordan wheat cv. Hourani and cv. Karim have similar biomass and yields to the spring barley cv. Rum (Ebrahim, 2008). However, in the present study, in both 2006 and 2007, the growth and yields of the durum wheat varieties were significantly lower than for spring barley cv. Rum.

AGDW of genotypes in 2007 was much lower than in 2006, associated with lower tillering in 2007. The decrease in fertile-shoot number in 2007 was possibly caused by a combination of: i) lower light conditions in the growth room vernalization phase; ii) relatively higher temperatures after transplantation (average maximum 33.9 ºC); iii) lower water available due to the soil type in 2007 than 2006 and iV) high soil bulk density might have cause root growth limitation.

Barley cv. Rum fertile-shoot number was consistently higher than for durum wheat as also reported by Simpson & Siddique (1994), while wheat cv. Hourani produced more fertile shoots than wheat cv. Karim. Drought generally decreased the shoot number for barley cv. Rum and wheat cv. Karim at harvest, while no significant effect was found for wheat cv. Hourani in the two years. The decrease in tillering with drought in durum

wheat and barley is frequently reported in previous investigations (Brisson *et al.*, 2001; Pandey *et al.*, 2001; Baburai Nagesh, 2006; Ebrahim, 2008).

One of the most common responses of crops to N fertilization is an increase in the number of fertile shoots. Ebrahim (2008) reported experiments with barley cv. Rum and wheat cv. Hourani showing an increase in the number of fertile tillers with N application in both glasshouse and field experiments. Increase in fertile shoots with N fertilizer was also described by Fischer (1993) in experiments with spring wheat in Australia. Similar results were found by Abad *et al.* (2004) for durum wheat growing in Spanish Mediterranean conditions; and in winter wheat by Pask (2009). However in this work overall N application effects on tillering were only apparent for barley cv. Rum in 2006.

Averaging across the three years, drought decreased barley cv. Rum green area per plant by 19.2% at anthesis. In 2006 it can be seen that GA under irrigation increases with N application until the end of the grain filling, while for N0, and drought senescence started after drought was imposed. For wheat cv. Hourani (2007) by GS55 drought had already decreased GA by 28%, after which senescence was accelerated. Larger effects of drought were observed for wheat cv. Karim (2007) with drought decreasing GA by 54%. The maintenance of GA for longer (particularly under irrigated treatments) allowed barley cv. Rum to keep growing after anthesis, while for both durum wheat varieties the increase in dry weight after anthesis was small (cv. Hourani) or negligible (cv. Karim).

Overall AGDW with time followed a similar pattern as that of the FS number. As previously mentioned, barley cv. Rum always had higher AGDW than the two durum wheat varieties in the study. Post-anthesis growth is closely and positively correlated with AGDW at harvest and grain yield, as described by Cossani *et al.* (2009). Drought generally decreased the AGDW at harvest for barley cv. Rum (also in 2008) and wheat cv. Hourani, though no effects of drought on AGDW were found for wheat cv. Karim. The negative effect of drought on AGDW was higher for barley cv. Rum (-40 to -33%) than for wheat cv. Hourani (-20 to -14%). In the literature the comparison between the performances of these two species in the field under optimal or in water and/ or N deficit conditions has often produced contradictory results. Simpson & Siddique (1994) in experiments in Mediterranean-type environment found a better performance for

barley than wheat, producing more biomass, higher HI and yields; while Ebrahim (2008) in Jordan field and glasshouse experiments found no difference at harvest between both species, or in their responses to water and N deficits. Lopéz-Castañeda & Richards (1994) in Australia found a higher AGDW and yield for barley when compared to durum wheat. Though recent works of Cossani *et al.* (2007; 2009) in Spain point out for generally similar performances between durum wheat and barley genotypes, but an ability of wheat to maintain yield better at sites of relatively lower yield potential.

Benefits of N fertilization on plant production are well known (Novoa & Loomis, 1981). N generally increases the overall plant growth and yield (Brown *et al.*, 1987b; Latiri-Souki *et al.*, 1998; Lloveras *et al.*, 2001; Ebrahim, 2008; Pask, 2009). However, in the present study, N application effects were generally not significant and often inconsistent or contradictory. For barley cv. Rum the only N effect on AGDW was a slight increase with N50 under irrigation but not with N100 in 2006; while for wheat cv. Hourani both N application levels decreased the AGDW in 2007, under both droughted and full irrigated treatments. Soils in the south Mediterranean are generally poor, having a very low N concentration. N fertilizers, when applied, do not exceed the 50 kg N ha^{-1} for barley cv. Rum and 100 kg N ha^{-1} wheat cv. Hourani and cv. Karim (Thabet *et al.*, 2009). In 2006, not only the initial soil N was more than those found in the South Mediterranean, but also due to the particular environment of the soil columns, soil water and high temperatures throughout the soil profile made the soil prone to mineralisation and therefore increasing the available soil mineral N. In this way soil N availability in the N0 treatment was increased and the N effects were only small, and inconsistent. Reasons for a lack of an N effect in 2007 might be also associated with the soil medium used, though the N concentration in the soil was extremely large by Mediterranean standards it was not really available to the plants, therefore the low growth in 2007 compared to 2006. The unavailability of soil N is associated with the fact that the soil used was constituted by 80% of sand and, consequently, prone to N leaching in the irrigated treatment to the bottom layers of the soil column, were there was an insufficient amount of roots to extract it effectively. For the droughted plants, the N in the soil was not fully available, since the low soil moisture content does not permit an effective N uptake. Figure 5.19 illustrates this fact well, with the higher N content in the soil at harvest being in the upper soil layers for the drought treatments and the opposite

being observed in the irrigation treatments. Additionally the bulk density was exceptionally large in 2007 (1.85 g cm^{-3}). It is well known that mechanical impedance caused by high bulk density can strongly reduce root extension and aboveground growth decreasing yields (Atwell, 1993; Bingham, 2001; Bingham & Bengough, 2003; Clark *et al.*, 2003). Young *et al.* (1997) experiments with wheat and barley seedlings showed that a large and rapid decrease of leaf elongation rates occurred after mechanical impedance of the roots was increased, demonstrating that mechanical impedance of the roots can have a strong negative effect on the aboveground growth even when water and nutrients in the field are abundantly available. This decrease in growth is associated with loss of cell turgor induced by hormone signals (Young *et al.*, 1997). Bingham & Bengough (2003) subjected spring wheat and barley seedlings to different mechanical impedance resistances (bulk densities of 1.1 and 1.4 g cm^{-3}), resulting in smaller leaves and slower tiller formation, consequently decreasing the whole plant weight by 23% and the root length by 46% for barley, and 30% cf. and 45%, respectively for wheat. A decrease in SRL was also reported (Bingham & Bengough, 2003). There is a lack of literature regarding the comparison of spring barley and durum wheat and their capacity to withstand or adapt to mechanical impedance. Recent soil column pot experiments of Price (2009) comparing different wheat varieties and their ability to penetrate 5% and 30% wax layers revealed a higher penetration capacity for wheat cv. Hourani (ratio 30%:5% ≈ 40) than wheat cv. Karim (ratio 30%:5% ≈ 27).

The AGDW partitioning between plant organs revealed different allocation patterns according to genotypes and years. In 2006 neither irrigation nor N application treatments changed the biomass allocation for different plant organs at harvest. The major difference occurred between genotypes with a 132% higher investment in leaves by wheat cv. Hourani than barley cv. Rum, and a 40% higher investment in grains for the latter compared to the former. At harvest in 2007 wheat cv. Hourani invested relatively more of its biomass in leaves than wheat cv. Karim or barley cv. Rum. For barley cv. Rum and wheat cv. Hourani drought generally increased the proportion of AGDW allocated to grain, but decreased it for wheat cv. Karim.

Evaluating the distribution of straw weight per tiller cohort revealed, independently of year and treatment applied, for both barley cv. Rum and durum wheat that infertile shoots were only produced by the plants if T4+ cohort was present, i.e. when the plants

had more than 5 shoots. In 2006, straw weight in IS was only significant for wheat cv. Hourani (5.5%) in 2006 and barley cv. Rum in 2007 and 2008 (13.9 and 4.5%, respectively). Effects of the treatments on partitioning to IS was only found for barley cv. Rum in 2007, with 22.3% of TSW in IS for the irrigated plants compared to 4.5 % to the drought plants. For barley cv. Rum in 2007 the tiller production phase was prolonged to the booting phase of the main shoot, and production of T4+ tillers occurred post-anthesis, when temperatures were high and less time for grain filling was available. The leaching of N deeper in the profile where the RLD was lower and insufficient to acquire all the available N might also have contributed to the high percentage of IS for the irrigated plants. Overall, the differences in the allocation of straw weight per tiller cohort between genotypes and treatments seemed dependent on the number of tillers produced and consequently biomass plant^{-1}, and not due to a particular change in partitioning between tiller cohorts.

4.8.2 Grain yield responses

For wheat cv. Hourani and barley cv. Rum, grain yield decreased from 2006 to 2007 but to a higher extent for the latter. Yield for barley cv. Rum was generally higher than for wheat cv. Hourani or wheat cv. Karim. Although the number of grains per ear was not significantly different for barley cv. Rum than durum wheat varieties in study, the number of ears per plant was higher for barley and hence the higher yields. Higher yields for barley cv. Rum compared to wheat cv. Hourani were previously found by Ebrahim (2008) in glasshouse (30% more) and field experiments (53% more). Furthermore, Cossani *et al.* (2009) in field experiments in Spain found a tendency for higher yields for barley when compared to durum wheat under well irrigated and high N availability conditions (below 50 kg N ha^{-1}), but found no advantage of barley over wheat under nutrient or water limitation conditions.

For barley cv. Rum, drought consistently decreased the number of ears and grains per plant, resulting in lower yields under drought. For wheat cv. Hourani, similar effects to those described for barley cv. Rum were observed in 2006, but not in 2007. For wheat cv. Karim drought decreased the ear number but tended to increase the GN per ear when

compared to full irrigation; these two factors cancelled out resulting in no change in yield between irrigation treatments. In this experiment, treatment effects were related mainly to the tiller growth, more than biomass partitioning. Therefore the absence of a drought effect on yield in 2007 for durum wheat varieties might be associated with its generally poor tillering in this experiment. In 2006 for barley cv. Rum, N50 increased yield by 47% but only under irrigation, due to an increase in ears and GN. For wheat cv. Hourani in 2006, N application was found to increase GN under irrigation while decreasing GN under drought, with effects in the opposite direction found for IGW.

The benefits of N on crop yields are well known, and increases in plant weight and yield with N application in Mediterranean field-grown barley and durum wheat are widely reported (Cooper *et al.*, 1987; Ebrahim, 2008; Cabrera-Bosquet *et al.*, 2009; Cossani *et al.*, 2009). As described by Cossani *et al.* (2009), yield in barley and durum wheat is closely related with the grain number per unit area ($y = 0.046 x - 0.48$; $R^2 = 0.97$; $p \leq 0.001$), and this, in turn, with ear number per unit area. HI is the ratio of yield to AGDW (Passioura, 1983; Passioura, 2006). According to Passioura (1983) HI is closely related with the pattern of water supply, an early drought tends to give higher HI. Averaging across all experiments and treatments, wheat cv. Karim had the highest HI (0.55), followed by barley cv. Rum (0.48) and wheat cv. Hourani (0.46). In 2007 HI for barley cv. Rum was 21% lower than for the 3 year average, due to a large number of IS under irrigation (14% of the total AGDW). N had no effect on HI. Drought increased HI for barley cv. Rum and wheat cv. Hourani, and decreased HI for wheat cv. Karim. HI effects might be closely related with the glasshouse microclimate conditions in the different years. In 2006 and 2008 glasshouse temperatures after transplantation were relatively lower when compared to 2007, for that reason not only the plant development was relatively slow but also evapotranspiration was lower, and consequently the initial drought treatment of 50% AW_{FC} was slowly imposed, and the HI was not significantly affected. In 2007 in the days after transplantation temperatures were relatively high increasing the speed of plant development and evapotranspiration, thus the initial 50% WA_{FC} drought was probably felt more rapidly and intensely for barley cv. Rum and wheat cv. Hourani hence increasing HI. For wheat cv. Karim the increase in drought stress might have been significantly felt only later in the season with 25% AW_{FC} having a negative impact on HI.

Analysing the distribution of total plant grain weight per tiller cohort, it is easily seen that the differences in yield observed by the treatments applied are mainly caused due to an increase in the total grain weight in higher tiller cohorts. Therefore, in the present glasshouse conditions it seems that increasing resource uptake and/or utilization to enhance tiller production and/or survival is key to enhancing yields under water and/or N stresses.

4.8.3 Plant water status

Water status traits have been proposed as criteria for drought improvement in wheat and barley (Merah, 2001). Furthermore, RWC due to its relation with cell volume might reflect better the water supply to the leaf and transpiration rate (Winter *et al.*, 1988b). Therefore at least for bread wheat RWC has been described as a better indicator of water status than water potential (Merah, 2001). Merah (2001) in experiments characterizing 144 genotypes of durum wheat under Mediterranean conditions showed a positive relationship between flag leaf RWC and yield and HI, suggesting its use as a selection tool for breeding.

In the present study the plant water status was measured as PWC, LWC and LRWC. Significant differences on PWC and LWC between the treatments applied were only observed in 2006 for barley cv. Rum, with full irrigation having 3 and 1.5% higher PWC and LWC, respectively, than the drought treatment at anthesis. Similar results were observed for wheat cv. Karim in 2007 with 6 and 3% increases, respectively. Differences in PWC and LWC between species at anthesis are influenced by the rate of plant development. Since the 25% AW_{FC} drought treatment was imposed relatively later for barley cv. Rum, it would be expected to have the highest water content in the leaf compared to both durum wheat varieties at respective developmental stages, and though that happened when compared to wheat cv. Karim it did not when compared to wheat cv. Hourani. This might be associated with a larger leaf weight for wheat cv. Hourani and therefore a higher facility for water storage per leaf.

For all genotypes, although differences in the total AGDW due to drought existed, LRWC at anthesis remained relatively constant, suggesting that plants were able to

adjust their total leaf area, hence growth, to the water available in the soil columns, suffering only a mild water stress, as observed by Cabrera-Bosquet *et al.* (2009) in pot experiments with durum wheat. However, averaging across years LRWC values at anthesis for the full irrigated treatment were generally higher for barley cv. Rum (81%) when compared to wheat cv. Hourani (78%) or wheat cv. Karim (74%). Probably associated with the time of anthesis occurring later in the season for durum wheat, where the transpiration demands are higher due to higher vapour pressure deficits.

4.8.4 Water-use efficiency

Water-use efficiency for barley cv. Rum was higher than for both durum wheat varieties, under full irrigation and drought, and when measured either as AGDW/ WU at harvest or as the slope of the cumulative AGDW by cumulative WU throughout the season. This would be generally consistent with the findings of Araus *et al.* (2003b) that barley is better adapted to the Mediterranean drought conditions than durum wheat. Similar results were found by Ebrahim (2008) for field grown barley cv. Rum and wheat cv. Hourani under rain-fed and supplemental irrigation treatments, and 3 levels of N fertilizer, with barley having a WUE 72% higher than durum wheat. Average WUE measured as AGDW/ WU varied from 0.81 to 1.53 g l^{-1} (2006) under full irrigation and 1.81 to 3.84 g l^{-1} under drought. While for wheat cv. Hourani it varied from 0.91 to 0.96 g l^{-1} and 1.35 to 2.43 g l^{-1}, respectively; and for wheat cv. Karim it was 0.78 and 1.12 g l^{-1} for full irrigation and drought, respectively. This increase of WUE with drought was also observed when calculated as the slope of the cumulative AGDW by cumulative WU. N effects were only observed in 2006, with N application increasing WUE under irrigation for wheat cv. Hourani and decreasing it under drought. In contrast for barley N50 increased WUE under drought. However Ebrahim (2008) in glasshouse experiments with barley cv. Rum and wheat cv. Hourani showed an increase of WUE with N application under both irrigation and drought treatments. In pot experiments using durum wheat Cabrera-Bosquet *et al.* (2007) found an increase of WUE with N application, though they did not find an increase in WUE with drought.

WUE_{grain} is a more economical measurement of the efficiency of use of water for barley and wheat, since it relates the water used to grain yield. WUE_{grain} for barley cv. Rum in 2006 was overall 130% higher than for wheat cv. Hourani, However in 2007 similar values were found amongst all genotypes. The low WUE_{grain} found in 2007 for barley cv. Rum when compared to 2006 is related to a high number of infertile tillers and low grain number in the main shoot due to high temperatures felt during booting. Similar to WUE, WUE_{grain} also increased with drought.

$\Delta^{13}C$ is inversely related to the transpiration efficiency; in this experiment it was measured in the grain. It provides a measurement integrated over time through grain formation to harvest. Using $\Delta^{13}C$ it was not possible to verify the differences in WUE amongst genotypes. However $\Delta^{13}C$ confirmed the lower WUE values under full irrigation for barley cv. Rum in 2006 and 2008, for wheat cv. Hourani in 2006, and for wheat cv. Karim in 2007.

Averaging across N and irrigation treatments, SPAD values at anthesis were consistently higher for barley cv. Rum than wheat cv. Hourani and wheat cv. Karim, 64% (2006) and 53% (2007) higher, respectively. Although not measuring chlorophyll content directly, SPAD is well correlated with it (Markwell *et al.*, 1995). Therefore the chlorophyll content per unit leaf area was higher for barley cv. Rum than durum wheat. Furthermore, at least for durum wheat, transpiration efficiency was shown to be positively correlated with chlorophyll content (Fotovat *et al.*, 2007). Additionally, a positive correlation between SPAD measurements and grain yield was reported (Cabrera-Bosquet *et al.*, 2009). Present results showed barley cv. Rum had a more efficient photosynthetic apparatus due to higher chlorophyll, permitting higher AGDW while having also higher WUE and WUE_{grain}. Although under field conditions increasing SPAD with N application has been reported for barley and durum wheat (Cabrera-Bosquet *et al.*, 2009), in this work N effects were generally not significant. However, drought decreased SPAD at anthesis for barley cv. Rum and wheat cv. Karim, but not for wheat cv. Hourani.

4.8.5 NUE

Irrigation increased or tended to increase, and N fertilizer decreased, N-uptake efficiency for all genotypes, but only significantly for barley cv. Rum. For barley cv. Rum and wheat cv. Hourani in 2007, NutE (grain DW / Nup) was higher under drought than irrigation. However, NutE was not significantly affected by irrigation treatments for wheat cv. Hourani in 2006 and wheat cv. Karim in 2007. Overall, NUE increased in response to irrigation and decreased in response to N fertilizer, mainly associated with the changes in NupE, though the interaction was not statistically significant across experiments. Overall NupE and NUE were higher for barley cv. Rum than durum wheat varieties. These results are consistent with previous reports in the literature for spring barley and durum wheat experiments (Cabrera-Bosquet *et al.*, 2007; Ebrahim, 2008), and winter wheat and barley (Delogu *et al.*, 1998). NUE was found to be closely related with NupE, as formerly observed by Muurinen *et al.* (2006).

4.9 CONCLUSIONS

The results in this section allow the following conclusions to be made:

1. In contrast to field experiments in Mediterranean conditions the AGDW and yields for barley cv. Rum were higher than for the durum wheat varieties in this study. Y and AGDW decreased with water deficits but to a higher extent for barley. In 2006 N50 treatment increased fertile shoot number, AGDW and Y for both barley and wheat;

2. WUE and WUE_{grain} values were higher for barley cv. Rum when compared to durum wheat. Drought had a positive impact on both variables for all genotypes;

3. Grain increased with water availability for barley cv. Rum (2006 and 2008), wheat cv. Hourani (2006) and wheat cv. Karim (2007). N application had no significant effect on $\Delta^{13}C$;

4. NUE was higher for barley cv. Rum than the durum wheat varieties used in this work. NUE for all genotypes decreased with N application and drought, due to differences in NupE. Drought consistently increased NutE for barley cv. Rum, had no effect for wheat cv. Karim, and had no effect for wheat cv. Hourani in 2006 but increased in 2007.

5 ROOT MORPHOLOGY

5.1 INTRODUCTION

The morphology of the root system determines the ability and capacity of the root system to acquire the soil resources. In the present study, root morphology adopts the definition of Lynch (1995), that is: the features of a single root system axis as an organ, including characteristics of the epidermis. Root weight, length, diameter and volume are the components of the root morphology presently considered. This chapter also includes an analysis of the distribution of the weight (RWD), diameter, length (RLD) and volume (RVD) of the root system of whole the plant within the soil profile. Other parameters related with tissue density (SRL and rV:rW) are also examined.

Mechanical impedance refers to the soil matrix resistance against the deformation caused by a growing root (Bennie, 1996), and is considered to be one of the main factors influencing the distribution of roots in the soil (Young & Bengough, 1989). As mechanical impedance increases, root elongation decreases due to an augment of the resistance of soil particles to displacement (Clark *et al.*, 2003). Therefore, roots have difficulty penetrating very hard soils and, consequently, the access to water and nutrients might become restricted leading to a decrease in crop yields (Stirzaker *et al.*, 1996; Clark *et al.*, 2003). Soil bulk density [BD = soil dry weight (g)/ volume of soil (cm^3)] is well correlated with mechanical impedance. For this reason a detailed analysis of the BD per soil-depth layer was performed in the present study.

The main objective of this chapter is to describe and quantify responses of root growth and root: shoot partitioning and related root morphological parameters of Mediterranean spring barley and durum wheat to water and/ or N stresses. The relationship between specific morphological rooting traits and expression of traits (length and volume) will be examined.

The specific hypotheses tested in this chapter are:

1. Mediterranean barley and durum wheat have similar root system morphology, in terms of weight, length, diameter and volume;

2. Comparable distribution of root morphological traits density (RWD, RLD, RVD and diameter) with depth between barley and durum wheat is observed;

3. Root weight and size (measured as volume and length) decrease with water application and increase with N availability, and spring barley and durum wheat responses should be broadly similar;

4. N fertilizer application effects on root DM growth are significantly larger under full irrigation than under drought;

5. Water and N deficits increase the biomass allocated to the roots, i.e. higher R:S;

6. Drought decreases mean root diameter (RD) favouring root expansion, whereas N application increases both;

7. Both specific root length (SRL) and root weight to volume ratio (rV:rW) will increase with drought and with N stress;

8. More uniform root system distribution, and a relatively higher proportion of roots deeper in the soil profile, occurs with water and N deficits (higher β: weight – βW, length – βL and volume – βV).

5.2 RESULTS

5.2.1 Soil bulk density

In Figure 5.1 the BD measured for each depth layer at the beginning of each experiment is presented. Bulk density values in the top 20 cm were higher for 2007 (1.86 g cm^{-3}) than 2008 (1.68 g cm^{-3}) and 2006 (1.56 g cm^{-3}; $p \leq 0.001$). This difference was maintained until 40 – 60 cm ($p \leq 0.05$) soil-depth, below which the soil to 100 cm in both 2007 and 2008 experiments had a similar BD (≈ 1.78 g cm^{-3}), while for 2006 the BD was 13% lower (Figure 5.1). The BD increased at the soil depth ≥ 125 cm, where a similar value was found for all years (1.86, 1.99 and 1.86 g cm^{-3}, 2006, 2007 and 2008 respectively). Averaging across layers BD values were: 1.61 g cm^{-3} for 2006, 1.85 g cm^{-3} for 2007 and 1.76 g cm^{-3} for 2008 (Figure 5.1).

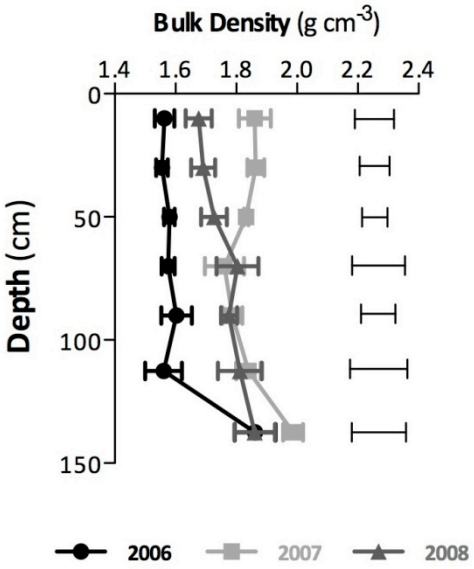

Figure 5.1 Bulk Density in the soil-depth layers of the soil columns for the 2006 (n = 3), 2007 (n = 4) and 2008 (n = 5) experiments. Error bars represent SE of the mean and SED for years.

5.2.2 Total Root Weight (TRW)

5.2.2.1 2006

The total root weight (TRW) was evaluated for three soil-depth horizons: 0 – 20, 20 – 40 and 40 – 60 cm at 67 DAS, and 0 – 20, 60 – 80 cm and 125 - 150 cm at anthesis and harvest. For barley cv. Rum at 67 DAS averaging across water and N treatments, the total root weight from the three horizons was 0.109 g and for wheat cv. Hourani 0.091 g (Table 5.1). As expected the TRW increased at anthesis with significant differences ($p \leq 0.001$) between species, 0.565 g for barley cv. Rum and 0.256 g for wheat cv. Hourani; no other statistically significant treatment effects were found at anthesis (Table 5.1).

At harvest, barley cv. Rum had a TRW 73% higher ($p \leq 0.001$) than wheat cv. Hourani (Table 5.1). There was also an increase ($p \leq 0.05$) of TRW from 0.159 g to 0.342 g with drought, but only for wheat cv. Hourani resulting in an interaction ($p \leq 0.05$) between species and irrigation (Table 5.1). There was a trend ($p = 0.058$) for N to decrease TRW for barley cv. Rum from an average of 0.560 g at N0 to 0.411 g with an application of 50 kg N ha^{-1} and to 0.330 g with 100 kg N ha^{-1} (Table 5.1). For wheat cv. Hourani N effects were only observed under irrigation, TRW decreasing by 16% with 50 kg N ha^{-1} and 25% with 100 kg N ha^{-1} (Table 5.1).

5.2.2.2 2007

In 2007 at 75 DAS averaging across water and N treatments TRW for barley cv. Rum for the three soil depths (0 – 20 cm, 40 – 60 cm and 80 – 100 cm) was 0.071 g, increasing to 0.110 g at anthesis and 0.179 g at harvest (Table 5.2). The treatment effects were only statistically significant at harvest with drought decreasing ($p \leq 0.01$) TRW by 23.3% (Table 5.2). Nitrogen application had no significant effects on TRW (Table 5.2).

For wheat cv. Karim when averaged across treatments at 75 DAS, the TRW for the three soil depths analysed was 0.057 g increasing to 0.144 g at anthesis and decreasing to 0.106 g at harvest (Table 5.2). Drought increased the TRW by 51.9% at anthesis and 54.5% at harvest ($p \leq 0.01$ and $p \leq 0.05$, respectively) (Table 5.2). At harvest, averaging across irrigation treatments, N application decreased ($p = 0.052$) TRW by 41% with 50 kg N ha^{-1} but by only 9% with 100 kg N ha^{-1}; no interaction between treatments was found (Table 5.2). Drought also slightly increased the TRW of wheat cv. Hourani (Table 5.2). N application decreased ($p \leq 0.01$) the TRW from 0.193 g to 0.131 g with 50 kg N ha^{-1} and to 0.133 g with 100 kg N ha^{-1} for the irrigated treatment (Table 5.2). For the droughted treatment, N application decreased the TRW from 0.209 g to 0.155 g with 50 kg N ha^{-1} and 0.141 g with 100 kg N ha^{-1} (Table 5.2).

5.2.2.3 2008

In 2008 at harvest there was a tendency for drought to decrease the TRW per column from 0.604 g to 0.465 g ($p = 0.112$) (Table 5.3).

Table 5.1 Total root weight (g) for three soil depths layers per column: 0 – 20, 20 – 40 and 40 – 60 cm at 67 DAS; 0 – 20, 60 – 80, > 125 cm at anthesis and harvest, for barley cv. Rum and durum wheat cv. Hourani subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) in 2006.

Species	Irrigation	Fertilizer N (kg N ha^{-1})	Total root weight (g)		
			67 DAS	Anthesis	Harvest
Barley cv. Rum	**Irrigated**	**0**	0.095	0.482	0.570
		50	0.145	0.533	0.404
		100	0.081	0.654	0.319
		Mean	*0.107*	*0.556*	*0.431*
	Droughted	**0**	0.109	0.553	0.549
		50	0.116	0.550	0.417
		100	0.111	0.619	0.341
		Mean	*0.112*	*0.574*	*0.436*
Wheat cv. Hourani	**Irrigated**	**0**	0.070	0.222	0.184
		50	0.122	0.314	0.154
		100	0.082	0.232	0.138
		Mean	*0.091*	*0.256*	*0.159*
	Droughted	**0**	0.089	0.260	0.329
		50	0.068	0.251	0.373
		100	0.116	0.257	0.324
		Mean	*0.091*	*0.256*	*0.342*
		SED (df)			
		Species (22)	0.010^{ns}	0.035^{***}	0.041^{***}
		Irrigation (22)	0.010^{ns}	0.035^{ns}	0.041^{*}
		Nitrogen (22)	0.012^{ns}	0.042^{ns}	0.050^{ns}
		*Species*Irrigation (22)*	0.014^{ns}	0.049^{ns}	0.059^{*}
		*Species*Nitrogen (22)*	0.017^{ns}	0.060^{ns}	0.071^{ns}
		*Irrigation*Nitrogen (22)*	0.017^{*}	0.060^{ns}	0.071^{ns}
		*Species * Irrigation * Nitrogen (22)*	0.025^{ns}	0.084^{ns}	0.100^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 5.2 Total root weight (g) for three soil depths layers per column: 0 – 20, 40 – 60 and 80 – 100 cm at 75 DAS; 0 – 20, 60 – 80, > 125 cm at anthesis and harvest, for barley cv. Rum, durum wheat cv. Karim and durum wheat cv. Hourani (only measured art harvest) subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) in 2007.

Irrigation	Fertilizer N (kg N ha^{-1})	Total root weight (g)						
		Barley cv. Rum			Wheat cv. Karim			Wheat cv. Hourani
		75 DAS	Anthesis	Harvest	75 DAS	Anthesis	Harvest	Harvest
Irrigated	**0**	0.075	0.107	0.207	0.060	0.120	0.103	0.193
	50	0.058	0.106	0.225	0.063	0.110	0.066	0.131
	100	0.074	0.107	0.176	0.056	0.113	0.082	0.133
	Mean	*0.069*	*0.107*	*0.202*	*0.060*	*0.114*	*0.083*	*0.152*
Droughted	**0**	0.056	0.105	0.168	0.069	0.216	0.151	0.209
	50	0.067	0.119	0.150	0.051	0.143	0.084	0.155
	100	0.094	0.115	0.147	0.045	0.162	0.151	0.141
	Mean	*0.072*	*0.113*	*0.155*	*0.055*	*0.173*	*0.129*	*0.168*
	SED (df)							
	Irrigation (20)	0.013^{ns}	0.014^{ns}	0.017^{**}	0.013^{ns}	0.016^{**}	0.017^{*}	0.015^{ns}
	Nitrogen (20)	0.016^{ns}	0.017^{ns}	0.020^{ns}	0.015^{ns}	0.020^{ns}	0.021^{ns}	0.018^{**}
	*Irrigation*Nitrogen (20)*	0.022^{ns}	0.024^{ns}	0.029^{ns}	0.022^{ns}	0.028^{ns}	0.030^{ns}	0.026^{**}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 5.3 Total root weight (g) per column for: 0 – 20 cm soil depth at 28 DAS; and 0 – 20, 60 – 80, > 125 cm soil depths at harvest for barley cv. Rum subjected to full irrigated and droughted treatments at 28 DAS and harvest in 2008.

Irrigation	Barley cv. Rum Total root weight (g)	
	28 DAS	Harvest
Irrigated	0.045	0.604
Droughted	0.043	0.465
SED (df)		
Irrigation (6)	0.007^{ns}	0.075^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

5.2.3 Root Weight Density (RWD) Distribution with Depth

5.2.3.1 2006

At 67 DAS the average root weight density with soil depth for barley cv. Rum was 28.7 g m^{-3} at 0 – 20 cm, 1.89 g m^{-3} at 20 – 40 cm and 0.38 g m^{-3} at 40 – 60 cm (Figure 5.2 a, d). For wheat cv. Hourani, the corresponding values were 23.7, 1.55 and 0.53 g m^{-3}, respectively (Figure 5.3 a, d).

At anthesis barley cv. Rum had a higher root weight density at all soil-depths ($p \leq 0.05$) than wheat cv. Hourani (Figure 5.2 b, e and Figure 5.3 b, e). Neither water nor nitrogen had a statistically significant effect on the root weight density at anthesis (Figure 5.2 b, e and Figure 5.3 b, e).

At harvest at 0 – 20 cm soil depth there was an effect of species ($p \leq 0.001$) with barley cv. Rum having an 87% higher RWD than wheat cv. Hourani (Figure 5.2 c, f and Figure 5.3 c, f). Drought increased ($p \leq 0.05$) RWD from 63.1 g m^{-3} to 80.4 g m^{-3}. This might be associated with reduced root mortality rather than enhanced root growth in the drought treatment from anthesis to harvest (Figure 5.2 c, f and Figure 5.3 c, f). There was an effect of N ($p \leq 0.05$) and an interaction between species and N ($p \leq 0.05$) at 0 – 20 cm soil-depth, with N application decreasing RWD by 36% with 50 kg N ha^{-1} and 42% with 100 kg N ha^{-1} for barley cv. Rum but not for wheat cv. Hourani (Figure 5.2 c, f and Figure 5.3 c, f).

For layers 60 – 80 cm and > 125 cm there was a trend for an interaction between species and irrigation ($p = 0.07$ and 0.08, respectively), with drought increasing root growth by 202% cf. and 176% respectively for wheat cv. Hourani but not for barley cv. Rum. Though, values for RWD of barley cv. Rum in the 60 – 80 cm soil depth were higher ($p \leq 0.05$) than those for wheat cv. Hourani (Figure 5.2 c, f and Figure 5.3 c, f).

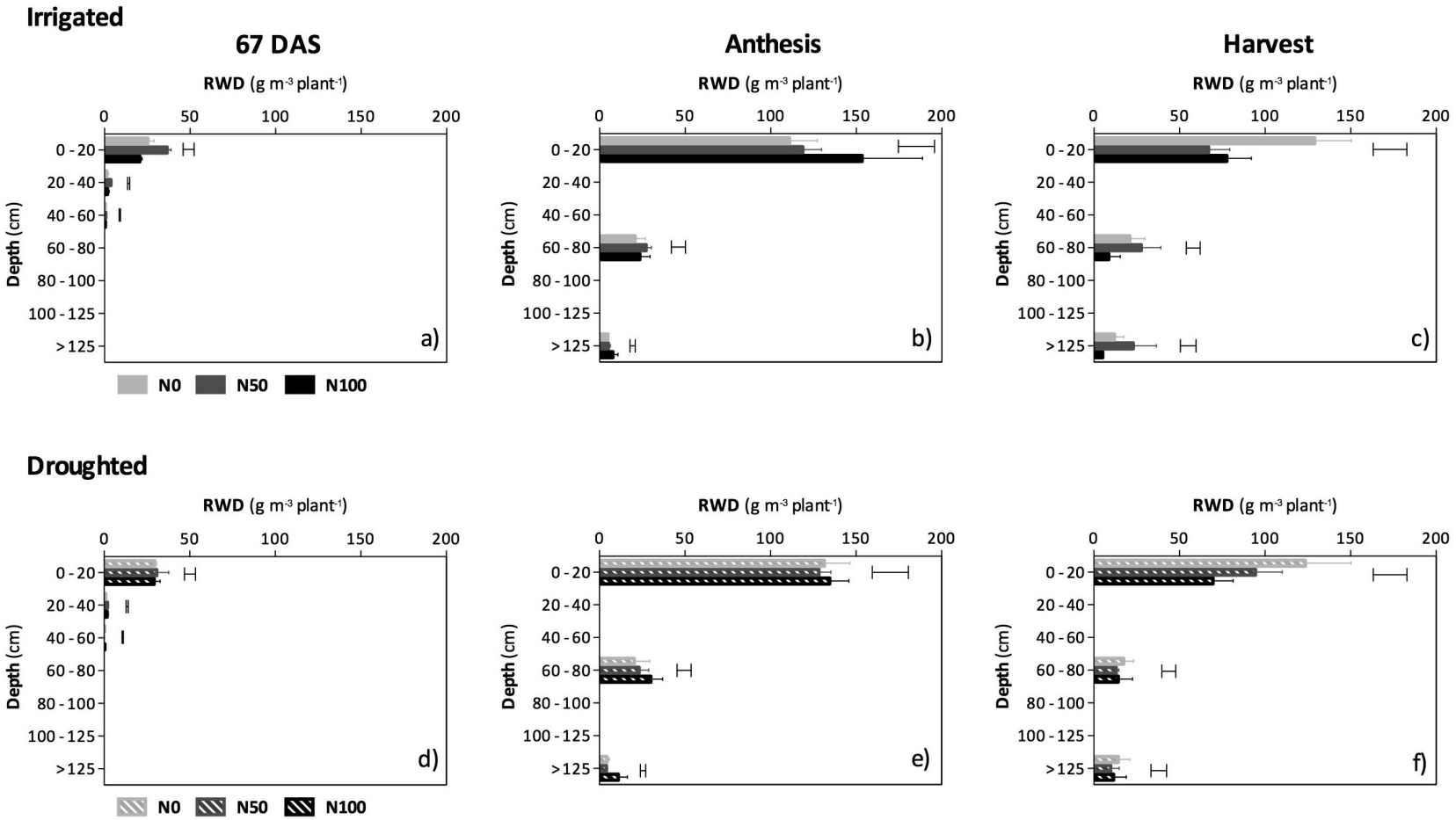

Figure 5.2 Root Weight Density (RWD, g m^{-3}) for different soil-depth layers for barley cv. Rum subjected to full irrigated (full bars) and droughted (striated bars) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 67 DAS (**a** & **d**), anthesis (**b** & **e**) and harvest (**c** & **f**) in 2006. Error bars represent SE of the mean and SED for species x irrigation x nitrogen (df = 22).

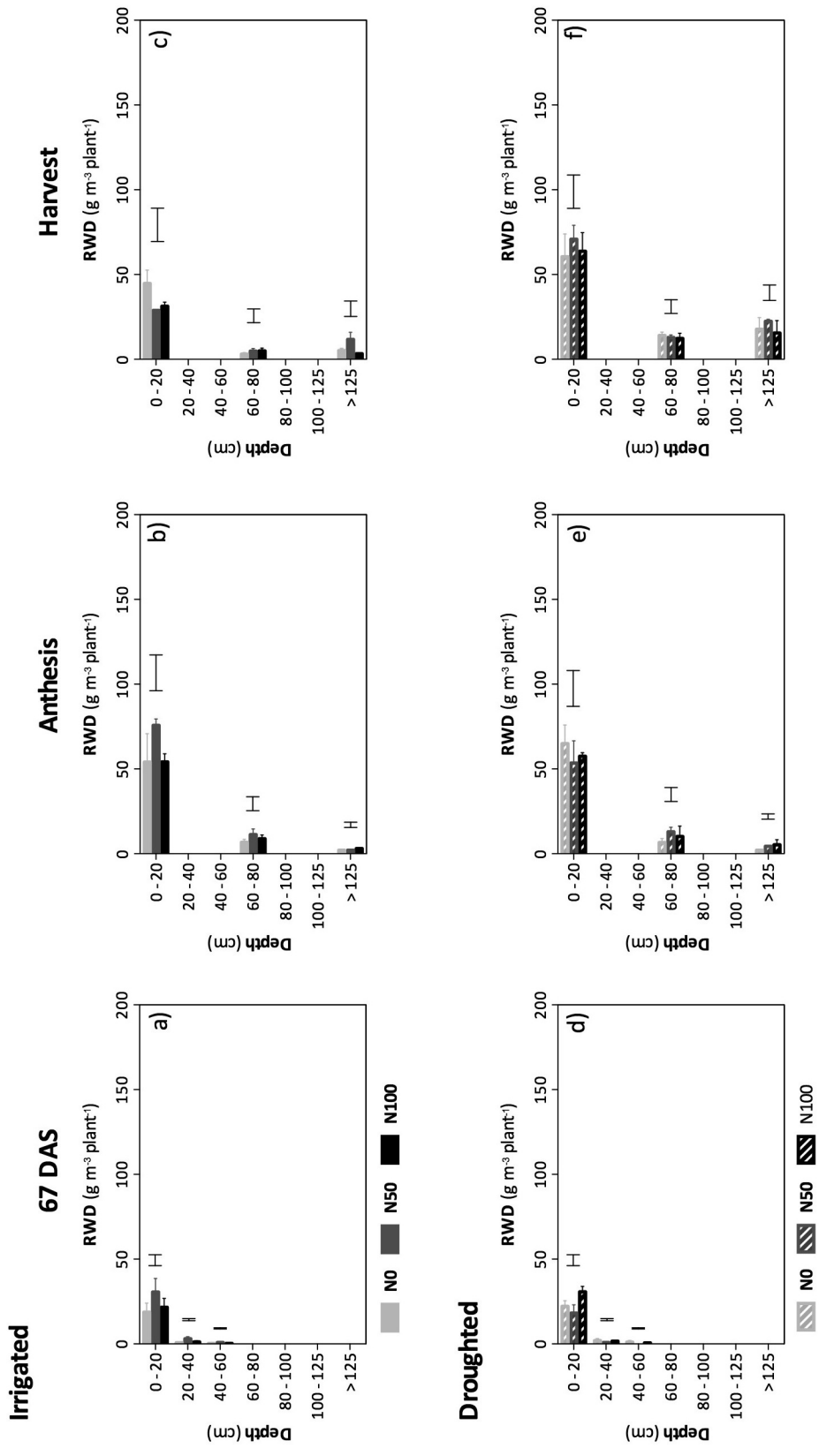

Figure 5.3 Root Weight Density (RWD, g m^{-3}) for different soil-depth layers for durum wheat cv. Hourani subjected to full irrigated (full bars) and droughted (striated bars) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 67 DAS (**a** & **d**), anthesis (**b** & **e**) and harvest (**c** & **f**) in 2006. Error bars represent SE of the mean and SED for species x irrigation x nitrogen (df = 22).

5.2.3.2 2007

For barley cv. Rum, as expected, at 75 DAS there were no significant effects of the treatments since it was before their application (Figure 5.4 a, d), RDW varying from 17.8 g m^{-3} at 0 – 20 cm to 0.47 g m^{-3} $plant^{-1}$ at 80 – 100 cm. At anthesis there was an overall increase of RWD at 0 – 20 cm to 26.5 g m^{-3} $plant^{-1}$, but there was no significant effect of water or N application (Figure 5.4 b, e). The RWD did not significantly change with any of the treatments at 60 – 80 cm, corresponding to an overall mean of 2.88 g m^{-3} $plant^{-1}$ (Figure 5.4 b, e). But at the soil depth > 125 cm drought increased ($p = 0.053$) RWD from 1.08 to 2.09 g m^{-3} $plant^{-1}$ (Figure 5.4 b, e). From anthesis to harvest, RWD increased at 0 – 20 cm though to a greater extent ($p \leq 0.001$) for the irrigated treatment (Figure 5.4 c, f). The opposite was detected deeper in the profile, with drought increasing ($p \leq 0.05$) the RWD by 61% (Figure 5.4 c, f).

For wheat cv. Karim at 75 DAS, RWD decreased from 14.5 g m^{-3} at 0 – 20 cm to 1.38 g m^{-3} at 40 – 60 cm and 0.34 g m^{-3} at 80 – 100 cm (Figure 5.5, a, d). At anthesis droughted plants had a higher ($p \leq 0.001$) RWD than the irrigated plants, 43.7 g m^{-3} cf. 29.0 g m^{-3} at 0 – 20 cm (Figure 5.5 b, e). Drought also increased ($p \leq 0.001$) the RWD by 72% at 60 – 80 cm (Figure 5.5 b, e). At this soil depth, the RWD decreased with N applied from 5.0 g m^{-3} at N0 to 3.4 g m^{-3} at N50 and 3.0 g m^{-3} at N100 (Figure 5.5 b, e). No effects were found for the depth > 125 cm (Figure 5.5 b, e). At harvest, at 0 – 20 cm drought increased ($p \leq 0.05$) RWD from 22.1 to 31.8 g m^{-3} $plant^{-1}$ (Figure 5.5 c, f). For the 0 – 20 cm soil depth, N application decreased ($p \leq 0.05$) the RWD at N50 and N100 (Figure 5.5 c, f). Drought also increased ($p \leq 0.001$) RWD at 60 – 80 cm (Figure 5.5 c, f). None of the treatments had a significant effect at a soil depth of > 125 cm (Figure 5.5 c, f).

For wheat cv. Hourani at harvest in 2007 (Figure 5.6 a, b), N application decreased ($p \leq 0.01$) the RWD for 0 – 20 cm, from 42.6 g m^{-3} for N0 to 30.8 and 31.2 g m^{-3} for N50 and N100, respectively (Figure 5.6 a, b). A similar ($p \leq 0.01$) N effect was also found at 60 – 80 cm soil depth (Figure 5.6 a, b). At the soil depth > 125 cm, drought ($p \leq 0.01$) increased the RWD from 2.60 to 7.91 g m^{-3} (Figure 5.6 a, b).

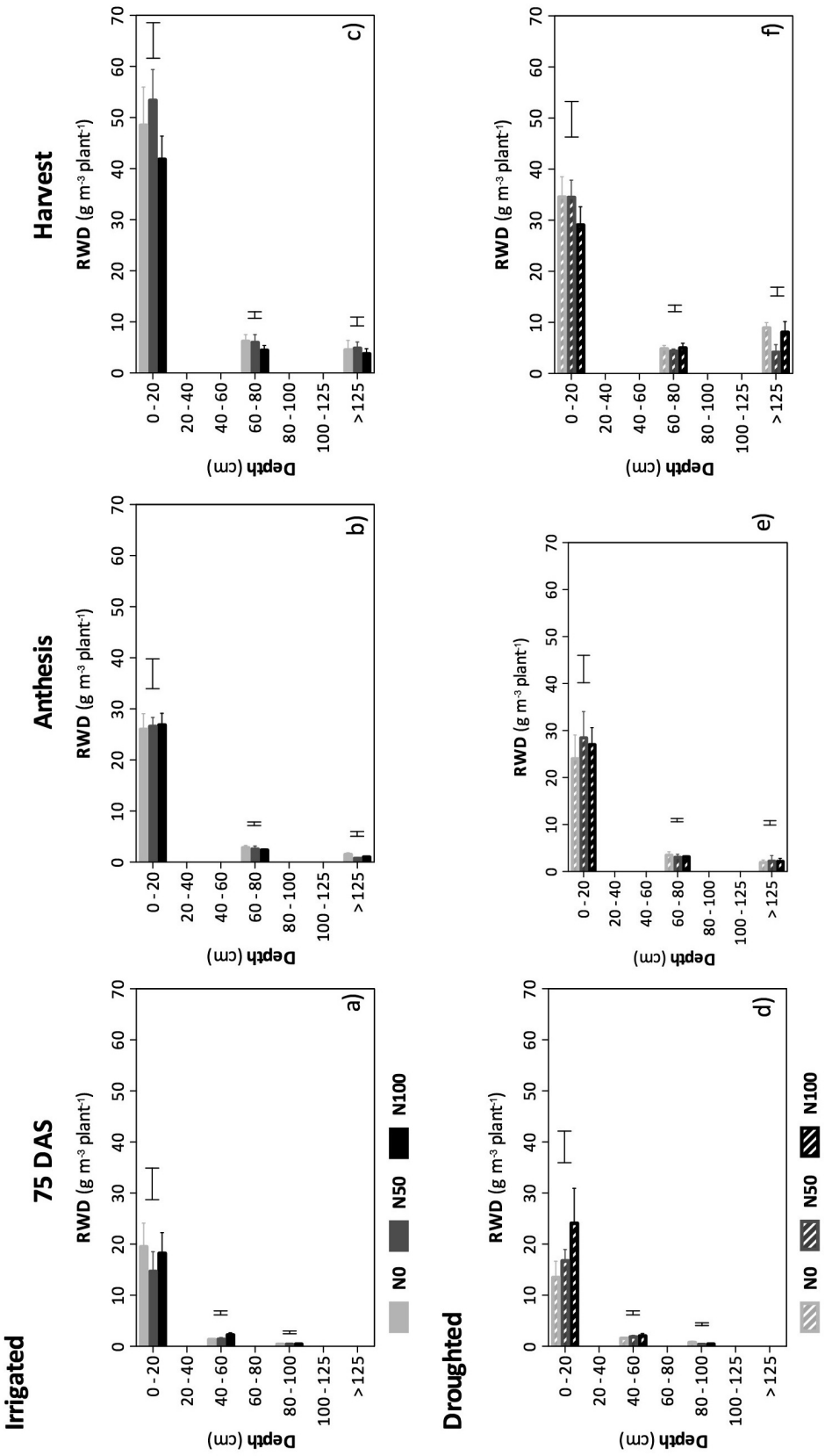

Figure 5.4 Root Weight Density (RWD, g m^{-3}) for different soil-depth layers for barley cv. Rum subjected to full irrigated (full bars) and droughted (striated bars) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 75 DAS (**a** & **d**), anthesis (**b** & **e**) and harvest (**c** & **f**) in 2007. Error bars represent SE of the mean and SED for irrigation x nitrogen (df = 24).

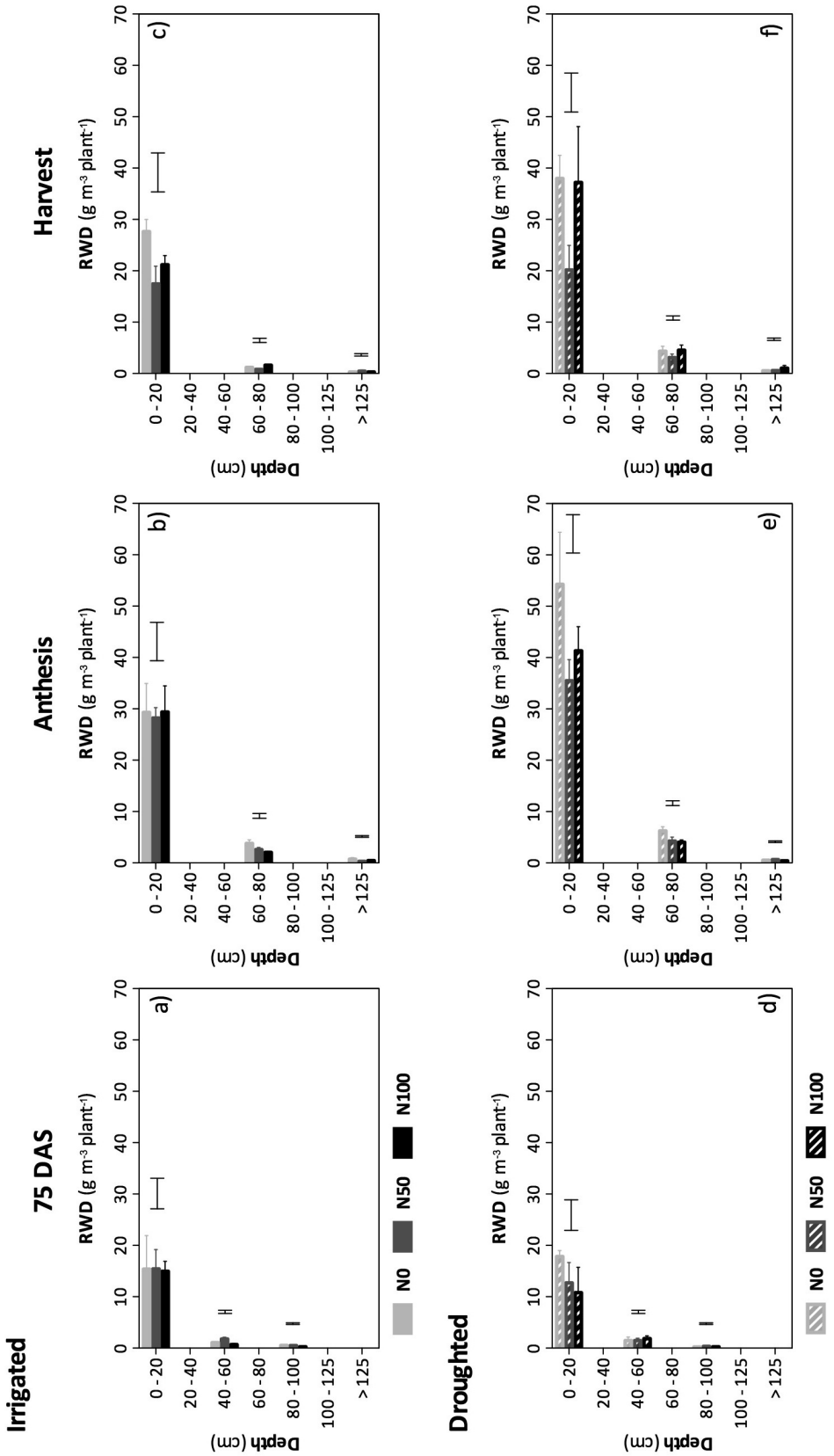

Figure 5.5 Root Weight Density (RWD, g m^{-3}) for different soil-depth layers for durum wheat cv. Karim subjected to irrigated (full bars) and droughted (striated bars) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 75 DAS (**a** & **d**), anthesis (**b** & **e**) and harvest (**c** & **f**) in 2007. Error bars represent SE of the mean and SED for irrigation x nitrogen (df = 24).

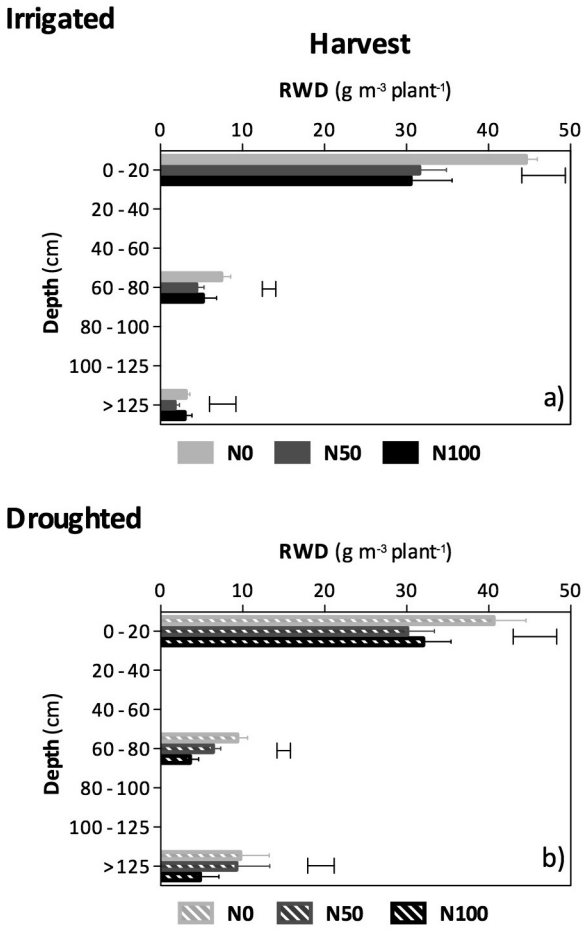

Figure 5.6 Root Weight Density (RWD, g m^{-3}) for different soil-depth layers for durum wheat cv. Hourani subjected to full irrigated (**a**, full bars) and droughted (**b**, striated bars) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) at harvest in 2007. Error bars represent SE of the mean and SED for irrigation x nitrogen (df = 24).

5.2.3.3 2008

As expected, the root weight density increased from 28 DAS to harvest, 12.4 to 97.2 g m^{-3}, respectively, for a soil depth of 0 – 20 cm (Figure 5.7 a, b). At harvest the only effect was at a soil depth ≥ 125 cm, with drought decreasing ($p \leq 0.01$) root weight density from 43.0 to 14.0 g m^{-3} $plant^{-1}$ (Figure 5.7 b).

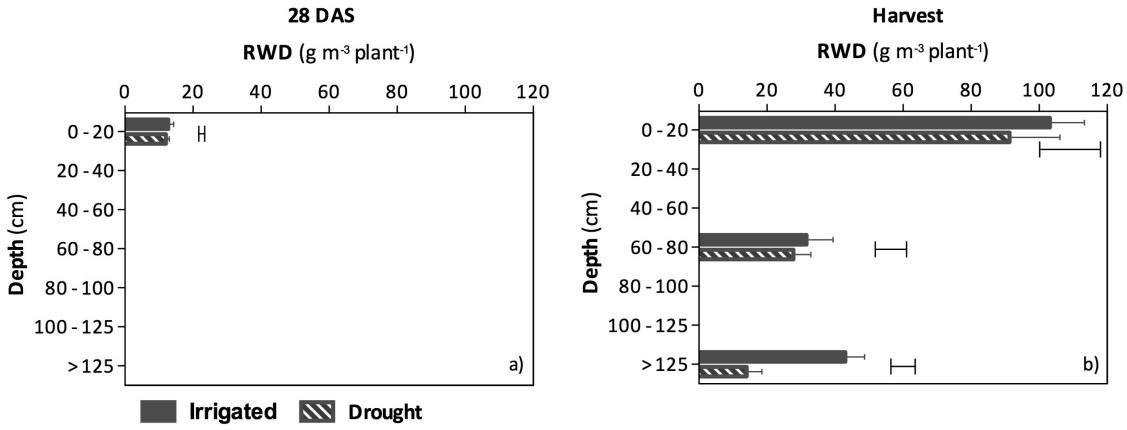

Figure 5.7 Root Weight Density (RWD, g m-3 plant^{-1}) for different soil depth layers for barley cv. Rum subjected to full irrigated (full bars) and droughted (striated bars) at 28 DAS (**a)** and harvest (**b**) in 2008. Error bars represent SE of the mean and SED for irrigation (df = 20).

5.2.4 Root Weight distribution with depth (β_W)

As previously explained (*vide* section 3.6.5.3) the distribution of weight with soil-depth was accessed according to the shape of the cumulative distribution of weight with depth (β_W). As β_W approaches 1 a greater proportion of root is distributed deeper in the soil profile.

5.2.4.1 2006

According to β_W values the relative proportion of root weight deeper in the profile increased with time for both barley cv. Rum and wheat cv. Hourani, though there were no significant differences between species, irrigation and nitrogen application (Table 5.4). Overall β_W increased from 0.871 early in the plant growth to 0.927 at harvest, representing a relative decrease of root weight in the top 20 cm from 94 to 78% (Table 5.4).

Table 5.4 Shape of the cumulative weight distribution with depth (β_W) estimated from three soil depths per column: 0 – 20, 20 – 40 and 40 – 60 cm at 67 DAS; 0 – 20, 60 – 80, > 125 cm at anthesis and harvest, for barley cv. Rum and durum wheat cv. Hourani subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 67 DAS, anthesis and harvest in 2006.

Species	Irrigation	Fertilizer N (kg N ha^{-1})	β_W		
			67 DAS	Anthesis	Harvest
Barley cv. Rum	**Irrigated**	**0**	0.834	0.918	0.908
		50	0.895	0.926	0.950
		100	0.870	0.914	0.894
		Mean	*0.866*	*0.919*	*0.917*
	Droughted	**0**	0.863	0.900	0.916
		50	0.870	0.914	0.921
		100	0.873	0.926	0.921
		Mean	*0.869*	*0.913*	*0.920*
Wheat cv. Hourani	**Irrigated**	**0**	0.847	0.908	0.905
		50	0.896	0.906	0.948
		100	0.896	0.915	0.919
		Mean	*0.880*	*0.909*	*0.924*
	Droughted	**0**	0.872	0.894	0.954
		50	0.860	0.933	0.952
		100	0.873	0.910	0.938
		Mean	*0.868*	*0.913*	*0.948*
		SED (df)			
		Species (22)	0.012^{ns}	0.009^{ns}	0.011^{ns}
		Irrigation (22)	0.012^{ns}	0.009^{ns}	0.011^{ns}
		Nitrogen (22)	0.015^{ns}	0.011^{ns}	0.014^{ns}
		*Species*Irrigation (22)*	0.017^{ns}	0.013^{ns}	0.016^{ns}
		*Species*Nitrogen (22)*	0.021^{ns}	0.016^{ns}	0.020^{ns}
		*Irrigation*Nitrogen (22)*	0.021^{ns}	0.016^{ns}	0.020^{ns}
		*Species*Irrigation*Nitrogen (22)*	0.030^{ns}	0.022^{ns}	0.028^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

5.2.4.2 2007

For barley cv. Rum drought increased the relative root weight distribution with depth with β_W of 0.898 cf. 0.914 at anthesis ($p \leq 0.05$) and 0.910 cf. 0.932 at harvest ($p \leq 0.01$; Table 5.5) in fully irrigated and droughted treatments, respectively. Similar effects were also observed for durum wheat at harvest, with drought decreasing the proportion of root weight in the top 20 cm from 94 to 87% for cv. Karim ($p \leq 0.001$) and 83 to 74% for cv. Hourani ($p \leq 0.01$; Table 5.5). For wheat cv. Hourani there was also an interaction between irrigation and N application ($p \leq 0.05$), with drought increasing the proportion of root weight deeper in the profile for 0 and 50 kg N ha^{-1} applications but not 100 kg N ha^{-1} (Table 5.5). Overall barley cv. Rum and wheat cv. Hourani had a similar distribution of root weight with depth at harvest, with around 80% of the root weight in the top 20 cm, while for wheat cv. Karim 90% of the root weight was in that soil-depth (Table 5.5).

5.2.4.3 2008

For barley cv. Rum in 2008 at harvest a higher proportion of the root weight ($\beta_W = 0.95$) was distributed deeper in the profile compared to previous years ($\beta_W \approx 0.92$ in both 2006 and 2007; Table 5.4, Table 5.5 and Table 5.6). In contrast to 2006 and 2007 (Table 5.4 and Table 5.5), in 2008 irrigation tended to increase ($p = 0.079$) the proportion of root weight deeper in soil profile (Table 5.6).

Table 5.5 Shape of the cumulative root weight distribution with depth (β_W) per column estimated from three soil depths: 0 – 20, 40 – 60 and 80 – 100 cm at 75 DAS; 0 – 20, 60 – 80, > 125 cm at anthesis and harvest, for barley cv. Rum, durum wheat cv. Karim and durum wheat cv. Hourani (only measured art harvest) subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) in 2007.

		β_W						
Irrigation	**Fertilizer N** (kg N ha^{-1})	**Barley cv. Rum**			**Wheat cv. Karim**			**Wheat cv. Hourani**
		75 DAS	**Anthesis**	**Harvest**	**75 DAS**	**Anthesis**	**Harvest**	**Harvest**
Irrigated	**0**	0.887	0.904	0.912	0.902	0.906	0.860	0.919
	50	0.897	0.894	0.909	0.907	0.887	0.874	0.905
	100	0.907	0.897	0.910	0.862	0.883	0.882	0.917
	Mean	*0.897*	*0.898*	*0.910*	*0.890*	*0.892*	*0.872*	*0.914*
Droughted	**0**	0.912	0.922	0.941	0.871	0.898	0.893	0.948
	50	0.897	0.905	0.916	0.906	0.899	0.915	0.945
	100	0.893	0.914	0.940	0.916	0.890	0.905	0.910
	Mean	*0.901*	*0.914*	*0.932*	*0.898*	*0.896*	*0.904*	*0.934*
	SED (df)							
	Irrigation (20)	0.009^{ns}	0.007^{*}	0.006^{**}	0.011^{ns}	0.005^{ns}	0.007^{***}	0.007^{**}
	Nitrogen (20)	0.011^{ns}	0.008^{ns}	0.007^{ns}	0.014^{ns}	0.007^{ns}	0.009^{ns}	0.009^{ns}
	*Irrigation*Nitrogen (20)*	0.016^{ns}	0.012^{ns}	0.010^{ns}	0.020^{*}	0.009^{ns}	0.012^{ns}	0.012^{*}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 5.6 Shape of the cumulative weight distribution with depth (β_W) per column estimated from: 0 – 20, 60 – 80, > 125 cm at soil depths at harvest for barley cv. Rum subjected to full irrigated and droughted treatments at harvest in 2008.

	Barley cv. Rum
Irrigation	β_W
	Harvest
Irrigated	0.961
Droughted	0.946
SED (df)	
Irrigation (6)	0.007^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

5.2.5 Root Shoot Ratio (R:S)

5.2.5.1 2006

In 2006 R:S decreased from an overall value of 0.31 at 67 DAS to 0.05 at anthesis and 0.02 at harvest for barley cv. Rum, and 0.10 and 0.03, respectively, for wheat cv. Hourani (Table 5.7). At anthesis wheat cv. Hourani had a 83% higher ($p \leq 0.01$) R:S than barley cv. Rum, but only 35% at harvest ($p \leq 0.05$; Table 5.7). There was also an increase of R:S with drought ($p \leq 0.001$) and an interaction between species and irrigation ($p \leq 0.05$) at anthesis and harvest: with drought increasing R:S by 200 and 187% respectively, for wheat cv. Hourani, but only by 17 and 53%, respectively, for barley cv. Rum (Table 5.7). N application had no significant effect on R:S.

5.2.5.2 2007

Overall R:S decreased from 75 DAS to harvest by 70% for barley cv. Rum and by 80% for wheat cv. Karim (Table 5.8). Water deficiency significantly increased R:S by 25% at anthesis and 30% at harvest for barley cv. Rum, and 70 and 85%, respectively, for wheat cv. Karim (Table 5.8). Drought also increased ($p \leq 0.01$) R:S by 50% for wheat cv. Hourani at harvest (Table 5.8). At anthesis for wheat cv. Karim there was an interaction between irrigation and N applied ($p \leq 0.05$), with drought increasing R:S for N0 or N100 but not for N50 (Table 5.8).

5.2.5.3 2008

In 2008 (Table 5.9) R:S at harvest was relatively high (0.064) when compared to previous years (0.022 in 2006 and 0.027 in 2007; Table 5.7 and Table 5.8), and irrigation did not significantly affect R:S (Table 5.9).

Table 5.7 Root shoot ratio (R:S) per column at 67 DAS, anthesis and harvest, for barley cv. Rum and durum wheat cv. Hourani subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) 2006.

Species	Irrigation	Fertilizer N (kg N ha^{-1})	R:S		
			67 DAS	Anthesis	Harvest
Barley cv. Rum	**Irrigated**	**0**	0.258	0.055	0.022
		50	0.399	0.061	0.014
		100	0.240	0.027	0.014
		Mean	*0.299*	*0.048*	*0.017*
	Droughted	**0**	0.281	0.082	0.029
		50	0.376	0.044	0.023
		100	0.281	0.042	0.026
		Mean	*0.313*	*0.056*	*0.026*
Wheat cv. Hourani	**Irrigated**	**0**	0.263	0.052	0.018
		50	0.366	0.046	0.014
		100	0.245	0.043	0.014
		Mean	*0.291*	*0.047*	*0.015*
	Droughted	**0**	0.309	0.146	0.038
		50	0.292	0.143	0.050
		100	0.408	0.142	0.041
		Mean	*0.336*	*0.144*	*0.043*
		SED (df)			
		Species (22)	0.030^{ns}	0.013^{**}	0.004^{*}
		Irrigation (22)	0.030^{ns}	0.013^{***}	0.004^{***}
		Nitrogen (22)	0.037^{ns}	0.016^{ns}	0.004^{ns}
		*Species*Irrigation (22)*	0.043^{ns}	0.018^{*}	0.005^{*}
		*Species*Nitrogen (22)*	0.053^{ns}	0.023^{ns}	0.006^{ns}
		*Irrigation*Nitrogen (22)*	0.053^{ns}	0.023^{ns}	0.006^{ns}
		*Species * Irrigation * Nitrogen (22)*	0.075^{ns}	0.032^{ns}	0.009^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 5.8 Root shoot ratio (R:S) per column at anthesis and harvest, for barley cv. Rum, durum wheat cv. Karim and, durum wheat cv. Hourani (only measured art harvest) subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) in 2007.

Irrigation	Fertilizer N (kg N ha^{-1})	R:S						
		Barley cv. Rum			Wheat cv. Karim			Wheat cv. Hourani
		75 DAS	Anthesis	Harvest	75 DAS	Anthesis	Harvest	Harvest
Irrigated	**0**	0.092	0.025	0.022	0.155	0.027	0.021	0.027
	50	0.079	0.025	0.026	0.152	0.026	0.022	0.023
	100	0.089	0.023	0.021	0.144	0.028	0.019	0.029
	Mean	*0.087*	*0.024*	*0.023*	*0.150*	*0.027*	*0.020*	*0.026*
Droughted	**0**	0.081	0.029	0.030	0.161	0.051	0.043	0.047
	50	0.089	0.031	0.027	0.137	0.042	0.026	0.041
	100	0.110	0.029	0.032	0.112	0.044	0.040	0.031
	Mean	*0.093*	*0.030*	*0.030*	*0.137*	*0.046*	*0.037*	*0.039*
	SED (df)							
	Irrigation (20)	0.012^{ns}	0.002^{*}	0.002^{**}	0.030^{ns}	0.004^{***}	0.003^{***}	0.004^{**}
	Nitrogen (20)	0.015^{ns}	0.003^{ns}	0.003^{ns}	0.037^{ns}	0.005^{ns}	0.004^{ns}	0.005^{ns}
	*Irrigation*Nitrogen (20)*	0.021^{ns}	0.004^{ns}	0.004^{ns}	0.052^{ns}	0.006^{*}	0.005^{ns}	0.007^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 5.9 Root shoot ratio (R:S) per column at 28 DAS and harvest for barley cv. Rum subjected to full irrigated and droughted treatments at 28 DAS and harvest in 2008.

Irrigation	Barley cv. Rum R:S	
	28 DAS	Harvest
Irrigated	0.811	0.062
Droughted	0.721	0.066
SED (df)		
Irrigation (6)	0.136^{ns}	0.596^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

5.2.6 Specific root length (SRL) and root volume: root weight ratio (rV:rW)

5.2.6.1 2006

In 2006, 67 DAS for barley cv. Rum and wheat cv. Hourani, the SRL calculated from the 3 soil layers analysed was respectively: 125.2 m g^{-1} and 136.7 m g^{-1}; and the rV:rW: 12.5 cm^3 g^{-1} and 11.0 cm^3 g^{-1} (Table 5.10). At anthesis there was no effect of any of the treatments on either SRL or rV:rW (Table 5.10). The average SRL was 136.8 m g^{-1} for barley cv. Rum and 149.1 m g^{-1} for wheat cv. Hourani; and the average rV:rW 10.4 cm^3 g^{-1} and 9.7 cm^3 g^{-1}, respectively. At harvest, full irrigation increased ($p \leq 0.05$) SRL by 36% for barley cv. Rum but only 11% for wheat cv. Hourani (Table 5.10). Wheat cv. Hourani had a higher SRL than barley cv. Rum, 170.5 cf. 135.3 m g^{-1} ($p< 0.05$; Table 5.10). For rV:rW the only significant effect was an interaction between species*irrigation, with drought decreasing the rV:rW by 30% for barley cv. Rum but with no effect for wheat cv. Hourani (Table 5.10).

5.2.6.2 2007

For barley cv. Rum in 2007 none of the treatments had a significant effect on the SRL, with average values of 139.8 (75 DAS), 136.3 (anthesis) and 140.3 m g^{-1} at harvest (Table 5.11). However there was a trend to an increase on SRL with drought at anthesis ($p = 0.074$, Table 5.11). At 75 DAS rV:rW for barley cv. Rum was 9.1 cm^3 g^{-1}, thereafter decreasing to an average value of 6.9 cm^3 g^{-1} at anthesis and harvest (Table 5.11). Drought increased rV:rW by 32% at anthesis ($p \leq 0.01$) and 23% at harvest ($p \leq 0.05$; Table 5.11).

For wheat cv. Karim SRL also decreased through time from 158.3 m g^{-1} (75 DAS) to ca. 100 m g^{-1} at harvest (Table 5.11). At anthesis there was an irrigation x nitrogen interaction ($p < 0.05$), with N application decreasing SRL by 43.1 m g^{-1} with 50 kg N

ha^{-1} and 48.1 m g^{-1} with 100 kg N ha^{-1} when irrigated, but not under drought (Table 5.11). At harvest, an increase ($p \leq 0.05$) was observed on SRL with N application, by 65% with N50 and 25% with N100 when irrigated, and 98% and 52%, respectively, when droughted (Table 5.11). Also a trend ($p = 0.079$) for an increase in SRL with drought (39%) was observed at harvest (Table 5.11). Similar to results for barley, the average rV:rW for wheat cv. Karim decreased through time to harvest (Table 5.11). There was an interaction ($p \leq 0.05$) between irrigation and nitrogen for rV:rW at anthesis, with N decreasing rV:rW when irrigated but not under drought (Table 5.11). At harvest drought increased rW:rV by 34% ($p \leq 0.05$) (Table 5.11). Nitrogen application had a positive effect ($p \leq 0.05$) on the rV:rW for both irrigated and droughted treatments, increasing by 50% at N50 and 38% at N100 (Table 5.11).

For wheat cv. Hourani at harvest in 2007 neither SRL or rV:rW were significantly affected by irrigation or N application (Table 5.11) with average values of 158.5 m g^{-1} and 8.0 cm^3 g^{-1}, respectively.

5.2.6.3 2008

For barley cv. Rum in 2008, in contrast to 2007, irrigation had no significant effect on SRL and rV:rW (Table 5.12). However, there was an increase of 159% for SRL from 28 DAS to harvest and 58% decrease in rV:rW (Table 5.12), indicating a relatively high decrease of mean root diameter over time.

Table 5.10 Specific root length (SRL, m g^{-1}) and Root volume: Root Weight ratio (rV:rW, cm^3 g^{-1}) per column for barley cv. Rum and durum wheat cv. Hourani subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 67 DAS, anthesis and harvest in 2006.

Species	Irrigation	Fertilizer N (kg N ha^{-1})	67 DAS		Anthesis		Harvest	
			SRL (m g^{-1})	rV:rW (cm^3 g^{-1})	SRL (m g^{-1})	rV:rW (cm^3 g^{-1})	SRL (m g^{-1})	rV:rW (cm^3 g^{-1})
Barley cv. Rum	**Irrigated**	**0**	127.6	10.8	150.9	9.9	168.8	9.6
		50	111.8	14.7	165.3	10.9	194.6	12.4
		100	144.2	12.0	125.7	10.6	131.2	7.4
		Mean	*127.9*	*12.5*	*147.3*	*10.4*	*164.9*	*9.8*
	Droughted	**0**	121.9	13.8	113.1	10.4	77.4	5.7
		50	126.1	12.8	131.2	10.0	111.9	7.4
		100	119.6	10.8	134.5	10.8	128.0	7.6
		Mean	*122.5*	*12.5*	*126.3*	*10.4*	*105.8*	*6.9*
Wheat cv. Hourani	**Irrigated**	**0**	145.5	10.6	163.6	9.2	153.4	6.7
		50	127.6	14.3	137.9	9.2	220.9	9.7
		100	165.6	8.0	155.7	9.1	165.7	8.4
		Mean	*146.2*	*11.0*	*152.4*	*9.2*	*180.0*	*8.3*
	Droughted	**0**	139.1	11.2	123.1	8.6	176.0	9.9
		50	135.6	10.5	176.6	12.5	152.9	8.1
		100	106.9	11.4	137.9	9.3	153.8	8.3
		Mean	*127.2*	*11.0*	*145.9*	*10.1*	*160.9*	*8.8*
		SED (df)						
		Species (22)	9.8^{ns}	0.9^{ns}	12.6^{ns}	0.7^{ns}	14.3^{*}	0.7^{ns}
		Irrigation (22)	9.8^{ns}	0.9^{ns}	12.6^{ns}	0.7^{ns}	14.3^{*}	0.7^{ns}
		Nitrogen (22)	12.0^{ns}	1.1^{ns}	15.4^{ns}	0.8^{ns}	17.5^{ns}	0.9^{ns}
		*Species*Irrigation (22)*	13.8^{ns}	1.3^{ns}	17.8^{ns}	1.0^{ns}	20.2^{ns}	1.0^{*}
		*Species*Nitrogen (22)*	16.9^{ns}	1.6^{ns}	21.8^{ns}	1.2^{ns}	24.8^{ns}	1.2^{ns}
		*Irrigation*Nitrogen (22)*	16.9^{ns}	1.6^{ns}	21.8^{ns}	1.2^{ns}	24.8^{ns}	1.2^{ns}
		*Species * Irrigation * Nitrogen (22)*	23.9^{ns}	2.2^{ns}	30.8^{ns}	1.7^{ns}	35.1^{ns}	1.7^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 5.11 Specific root length (SRL, m g^{-1}) and Root volume: Root Weight ratio (rV:rW, cm^3 g^{-1}) per column at 75 DAS, anthesis and harvest, for barley cv. Rum, durum wheat cv. Karim and durum wheat cv. Hourani (only measured art harvest) subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) in 2007

Irrigation	Fertilizer N (kg N ha^{-1})	Barley cv. Rum						Wheat cv. Karim						Wheat cv. Hourani	
		75 DAS		Anthesis		Harvest		75 DAS		Anthesis		Harvest		Harvest	
		SRL (m g^{-1})	rV:rW (cm^3 g^{-1})	SRL (m g^{-1})	rV:rW (cm^3 g^{-1})	SRL (m g^{-1})	rV:rW (cm^3 g^{-1})	SRL (m g^{-1})	rV:rW (cm^3 g^{-1})	SRL (m g^{-1})	rV:rW (cm^3 g^{-1})	SRL (m g^{-1})	rV:rW (cm^3 g^{-1})	SRL (m g^{-1})	rV:rW (cm^3 g^{-1})
Irrigated	**0**	114.0	8.3	125.8	6.3	139.0	6.4	171.0	11.3	136.4	7.0	67.9	3.8	162.9	8.0
	50	153.0	10.2	119.9	5.9	128.5	6.0	159.0	10.5	93.3	5.8	111.8	5.8	158.3	7.2
	100	168.0	9.9	116.8	5.6	138.0	6.0	111.0	8.7	88.3	4.7	85.2	4.7	161.6	8.3
	Mean	*145.0*	*9.5*	*120.8*	*6.0*	*135.2*	*6.2*	*147.0*	*10.1*	*106.0*	*5.8*	*88.3*	*4.8*	*160.9*	*7.8*
Droughted	**0**	150.0	8.8	179.6	8.3	156.1	8.2	104.0	7.2	89.4	5.2	81.6	4.8	161.2	8.8
	50	137.0	9.1	132.2	7.3	120.0	6.4	177.0	11.5	103.9	6.8	161.3	7.1	176.9	8.9
	100	117.0	8.2	143.2	7.9	160.2	8.1	228.0	14.0	97.5	6.1	124.3	7.2	129.9	7.1
	Mean	*134.7*	*8.7*	*151.7*	*7.8*	*145.4*	*7.6*	*169.7*	*10.9*	*96.9*	*6.0*	*122.4*	*6.4*	*156.0*	*8.3*
	SED (df)														
	Irrigation (20)	20.0^{ns}	1.0^{ns}	16.3^{ns}	0.6^{**}	13.0^{ns}	0.6^{*}	30.0^{ns}	1.5^{ns}	7.9^{ns}	0.5^{ns}	18.4^{ns}	0.6^{*}	13.8^{ns}	0.6^{ns}
	Nitrogen (20)	24.5^{ns}	1.3^{ns}	20.0^{ns}	0.7^{ns}	15.9^{ns}	0.7^{ns}	36.7^{ns}	1.8^{ns}	9.7^{ns}	0.6^{ns}	22.6^{*}	0.7^{*}	16.8^{ns}	0.7^{ns}
	*Irrigation*Nitrogen (20)*	34.7^{ns}	1.8^{ns}	28.3^{ns}	1.0^{ns}	22.5^{ns}	1.0^{ns}	51.9^{ns}	2.6^{ns}	13.7^{*}	0.8^{*}	31.9^{ns}	1.0^{ns}	23.8^{ns}	1.0^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 5.12 Specific root length (SRL, m g^{-1}) and root volume: root weight ratio (rV:rW, cm^3 g^{-1}) per column for barley cv. Rum subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 75 DAS, anthesis and harvest in 2007.

Irrigation	Barley cv. Rum			
	28 DAS		Harvest	
	SRL (m g^{-1})	rV:rW (cm^3 g^{-1})	SRL (m g^{-1})	rV:rW (cm^3 g^{-1})
Irrigated	99.1	18.5	277.8	11.5
Droughted	110.3	18.5	264.2	11.8
SED (df)				
Irrigation (6)	8.2^{ns}	1.7^{ns}	16.0^{ns}	0.9^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and *ns* for a non significant result for the ANOVA test.

5.2.7 Mean Root Diameter (RD)

5.2.7.1 2006

Throughout the season barley cv. Rum had higher mean root diameter (RD) than wheat cv. Hourani ($p < 0.05$, Table 5.13). Root diameter overall decreased from 0.358 mm at 67 DAS to 0.315 mm at anthesis and then to 0.284 mm at harvest for barley cv. Rum; and from 0.321 to 0.288 to 0.253 mm, respectively, for wheat cv. Hourani (Table 5.13). Nitrogen supply had no statistically significant effect on RD for both barley cv. Rum and wheat cv. Hourani (Table 5.13), whereas drought increased RD at anthesis ($p \leq 0.05$) and harvest ($p \leq 0.01$) for barley cv. Rum (7% and 5%, respectively) and wheat cv. Hourani (6% and 9%, respectively; Table 5.13).

5.2.7.2 2007

In 2007 the only statistically significant effect on RD of barley cv. Rum was a small increase with drought at harvest (Table 5.14). For wheat cv. Karim, drought increased

($p \leq 0.001$) RD by 6% but only at anthesis (Table 5.14). Nitrogen also overall increased RD at anthesis ($p < 0.05$) at N50 and N100 (Table 5.14).

Drought increased the RD for wheat cv. Hourani at harvest by 4% *(*$p < 0.05$) (Table 5.14). There was also an effect of N ($p < 0.05$) (Table 5.14) with 50 kg N ha^{-1} slightly decreasing the RD compared to the nil N treatment, but no increase with 100 Kg N ha^{-1}.

Though overall drought increased RD, the effects were probably not large enough to have any significant physiological advantage.

5.2.7.3 2008

In 2008, as seen in previous years, RD decreased with time, though no statistically significant effects of drought were observed (Table 5.15).

Table 5.13 Mean root diameter (mm) per column for barley cv. Rum and durum wheat cv. Hourani subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}) at 67 DAS, anthesis and harvest in 2006.

Species	Irrigation	Fertilizer N (kg N ha^{-1})	Mean root diameter (mm)		
			67 DAS	Anthesis	Harvest
Barley cv. Rum	**Irrigated**	**0**	0.329	0.292	0.271
		50	0.408	0.290	0.291
		100	0.324	0.332	0.267
		Mean	*0.354*	*0.305*	*0.276*
	Droughted	**0**	0.380	0.342	0.306
		50	0.366	0.312	0.290
		100	0.341	0.320	0.278
		Mean	*0.362*	*0.325*	*0.291*
Wheat cv. Hourani	**Irrigated**	**0**	0.307	0.274	0.236
		50	0.378	0.292	0.234
		100	0.236	0.274	0.257
		Mean	*0.307*	*0.280*	*0.243*
	Droughted	**0**	0.324	0.299	0.267
		50	0.315	0.301	0.261
		100	0.368	0.290	0.262
		Mean	*0.335*	*0.297*	*0.264*
		SED (df)			
		Species (22)	0.015^{*}	0.007^{**}	0.006^{***}
		Irrigation (22)	0.015^{ns}	0.007^{*}	0.006^{**}
		Nitrogen (22)	0.018^{*}	0.009^{ns}	0.008^{ns}
		*Species*Irrigation (22)*	0.021^{ns}	0.011^{ns}	0.009^{ns}
		*Species*Nitrogen (22)*	0.025^{ns}	0.013^{ns}	0.011^{ns}
		*Irrigation*Nitrogen (22)*	0.025^{**}	0.013^{ns}	0.011^{ns}
		*Species*Irrigation*Nitrogen (22)*	0.036^{ns}	0.018^{ns}	0.015^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 5.14 Mean root diameter (mm) per column for barley cv. Rum, durum wheat cv. Hourani and durum wheat cv. Rum subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 75 DAS, anthesis and harvest in 2007.

Irrigation	Fertilizer N (kg N ha^{-1})	Mean root diameter (mm)						
		Barley cv. Rum			Wheat cv. Karim			Wheat cv. Hourani
		75 DAS	Anthesis	Harvest	75 DAS	Anthesis	Harvest	Harvest
Irrigated	**0**	0.308	0.253	0.245	0.321	0.256	0.269	0.250
	50	0.300	0.253	0.245	0.302	0.282	0.277	0.243
	100	0.278	0.248	0.239	0.321	0.259	0.269	0.259
	Mean	*0.296*	*0.251*	*0.243*	*0.315*	*0.265*	*0.271*	*0.251*
Droughted	**0**	0.281	0.249	0.259	0.309	0.272	0.274	0.264
	50	0.294	0.267	0.262	0.302	0.289	0.251	0.252
	100	0.300	0.267	0.252	0.289	0.281	0.273	0.264
	Mean	*0.292*	*0.261*	*0.258*	*0.300*	*0.281*	*0.266*	*0.260*
	SED (df)							
	Irrigation (20)	0.008^{ns}	0.007^{ns}	0.006^{*}	0.010^{ns}	0.005^{**}	0.009^{ns}	0.004^{*}
	Nitrogen (20)	0.010^{ns}	0.009^{ns}	0.007^{ns}	0.012^{ns}	0.006^{*}	0.011^{ns}	0.005^{*}
	*Irrigation*Nitrogen (20)*	0.014^{ns}	0.013^{ns}	0.010^{ns}	0.017^{ns}	0.009^{ns}	0.015^{ns}	0.007^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 5.15 Mean root diameter (mm) per column for barley cv. Rum subjected to full irrigated and droughted treatments at 28 DAS and harvest in 2008.

Irrigation	Barley cv. Rum	
	Mean root diameter (mm)	
	28 DAS	Harvest
Irrigated	0.489	0.230
Droughted	0.462	0.239
SED (df)		
Irrigation (6)	0.024^{ns}	0.007^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

5.2.8 Mean Root diameter distribution with depth

5.2.8.1 2006

In 2006 overall RD decreased with time and depth for both barley cv. Rum and wheat cv. Hourani (Figure 5.8 and Figure 5.9). At anthesis the RD decrease by 25.3% from 0 – 20 to 60 – 80 cm soil depth and by 35.7% to > 125 cm for barley cv. Rum (Figure 5.8 b, e); and by 10.3 and 14.2%, respectively, for wheat cv. Hourani (Figure 5.9 b, e). At harvest similar decreases with depth were observed (Figure 5.9 c, f).

In 2006 at 67 DAS barley cv. Rum had a higher ($p \leq 0.05$) RD than wheat cv. Hourani, but only at the 0 -20 cm soil depth (Figure 5.8 a, d and Figure 5.9 a, d). This sampling was before the irrigation and nitrogen treatments were applied. At anthesis effects were only observed at 0 – 20 cm, with barley cv. Rum having a higher RD than wheat cv. Hourani ($p \leq 0.05$); and drought increasing ($p \leq 0.05$) RD by 12% and10%, respectively (Figure 5.8 b, e and Figure 5.9 b, e).

At harvest barley cv. Rum again had greater ($p \leq 0.05$) mean RD than wheat cv. Hourani at 0 – 20 cm by 10% (Figure 5.8 c, f and Figure 5.9 c, f). In this soil layer, drought also increased ($p \leq 0.01$) the mean RD by 14% (Figure 5.8 c, f and Figure 5.9 c, f). An interaction between species and irrigation ($p \leq 0.05$) was observed at 0 – 20 cm, with drought having neutral effects for wheat cv. Hourani but increasing RD for barley cv. Rum. At the soil-depth of 60 – 80 cm barley cv. Rum continued to have a higher ($p \leq 0.01$) mean RD than wheat cv. Hourani, 0.245 cf. 0.219 mm (Figure 5.8 c, f and Figure 5.9 c, f). At this depth there was an interaction between species and irrigation ($p \leq 0.01$), with drought: decreasing RD, more for wheat than barley (Figure 5.8 c, f and Figure 5.9 c, f). At the depth > 125 cm the only significant effect was for the irrigation treatment: the droughted plants having a RD of 0.251 mm and the irrigated ones 0.226 mm (Figure 5.8 c, f and Figure 5.9 c, f).

For barley cv. Rum at anthesis the RD was more uniformly distributed with depth under irrigation decreasing by 21% from 0 – 20 cm to 60 – 80 cm and 33% to > 125 cm,

whilst under drought the decrease was 29% and 38% respectively (Figure 5.8. b, e). From anthesis to harvest there was a slight decrease (10%) in RD in all 0 – 20 and 60 – 80 cm soil depths, and an increase (7%) deeper > 125 cm in the soil profile (Figure 5.8. b, c, e, f). The decrease in RD with depth at harvest was less under irrigation than under drought (Figure 5.8. e).

For wheat cv. Hourani at anthesis the RD of the irrigated plants was evenly distributed in the soil profile, but for the droughted plants there was a decrease of 15% from the top 20 cm to the 60 – 80 cm and a further 18% to > 125 cm soil-depth (Figure 5.9 b, e). Mean RD for wheat cv. Hourani at 0 - 20 cm did not change from anthesis to harvest (approximately 0.3 mm), but for the 60 – 80 cm and > 125 cm soil-depth there was a decrease in RD for both irrigated and droughted plants (Figure 5.9 b, c, e, f).

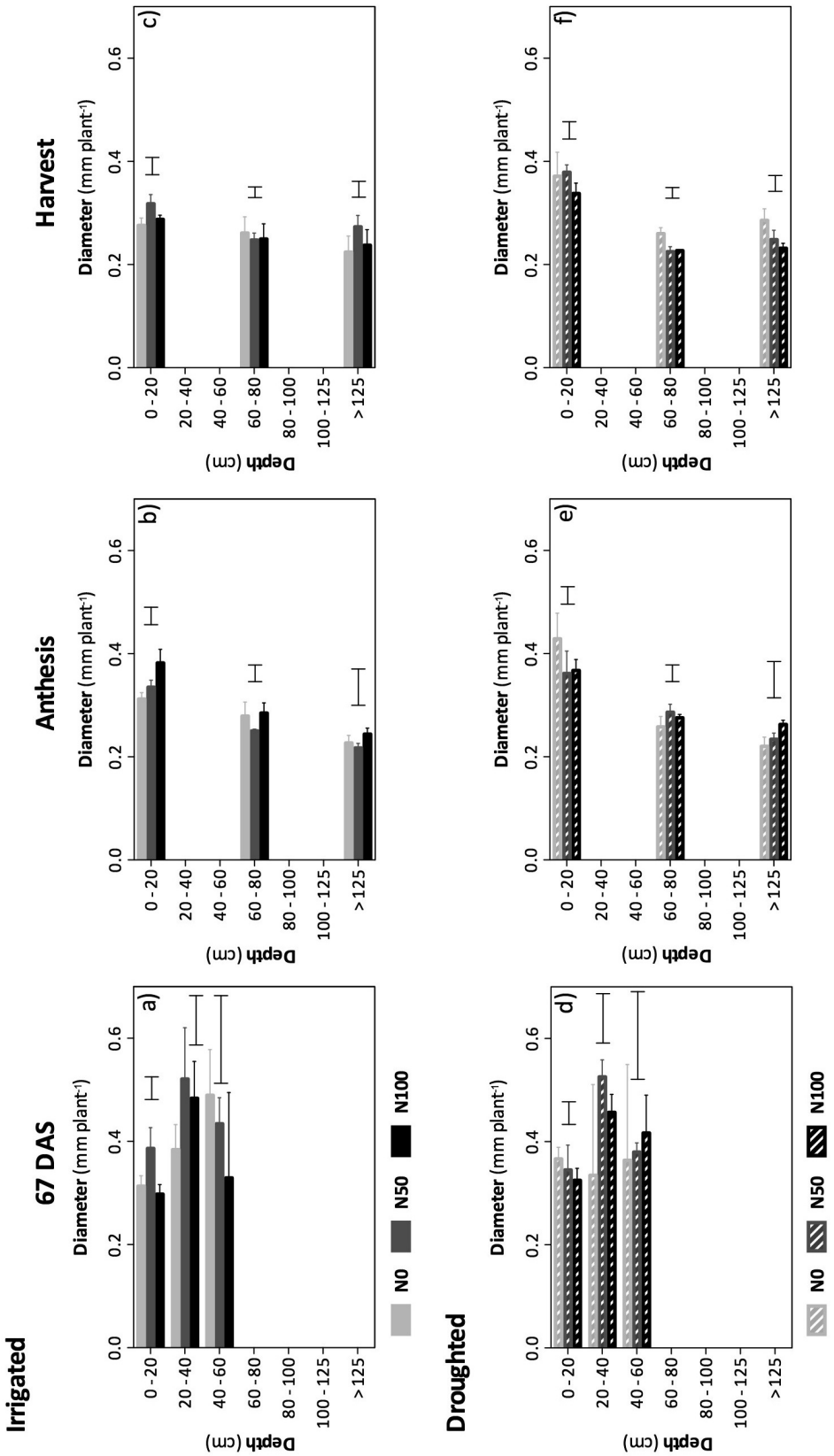

Figure 5.8 Mean root diameter (mm) for different soil depth layers for barley cv. Rum subjected to full irrigated (full bars) and droughted (striated bars) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 67 DAS (**a** & **d**), anthesis (**b** & **e**) and harvest (**c** & **f**) in 2006. Error bars represent SE of the mean and SED for species*irrigation*nitrogen (df = 22).

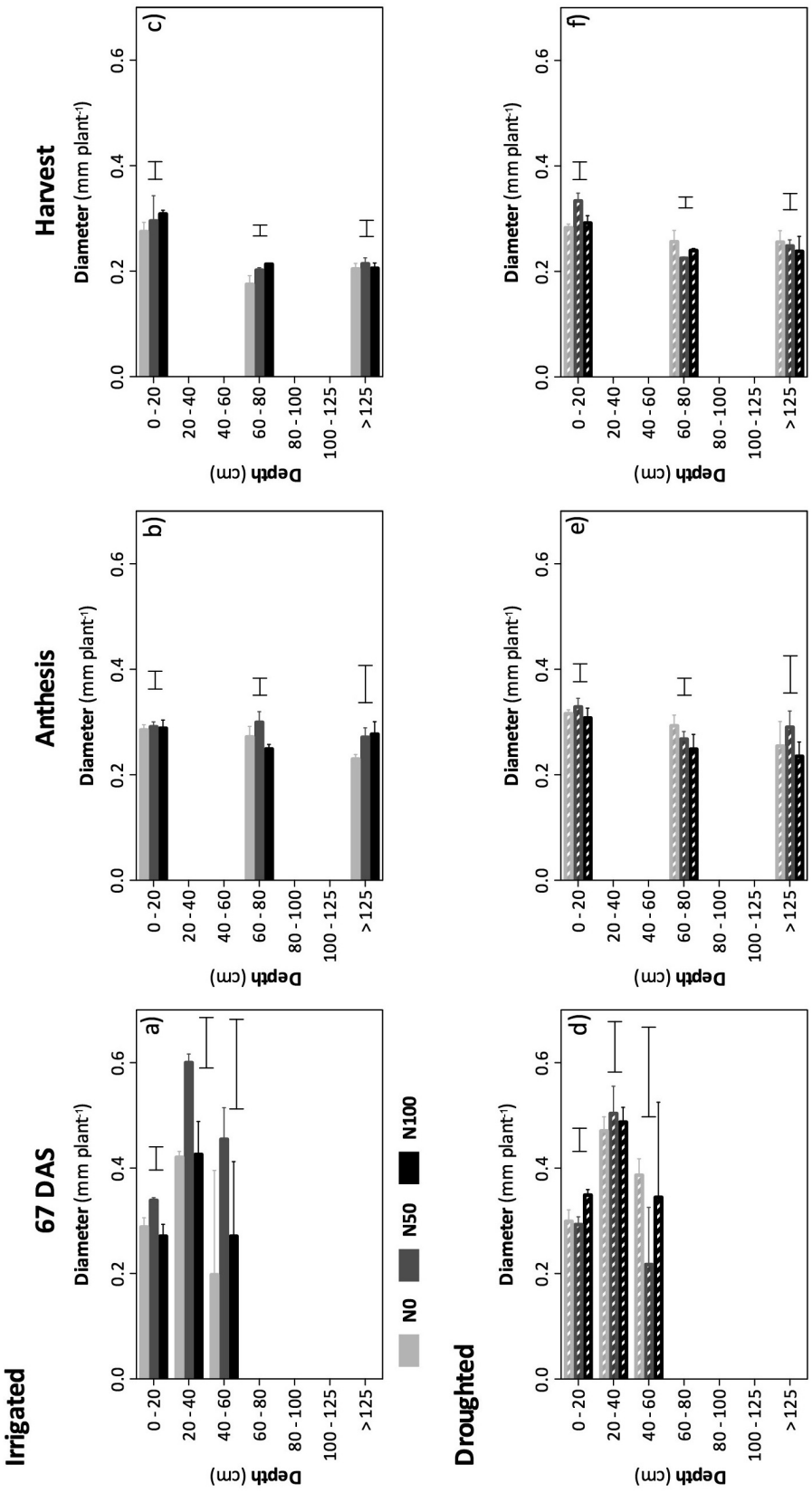

Figure 5.9 Mean root diameter (mm) for different soil depth layers for durum wheat cv. Karim subjected to full irrigated (full bars) and droughted (striated bars) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 67 DAS (**a** & **d**), anthesis (**b** & **e**) and harvest (**c** & **f**) in 2006. Error bars represent SE of the mean and SED for species x irrigation x nitrogen (df = 22).

5.2.8.2 2007

For barley cv. Rum in 2007 at 75 DAS the overall RD decreased from 0.306 mm at 0 – 20 cm to 0.253 mm at 40 – 60 cm and then to 0.261 mm at 80 – 100 cm soil-depth (Figure 5.10 a, b). At anthesis for the soil depths 60 – 80 and > 125 cm, drought increased RD by 25% ($p \leq 0.001$) and 8% ($p \leq 0.05$), respectively (Figure 5.10, b & e). At harvest, drought increased the RD at lower soil depths by 0.023 mm ($p \leq 0.001$) at 60 – 80 cm and 0.040 ($p \leq 0.01$) at > 125 cm (Figure 5.10 c, f). At anthesis and harvest RD decreased with depth for all treatments though it was more accentuated for the irrigated plants (Figure 5.10 b, c, e, f). For wheat cv. Karim at anthesis at soil depth of 60 - 80 cm drought increased ($p \leq 0.001$) RD by 20% (Figure 5.11 b, e). Increasing N supply increased ($p \leq 0.01$) RD at soil depth > 125 cm by 2% at N50 and by 17% at N100 (Figure 5.11 b, e). At harvest at 60 – 80 cm drought increased ($p \leq 0.001$) RD by 0.042 mm (Figure 5.11 c, f). There was a decrease in RD with soil-depth, of 37% from the top 20 cm to 60 - 80 cm and a further 35% to > 125 cm under irrigation and 24 and 33%, respectively, under drought (Figure 5.11 b, e). At harvest similar decreases with soil depth were observed (Figure 5.11 c, f). The effects of irrigation and applied N for wheat cv. Hourani in 2007 were only evaluated at harvest (Figure 5.12). At soil depths of 0 – 20 and 60 – 80 cm there were no significant effects of water or nitrogen on RD (Figure 5.12), but at > 125 cm soil layer drought significantly increased the mean root diameter by 10% (Figure 5.12). Overall the RD distribution with depth was similar for all treatments decreasing by ca., 28 – 30% from the top layer to 60 – 80 cm and in turn from this layer to > 125 cm soil depth (Figure 5.12).

5.2.8.3 2008

In 2008 irrigation had no significant effect on the RD at any stage (Figure 5.13). The overall mean at 28 DAS was 0.475 mm at 0 – 20 cm decreasing at harvest to 0.245 mm (Figure 5.13). The decrease in RD with depth observed in previous years (*vide* section

5.2.8.1 and 5.2.8.2) was only observed for the droughted treatment, 14% from the top 20 cm to 60 – 80 cm and 16% to > 125 cm (Figure 5.13 b).

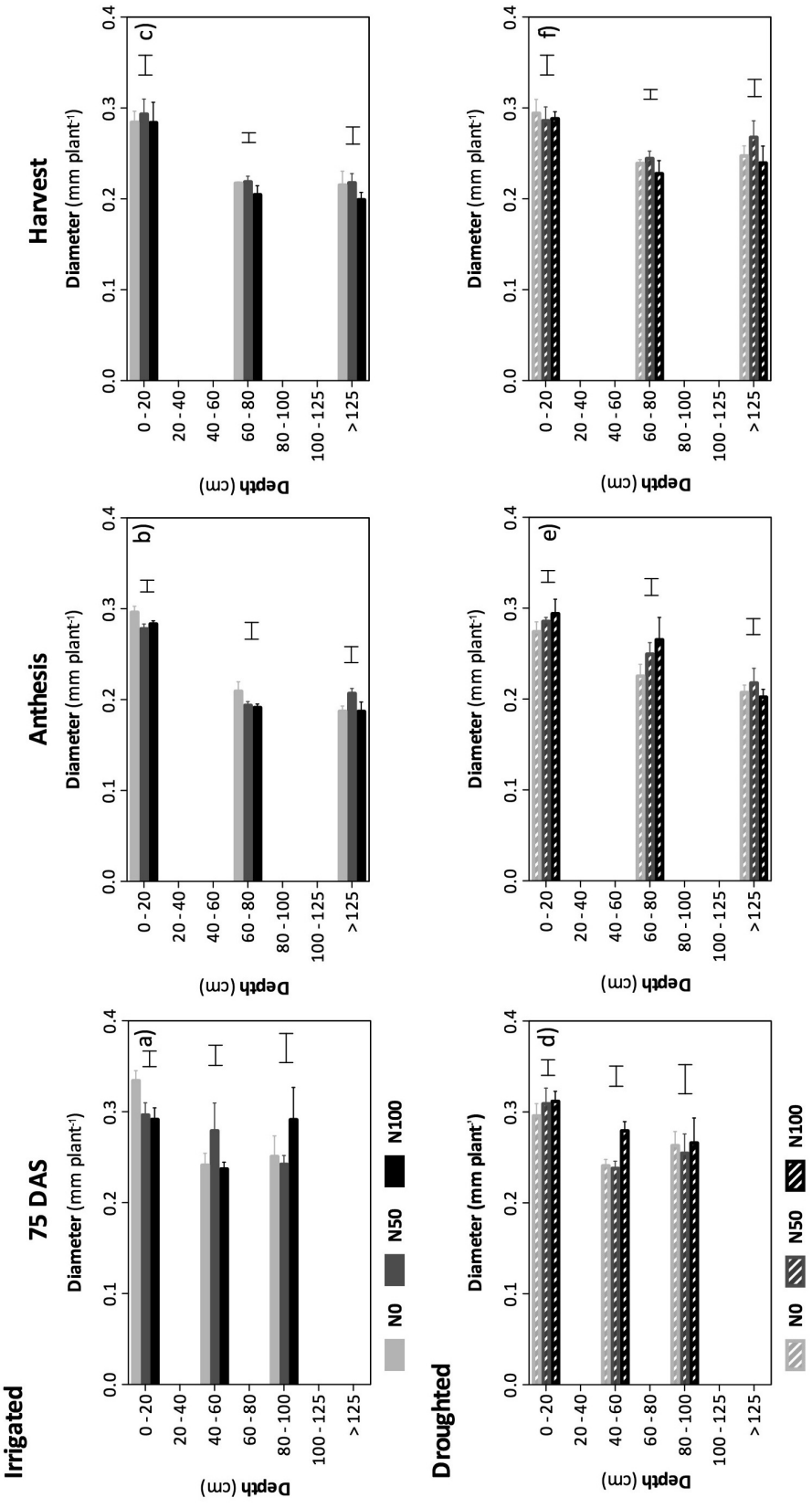

Figure 5.10 Mean root diameter (mm) for different soil-depth layers for barley cv. Rum subjected to full irrigated (full bars) and droughted (striated bars) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 75 DAS (**a** & **d**), anthesis (**b** & **e**) and harvest (**c** & **f**) in 2007. Error bars represent SE of the mean and SED for irrigation x nitrogen (df = 24).

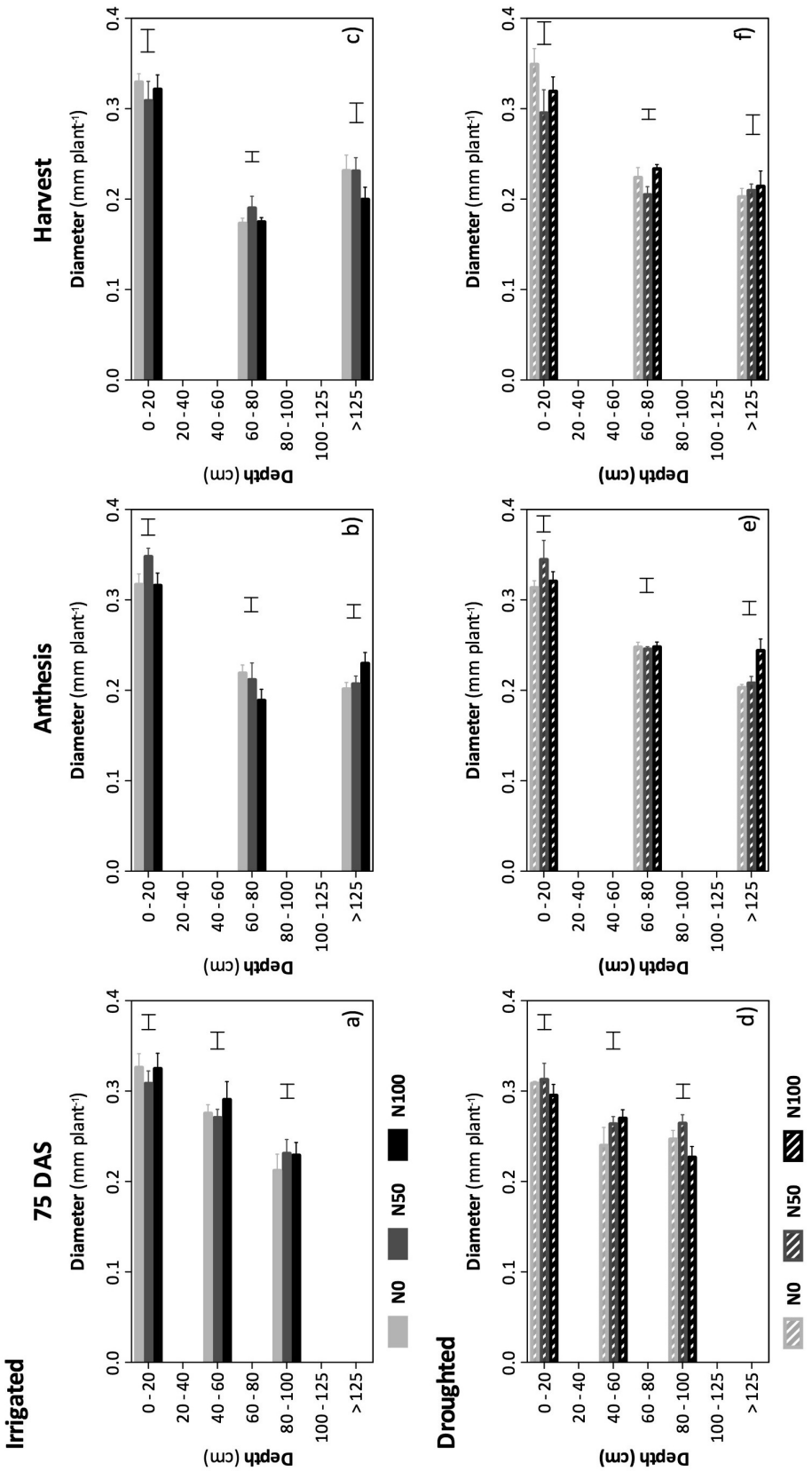

Figure 5.11 Mean root diameter (mm) for different soil depth layers for durum wheat cv. Karim subjected to full irrigated (full bars) and droughted (striated bars) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 75 DAS (**a** & **d**), anthesis (**b** & **e**) and harvest (**c** & **f**) in 2007. Error bars represent SE of the mean and SED for irrigation x nitrogen (df = 24).

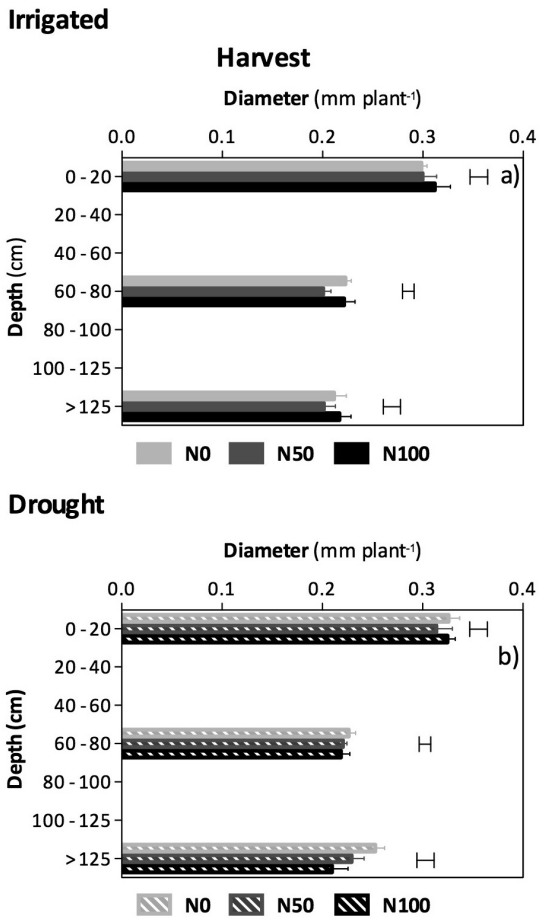

Figure 5.12 Mean root diameter (mm) for different soil depth layers for durum wheat cv. Hourani subjected to full irrigated (**a**, full bars) and droughted (**b**, striated bars) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) at harvest in 2007. Error bars represent SE of the mean and SED for irrigation x nitrogen (df = 24).

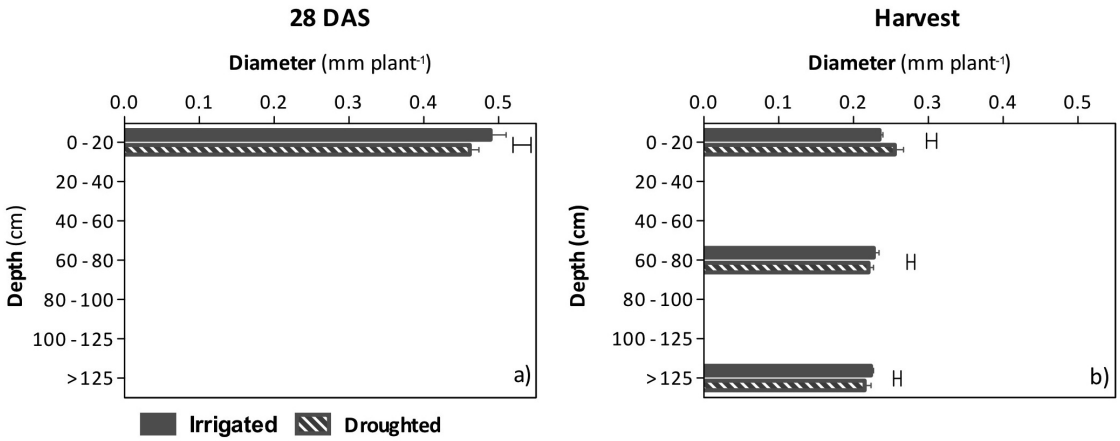

Figure 5.13 Mean root diameter (mm) for barley cv. Rum subjected to full irrigated (full bars) and droughted (striated bars) treatments, at 28 DAS (days after sowing, **a**) and harvest (**b**) in 2008. Error bars represent SE of the mean and SED for irrigation (df = 8).

5.2.9 Total Root Length (TRL)

Due to the difficulty of analysing the complete root system, the total root length (TRL) was calculated as the sum of the root length of the layers analysed, therefore it is not the true root length. For the first sampling point, in 2006, this was the root length in the 0 – 60 cm soil depth, in 2007 the soil-depths 0 – 20, 40 – 60 cm and 80 – 100 cm, and in 2008 the 0 – 20 cm soil-depth. At anthesis and harvest sampling points, the TRL was the sum of the root lengths in the 0 – 20, 60 – 80 and > 125 cm soil-depths.

5.2.9.1 2006

In 2006 at 67 DAS the average total root length (TRL) across treatments was 13.3 m for barley cv. Rum and 11.7 m for wheat cv. Hourani (Table 5.16).

At anthesis the difference between crop species increased ($p \leq 0.001$), with wheat cv. Hourani having 50% less TRL than barley cv. Rum (Table 5.16). Applied N significantly increased TRL for both species by 14 m at N50 and 15 m at N100 for barley cv. Rum; and 12 and 5 m, respectively, for wheat cv. Hourani when averaged across irrigation treatments (Table 5.16).

At harvest barley cv. Rum had a TRL 42% greater ($p \leq 0.05$) than wheat cv. Hourani (Table 5.16). The species x irrigation interaction was significant ($p \leq 0.001$) at harvest, with drought decreasing root length by 25 m for barley cv. Rum but increasing root length by 25 m for wheat cv. Hourani (Table 5.16).

Table 5.16 Total root length (m) per column for combined soil-depths: 0 – 20, 20 – 40 and 40 – 60 cm at 67 DAS; 0 – 20, 60 – 80, > 125 cm at anthesis and harvest, for barley cv. Rum and durum wheat cv. Hourani subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 67 DAS, anthesis and harvest in 2006.

Species	Irrigation	Fertilizer N (kg N ha^{-1})	Total root length (m)		
			67 DAS	Anthesis	Harvest
Barley cv. Rum	**Irrigated**	**0**	11.9	69.7	93.3
		50	16.2	87.7	79.8
		100	11.9	76.0	38.8
		Mean	*13.3*	*77.8*	*70.6*
	Droughted	**0**	13.3	61.3	43.3
		50	13.2	71.9	46.8
		100	13.4	84.2	47.2
		Mean	*13.3*	*72.5*	*45.8*
Wheat cv. Hourani	**Irrigated**	**0**	9.6	31.7	28.3
		50	15.1	43.4	34.4
		100	12.5	35.6	23.0
		Mean	*12.4*	*36.9*	*28.6*
	Droughted	**0**	12.2	30.5	55.4
		50	8.7	42.8	56.0
		100	12.3	36.2	49.2
		Mean	*11.1*	*36.5*	*53.5*
		SED (df)			
		Species (22)	1.0^{ns}	4.2^{***}	6.9^{*}
		Irrigation (22)	1.0^{ns}	4.2^{ns}	69^{ns}
		Nitrogen (22)	1.3^{ns}	5.1^{*}	8.4^{ns}
		*Species*Irrigation (22)*	1.5^{ns}	5.9^{ns}	9.7^{***}
		*Species*Nitrogen (22)*	1.8^{ns}	7.2^{ns}	11.9^{ns}
		*Irrigation*Nitrogen (22)*	1.8^{*}	7.2^{ns}	11.9^{ns}
		*Species*Irrigation*Nitrogen (22)*	2.5^{ns}	10.2^{ns}	16.8^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

5.2.9.2 2007

In 2007 TRL for barley cv. Rum was smaller than in 2006 (14 m at anthesis and 25 m at harvest compared to 75 and 58 m, respectively, in 2006, Table 5.16 and Table 5.17). The average TRL increased from 9 m at 75 DAS to 14 m at anthesis and to 25 m at harvest (Table 5.17). Neither irrigation nor nitrogen supply significantly changed the TRL for barley cv. Rum in 2007, with the only relevant trend a slight increase ($p \leq 0.094$) of 3.4 m with drought at anthesis (Table 5.17).

The total root length almost doubled from 75 DAS to anthesis and then declined at harvest for wheat cv. Karim in 2007 (Table 5.17). Drought increased the TRL by 34% at anthesis and by 49% at harvest ($p \leq 0.01$ and $p \leq 0.001$ respectively, Table 5.17). Nitrogen application decreased ($p \leq 0.01$) TRL at anthesis by 5 m at N50 and by 6 m with at N100 under irrigation, and by 3 and 2 m, respectively, under drought ($p< 0.05$) (Table 5.17).

For wheat cv. Hourani at harvest in 2007 there was no effect of irrigation regime on TRL (Table 5.17), although N decreased ($p \leq 0.01$) TRL by 26 and 39% with 50 and 100 kg N ha^{-1}, respectively (Table 5.17).

5.2.9.3 2008

In 2008 TRL increased from 4.5 m at 28 DAS to 144 m at harvest when averaged across irrigation treatments, and drought decreased ($p \leq 0.05$) the TRL by 45 m (Table 5.18).

Table 5.17 Root total length (m) per column for combined soil-depths: 0 – 20, 40 – 60 and 80 – 100 cm at 75 DAS; 0 – 20, 60 – 80, > 125 cm at anthesis and harvest, for barley cv. Rum, durum wheat cv. Karim and durum wheat cv. Hourani (only measured art harvest) subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) in 2007.

Irrigation	FertilizerN (kg N ha^{-1})	Total root length (m)						
		Barley cv. Rum			Wheat cv. Karim			Wheat cv. Hourani
		75 DAS	Anthesis	Harvest	75 DAS	Anthesis	Harvest	Harvest
Irrigated	**0**	7.8	13.3	27.8	6.9	15.5	7.0	31.8
	50	7.6	12.7	29.5	8.4	10.2	5.8	20.5
	100	10.5	12.3	24.6	6.3	9.5	7.0	21.2
	Mean	*8.6*	*12.8*	*27.3*	*7.2*	*11.7*	*6.6*	*24.5*
Droughted	**0**	7.1	16.5	25.9	7.3	17.3	12.4	33.3
	50	9.2	15.9	18.2	6.1	14.6	10.7	27.8
	100	9.7	16.0	23.7	7.7	15.2	15.8	18.8
	Mean	*8.7*	*16.1*	*22.6*	*7.1*	*15.7*	*13.0*	*26.6*
	SED (df)							
	Irrigation (20)	0.9^{ns}	1.9^{ns}	2.8^{ns}	0.8^{ns}	1.1^{**}	1.4^{***}	2.6^{ns}
	Nitrogen (20)	1.1^{ns}	2.4^{ns}	3.4^{ns}	1.0^{ns}	1.4^{*}	17^{ns}	3.2^{**}
	*Irrigation*Nitrogen (20)*	1.5^{ns}	3.3^{ns}	4.9^{ns}	1.4^{ns}	1.9^{ns}	2.4^{ns}	4.6^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 5.18 Root total length (m) per column for 0 – 20 cm soil depth at 28 DAS and for combined 0 – 20, 60 – 80, > 125 cm soil-depths at harvest for barley cv. Rum subjected full to irrigated and droughted treatments at 28 DAS and harvest in 2008.

Irrigation	Barley cv. Rum Total root length (m)	
	28 DAS	Harvest
Irrigated	4.3	166.4
Droughted	4.7	121.7
SED (df)		
Irrigation (6)	3.4^{ns}	15.42^{*}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

5.2.10 Root Length Density (RLD) Distribution with Depth

5.2.10.1 2006

As expected at 67 DAS there were no significant differences for RLD between species or treatments, with average values of 0.343, 0.040 and 0.009 cm cm^{-3} for the soil layers 0 – 20, 20 – 40 and 40 – 60 cm for barley cv. Rum (Figure 5.14 a, d); and 0.321, 0.032 and 0.010 cm cm^{-3}, respectively, for wheat cv. Hourani (Figure 5.15 a, d).

At anthesis for all the three soil layers barley cv. Rum had higher RLD than wheat cv. Hourani ($p < 0.01$) (Figure 5.14 b, e and Figure 5.15 b, e).

At harvest at 0 – 20 cm barley cv. Rum had a RLD 101% higher ($p \leq 0.001$) than wheat cv. Hourani (Figure 5.14 c, f and Figure 5.15 c, f). At this soil-depth, there was an effect of irrigation ($p \leq 0.01$) and interaction between irrigation and species ($p \leq 0.01$), with drought decreasing RLD for barley cv. Rum but with no effect for wheat cv. Hourani (Figure 5.14 c, f and Figure 5.15 c, f). There was also a nitrogen ($p = 0.053$) and an irrigation x nitrogen effect ($p \leq 0.01$), with N application decreasing RLD for both species under irrigation although not under drought (Figure 5.14 c, f and Figure 5.15 c, f). At the 60 – 80 cm soil-depth barley cv. Rum had a 62% higher RLD than wheat cv. Hourani ($p = 0.054$; Figure 5.14 c, f); whereas deeper in the profile (>125 cm), there were no significant differences between the treatments (Figure 5.14 c, f and Figure 5.15 c, f).

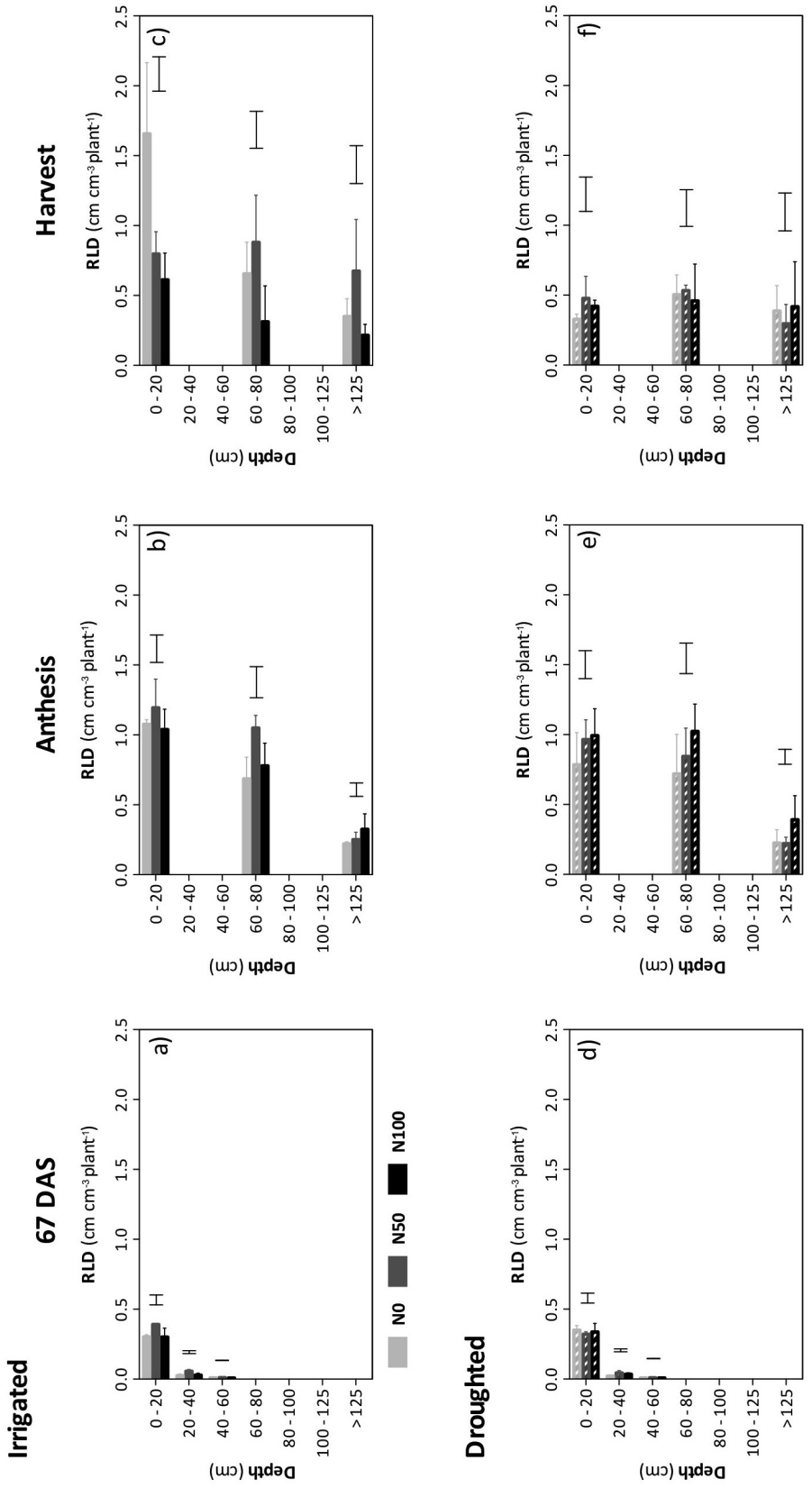

Figure 5.14 Root length density (RLD, cm cm^{-3}) for different soil depth layers for barley cv. Rum subjected to full irrigated (full bars) and droughted (striated bars) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 67 DAS (**a** & **d**), anthesis (**b** & **e**) and harvest (**c** & **f**) in 2006. Error bars represent SE of the mean and SED for species x irrigation x nitrogen (df = 22).

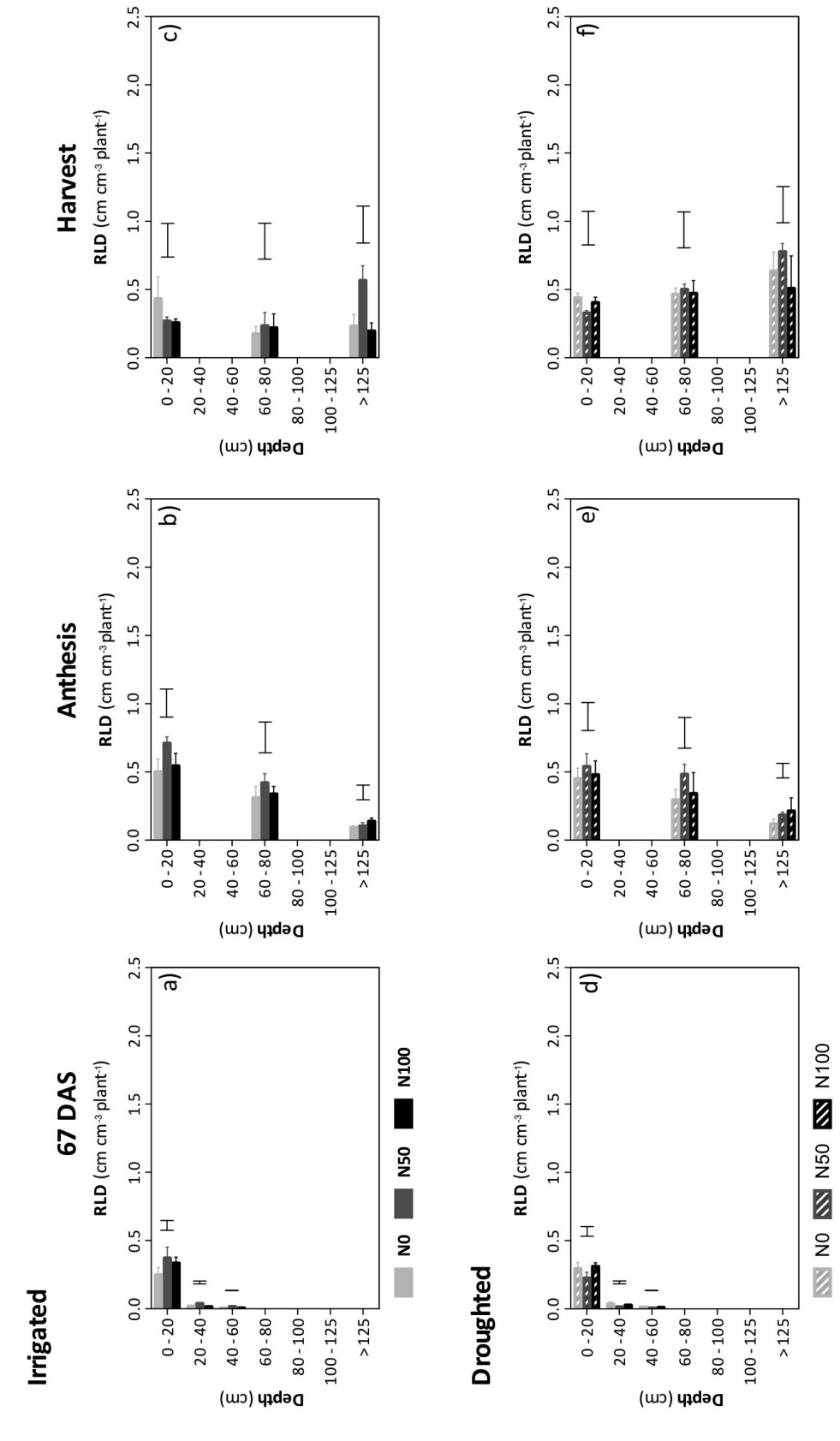

Figure 5.15 Root length density (RLD, cm cm^{-3}) for different soil depth layers for durum wheat cv. Hourani subjected to full irrigated (full bars) and droughted (striated bars) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) at 67 DAS (**a** & **d**), anthesis (**b** & **e**) and harvest (**c** & **f**) in 2006. Error bars represent SE of the mean and SED for species x irrigation x nitrogen (df = 22).

5.2.10.2 2007

For barley cv. Rum 75 DAS in 2007 the usual exponential decrease of the RLD with soil-depth was observed (Figure 5.16 a, d). At anthesis RLD under drought at depth > 125 cm was higher ($p \leq 0.05$) than under irrigation, although drought had no effect on RLD in the rest of the soil profile (Figure 5.16 b, e). Drought, however, decreased ($p \leq 0.01$) RLD at harvest for both 0 – 20 and 60 – 80 cm soil-depths by 29 and 41%, respectively (Figure 5.16 c, f). Deeper in the profile there was an interaction between irrigation and N ($p \leq 0.05$) with drought increasing RLD > 125 cm by 39% for 0 and 36% for 100 kg N ha^{-1} application but not for 50 kg N ha^{-1} (Figure 5.16 c, f).

In 2007 for wheat cv. Karim at anthesis, drought increased RLD by 35% at 0 – 20 cm ($p \leq 0.01$) and 41% at 60 – 80 cm ($p \leq 0.05$) (Figure 5.17 b, e). N50 decreased the RLD by 0.076 cm cm^{-3} ($p < 0.01$) and N100 by 0.093 cm cm^{-3} ($p < 0.01$, Figure 5.17 b, e) compared to N0. No significant effects were observed at > 125 cm (Figure 5.17 b, e). At harvest drought increased RLD of all soil layers, by 30% ($p \leq 0.05$) at 0 – 20 cm, 181% ($p \leq 0.001$) at 60 – 80 cm and 205% ($p \leq 0.05$) at >125 cm (Figure 5.17 c, f).

Overall values of RLD at anthesis were similar for wheat cv. Karim and barley cv. Rum (0.128 cf. 0.134 cm cm^{-3}, respectively; Figure 5.16 b, e and Figure 5.17 b, e). Though the highest values of RLD for barley cv. Rum were in the top 20 cm (Figure 5.16 b, e), for wheat cv. Karim they were in the 60 – 80 cm soil depth (Figure 5.17 b, e). At harvest the overall RLD was 62% higher for barley cv. Rum than for wheat cv. Karim (Figure 5.16 c, f and Figure 5.17 c, f).

At harvest in 2007 for wheat cv. Hourani, drought decreased ($p \leq 0.05$) RLD by 21% at 0 – 20 cm and in contrast increased ($p \leq 0.05$) RLD by 100% at > 125 cm (Figure 5.18). At the soil depth 60 – 80 cm, N50 and N100 decreased RLD by 32 and by 44%, respectively, compared to N0 (Figure 5.18).

In summary, drought generally increases the RLD deeper in the profile (> 125 cm) for barley cv. Rum at anthesis and harvest (Figure 5.16 b, c, e, f) and for durum wheat (cv. Karim and Hourani) at harvest (Figure 5.17 c, f and Figure 5.18). Drought also increased the RLD at 0 – 20 and 60 – 80 cm soil-depths at anthesis and harvest, but only

for wheat cv. Karim (Figure 5.17 b, c, e, f). Irrigation increased the RLD at harvest for wheat cv. Hourani at 0 – 20 cm soil-depth (Figure 5.18), and for barley cv. Rum at 0 – 20 and 60 – 80 cm soil depths (Figure 5.17 c, f). Nitrogen application decreased RLD for durum wheat but only at harvest and at the soil-depth 60 – 80 cm (Figure 5.17 c, f and Figure 5.18).

5.2.10.3 2008

For barley cv. Rum at harvest in 2008 the typical decrease of the RLD with depth was found under drought but not under irrigation (Figure 5.19). Drought decreased RLD at all soil layers but only significantly at the soil depth > 125 cm (Figure 5.19).

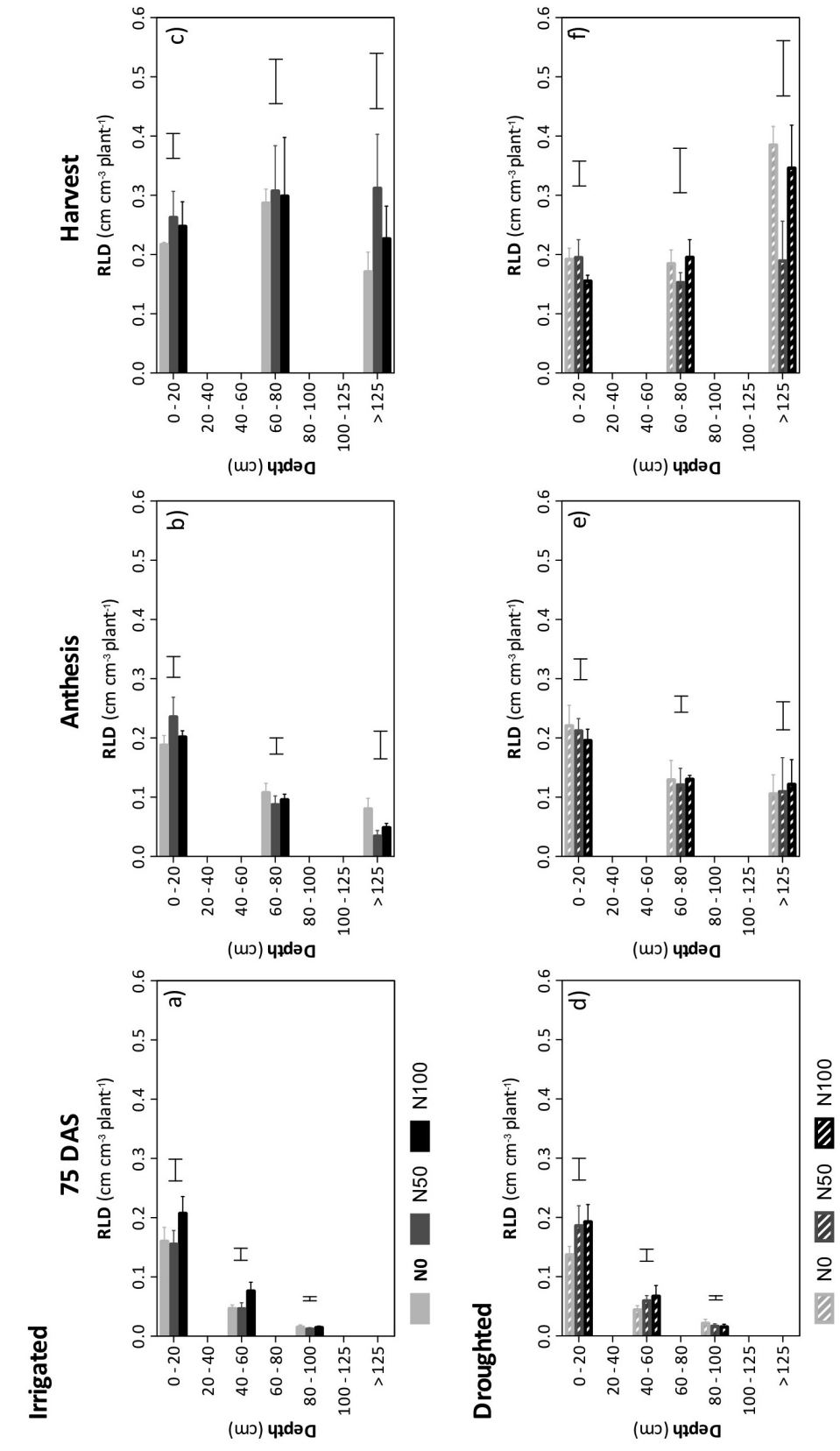

Figure 5.16 Root length density (RLD, cm cm^{-3}) for different soil depth layers for barley cv. Rum subjected to full irrigated (full bars) and droughted (striated bars) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) at 75 DAS (days after sowing, **a** & **d**), anthesis (**b** & **e**) and harvest (**c** & **f**) in 2007. Error bars represent SE of the mean and SED for species x irrigation x nitrogen (df = 24).

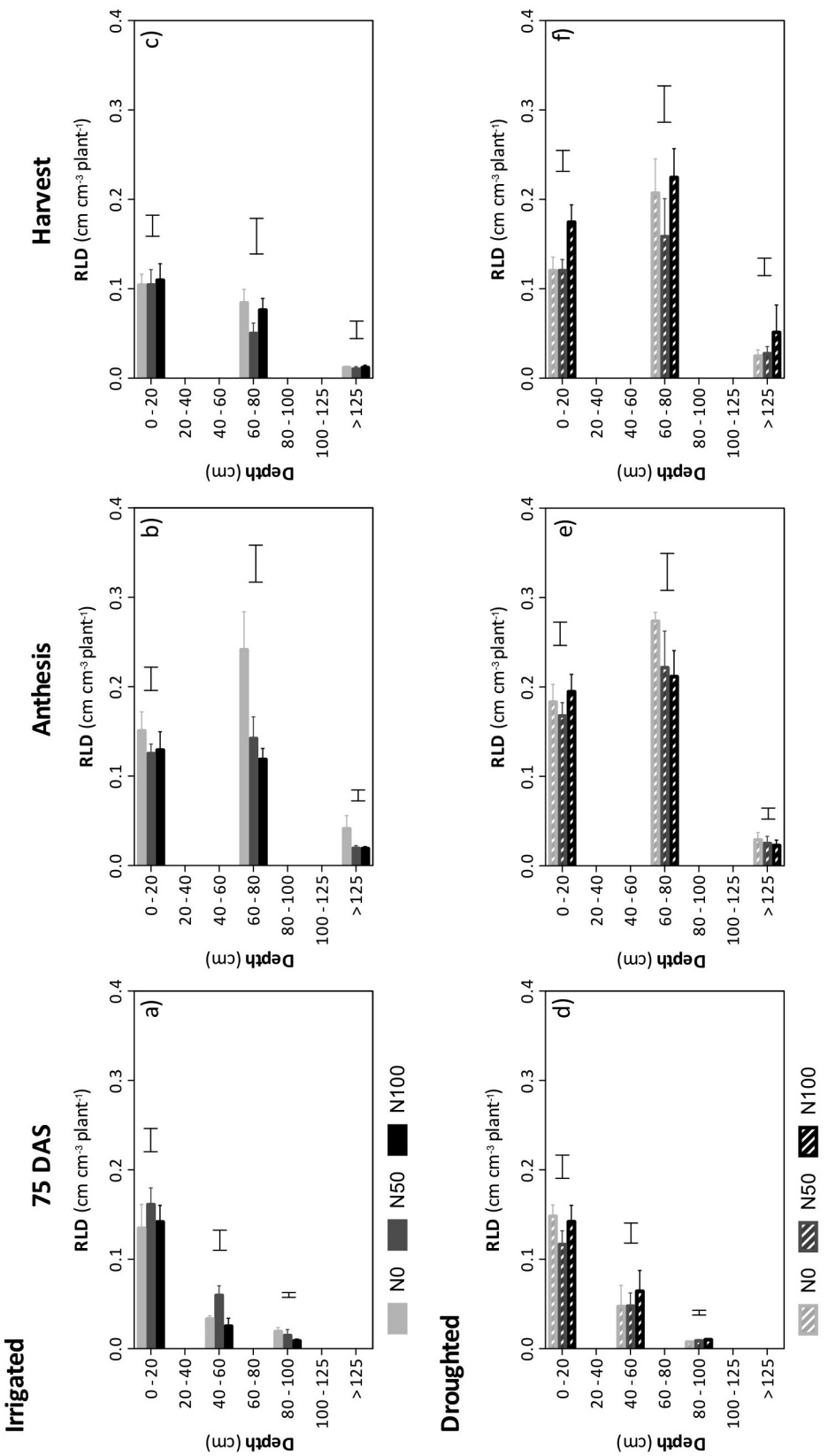

Figure 5.17 Root length density (RLD, cm cm^{-3}) for different soil depth layers for durum wheat cv. Karim subjected to full irrigated (full bars) and droughted (striated bars) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 75 DAS (days after sowing, **a** & **d**), anthesis (**b** & **e**) and harvest (**c** & **f**) in 2007. Error bars represent SE of the mean and SED for species x irrigation x nitrogen (df = 24).

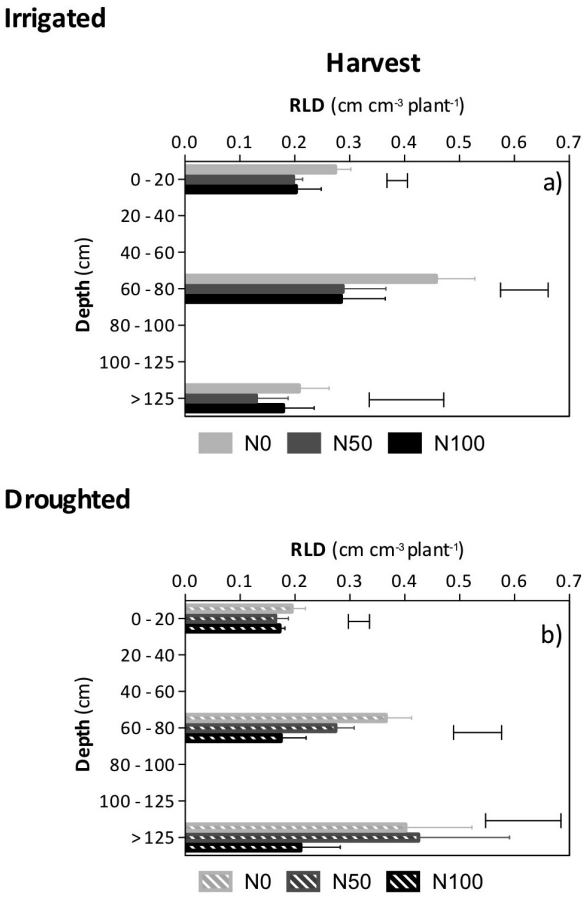

Figure 5.18 Root length density (RLD, cm cm^{-3}) for different soil depth layers for durum wheat cv. Hourani subjected to full irrigated (**a**, full bars) and droughted (**b**, striated bars) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) at harvest in 2007. Error bars represent SE of the mean and SED for species x irrigation x nitrogen (df = 0.24).

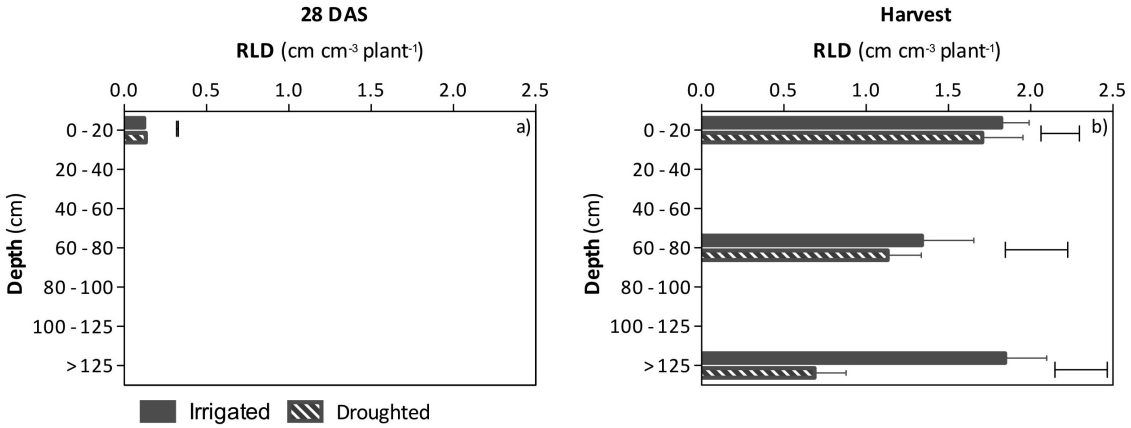

Figure 5.19 Root length density (RLD, cm cm^{-3}) for barley cv. Rum subjected to full irrigated (full bars) and droughted (striated bars) treatments, at 28 DAS (days after sowing, **a**) and harvest (**b**) in 2008. Error bars represent SE of the mean and SED for irrigation (df = 8).

5.2.11 Root length distribution with depth (β_L)

5.2.11.1 2006

The β_L estimated from the soil-depth layers analysed (*vide* section 3.6.5.3) generally increased with time for both barley cv. Rum and wheat cv. Hourani in 2006 (Table 5.19). This represented a decrease from 89% of root length in the top 20 cm at 67 DAS to only 55% at harvest for barley cv. Rum; and 91 and 38%, respectively, for wheat cv. Hourani (Table 5.19). There were no significant effects of irrigation or N application in root length distribution with soil-depth. However at harvest, when averaged across irrigation and N treatments, a trend (p = 0.11) could be identified for a higher β_L for wheat cv. Hourani (0.977) than barley cv. Rum (0.961; Table 5.19). Similarly, there was a trend for drought (p = 0.12) to increase the proportion of root length deeper in the soil profile, increasing β_L from 0.961 under irrigation to 0.977 under drought, when averaged across species and treatments.

5.2.11.2 2007

In 2007 for barley cv. Rum β_L increased with time from an overall value of 0.940 at 75 DAS to 0.981 at harvest, representing an increase in the proportion of root length at depth (Table 5.20). For wheat cv. Karim β_L also increased with time but only to anthesis (Table 5.20). Deeper root distribution (higher β_L) was found under drought at anthesis for barley cv. Rum ($p \leq 0.05$) and harvest for wheat cv. Karim ($p \leq 0.001$) and wheat cv. Hourani (p = 0.068; Table 5.20). For wheat cv. Karim N application slightly decreased ($p \leq 0.05$) the proportion of root length deeper in the profile (Table 5.20). Overall wheat cv. Karim (β_L = 0.965) at harvest had relatively less roots deeper in the profile than barley cv. Rum (β_L = 0.981) and wheat cv. Hourani (β_L = 0.979; Table 5.20).

Table 5.19 Shape of the cumulative length distribution with depth (β_L) per column estimated from three soil depths: 0 – 20, 20 – 40 and 40 – 60 cm at 67 DAS; 0 – 20, 60 – 80, > 125 cm at anthesis and harvest, for barley cv. Rum and durum wheat cv. Hourani subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 67 DAS, anthesis and harvest in 2006.

Species	Irrigation	Fertilizer N (kg N ha^{-1})	β_L		
			67 DAS	Anthesis	Harvest
Barley cv. Rum	**Irrigated**	**0**	0.887	0.962	0.945
		50	0.907	0.969	0.968
		100	0.888	0.968	0.945
		Mean	*0.894*	*0.966*	*0.953*
	Droughted	**0**	0.893	0.957	0.977
		50	0.902	0.966	0.977
		100	0.896	0.971	0.955
		Mean	*0.897*	*0.964*	*0.970*
Wheat cv. Hourani	**Irrigated**	**0**	0.880	0.957	0.960
		50	0.905	0.958	0.986
		100	0.863	0.964	0.964
		Mean	*0.883*	*0.960*	*0.970*
	Droughted	**0**	0.901	0.963	0.986
		50	0.886	0.974	0.987
		100	0.896	0.964	0.977
		Mean	*0.894*	*0.967*	*0.983*
		SED (df)			
		Species (22)	0.008^{ns}	0.006^{ns}	0.009^{ns}
		Irrigation (22)	0.008^{ns}	0.006^{ns}	0.009^{ns}
		Nitrogen (22)	0.009^{ns}	0.007^{ns}	0.011^{ns}
		*Species*Irrigation (22)*	0.011^{ns}	0.008^{ns}	0.013^{ns}
		*Species*Nitrogen (22)*	0.013^{ns}	0.010^{ns}	0.016^{ns}
		*Irrigation*Nitrogen (22)*	0.013^{ns}	0.010^{ns}	0.016^{ns}
		*Species*Irrigation*Nitrogen (22)*	0.018^{ns}	0.015^{ns}	0.023^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 5.20 Shape of the cumulative length distribution with depth (β_L) per column estimated from three soil depths: 0 – 20, 40 – 60 and 80 – 100 cm at 75 DAS; 0 – 20, 60 – 80, > 125 cm at anthesis and harvest, for barley cv. Rum, durum wheat cv. Karim and durum wheat cv. Hourani (only measured art harvest) subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) in 2007.

		β_L						
Irrigation	**Fertilizer N** (kg N ha^{-1})	**Barley cv. Rum**			**Wheat cv. Karim**			**Wheat cv. Hourani**
		75 DAS	**Anthesis**	**Harvest**	**75 DAS**	**Anthesis**	**Harvest**	**Harvest**
Irrigated	**0**	0.940	0.968	0.979	0.948	0.975	0.962	0.978
	50	0.935	0.950	0.980	0.947	0.969	0.949	0.974
	100	0.943	0.962	0.981	0.919	0.967	0.961	0.978
	Mean	*0.939*	*0.960*	*0.980*	*0.938*	*0.971*	*0.957*	*0.977*
Droughted	**0**	0.944	0.969	0.987	0.929	0.973	0.974	0.985
	50	0.940	0.965	0.975	0.942	0.971	0.972	0.985
	100	0.941	0.976	0.985	0.942	0.968	0.972	0.975
	Mean	*0.942*	*0.970*	*0.982*	*0.938*	*0.971*	*0.973*	*0.982*
	SED (df)							
	Irrigation (20)	0.006^{ns}	0.005^{*}	0.002^{ns}	0.006^{ns}	0.001^{ns}	0.002^{***}	0.003^{ns}
	Nitrogen (20)	0.007^{ns}	0.006^{ns}	0.003^{ns}	0.007^{ns}	0.002^{*}	0.003^{ns}	0.003^{ns}
	*Irrigation*Nitrogen (20)*	0.010^{ns}	0.008^{ns}	0.004^{ns}	0.010^{ns}	0.003^{ns}	0.004^{ns}	0.005^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

5.2.11.3 2008

For barley cv. Rum at harvest in contrast to previous years (Table 5.19 and Table 5.20) in 2008 irrigation increased ($p \leq 0.05$) β_L (Table 5.21). Thus under irrigation 15% of root length was below 100 cm compared to only 5% under drought (Table 5.21).

Table 5.21 Shape of the cumulative length distribution with depth (β_L) per column estimated from: 0 – 20, 60 – 80, > 125 cm at soil depths at harvest for barley cv. Rum subjected to full irrigated and droughted treatments at harvest in 2008.

Irrigation	**Barley cv. Rum** β_L
	Harvest
Irrigated	0.982
Droughted	0.971
SED (df)	
Irrigation (6)	*0.005**

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and *ns* for a non significant result for the ANOVA test.

5.2.12 Sub-traits affecting Root Length

The relationship between TRL and plant growth (AGDW), biomass partitioning to roots (R:S) and biomass investment in potential soil resources acquisition (SRL) can be simply described as:

$$TRL = AGDW \times R:S \times SRL \qquad \textbf{Equation 4.3}$$

Therefore increasing any of the parameters in the model, while holding the others constant, will lead to an increase in TRL. In Figure 5.20 – 22 is presented the linear regressions between TRL (measured at 0-20, 60-80 and > 125 cm) and: R:S, AGDW and the root morphology traits, TRW and SRL, for all genotypes and experiments. As expected for all genotypes the TRL, within and across years, was well correlated with

TRW (Table 5.22, Table 5.23 and Table 5.24), R^2 = 0.66 for barley cv. Rum, 0.78 for wheat cv. Hourani and 0.66 for wheat cv. Karim.

For barley cv. Rum, across years, both R:S and SRL were found to explain a high percentage of the TRL variation (R^2 = 0.51 and 0.60, respectively). A significant regression between AGDW and TRL was also found, but it explained only a small percentage of the variation in TRL (R^2 = 0.12; Figure 5.20 and Table 5.22).

For wheat cv. Hourani although SRL explained a high percentage of the variation found in TRL (43%) in 2007 it explained overall (2006-07) only 15% of the variation in TRL (Figure 5.21 and Table 5.23). From Figure 5.21 and Figure 5.22, it can be seen that for both durum wheat varieties TRL was correlated more strongly with R:S than AGDW (R^2 = 0.36 and 0.23 cf. for wheat cv. Hourani and 0.28 and 0.17 for wheat cv. Karim, respectively).

For all genotypes, when analysed across years, a significant correlation was found between TRL and all parameters in equation 4.3, though differences were apparent between durum wheat and barley. For durum wheat TRL was positively associated with AGDW and R:S, whereas for barley TRL was positively associated with R:S and SRL.

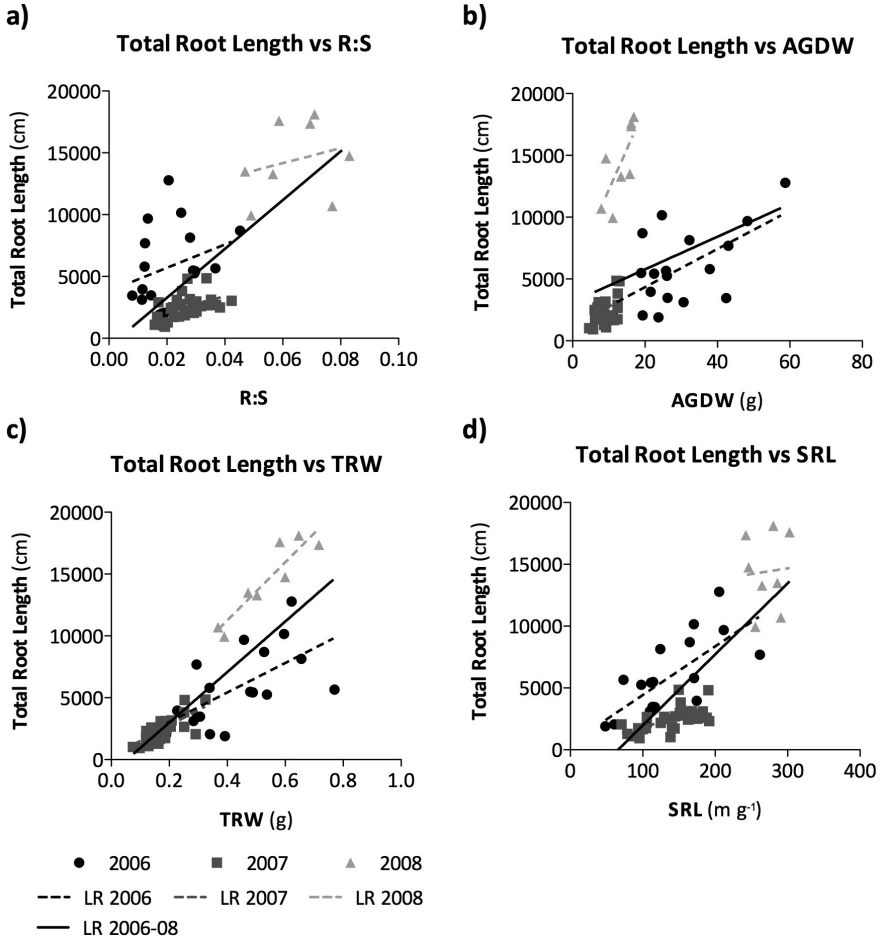

Figure 5.20 Linear regression (LR) between total root length (TRL) measured in 3 soil-depths layers (0-20, 60-80 and > 125 cm) per column and: **a**) root to shoot ratio (R:S), **b**) aboveground dry weight (AGDW), **c**) total root dry weight (TRW) and **d**) specific root length (SRL) at harvest for barley cv. Rum plants analysed in the 2006, 2007 and 2008 experiments. Data include full irrigation and drought treatments, as well as N application treatments (0, 50 and 100 kg N ha^{-1}, equivalents). Slopes and R^2 values for the linear regressions are presented in Table 5.22.

Table 5.22 Linear regressions between total root length (TRL) measured in 3 soil-depths layers (0-20, 60-80 and > 125 cm) per column and: root to shot ratio (R:S), aboveground dry weight (AGDW), total root weight (TRW) and specific root length (SRL) at harvest for barley cv. Rum plants analysed in the 2006, 2007 and 2008 experiments. Data include full irrigation and drought treatments, as well as N application treatments (0, 50 and 100 kg N ha^{-1}, equivalents). For fitted curves see Figure 5.20.

TRL vs	Barley cv. Rum							
	2006 (*df = 16*)		**2007** (*df = 28*)		**2008** *(df = 6)*		**2006-08** (*df = 54*)	
	Equation	**R^2**	**Equation**	**R^2**	**Equation**	**R^2**	**Equation**	**R^2**
R:S	$y=9.4x10^4x+3823$	0.09^{ns}	$y=6.7x10^4x+726$	0.24^{**}	$y=6.1x10^4x+10527$	0.06^{ns}	$y=19.7x10^4x-672$	0.51^{***}
AGDW	y=155x+1248	0.36^{**}	y=195x+785	0.23^{**}	y=657x+5646	0.54^{*}	y=132x-3140	0.12^{**}
TRW	$y=1.2x10^4x+650$	0.38^{**}	$y=1.2x10^4x+271$	0.52^{***}	$y=2.3x10^4x+1867$	0.85^{**}	$y=2.0x10^4x-1096$	0.66^{***}
SRL	y=39.4x+495	0.50^{***}	y=16.6x+170	0.37^{***}	y=9.3x+11897	0.00^{ns}	y=57.5x-3779	0.60^{***}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non Significant result for simple linear regression.

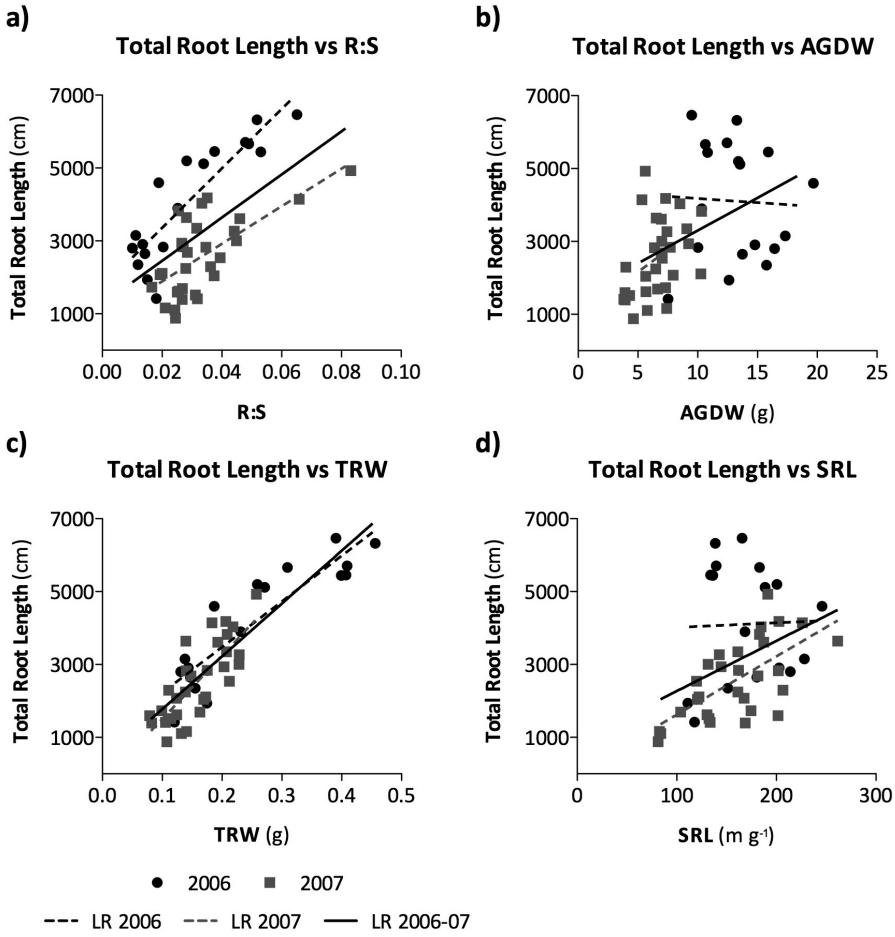

Figure 5.21 Linear regression (LR) between total root length (TRL) measured in 3 soil-depths layers (0-20, 60-80 and > 125 cm) per column and: **a**) root to shoot ratio (R:S), **b**) aboveground dry weight (AGDW), **c**) total root dry weight (TRW) and **d**) specific root length (SRL) at harvest for durum wheat cv. Hourani in the 2006 and 2007 experiments. Data include full irrigated and droughted treatments, as well as N application treatments (0, 50 and 100 kg N ha^{-1}, equivalents). Slopes and R^2 values for the linear regressions are presented in Table 5.23.

Table 5.23 Linear regression between total root length (TRL) measured in 3 soil-depths layers (0-20, 60-80 and > 125 cm) per column and: root to shoot ratio (R:S), aboveground dry weight (AGDW), total root weight (TRW) and specific root length (SRL) at harvest for durum wheat cv. Hourani in the 2006 and 2007 experiments. Data include full irrigated and droughted treatments, as well as N application treatments (0, 50 and 100 kg N ha-1, equivalents). For fitted curves see Figure 5.21.

TRL vs	Wheat cv. Hourani					
	2006 (*df = 16*)		**2007** (*df = 28*)		**2006-07** (*df = 46*)	
	Equation	**R^2**	**Equation**	**R^2**	**Equation**	**R^2**
R:S	$y=8.2x10^4x+1727$	0.78^{***}	$y=5.1x10^4x+859$	0.44^{***}	$y=5.9x10^4x+1274$	0.36^{***}
AGDW	y=-22.8x+4407	0.00^{ns}	y=242x+952	0.16^{*}	y=180x+1502	0.23^{***}
TRW	$y=1.2x10^4x+971$	0.81^{***}	$y=1.7x10^4x-240$	0.62^{***}	$y=1.4x10^4x-324$	0.78^{***}
SRL	y=1.3x+3891	0.00^{ns}	Y=16.0x+20.3	0.43^{***}	y=13.8x+892	0.15^{**}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non Significant result for simple linear regression.

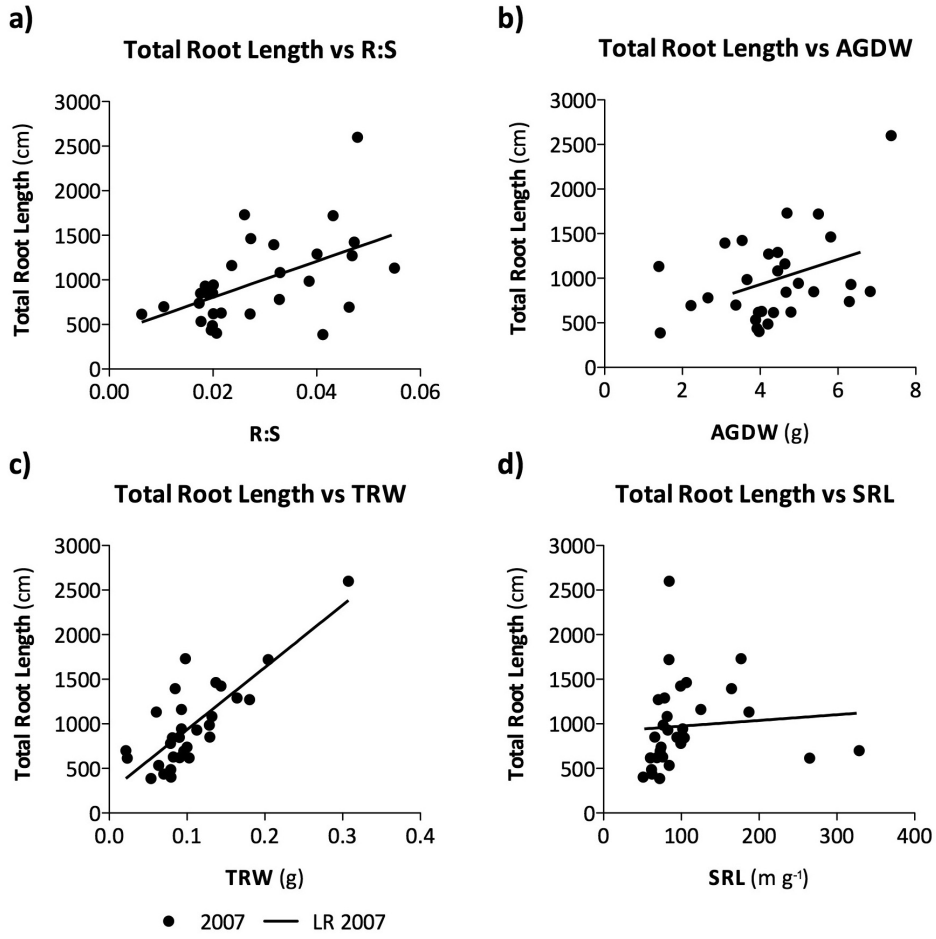

Figure 5.22 Linear regression (LR) between total root length (TRL) measured in 3 soil-depths layers (0-20, 60-80 and > 125 cm) per column and: **a**) root to shoot ratio (R:S), **b**) aboveground dry weight (AGDW), **c**) total root dry weight (TRW) and **d**) specific root length (SRL) at harvest for durum wheat cv. Karim in the 2007 experiment. Data include full irrigated and droughted treatments, as well as N application treatments (0, 50 and 100 kg N ha^{-1}, equivalents). Slopes and R^2 values for the linear regressions are presented in Table 5.24.

Table 5.24 Simple linear regression between total root length (TRL) measured in 3 soil-depths layers (0-20, 60-80 and > 125 cm) per column and: R:S, AGDW, TRW and SRL at harvest for durum wheat cv. Karim plants analysed in the 2007 experiment. Data includes full irrigated and droughted treatments, as well as N application treatments (0, 50 and 100 kg N ha^{-1}, equivalents). To fitted curves see Figure 5.22.

TRL vs	**Wheat cv. Karim 2007** (*df = 28*)	
	Equation	**R^2**
R:S	$y=2.0x10^4x+400$	0.28^{**}
AGDW	$y=141x+366$	0.17^{*}
TRW	$y=0.70x10^4x+238$	0.64^{***}
SRL	$y=0.64x+910$	0.01^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non Significant result for simple linear regression.

5.2.13 Total root volume (TRV)

As for the TRL the total root volume (TRV) is generally estimated as a combination of 3 layers, corresponding to the top, mid and bottom layers of the root system distribution through the soil profile (*vide* section 5.2.9).

5.2.13.1 2006

Throughout development to harvest TRV was higher for barley cv. Rum than wheat cv. Hourani,($p \leq 0.05$) (Table 5.25). At anthesis there was an interaction of species and nitrogen, with N increasing TRV for barley cv. Rum, but not for wheat cv. Hourani (Table 5.25). At harvest, besides the effect of species, there was an interaction between species and irrigation, with drought decreasing (-30%) TRV for barley cv. Rum but increasing it (123%) for wheat cv. Hourani ($p \leq 0.01$) (Table 5.25).

5.2.13.2 2007

For barley cv. Rum in 2007 at anthesis drought increased ($p \leq 0.05$) TRV by 0.23 cm^3 but had no effect at harvest (Table 5.26). For wheat cv. Karim, drought increased ($p \leq 0.001$) TRV by 50% at anthesis and 97% at harvest (Table 5.26). Although drought had no effect on TRV of wheat cv. Hourani at harvest, N application decreased TRV by 0.53 cm^3 at N50 and by 0.62 cm^3 at N100 compared to N0 (Table 5.26).

5.2.13.3 2008

Overall values for TRV in 2008 were higher than previous years (6.23 cm^3, compared to 3.62 cm^3 in 2006 and 1.23 cm^3 in 2007). Drought tended to decrease TRV at harvest ($p \leq 0.12$; Table 5.27).

Table 5.25 Total root volume per column (cm^3) for three soil depths: 0 – 20, 20 – 40 and 40 – 60 cm at 67 DAS; 0 – 20, 60 – 80 and > 125 cm at anthesis and harvest, for barley cv. Rum and durum wheat cv. Hourani subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 67 DAS, anthesis and harvest in 2006.

Species	Irrigation	Fertilizer N kg N ha^{-1})	Total root volume (cm^3)		
			67 DAS	Anthesis	Harvest
Barley cv. Rum	**Irrigated**	**0**	1.03	4.61	5.33
		50	2.18	5.77	5.28
		100	1.01	6.52	2.16
		Mean	*1.41*	*5.63*	*4.26*
	Droughted	**0**	1.50	5.59	3.19
		50	1.45	5.52	3.11
		100	1.21	6.58	2.65
		Mean	*1.39*	*5.90*	*2.98*
Wheat cv. Hourani	**Irrigated**	**0**	0.74	1.88	1.24
		50	1.69	2.89	1.54
		100	0.54	2.11	1.16
		Mean	*0.99*	*2.29*	*1.31*
	Droughted	**0**	1.00	2.14	3.12
		50	0.69	3.11	3.00
		100	1.32	2.41	2.69
		Mean	*1.00*	*2.55*	*2.94*
		SED (df)			
		Species (22)	0.16^{*}	0.27^{***}	0.43^{**}
		Irrigation (22)	0.16^{ns}	0.27^{ns}	0.43^{ns}
		Nitrogen (22)	0.19^{*}	0.33^{*}	0.53^{ns}
		*Species*Irrigation (22)*	0.22^{ns}	0.38^{ns}	0.61^{**}
		*Species*Nitrogen (22)*	0.27^{ns}	0.46^{*}	0.75^{ns}
		*Irrigation*Nitrogen (22)*	0.27^{**}	0.46^{ns}	0.75^{ns}
		*Species*Irrigation*Nitrogen (22)*	0.38^{ns}	0.65^{ns}	1.06^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 5.26 Total root volume (cm^3) per column for three soil depths: 0 – 20, 40 – 60 and 80 – 100 cm at 75 DAS; 0 – 20, 60 – 80, > 125 cm at anthesis and harvest, for barley cv. Rum, durum wheat cv. Karim and durum wheat cv. Hourani (only measured art harvest) subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) in 2007.

Irrigation	Fertilizer (kg N ha^{-1})	Total root volume (cm^3)						
		Barley cv. Rum			Wheat cv. Karim			Wheat cv. Hourani
		75 DAS	Anthesis	Harvest	75 DAS	Anthesis	Harvest	Harvest
Irrigated	**0**	0.59	0.68	1.30	0.53	0.81	0.39	1.6
	50	0.51	0.62	1.41	0.59	0.63	0.33	0.9
	100	0.66	0.59	1.07	0.48	0.50	0.38	1.1
	Mean	*0.58*	*0.63*	*1.26*	*0.53*	*0.64*	*0.37*	*1.2*
Droughted	**0**	0.45	0.82	1.36	0.51	1.00	0.72	1.8
	50	0.60	0.89	0.97	0.45	0.95	0.54	1.4
	100	0.70	0.87	1.24	0.52	0.94	0.92	1.0
	Mean	*0.58*	*0.86*	*1.19*	*0.49*	*0.96*	*0.73*	*1.4*
	SED (df)							
	Irrigation (20)	0.07^{ns}	0.10^{*}	0.15^{ns}	0.08^{ns}	0.06^{***}	0.07^{***}	0.15^{ns}
	Nitrogen (20)	0.09^{ns}	0.13^{ns}	0.19^{ns}	0.10^{ns}	0.07^{ns}	0.09^{ns}	0.18^{**}
	*Irrigation*Nitrogen (20)*	0.12^{ns}	0.18^{ns}	0.26^{ns}	0.14^{ns}	0.10^{ns}	0.12^{ns}	0.26^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 5.27 Total root weight (g) per column for: 0 – 20 cm soil depth at 28 DAS; 0 – 20, 60 – 80, > 125 cm at soil depths at harvest for barley cv. Rum subjected to full irrigated and droughted treatments at 28 DAS and harvest in 2008.

Irrigation	Barley cv. Rum Total root volume (cm^3)	
	28 DAS	Harvest
Irrigated	0.83	6.94
Droughted	0.79	5.52
SED (df)		
Irrigation (6)	0.14^{ns}	0.99^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

5.2.14 Root Volume Density (RVD) Distribution with Depth

5.2.14.1 2006

In 2006 at 67 DAS barley cv. Rum had a RVD 31% higher than wheat cv. Hourani at 0 – 20 cm soil depth (Figure 4.23 a & d and Figure 5.24 a & d).

At anthesis barley cv. Rum had a higher ($p \leq 0.001$) RVD than wheat cv. Hourani at 0 – 20 and 60 – 80 cm soil-depths (Figure 4.23 b, e and Figure 5.24 b & e). However, neither irrigation nor N significantly affected RVD (Figure 4.23 b, e and Figure 5.24 b, e).

Root volume density at harvest was higher for barley cv. Rum than wheat cv. Hourani at both the 0 - 20 and 60 – 80 cm soil depths ($p \leq 0.001$ and 0.05 respectively; Figure 4.23 c, f and Figure 5.24 c, f). There was an interaction between species and irrigation at 0 – 20 ($p \leq 0.01$) and 60 – 80 cm ($p \leq 0.05$) and a trend at > 125 cm ($p = 0.08$) for drought to decrease RVD for barley cv. Rum but to increase RVD for wheat cv. Hourani (Figure 4.23 c, f and Figure 5.24 c, f).

5.2.14.2 2007

From 75 DAS to harvest barley cv. Rum overall had an almost constant value of RVD at ca. 0.135 cm^3 dm^{-3} in the top 20 cm (Figure 5.25). At anthesis, drought increased RVD by 114% ($p \leq 0.01$) at 60 – 80 cm and by 180% ($p \leq 0.05$) at > 125 cm (Figure 5.25 b, e). At harvest the irrigated plants had a higher RVD ($p \leq 0.01$) than the droughted plants at all depths (Figure 5.25). For wheat cv. Karim at anthesis in 2007, drought increased RVD at both 0 – 20 and 60 – 80 cm soil depths ($p \leq 0.001$) (Figure 5.26 b, e). Also N application decreased the RVD at the soil depth 0 – 20 cm, by 31% at N50 and by 41% at N100 compared to the nil N treatment (Figure 5.26 b, e). Drought at harvest increased RVD for both 0 – 20 cm ($p \leq 0.05$) and 60 – 80 cm ($p \leq 0.001$) soil

layers, although no significant effects were found for the > 125 cm soil layer (Figure 5.26 c, f).

For wheat cv. Hourani at harvest N application decreased ($p \leq 0.05$) RVD at 0 – 20 cm and 60 – 80 cm (Figure 5.27). Drought caused no significant effects in the top and middle layers of the soil profile but at > 125 cm significantly increased RVD by 155% (Figure 5.27 a, b).

5.2.14.3 2008

As expected, for barley cv. Rum the RVD increased from 28 DAS to harvest (Figure 5.28). At harvest the only significant effect was a decrease by 65% of RVD with drought at the soil depth of > 125 cm (Figure 5.28 b).

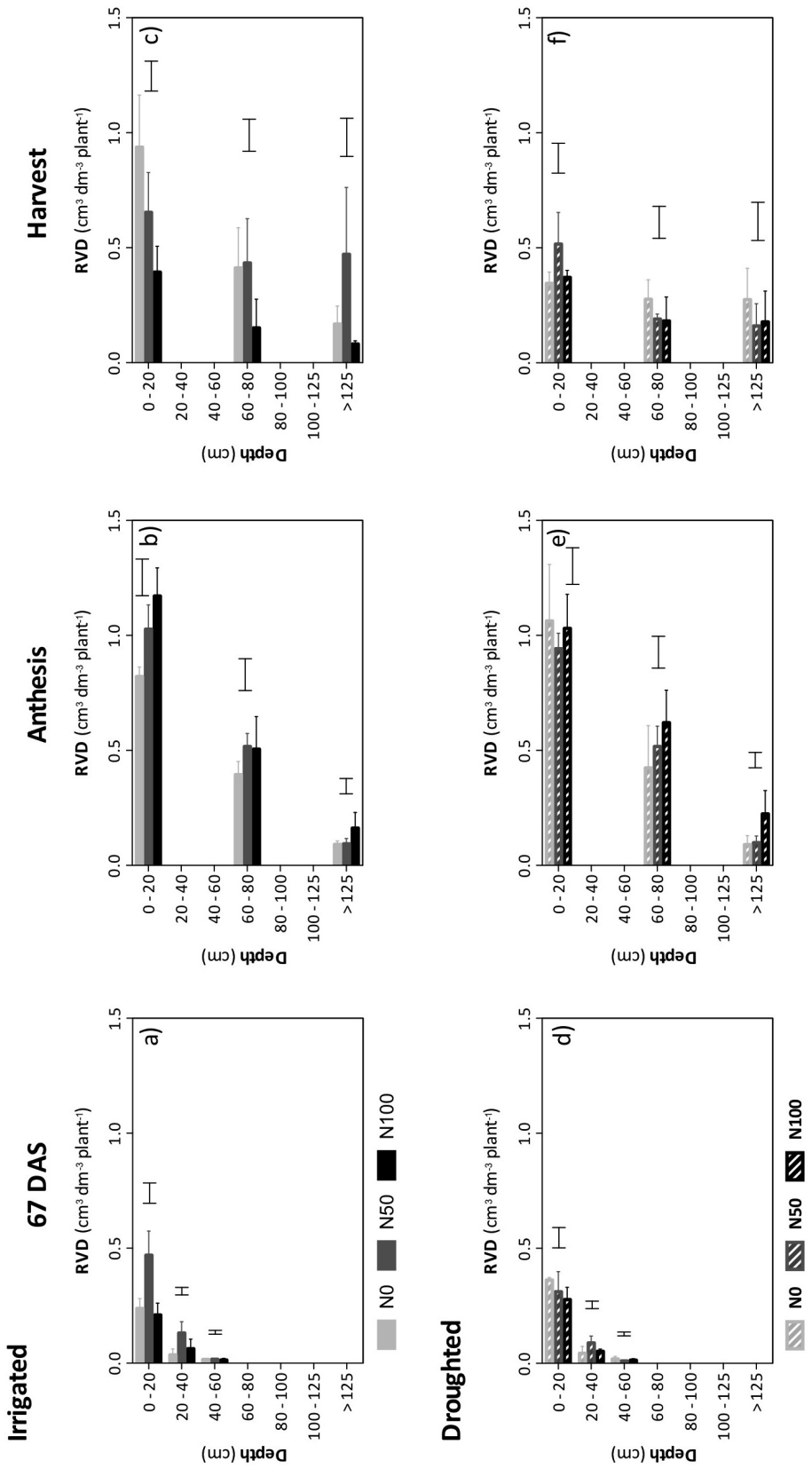

Figure 5.23 Root volume density (RVD, $cm^3\ dm^{-3}$) for barley cv. Rum subjected full to irrigated (solid bars and droughted (striated bars) at three levels of N fertilizer (N0 – 0 kg N ha^{-1}, N50 – 50 kg N ha^{-1} and N100 – 100 kg N ha^{-1}, equivalents), at 67 DAS (days after sowing, **a** & **d**), anthesis (**b** & **e**) and harvest (**c** & **f**) in 2006. Error bars represent SE of the mean and SED for species x irrigation x nitrogen (df = 22).

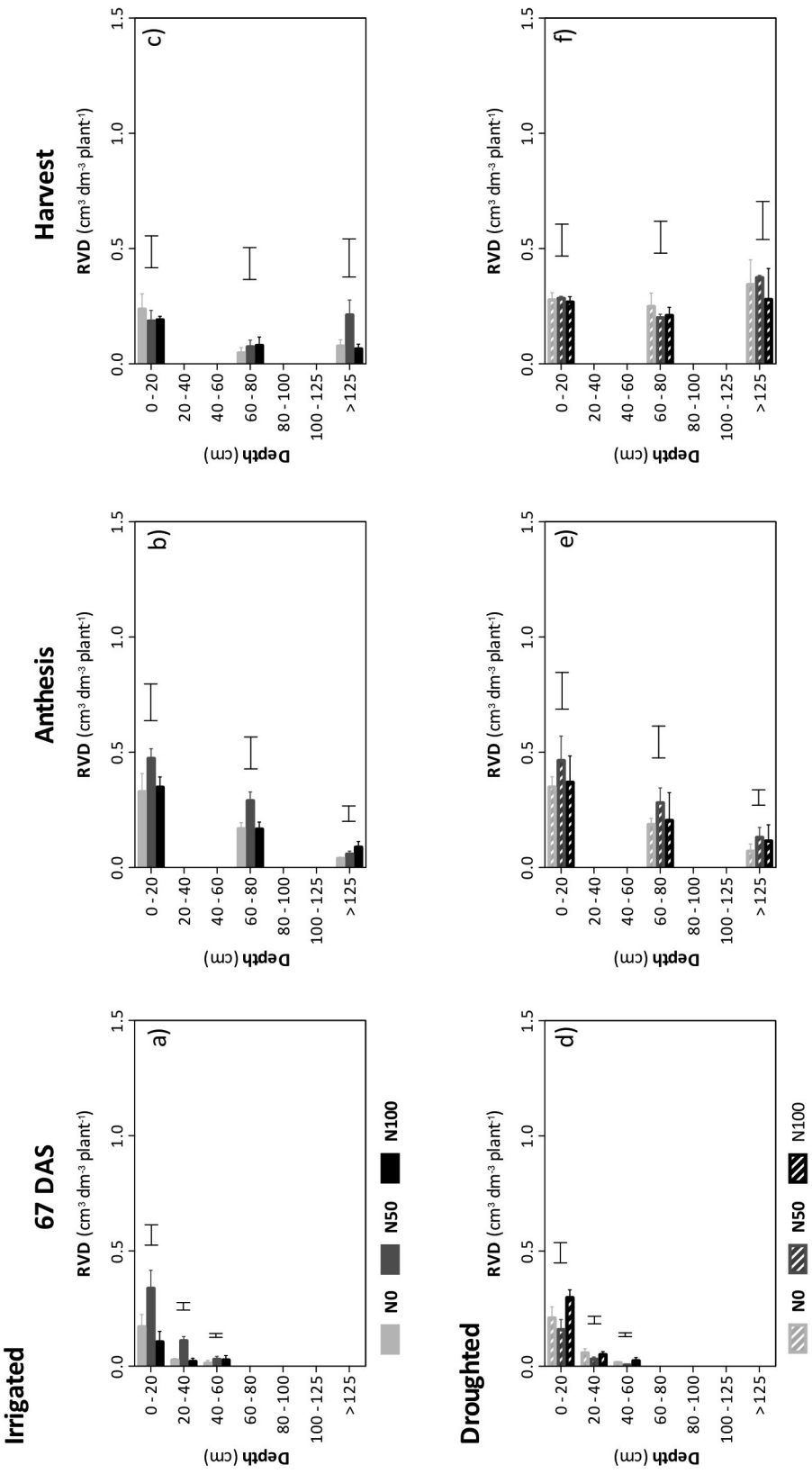

Figure 5.24 Root volume density (RVD, $cm^3\ dm^{-3}$) for durum wheat cv. Hourani subjected full to irrigated (solid bars and droughted (striated bars) at three levels of N fertilizer (N0 – 0 kg N ha^{-1}, N50 – 50 kg N ha^{-1} and N100 – 100 kg N ha^{-1}, equivalents), at 67 DAS (days after sowing, **a** & **d**), anthesis (**b** & **e**) and harvest (**c** & **f**) in 2006. Error bars represent SE of the mean and SED for species x irrigation x nitrogen (df = 22).

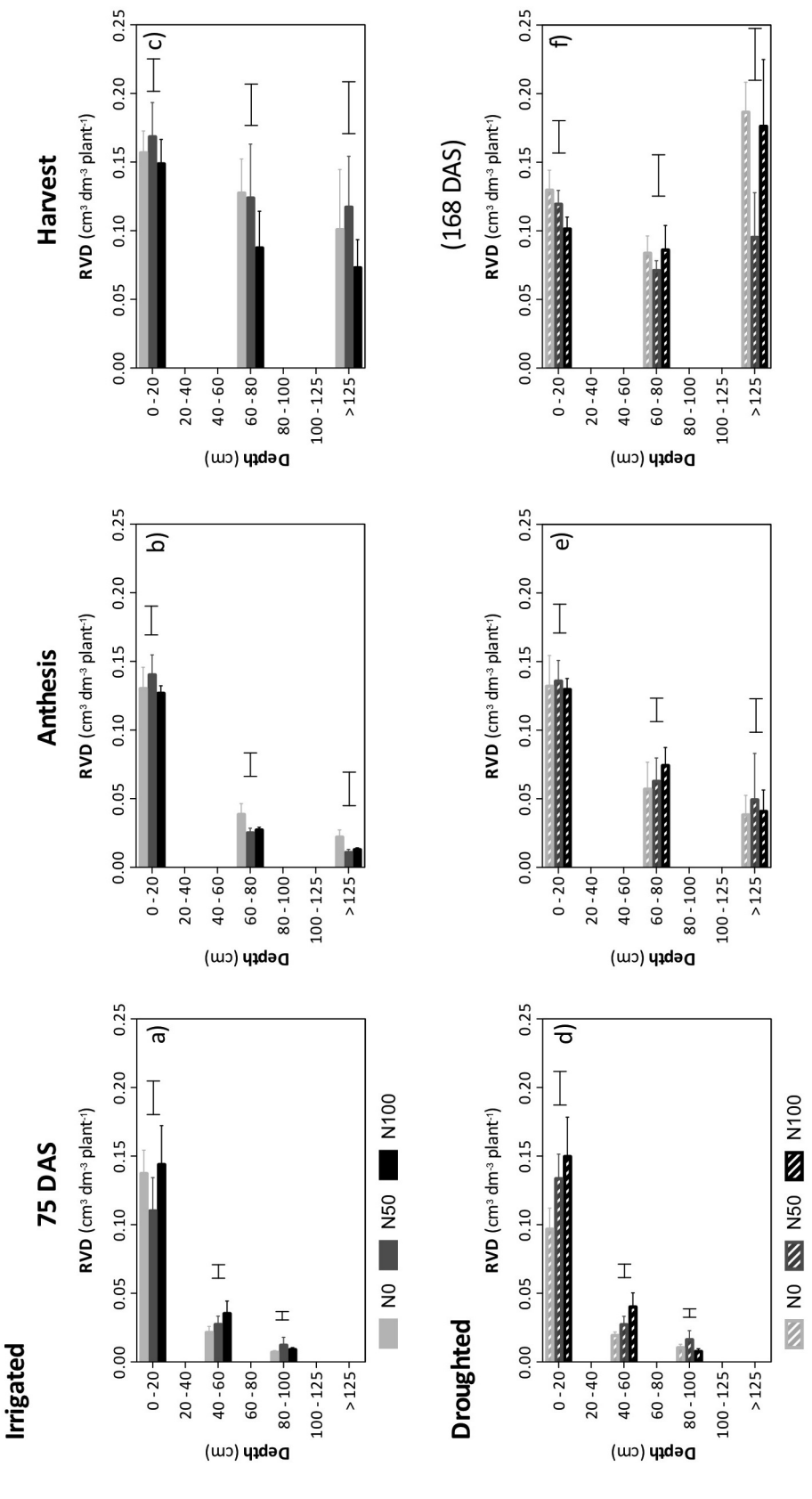

Figure 5.25 Root volume density (RVD, cm^3 dm^{-3}) for different soil depth layers for barley cv. Rum subjected to full irrigated (solid bars) and droughted (striated bars) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 75 DAS (**a** & **d**), anthesis (**b** & **e**) and harvest (**c** & **f**) in 2007. Error bars represent SE of the mean and SED for irrigation x nitrogen (df = 24).

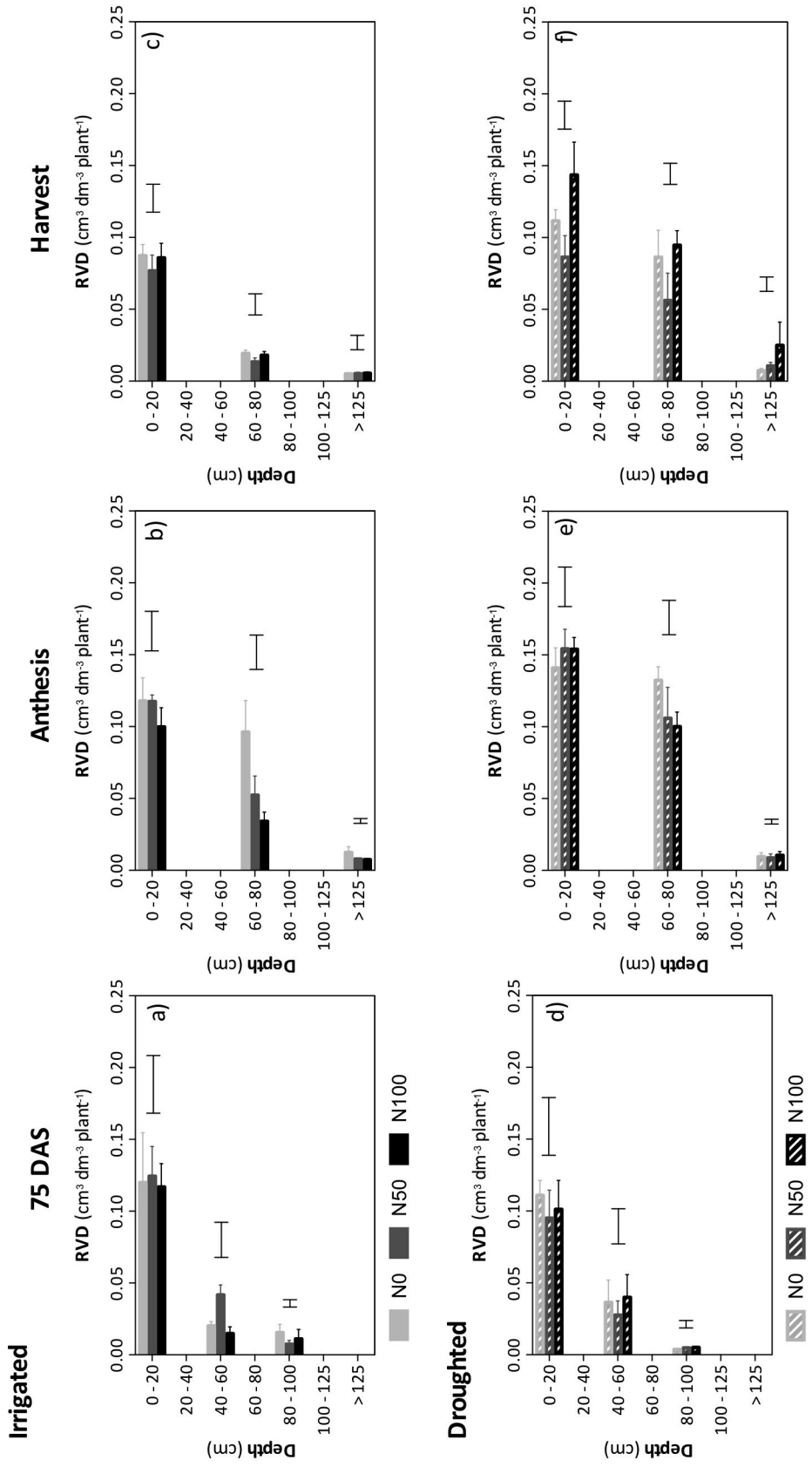

Figure 5.26 Root volume density (RVD, $cm^3\ dm^{-3}$) for different soil depth layers for durum wheat cv. Karim subjected to full irrigated (solid bars) and droughted (striated bars) treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 75 DAS (**a** & **d**), anthesis (**b** & **e**) and harvest (**c** & **f**) in 2007. Error bars represent SE of the mean and SED for irrigation x nitrogen (df = 24).

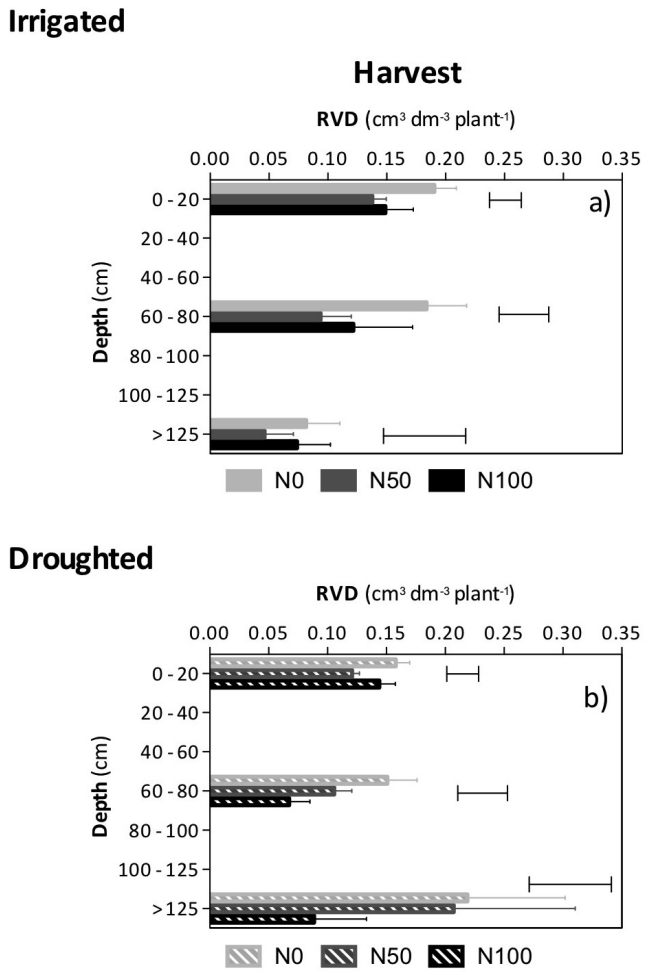

Figure 5.27 Root length density (RVD, cm^{-3} dm^{-3}) at harvest for durum wheat cv. Hourani subjected to full rrigated (**a**, solid bars) and droughted (**b**, striated bars), at three levels of N fertilizer (N0 – 0 kg N ha^{-1}, N50 – 50 kg N ha^{-1} and N100 – 100 kg N ha^{-1}, equivalents) in 2007. Error bars represent SE of the mean and SED for irrigation x nitrogen (df = 24).

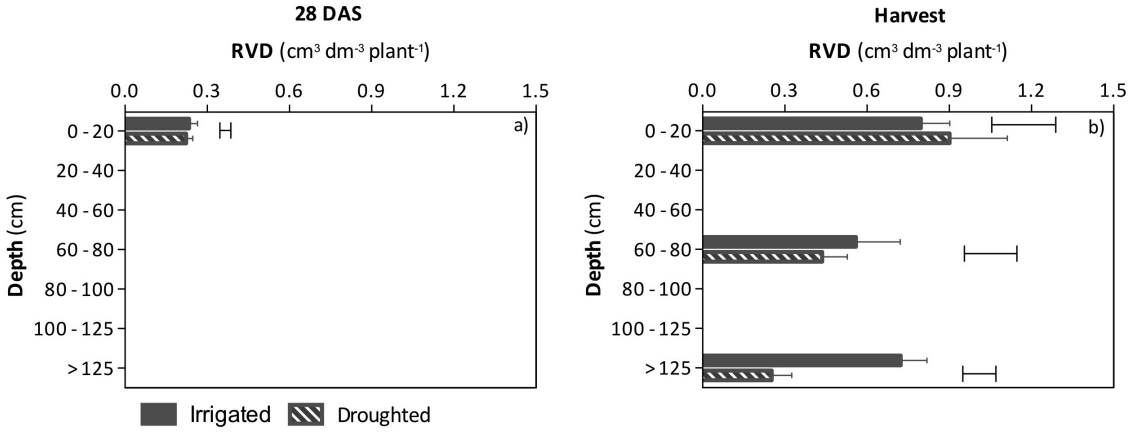

Figure 5.28 Root length density (RLD, cm cm^{-3}) for barley cv. Rum subjected to full irrigated (full bars) and droughted (striated bars) treatments, at 28 DAS (days after sowing, **a**) and harvest (**b**) in 2008. Error bars represent SE of the mean and SED for irrigation (df = 8).

5.2.15 Root volume distribution with depth (β_V)

5.2.15.1 2006

As expected the proportion of root volume deeper in the profile increased with time from an overall β_V of 0.921 at 67 DAS to 0.950 at harvest for barley cv. Rum and 0.924 to 0.956, respectively, for wheat cv. Hourani (Table 5.28).

The distribution of root volume with depth β_V was estimated on the basis of the 3 layers analysed at different growth stages. For barley cv. Rum and wheat cv. Hourani in 2006 N application had no significant effect on β_V at any of the sampling points (Table 5.28). However there was a trend (p = 0.11) for an increase in the proportion of the volume deeper in the soil profile (higher β_V) for wheat cv. Hourani (0.969) compared to barley cv. Rum (0.950). Similarly there was a trend (p = 0.16) for an increase in β_V with water deficits (Table 5.28) for both species.

5.2.15.2 2007

For barley cv. Rum the β_V increased from 75 DAS to harvest for both irrigated and droughted treatments, though more so for the drought treatment (Table 5.29). Drought increased the proportion of root volume deeper in the profile at both anthesis ($p \leq$ 0.001) and harvest ($p \leq 0.05$; Table 5.29).

Similar to barley cv. Rum, β_V for wheat cv. Karim increased with time to anthesis (Table 5.29). The increase in β_V with time was higher under drought than under irrigation ($p \leq 0.001$; Table 5.29). At harvest droughted plants had a higher ($p \leq 0.05$) β_V than the irrigated plants (Table 5.29). At anthesis N application also decreased ($p \leq$ 0.05) the β_V from 0.964 with nil N applied to 0.950 with both 50 and 100 Kg N ha^{-1} (Table 5.29).

For wheat cv. Hourani there was a tendency for drought to increase the proportion (p = 0.10) of root volume deeper in the profile, particularly for the 0 and 50 Kg N ha^{-1}

treatments corresponding overall to 2% of root volume below 100 cm soil-depth under irrigation and 7% with drought (Table 5.29).

5.2.15.3 2008

Contrastingly to 2007 (Table 5.29) in 2008 β_V increased (p = 0.06) with irrigation at harvest (Table 5.30).

Table 5.28 Shape of the cumulative volume distribution with depth (β_V) per column estimated from three soil depths: 0 – 20, 20 – 40 and 40 – 60 cm at 67 DAS; 0 – 20, 60 – 80, > 125 cm at anthesis and harvest, for barley cv. Rum and durum wheat cv. Hourani subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents), at 67 DAS, anthesis and harvest in 2006.

Species	Irrigation	Fertilizer N kg N ha^{-1})	β_V		
			67 DAS	Anthesis	Harvest
Barley cv. Rum	**Irrigated**	**0**	0.908	0.952	0.937
		50	0.926	0.953	0.960
		100	0.918	0.948	0.936
		Mean	*0.917*	*0.951*	*0.944*
	Droughted	**0**	0.924	0.930	0.969
		50	0.928	0.955	0.957
		100	0.922	0.958	0.939
		Mean	*0.925*	*0.947*	*0.955*
Wheat cv. Hourani	**Irrigated**	**0**	0.911	0.953	0.941
		50	0.938	0.958	0.983
		100	0.926	0.962	0.949
		Mean	*0.925*	*0.958*	*0.957*
	Droughted	**0**	0.928	0.959	0.984
		50	0.916	0.966	0.985
		100	0.920	0.947	0.975
		Mean	*0.922*	*0.957*	*0.981*
		SED (df)			
		Species (22)	0.010^{ns}	0.090^{ns}	0.012^{ns}
		Irrigation (22)	0.010^{ns}	0.090^{ns}	0.012^{ns}
		Nitrogen (22)	0.013^{ns}	0.011^{ns}	0.014^{ns}
		*Species*Irrigation (22)*	0.015^{ns}	0.013^{ns}	0.017^{ns}
		*Species*Nitrogen (22)*	0.018^{ns}	0.016^{ns}	0.021^{ns}
		*Irrigation*Nitrogen (22)*	0.018^{ns}	0.016^{ns}	0.021^{ns}
		*Species*Irrigation*Nitrogen (22)*	0.025^{ns}	0.022^{ns}	0.029^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 5.29 Shape of the cumulative volume distribution with depth (β_V) per column estimated from three soil depths: 0 – 20 cm, 40 – 60 cm and 80 – 100 cm at 75 DAS; 0 – 20 cm, 60 – 80 cm, > 125 cm at anthesis and harvest, for barley cv. Rum, durum wheat cv. Karim and durum wheat cv. Hourani (only measured art harvest) subjected to full irrigated and droughted treatments at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents) in 2007.

		β_V						
Irrigation	**Fertilizer N** (kg N ha^{-1})	**Barley cv. Rum**			**Wheat cv. Karim**			**Wheat cv. Hourani**
		75 DAS	**Anthesis**	**Harvest**	**75 DAS**	**Anthesis**	**Harvest**	**Harvest**
Irrigated	**0**	0.917	0.943	0.971	0.926	0.963	0.925	0.968
	50	0.927	0.925	0.973	0.936	0.943	0.918	0.958
	100	0.931	0.932	0.966	0.901	0.942	0.925	0.965
	Mean	*0.925*	*0.933*	*0.970*	*0.921*	*0.949*	*0.923*	*0.964*
Droughted	**0**	0.933	0.955	0.985	0.912	0.965	0.957	0.983
	50	0.924	0.953	0.972	0.930	0.956	0.957	0.981
	100	0.932	0.965	0.979	0.932	0.957	0.960	0.958
	Mean	*0.929*	*0.958*	*0.979*	*0.925*	*0.959*	*0.958*	*0.974*
	SED (df)							
	Irrigation (20)	0.007^{ns}	0.006^{***}	0.004^{*}	0.008^{ns}	0.003^{**}	0.005^{*}	0.006^{ns}
	Nitrogen (20)	0.008^{ns}	0.008^{ns}	0.005^{ns}	0.010^{ns}	0.004^{**}	0.007^{ns}	0.007^{ns}
	*Irrigation*Nitrogen (20)*	0.012^{ns}	0.011^{ns}	0.007^{ns}	0.014^{ns}	0.006^{ns}	0.009^{ns}	0.010^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

Table 5.30 Shape of the cumulative volume distribution with depth (β_V) per column estimated from: 0 – 20, 60 – 80, > 125 cm soil depths at harvest for barley cv. Rum subjected to full irrigated and droughted treatments at harvest in 2008.

	Barley cv. Rum
	β_V
Irrigation	**Harvest**
Irrigated	0.980
Droughted	0.963
SED (df)	
Irrigation (6)	0.008^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the ANOVA test.

5.3 DISCUSSION

Barley and wheat root systems in the field at anthesis usually extend below 100 cm (Gregory *et al.*, 1992; Hoad *et al.*, 2001). Although only a small fraction of the root system is typically below 100 cm its importance for water uptake is crucial, particularly in drying conditions, where relatively more water will remain deeper in the soil profile (Canadell *et al.*, 1996). Gregory *et al.* (1978a; 1978b) demonstrated that for winter wheat only 3% of total root weight was found below 100 cm, however it was responsible for 20% of the water transpired during drying periods. In the present study, for both durum wheat varieties and barley roots rapidly extended to the bottom layers of the soil profile, reaching ≥ 125 cm by anthesis.

5.3.1 Responses of R:S and root growth to N applied and water deficits

5.3.1.1 Biomass partitioning

The most common effect of N and/ or water deficits on biomass partitioning is an increase in the relative biomass allocated to the roots (Brouwer, 1983; Ryser & Lambers, 1995). In pot glasshouse experiments, Karrou & Maranville (1994a) using Moroccan bread wheat varieties found R:S values in the range of 0.143 – 0.180 at anthesis, when growing in non stressed conditions. R:S increased, decreased or remained constant with drought depending on the cultivar. While optimum N application decreased root dry matter and R:S compared to nil N. Moreover under severe water stress the effects of N were not observed (Karrou & Maranville, 1994a). Barraclough *et al.* (1989) for field-grown winter wheat in the UK also found an increase in R:S with low N, whereas water supply reduced it. In soil column experiments, Ebrahim (2008) found an increase in root to total plant dry weight ratio with drought for barley cv. Rum and wheat cv. Hourani at harvest, whereas N application had no significant effect on the relative biomass partitioning to roots. For nine spring wheat

cultivars (ranging from semi-dwarf modern varieties to old varieties) and one barley cultivar, growing under Mediterranean type ecosystem in Australia, Siddique *et al.* (1990) found R:S values of 0.51 – 0.70 decreasing to around 0.44 at harvest. In the present study, all R:S values were much lower than the above-mentioned findings. Overall the average R:S for barley cv. Rum at anthesis and harvest across experiments was 0.040 and 0.037, respectively, while for wheat it was cv. Hourani 0.096 and 0.031, respectively, and wheat cv. Karim 0.037 and 0.029. Bulk density in the soil columns was extremely high, averaging 1.61, 1.85 and 1.76 g cm^{-3}, for 2006, 2007 and 2008 experiments, while the reported value in field experiments in Jordan (Ebrahim, 2008) was 1.01 g cm^{-3}. Therefore some limitations to root growth due to mechanical impedance might have occurred in the soil columns in the present study, and if so the susceptibility to soil strength must be higher for the durum wheat varieties in study than for barley.

For all genotypes R:S increased with drought at anthesis and harvest (except for barley cv. Rum in 2008); though this response was higher for wheat cvs. Hourani and Karim than for barley cv. Rum. N application generally did not change the biomass allocation pattern.

5.3.1.2 TRW and RWD distribution with depth

In the present study, there was a large difference between the root growth in different years and amongst genotypes. Barley cv. Rum had generally higher TRW than the durum wheat genotypes. However, the opposite is usually described in the literature for the same genotypes when grown in the field in the Mediterranean (Ebrahim, 2008). Total root weight for barley cv. Rum at harvest in 2006 was 0.43 g, 0.18 g in 2007 and 0.53 g in 2008. Wheat cv. Hourani root weight was 0.25 g in 2006 and 0.16 g in 2007, whereas for wheat cv. Karim in 2007 it was 0.179 g. The low values of TRW in 2007 might be associated with the very high bulk (> 1.8 g cm^{-3}), especially in the top 50 cm. This might be particularly so for wheat cv. Karim that was found to have a very low soil penetration capability compared to wheat cv. Hourani (Price, 2009).

Different patterns of root growth were also observed for different years and genotypes. For barley cv. Rum in 2006 and wheat cv. Karim in 2007, root weight increased to anthesis after which it decreased to harvest due to root death as described in previous investigations for winter (Gregory *et al.*, 1978b) and spring wheat (Siddique *et al.*, 1990; Ebrahim, 2008). However, in 2007 for barley cv. Rum TRW increased until harvest, as observed for this genotype growing in a similar column experiment by Ebrahim (2008); and as described more generally by Borg *et al* (1986).

Contrasting responses of TRW to water deficits were found between genotypes. While for barley cv. Rum TRW was not affected (2006) or decreased (2007 and 2008) with drought, for durum wheat cv. Hourani and cv. Karim it increased under drought. Similar responses to that presently reported for barley were also found for winter bread wheat (Baburai Nagesh, 2006), spring bread wheat and barley (Ebrahim, 2008) grown in similar soil column experiments. The positive effects of water deficits on root weight of durum wheat genotypes observed in this experiment were also previously reported by Blum *et al.* (1983) for different 'drought adapted' spring durum wheat varieties under mild water stress; though for drought-susceptible varieties or under severe water stresses total root weight decreased.

N application is usually reported to increase TRW in both durum wheat and spring barley (Brown *et al.*, 1987b; Hamblin *et al.*, 1990; Ebrahim, 2008), but in this study N applications tended to have a negative impact on root weight at harvest for both spring barley (2006) and durum wheat genotypes (2006 and 2007).

Drew *et al.* (1973) demonstrated that when barley seedlings were locally exposed to concentrated supply of N, lateral root (LR) proliferation would occur, increasing the number and extension of both first- and second-order laterals in the nutrient rich zone. More recently works of Zhang *et al.* (1999; 2000) and Linkohr *et al.* (2002) with *Arabidopsis* demonstrated that besides the increase in LR when N occurs in patches, like in the heterogeneous soil environment, in a more homogenous medium with high N concentration LR is suppressed. So in a field situation LR is systemically inhibited in response to global high N levels, and locally induced in response to N-rich patches (Osmont *et al.*, 2007). This response was reportedly to be associated with the nitrate-inducible Arabidopsis MADS box transcription factor NITRATE-REGULATED1 (ANR1) but it is also affected by N transporters in particular NRT2 (Osmont *et al.*,

2007). This regulation is a promising tool since the actual architecture of the root system can be modified, for example from the less efficient dichotomous architecture to the more cost effective herringbone type of structure (Fitter, 1985; Fitter *et al.*, 1991). Transferring this information to wheat and barley could therefore be valuable for use in screening for improved nitrogen- and/or water-uptake efficiency (NupE and WupE, respectively).

Not only did genotypes differ in the total root growth dynamic with time and responses to N application and irrigation, they also differed in the distribution of the biomass allocated to the root with soil depth. The increase of root weight (RW) with water deficits for wheat cv. Hourani was due to an increase in root weight density in all soil layers in 2006, but only deeper in the profile in 2007. While under irrigation there was higher root mortality in the top and mid layers of the soil profile after anthesis than under drought. For wheat cv. Karim drought treatment favoured root growth to 80 cm soil depth with neutral effects below this.

For barley cv. Rum in 2006 at 0 – 20 cm and 60 – 80 cm root mortality occurred, and it was higher under irrigation; partly as a consequence of this RWD was higher for the droughted plants in these soil layers. In 2007 RWD at > 125 cm was higher under drought while at 0 – 20 and 60 – 80 cm RWD it increased under irrigation. In 2008 irrigation increased the RWD in all layers, but only significantly deeper in the soil profile.

Effects of N application on RWD were generally low and inconsistently observed. For all species when effects were observed they were negative. Decreasing RWD with higher N supply at harvest was found for all the genotypes at 0 – 20 cm soil-depth, but at 60 – 80 cm soil-depth for wheat genotypes only.

The root weight distribution with depth estimated by β_W indicated a relatively higher proportion of root weight deeper in the profile with time. In 2006 and 2007 wheat cv. Hourani and barley cv. Rum had a β_W around 0.92 while for wheat cv. Karim (2007) its value was relatively lower (0.89), corresponding to 80 and 90%, respectively, of roots in the top 20 cm. The shape of the root weight distribution with soil-depth did not change with N application, though water tended to increase the proportion of weight deeper in the soil profile. At harvest the proportion of root weight below 20 cm increased with

drought: by 54% and 61% for wheat cv. Hourani and barley cv. Rum, respectively, and by 106% for wheat cv. Karim.

5.3.2 Effects on total root length and total root volume

In field experiments in Jordan, Ebrahim (2008) found at anthesis a TRL 150% higher for durum wheat cv. Hourani when compared to barley cv. Rum, and an increase by ca, 46% with N application, but no differences between rain-fed and supplemental irrigation. However in the present study TRL as well as TRV were generally higher for barley cv. Rum than durum wheat. N application increased TRL and TRV at anthesis for both barley cv. Rum and wheat cv. Hourani in 2006. However, it had a negative impact for both durum wheat varieties in 2007 and no significant effect for barley cv. Rum in 2007 and 2008. High temperatures in the glasshouse and initial high moisture content, made the soil in the column prone to mineralization. Hence the N concentration in the soil might have been too high, and possible causing lateral root inhibition (Linkohr *et al.*, 2002), and therefore reducing TRL and TRV. Drought generally decreased both TRL and TRV for barley cv. Rum, whereas the opposite was found for both durum wheat varieties. A similar decrease of TRL with drought and an increase with N application was reported for two durum wheat varieties growing in controlled environment conditions in the United States by Karrou *et al.* (1994a).

5.3.2.1 RLD and RVD distribution with depth

The larger a root system is, the more effectively it will exploit soil resources. However inter-root competition sets a natural ceiling for the optimum density of roots in the soil (Foulkes *et al.*, 2009). Root size can be defined in terms of: weight, projected and surface area, volume, and root length. However, calculations made by van Noordwijk (1983) confirmed the Faiz and Weatherley (1977) experimental results, that soil-root contact resistance offers the major resistance to water flow. Therefore, root length per volume of soil usually defined as root length density – RLD, would be the most

appropriate parameter to describe the potential water and N uptake. Furthermore, van Noordwijk (1983) predicted a critical RLD value of about 1 cm cm^{-3} to extract all the available water and N in the soil. These predictions agree with the values reported for winter wheat by Barraclough *et al.* (1989) and for barley by Gregory and Brown (1989). In addition Brown *et al*. (1987a) found that above a RLD of 1 cm cm^{-3} for barley the rate of water extraction (mm day^{-1}) would not increase.

Higher root diameter was not only proven to increase the volume of soil available that could be exploited by a single root axes (Equation 2.9), but it is also positively correlated with water transport. However, finer roots have a greater return for unit investment (equation 2.10; Nye, 1973; Fitter, 1987; Fitter *et al.*, 1991). Since root volume incorporates the information of both root length and root diameter, it was decided to study the root volume density (RVD), to evaluate if a better relationship could be found between this parameter and potential resource uptake than RLD (*vide* section 5.3.3).

A simple model to describe the RLD or RVD distribution with depth and plant traits can be defined as:

$$RLD_X = AGDW \times R:S \times SRL \times \beta_L \qquad \textbf{Equation 4.5}$$

$$RVD_X = AGDW \times R:S \times rV:rW \times \beta_V \qquad \textbf{Equation 4.6}$$

Where X refers to the soil depth in analysis.

In field conditions the RLD in the top 20 cm usually exceeds the 1 cm cm^{-3} at anthesis and exponentially decreases with soil depth. For different barley varieties growing in Syria, Gregory *et al.* (1984) reported RLD values at anthesis raging from 3 cm cm^{-3} without fertilizer to an extremely high value of 9 cm cm^{-3} when N and P fertilizer was applied. While Barraclough *et al.* (1989) described a RLD values between 6 cm cm^{-3} under drought and low N conditions, to 12 cm cm^{-3} with irrigation and N fertilizer at anthesis for field-grown winter wheat in the UK. However relatively low RLD values in the top 10 cm, ca. 0.35 and 0.38 cm cm^{-3}, have been described by Thomas *et al.* (1995) for two different barley varieties growing in Australia under favourable conditions. Also in field experiments in Jordan Ebrahim (2008) found RLD values at anthesis on the top

20 cm of: 1.05 cm cm^{-3} for wheat cv. Hourani and 0.85 cm cm^{-3} for barley cv. Rum, both growing with supplemental and N fertilizer. In this work the values found in 2006 at anthesis for barley cv. Rum were comparable to those found by Ebrahim (2008), ranging from 1.10 cm cm^{-3} with irrigation to 0.91 cm cm^{-3} under drought (when averaged across N treatments). In contrast, wheat cv. Hourani had a poor root growth, with a RLD on the top 20 cm being only 53% of that found for barley. The difference in root growth was associated with an overall plant growth restriction, where the overall above ground weight (across N and irrigation treatments) for wheat cv. Hourani was only 47% of the one found for barley cv. Rum (*vide* section 4.2.5). Wheat cv. Karim in the 2007 also had generally poor growth (*vide* section 4.2.5), probably in part contributed by its susceptibility to mechanical impedance (Price, 2009).

For barley cv. Rum and wheat cv. Hourani, irrigation generally increased RLD in the top of the soil profile, while compensatory growth in deeper soil depths occurred under drought. Comparable results to these were previously described for field-grown barley in Syria (Cooper *et al.*, 1987), winter wheat in the UK (Barraclough *et al.*, 1989) and in China (Zhang *et al.*, 2004). Also in soil-column experiments for the same species (Ebrahim, 2008) and for winter wheat (Baburai Nagesh, 2006) similar decreases in RLD with drought were reported. For wheat cv. Karim, drought increased RLD throughout the soil profile, but to a higher extent in the mid and top layers. This might be associated with the high susceptibility of this genotype to soil strength (Price, 2009), so that due to the inability to increase root growth deeper in the profile where bulk density values were extremely high (1.99 g cm^{-3}) compensatory growth occurred in upper depths. Similar results were found for winter wheat experiments in the UK under field conditions (Barraclough & Weir, 1988).

In numerous experiments for barley and wheat, root growth is usually described to reach its peak at around anthesis (Gregory *et al.*, 1978b; Barraclough & Leigh, 1984; Siddique *et al.*, 1990), and although it can continue to increase later if water is available (Thomas *et al.*, 1995) the growth rate is highly reduced. In this experiment the most intensive drought was imposed at the date of anthesis for barley cv. Rum. Therefore, while for barley cv. Rum the highest level of stress was initiated when the root length was already largely complete, for both durum wheat varieties (since they reached GS61 later in the season; *vide* section 6.3) they were more able to respond to drought by increasing RLD under drought compared to that under irrigation.

Results of field experiments with barley in Syria (Gregory *et al.*, 1984; Cooper *et al.*, 1987; Gregory & Brown, 1989), soil-column and field experiments with barley and in durum wheat in Jordan (Ebrahim, 2008), and field experiments in winter wheat in the UK (Barraclough *et al.*, 1989) showed an increase in RLD with N application. In addition effects of N tend to be higher under well-watered conditions (Barraclough *et al.*, 1989; Ebrahim, 2008). This is in contrast with the present results, where generally N had no or negative effect on RLD, especially with full irrigation. As explained beforehand, soils in the column system were highly susceptible to mineralization, and so high N levels would be present even in the N0 treatment. Therefore 'extreme' N levels in the N50 and N100 might have had a negative impact on lateral root formation (Linkohr *et al.*, 2002). Agreeing with recent field experiments with winter wheat in Czech Republic, where a 100 kg ha^{-1} had no effect in relation to nil N applications while a high rate of 200 kg N h^{-1} tend to reduced root growth (Svoboda & Haberle, 2006).

When quantifying the RLD distribution with depth according to $\beta_{L,}$ results showed that for all species there was, as expected, a general increase in the proportion of roots deeper in the profile with time, as described by King *et al.* (2003). Drought generally increased β_L for all genotypes, corresponding to a high proportion of roots deeper in the profile with drought agreeing with results acquired for winter wheat by Barraclough *et al.* (1989).

There is a lack of published data on the RVD distribution with depth in cereals. However, information obtained by a study comparing the conventional and bed planting systems in India by Aggarwal *et al.* (2006) in wheat showed that RVD distribution follows a similar pattern as that for RLD. Although giving generally a similar pattern, it was found that RVD would be more sensible parameter to describe effects of the mechanical impedance caused by the conventional planting system than RLD.

RVD generally followed the decrease with depth, described previously for RLD. Barley cv. Rum at harvest in 2006 for the 0-20 and 60-80 cm soil depth layers had a higher RVD than wheat cv. Hourani, but not in 2007, while wheat cv. Karim had the lowest RVD, especially deeper in the profile.

Inconsistent responses of RVD to drought were found for barley cv. Rum. While water limitations generally decreased RVD at harvest in 2006 and 2008, in 2007 there was an increase in RVD at anthesis with drought revealing a higher exploration rate deeper in

the profile in search for water. At harvest RVD in top and mid soil depths, irrigated plants had a higher RVD, but deeper in the profile droughted plants again were able to compensate and increase RVD. A similar pattern was observed for wheat cv. Hourani in 2006 and 2007. For wheat cv. Karim in 2007 the RVD was always higher under drought.

N application was found to decrease RVD in the top layers of the soil profile, though not consistently between years. The proportion of RVD consistently increased deeper in the profile with drought (β_V).

5.3.3 Effects of N and drought on rV:rW and SRL

The rV:rW relates to root tissue density and was found to be positively correlated with root growth and negatively correlated with root longevity. Water and N deficits are reported to increase root tissue density (Ryser, 1996) and thus decrease SRL; consequently root length and volume would be negatively affected hence lower RLD and RVD values. Usually under N and water deficits, root tissue extension tends to decrease, lowering rV:rW (Ryser & Lambers, 1995). In this study rV:rW decreased with time indicating an increase in root tissue density for all genotypes. As expected for barley cv. Rum drought increased root tissue density in 2006, though it decreased in 2007, and had no effect in 2008. Drought and N supply had no consistent effects on rV:rW for wheat cv. Karim or cv. Hourani.

The translation of the biomass allocated to the roots into potential resource acquisition is given by SRL. Although useful it is a very complex and difficult parameter to analyse, since it depends on both tissue density and root diameter. Specific root length has been reported to increase, decrease or not change with nutrient deficiency (Ryser, 1998). In this study SRL when averaged across years and treatments was at harvest generally higher for wheat cv. Hourani (164.5 m g^{-1}) than barley cv. Rum (137.8 m g^{-1}) or wheat cv. Karim (105.4 m g^{-1}). Effects of drought on SRL were inconsistent. Drought for barley decreased SRL in 2006, increased it in 2007 and had no effect in 2008. For wheat cv. Hourani, water deficits consistently decreased SRL, and for wheat cv. Karim the opposite was found. An increase in SRL with drought was reported by Li *et al.*

(2001) in winter wheat growing in China and in CE experiments in the UK by Baburai Nagesh (2006). A similar increase was also reported by Ebrahim (2008) in barley and durum wheat growing in field and soil columns in Jordan.

The increase in SRL with drought for wheat cv. Karim in the present study was related to an increase in rV:rW; this was a decrease in root tissue density with no change in mean root diameter (RD). For wheat cv. Hourani the decrease in SRL with drought was associated with a relatively constant root tissue density, and was therefore related with an increase in RD under drought, particularly deeper in the soil profile. This would probably enhance the ability to penetrate the soil as well as improving water conductance under dry conditions (Ryser, 1998). Similarly drought consistently increased the RD for barley cv. Rum, though changes in SRL were mainly related with rV:rW. At harvest N application increased SRL for wheat cv. Karim due to a decrease in root tissue density as described by (Ryser, 1998). However, for two different grass species SRL was reported to decrease with N application (Arredondo & Johnson, 1999).

5.3.3.1 Root sub-traits affecting TRL and TRV

As previously mentioned RLD was found to be well correlated with potential resource uptake. So from a breeding perspective increasing RLD, and optimizing its distribution with depth (β_L), seems the best approach to increase both NupE and WU under abiotic stress. Increasing RLD and its distribution with depth can be achieved by increasing any of the terms in the Equation 4.5, while maintaining the others. If RVD is considered the better descriptor of potential resource uptake, then Equation 4.6 applies instead.

For all genotypes the trait that best explained the variation for different years and treatments in TRL and TRV was the TRW. For barley cv. Rum and wheat cv. Hourani variation in TRL related not only to R:S but also to SRL or rV:rW. In contrast, for wheat cv. Karim no relationship was found between SRL and rV:rW to TRL and TRV. For barley cv. Rum SRL seems a promising trait for breeding to increase RLD at depth whilst maintaining AGDW.

5.4 CONCLUSIONS

Soil columns are a common method used in root morphology studies (Gregory *et al.*, 1997; Ismail & Davies, 1998; Baburai Nagesh, 2006; Ebrahim, 2008; Place *et al.*, 2008). It not only provides easy access to roots, but if the size is right it imposes less mechanical constraints to root growth than pots. In all the experiments carried out, roots of all genotypes reached the bottom of the column, and no root coiling or air pruning through the water drainage holes was observed. Regarding the diameter of the soil columns, few roots were found growing near the edges, even when the RLD was higher than 1 cm cm^{-3} such as in the 2008 experiment. The 15 cm diameter x 150 cm depth columns seems to be the appropriate dimensions to grow individual plants of spring barley and wheat genotypes in controlled environments, first because the disturbance of the root growth, due to pot size limitations seems small, and second because though heavy (ca. 56 kg at FC) they are still manageable. However the bulk density might be an issue when using this type of system, especially when using sand based soil medium. The bulk density in all the three experiments was relatively high, but especially in 2007 where not only root but also the overall plant growth was affected. It is possible to fill the columns to a certain bulk density, however during irrigation the soil might sink and compaction will occur. If working with species with particular susceptibility to mechanical impedance, it is suggested to use compost based medium. However, this will make the extraction of roots from the soil more difficult. Although some constraints to root growth may have occurred in the experiments, the general response to treatments is quantitatively comparable to data in previous soil column and field investigations reported in the literature. Therefore, if used with caution, present results indicate the use of soil columns is a suitable methodology representative of the field environment for phenotyping barley and durum wheat to quantify agronomic and genotypic variation in rooting traits.

Addressing the specific hypothesis stated in the beginning of the chapter, one can therefore conclude:

1. Barley had a relatively larger TRL, TRV or TRW than durum wheat cv. Hourani.

2. Similar distribution of root morphological traits with soil-depth (RWD, RLD, RVD and RD) was found between barley cv. Rum and wheat cv. Hourani, however wheat cv. Karim showed less distribution of roots deeper in the profile due to high susceptibility to mechanical impedance.

3. Contrasting responses of rooting traits to water deficits between barley and durum wheat varieties in study were observed. TRW decreased for barley cv. Rum with water limitations, whereas it increased for durum wheat. Corresponding effects were found for TRL and TRV. N application generally decreased TRW, TRV and TRL for durum wheat cultivars. While for barley cv. Rum it increased TRW, TRL and TRV, at anthesis.

4. Effects of N on TRW were similar under full irrigated and droughted treatments.

5. R:S was found to increase with drought for all genotypes, though more strongly for durum wheat cultivars, whilst N application had no significant effect.

6. RD was broadly similar between genotypes, increasing with water deficits though generally unaffected by N applications.

7. Barley cv. Rum revealed a high plasticity in its response to drought in terms of SRL and rV:rW: decreasing (2006), increasing (2007) or not being affected (2008) by water deficits. While tissue density (here accessed by rV:rW) for wheat cv. Hourani was generally constant and only in one experiment SRL decreased with drought

(2006). SRL for wheat cv. Karim tend to increase with drought and N application, due to a decrease in tissue density (higher rV:rW).

8. Proportion of root weight (β_W), length (β_L) and volume (β_W) deeper in the profile consistently increased with drought. N had generally no effect on β values. Similar proportion of roots deeper in the profile for barley cv. Rum (higher β_W) and wheat cv. Hourani. However β_W values for wheat cv. Karim where relatively low demonstrating a lower penetration capability.

6 RESOURCE CAPTURE

6.1 INTRODUCTION

As previously described in the literature, RLD is the rooting trait that is most often related to proportional resource uptake. In addition, there is evidence that a RLD of 1 cm cm^{-3}, at least for barley and wheat, may potentially acquire all the available water and N in the soil, and that value limits the maximum rate of water extraction (Brown *et al.*, 1987a; Barraclough *et al.*, 1989; Gregory & Brown, 1989).

King *et al*. (2003) using data for barley from Gregory and Brown (1989) defined the following equation: $\phi = 1 - e^{k_{RLD}}$. This relates the proportional resource uptake, particularly water and nitrogen, to the RLD (cm cm^{-3}), through the resource capture coefficient parameter (k, cm^2). k essentially defines the potential proportional resource uptake from the soil, that a plant can achieve by a specific RLD. High k values indicate that fewer roots are needed to extract the available resources. Or if considered a fixed RLD, larger k values lead to a more rapid resource depletion. Regarding water uptake, a k of ca. 2 cm^2 was found for barley, and a value of ca. 0.4 cm^2 its theoretically expected for phosphorous due to its immobility (Bingham & Hoad, 2000; King *et al.*, 2003). Proportional nitrogen uptake (as nitrate) is usually assumed to be the same as water, since both are transported to the root surface mainly by mass flow of solution (Tinker & Nye, 2000; King *et al.*, 2003). Therefore, k values for N are predicted to follow those for water, and C_{RLD} values should be broadly similar. Furthermore, theoretical calculations of van Noordwijk (1983) and modelling analysis by Robinson and Rorison (1983) predicted that a RLD of 1 cm cm^{-3} would extract most of the nitrate available in the soil. Therefore, to calculate k for spring barley and durum wheat and compare with these previously reported, an estimate of the critical RLD is one of the main aims of this chapter.

Higher root diameter was not only shown to increase the volume of soil able to be exploited by a single root axis (Equation 2.9), but it is also positively correlated with the water transport in the plant. However, finer roots have a greater return per unit investment (equation 2.10; Nye, 1973; Fitter, 1987; Fitter *et al.*, 1991). Since root volume incorporates the information of both root length and root diameter, it was

decided to examine if a better relationship could be found between root volume density (RVD) and potential resource uptake than RLD.

This chapter describes the below-ground resource uptake (water and nitrogen) by durum wheat and spring barley in glasshouse experiments carried out in 2006, 2007 and 2008; and quantitatively relates the water uptake (WU) with the root system morphology. The main objective of this chapter is to quantify the ability of the root systems of durum wheat and spring barley to acquire water and nitrogen from the soil, including the quantification of the relationship between RLD and water capture in order to estimate a critical RLD: C_{RLD}. This is the RLD value below which there is an insufficient amount of roots to acquire 90% of the potentially available water and N in the soil. Effects of genotype, as well as of water and N applied on the C_{RLD} will be evaluated. Results will also be analysed to test whether the RVD, which incorporates not only the length but also the diameter of the root system, is better related to the potential resource capture than RLD.

The specific hypotheses to be tested in this chapter are:

1. The percentage of cumulative water use extracted from deeper in the profile increases with drought;

2. Increasing water availability increases seasonal water uptake (WU) and nitrogen uptake (Nup), in similar proportion for barley and wheat;

3. N application increases seasonal water use, and in the same proportion for barley and wheat;

4. A resource capture coefficient (k) can be defined from the relationship between RLD and ϕ (proportional resource capture) for water and N in barley and durum wheat, and its value does not differ significantly between these species, hence Critical RLD does not differ.

6.2 RESULTS

6.2.1 Soil water content

The soil water content per column measured gravimetrically during 2006 and per soil depth using the theta-probe method (section 3.1.2.2) in 2007 and 2008 is presented in Figure 6.1 to 6.5; the points of irrigation application can be seen by the peaks in the temporal pattern of the soil-moisture per column for 2006 (Figure 6.1) or in the 0 – 20 cm soil-depth in 2007 and 2008 (Figure 6.2 to Figure 6.5). A detailed table with dates and amounts of water applied for each treatment and year is presented in Tables 3.3, 3.5 and 3.6.

6.2.1.1 2006

For barley cv. Rum under irrigation, N50 generally had a slightly higher water extraction (lower soil moisture before irrigations) through time, followed by N100 and N0; though at harvest the soil moisture was higher for N100 (Figure 6.1 a). For wheat cv. Hourani under irrigation there was not a clear difference in the pattern of soil water extraction through time for the different N treatments, but nevertheless at harvest the soil moisture at N0 was higher than for N50 or N100 (Figure 6.1 b). Under irrigation barley cv. Rum generally depleted the soil moisture more than wheat cv. Hourani (Figure 6.1 a, b). Under drought, both genotypes showed similar decreases in soil moisture content through time, except at 102 DAS where a relatively higher extraction was recorded for barley cv. Rum with an application of N100, corresponding to anthesis for this genotype (Figure 6.1 c, d).

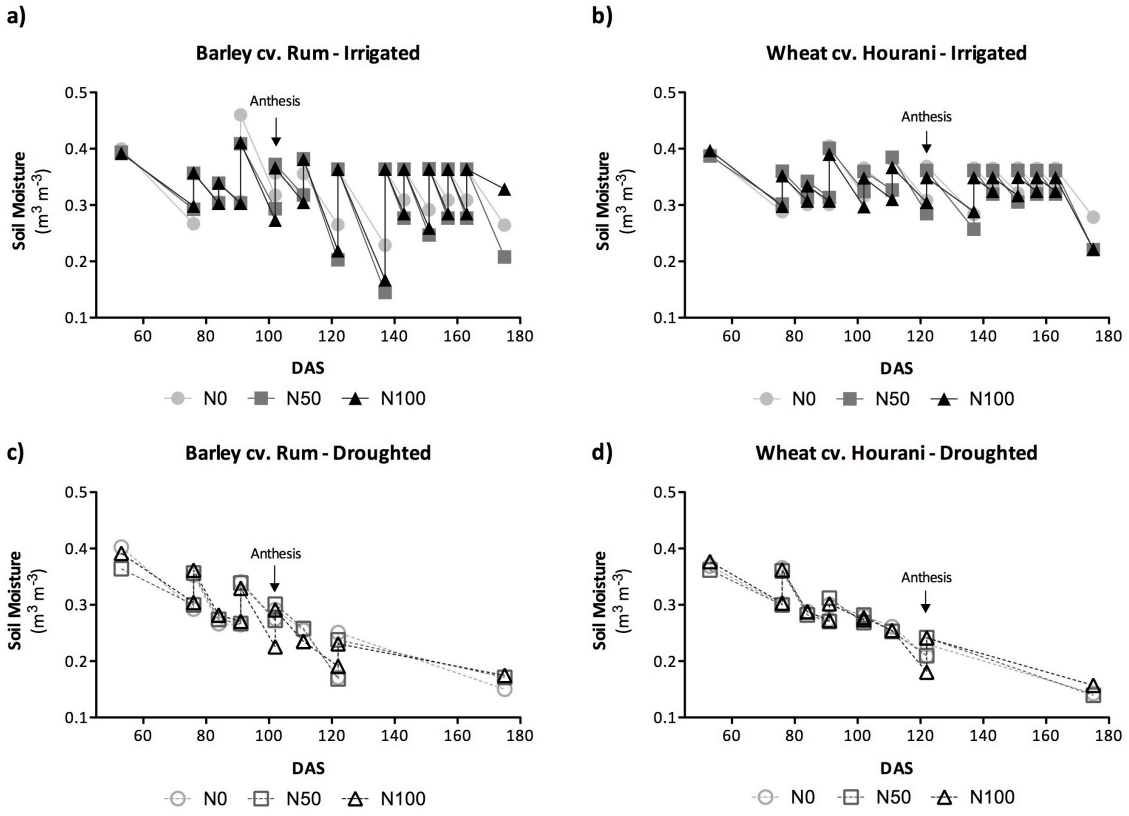

Figure 6.1 Soil moisture through time per soil column from 53 DAS to harvest during the 2006 experiment for barley cv. Rum and durum wheat cv. Hourani, in the fully irrigated (**a** and **b**) and droughted (**c** and **d**) treatments at three levels of N fertilizer: 0 kg N ha^{-1} (N0), 50 kg N ha^{-1} (N50), and 100 kg N ha^{-1} (N100), equivalents.

6.2.1.2 2007

In 2007 the use of the ThetaProbe (type ML2x, Delta-T Devices Ltd. Cambridge, UK) soil moisture system (section 3.1.2.2) permitted a more detailed analysis of the changes in soil moisture through time (Figure 6.2 to Figure 6.5). Here the irrigation can be detected by the increase in soil moisture at 0 – 20 cm soil depth. For all the genotypes it was possible to see that at the start of the experiment the soil deeper in the profile (> 125 cm soil-depth) was saturated, so that the initial decrease (approximately up to 83 DAS) might be associated with the loss of water through the drainage holes and not due to transpiration. As can be seen from Figure 6.2 to 6.4, irrigation applications generally reached the 40 – 60 cm soil-depth but only in the full irrigation treatment.

For both barley cv. Rum (Figure 6.2) and wheat cv. Hourani (Figure 6.4) under irrigation, the soil moisture at >125 cm soil-depth decreased to values below FC (≈

0.150 m^3 m^{-3}), while for wheat cv. Karim (Figure 6.3) the extraction never fell significantly below that value. Under drought, averaged across N treatments, for barley cv. Rum and wheat cv. Hourani the volumetric soil moisture reached at harvest was 7% (Figure 6.2 and Figure 6.4) though average values for wheat cv. Karim were 13% (Figure 6.3). This reduced extraction deeper in the profile for wheat was also associated with lower RLD and RVD for this genotype compared to wheat cv. Hourani and barley cv. Rum (Figure 5.16 to 5.18 and Figure 5.25 to 5.27, respectively).

Though the theta-probe calibration showed a close relationship between the voltage values measured and the volumetric soil water content gravimetrically determined, the time-course of soil moisture occasionally showed some unusual values. Although the soil moisture measurements were always performed using the same access holes, sporadically as soil was drying, some soil would fall out from the column during the moisture readings. Periodically the columns had to be moved so others could be accessed. These two facts might have been responsible for some of the sudden changes in soil moisture showed in Figure 6.2 to 6.4.

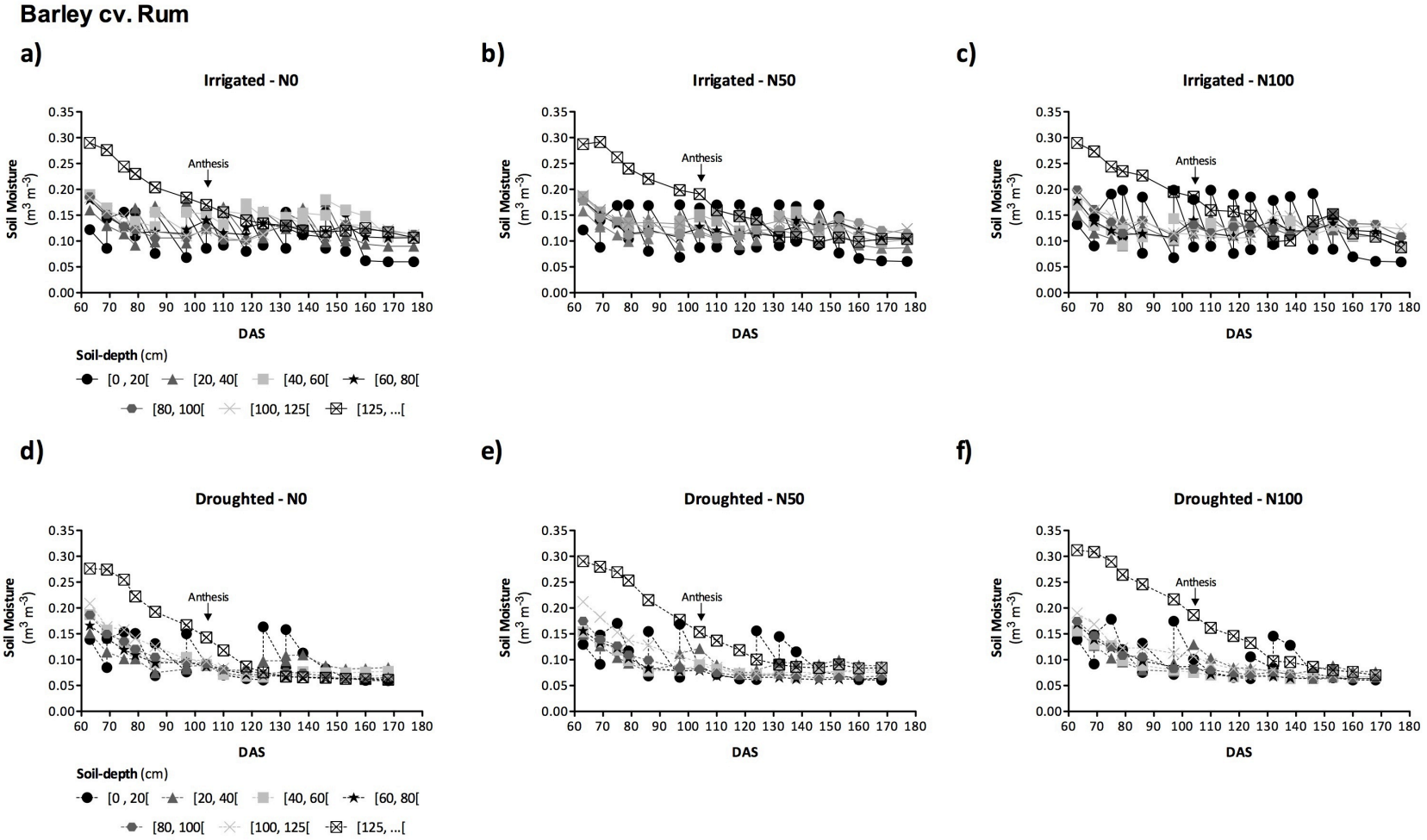

Figure 6.2 Soil moisture content for different soil-depth layers in columns from 57 DAS to harvest in the 2007 experiment for barley cv. Rum, under fully irrigated (full lines) and droughted treatments (broken lines) at three levels of N fertilizer: 0 kg N ha^{-1} (N0 – **a** and **d**), 50 kg N ha^{-1} (N50 – **b** and **e**), and 100 kg N ha^{-1} (N100 – **c** and **f**), equivalents.

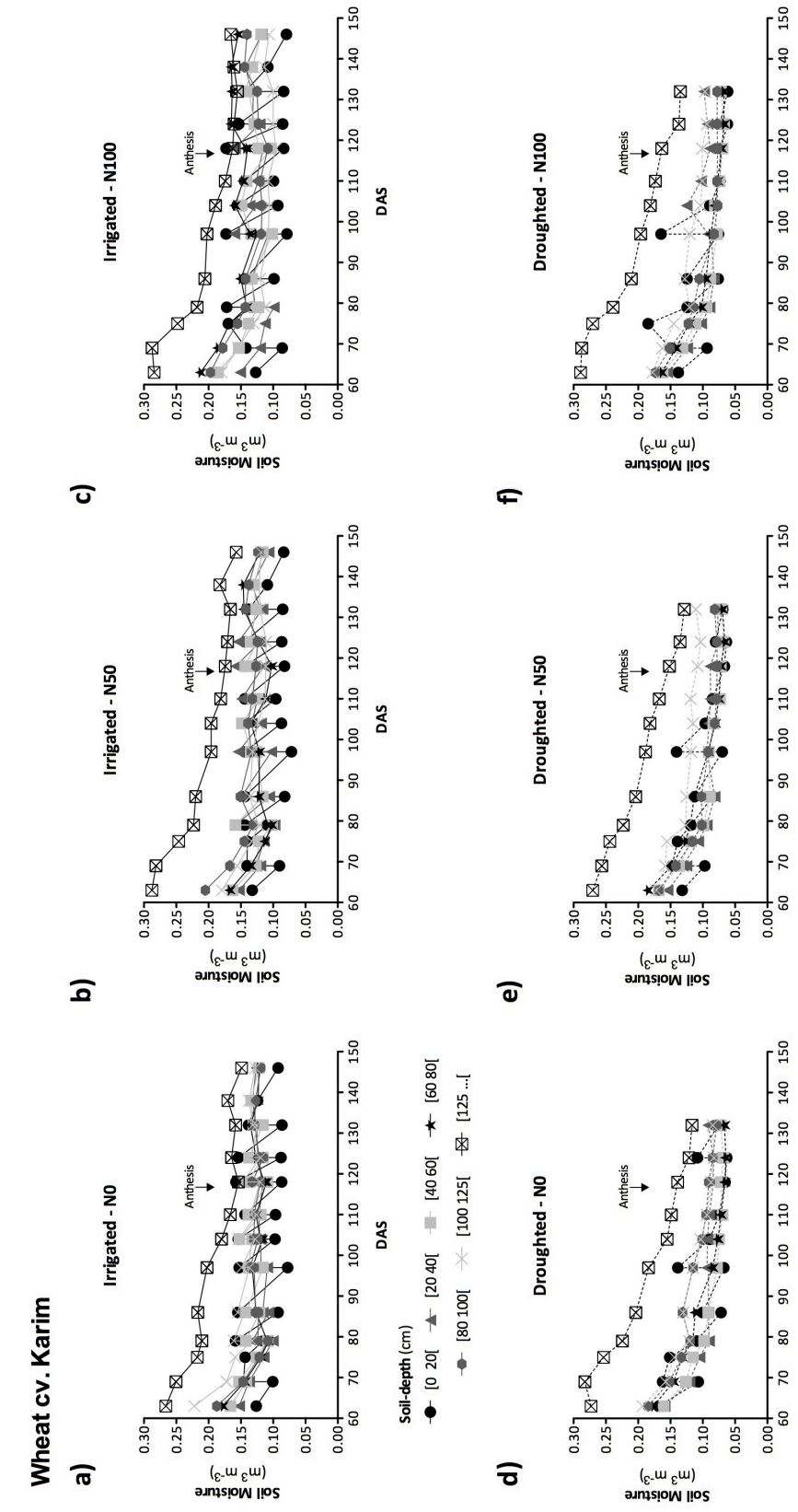

Figure 6.3 Soil moisture content for different soil-depth layers in columns from 57 DAS to harvest in the 2007 experiment for durum wheat cv. Karim, under fully irrigated (full lines) and droughted treatments (broken lines) at three levels of N fertilizer**:** 0 kg N ha^{-1} (N0 – **a** and **d**), 50 kg N ha^{-1} (N50 – **b** and **e**), and 100 kg N ha^{-1} (N100 – **c** and **f**), equivalents.

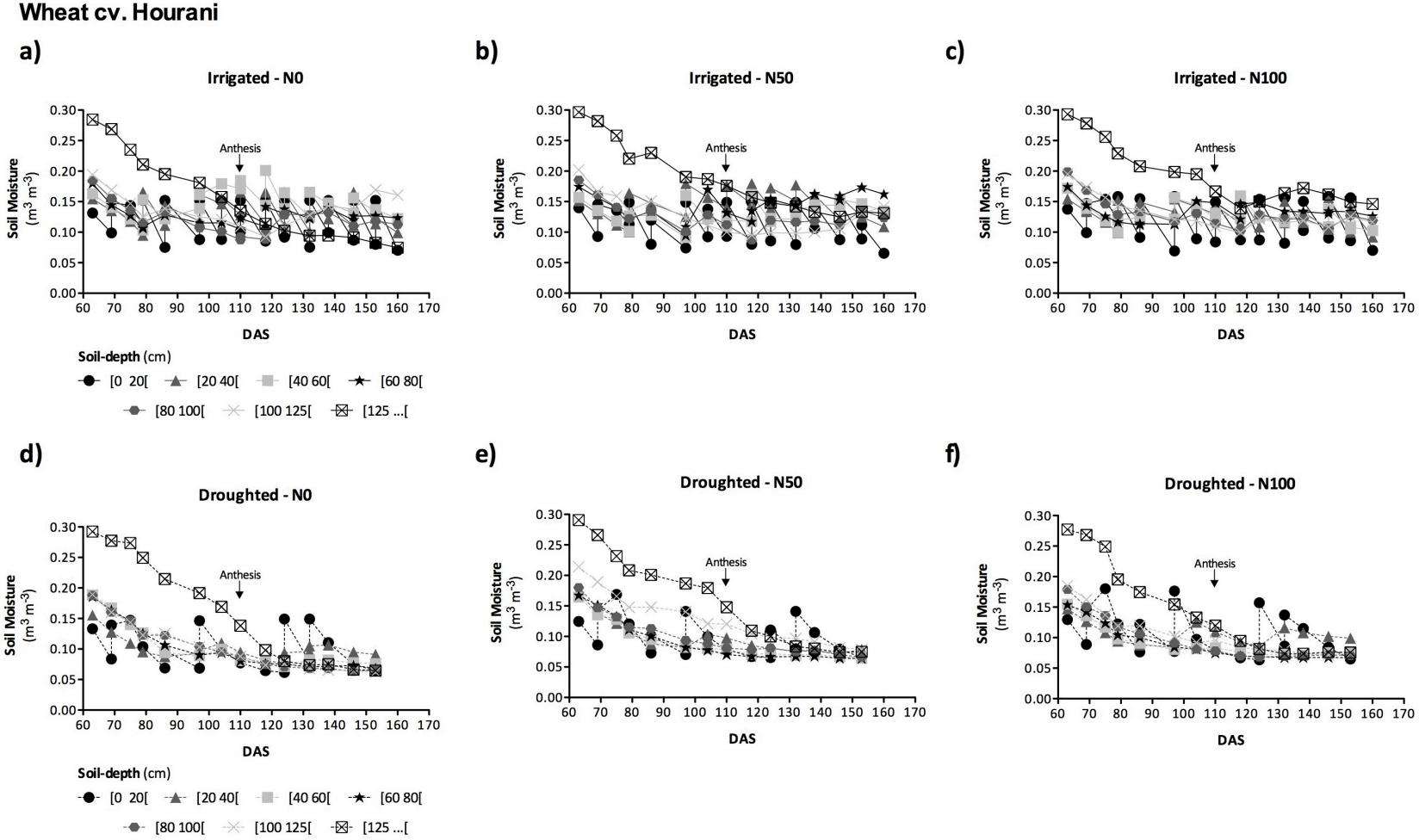

Figure 6.4 Soil moisture content for different soil-depth layers in columns from 57 DAS to harvest in the 2007 experiment for durum wheat cv. Hourani, under fully irrigated (full lines) and droughted treatments (broken lines) at three levels of N fertilizer: 0 kg N ha^{-1} (N0 – **a** and **d**), 50 kg N ha^{-1} (N50 – **b** and **e**), and 100 kg N ha^{-1} (N100 – **c** and **f**), equivalents.

6.2.1.3 2008

For barley cv. Rum in 2008 under irrigation the applied water reached the 100 – 125 cm soil-depth layer and occasionally the > 125 cm soil layer, although under drought applied water only reached the upper two layers of the soil profile (Figure 6.5). Generally, as expected, extraction was higher (lower soil moisture) for the 0 – 20 cm layer followed by the 20 – 40 cm soil layer (Figure 6.5). Under well-watered conditions at most soil-depth layers the moisture content after irrigation surpassed the value at FC (≈ 0.247 m^3 m^{-3}), though after anthesis the moisture in the top layers of the soil profile occasionally reached permanent wilting point (WT ≈ 0.123 m^3 m^{-3}) after one week without irrigation (Figure 6.5 a). But at soil-depths below 20 cm the moisture content was always higher than WT. Under drought conditions the soil moisture in the soil layers from 0 to 60 cm occasionally reached the estimated wilting point, and in some cases was lower than that, demonstrating that the WT was slightly lower than the estimated value (Figure 6.5 b).

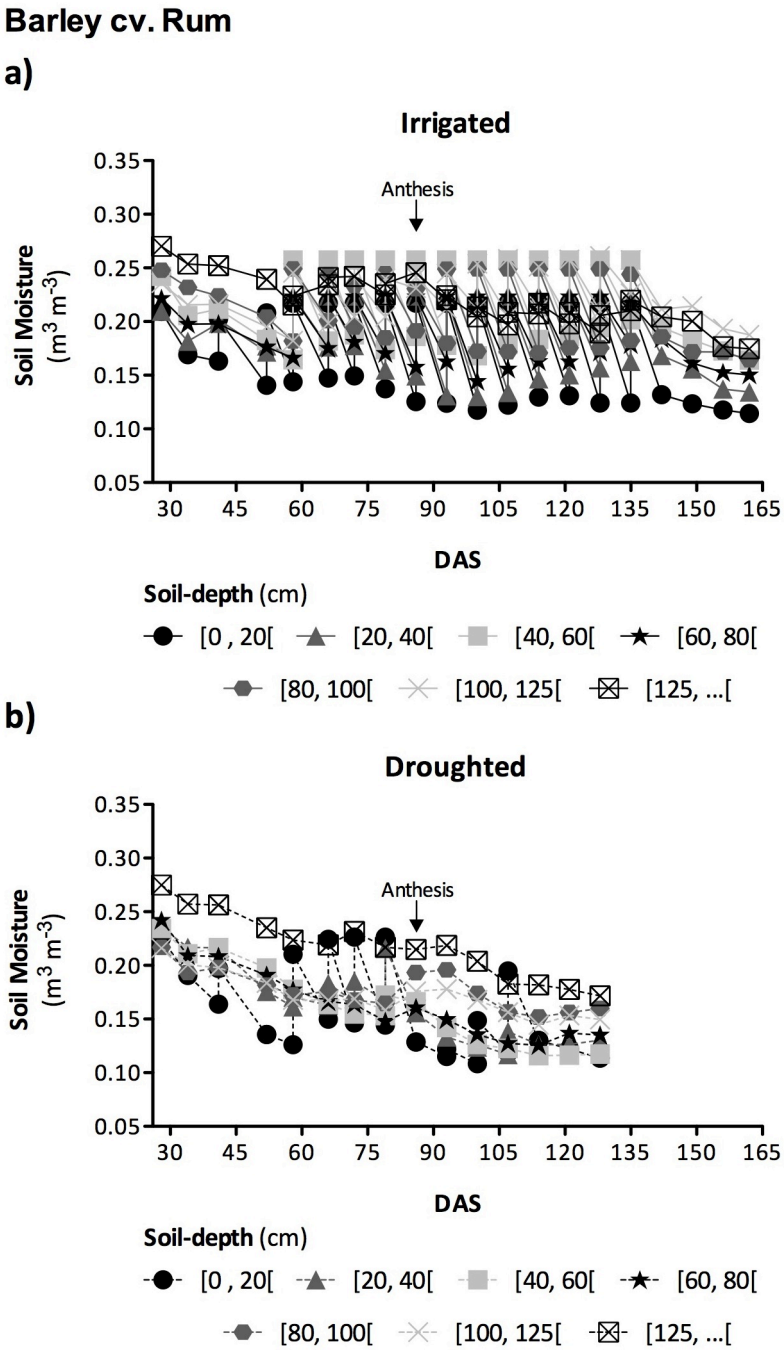

Figure 6.5 Soil moisture content for different soil-depth layers in columns from 28 DAS to harvest in the 2008 experiment for barley cv. Rum, under **a**) fully irrigated (full lines) and **b**) droughted treatments (broken lines).

6.2.2 Water uptake

The cumulative water uptake for the 2006, 2007 and 2008 experiments through time is shown in Figure 6.6, Figure 6.7 and Figure 6.11, respectively. The total water used for the different species and years was quite different, with a higher water use (WU) for

2006 (Figure 6.6) than in other years. WU was higher for barley cv. Rum, followed by wheat cv. Hourani and wheat cv. Karim. However, differences in WU between species were higher under irrigation than under drought, e.g. in 2006, when averaged across N treatments, WU at harvest for barley cv. Rum was 60% higher than for wheat cv. Hourani under irrigation, while under drought the difference was only 8%.

6.2.2.1 2006

In 2006 at 67 DAS wheat cv. Hourani had a higher WU than barley cv. Rum ($p \leq 0.001$). However, the opposite was found at 102 DAS, with barley cv. Rum (GS61) using 1.14 l plant^{-1} more water than wheat cv. Hourani ($p \leq 0.01$; GS55) (Figure 6.6). At anthesis drought decreased the water used by 47% for barley cv. Rum and 61% wheat cv. Hourani ($p \leq 0.001$), but no significant effect of nitrogen application on water uptake was found (Figure 6.6).

At 123 DAS water uptake for barley cv. Rum (GS71) was 55% higher ($p \leq 0.001$) than for wheat cv. Hourani (GS61). Restricted water availability decreased WU by 52% for barley cv. Rum and 58% for wheat cv. Hourani (Figure 6.6; $p \leq 0.001$). At this stage there was a trend ($p = 0.08$) for N application to increase WU by 20% with N50 and 35% with N100 compared to the N0 treatment for barley cv. Rum and 6% cf. and 16%, respectively, for wheat cv. Hourani (Figure 6.6).

At harvest at 175 DAS (Figure 6.6) the WU under drought was similar for both species (5.8 l plant^{-1} for barley cv. Rum cf. 5.4 l plant^{-1} for wheat cv. Hourani). However, under irrigation barley cv. Rum used 8.8 l more water than wheat cv. Hourani (Figure 6.6), resulting in a significant species x irrigation treatment interaction ($p \leq 0.001$). Drought decreased WU for barley cv. Rum and for wheat cv. Hourani by 76% and 65%, respectively ($p \leq 0.001$; Figure 6.6). There was an interaction between species x irrigation x nitrogen ($p \leq 0.05$) such that under irrigation N50 increased WU by 42% for barley cv. Rum, but only by 18% for wheat cv. Hourani. A further increase of N applied at N100 decreased WU in relation to N50, by 14% for barley cv. Rum and 20% for wheat cv. Hourani (Figure 6.6). Under drought both genotypes showed no response to N application (Figure 6.6).

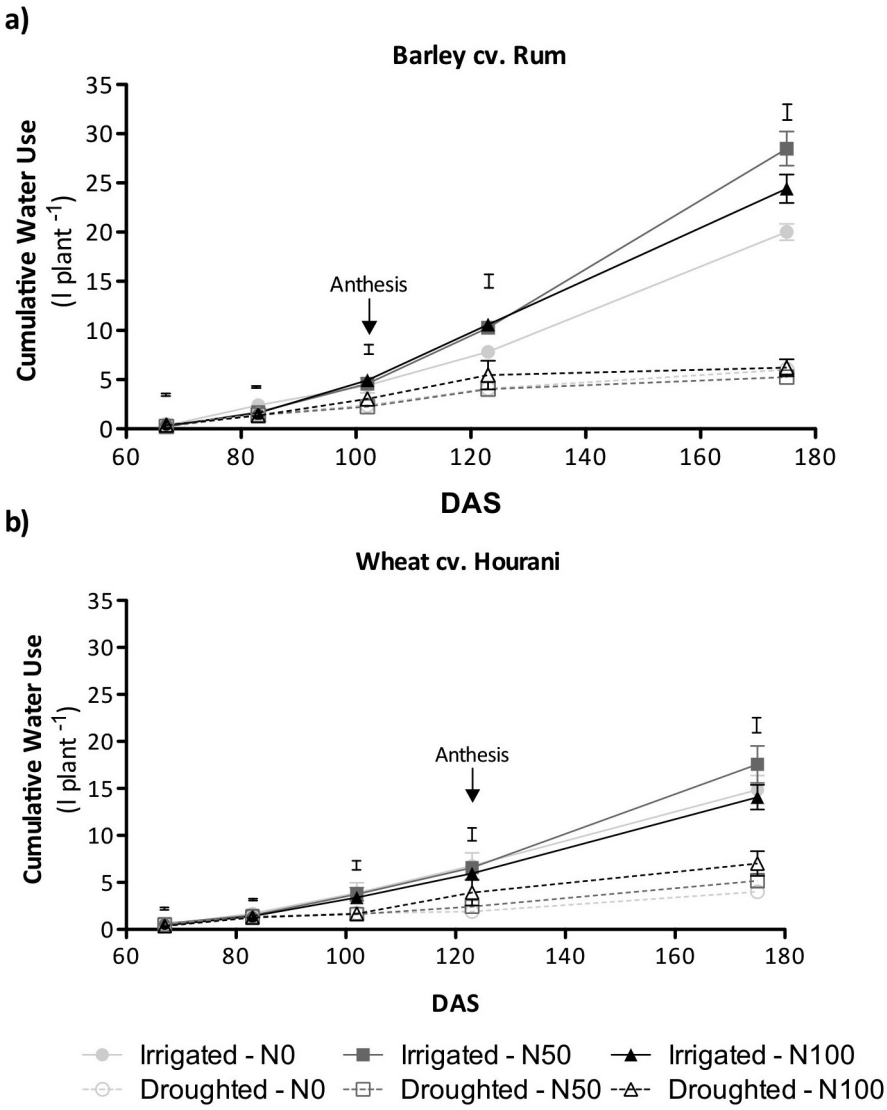

Figure 6.6 Cumulative water use per plant from 53 DAS in the 2006 experiment, for **a**) barley cv. Rum and **b**) durum wheat cv. Hourani under fully irrigated (closed symbols and full lines) and droughted treatments (closed symbols and broken lines) treatments at three levels of N fertilizer: 0 kg N ha^{-1} (N0), 50 kg N ha^{-1} (N50), and 100 kg N ha^{-1} (N100), equivalents. Error bars represent SE of the mean and SED for species x irrigation x nitrogen. (df = 22).

6.2.2.2 2007

In 2007, for barley cv. Rum averaging across irrigation and N treatments, water use increased from 1.22 l at 75 DAS to 3.65 l $plant^{-1}$ at anthesis (Figure 6.7, a). At anthesis drought decreased WU ($p \leq 0.001$) by 20% but there was no effect of N fertilizer application on WU (Figure 6.7, a). At harvest WU under irrigation was 9.5 l $plant^{-1}$, 88% higher ($p \leq 0.001$) than under drought (Figure 6.7 a). N application did not significantly affect the WU for barley cv. Rum.

For wheat cv. Karim overall water use per plant at 75 DAS was 1.20 l, increasing to a 3.9 l at anthesis and 4.8 l at harvest (Figure 6.7 b). Drought decreased ($p \leq 0.001$) WU by 1.1 l plant^{-1} at anthesis and 2.3 l plant^{-1} at harvest, while nitrogen had no significant effect on WU (Figure 6.7, b).

For wheat cv. Hourani WU increased from 1.1 l plant^{-1} at 75 DAS to 3.6 l plant^{-1} at anthesis (Figure 6.7, c). Drought decreased ($p \leq 0.001$) WU by 16 and 42% at anthesis and harvest, respectively (Figure 6.7, c); and nitrogen decreased WU ($p \leq 0.001$) by 12 and 9% with N50 and N100, respectively (Figure 6.7, c).

When examining the cumulative water used through time for individual soil-depth layers (Figure 6.8 to 6.10) for all genotypes and treatments, the layer that accounted for most of the total water uptake was the 0 – 20 cm soil layer. For all genotypes under irrigation more water was taken up from either of the 0 – 20 or 20 – 40 cm soil-depths than all the others combined. The cumulative WU at 0 – 20 cm tended to increase with applied N, but at 20 – 40 cm tended to decrease with N applied (Figure 6.8 to 6.10).

Although RLD and RVD were relatively low at > 125 cm soil-depth, the relative contribution to water uptake seemed to be important, representing around 9% of the total water uptake for barley cv. Rum and wheat cv. Karim, and 7% for wheat cv. Hourani under irrigation (Figure 6.8 to 5610). Under drought, the percentage of uptake at ≥ 125 cm across N treatments was around 16% for all genotypes and the second highest for the total WU after 0-20 cm, due to a higher soil moisture stored in this layer initially at the start of the experiment.

Considering the percentage of cumulative water in the 0 – 80 and > 80 cm soil-depths (Table 6.1), for all genotypes relatively ($p \leq 0.001$) more water was obtained deeper in the soil profile under drought at anthesis and harvest than under irrigation. Under drought the average contribution was ca. 60% for the 0 – 80 cm soil-depth and ca. 40% at > 80 cm at both anthesis and harvest (Table 6.1). Under irrigation, averaging across N treatments, at anthesis the average contribution from soil below 80 cm for barley cv. Rum and wheat cv. Karim was ca. 29% and for wheat cv. Hourani was ca. 33%, decreasing to 24% – 25% for all genotypes at harvest (Table 6.1).

An interaction between irrigation and N applied was observed for wheat cv. Karim at anthesis ($p \leq 0.05$) and harvest ($p \leq 0.01$), with N application increasing the percentage of WU below 80 cm under irrigation, while decreasing the percentage obtained at depth under drought. Averaging across irrigation treatments for wheat cv. Hourani there was an effect of N on percentage water uptake occurring at depth, with N100 decreasing the percentage below 80 cm by 6% at anthesis ($p \leq 0.05$); and N50 increasing this percentage by 11% at harvest (Table 6.1).

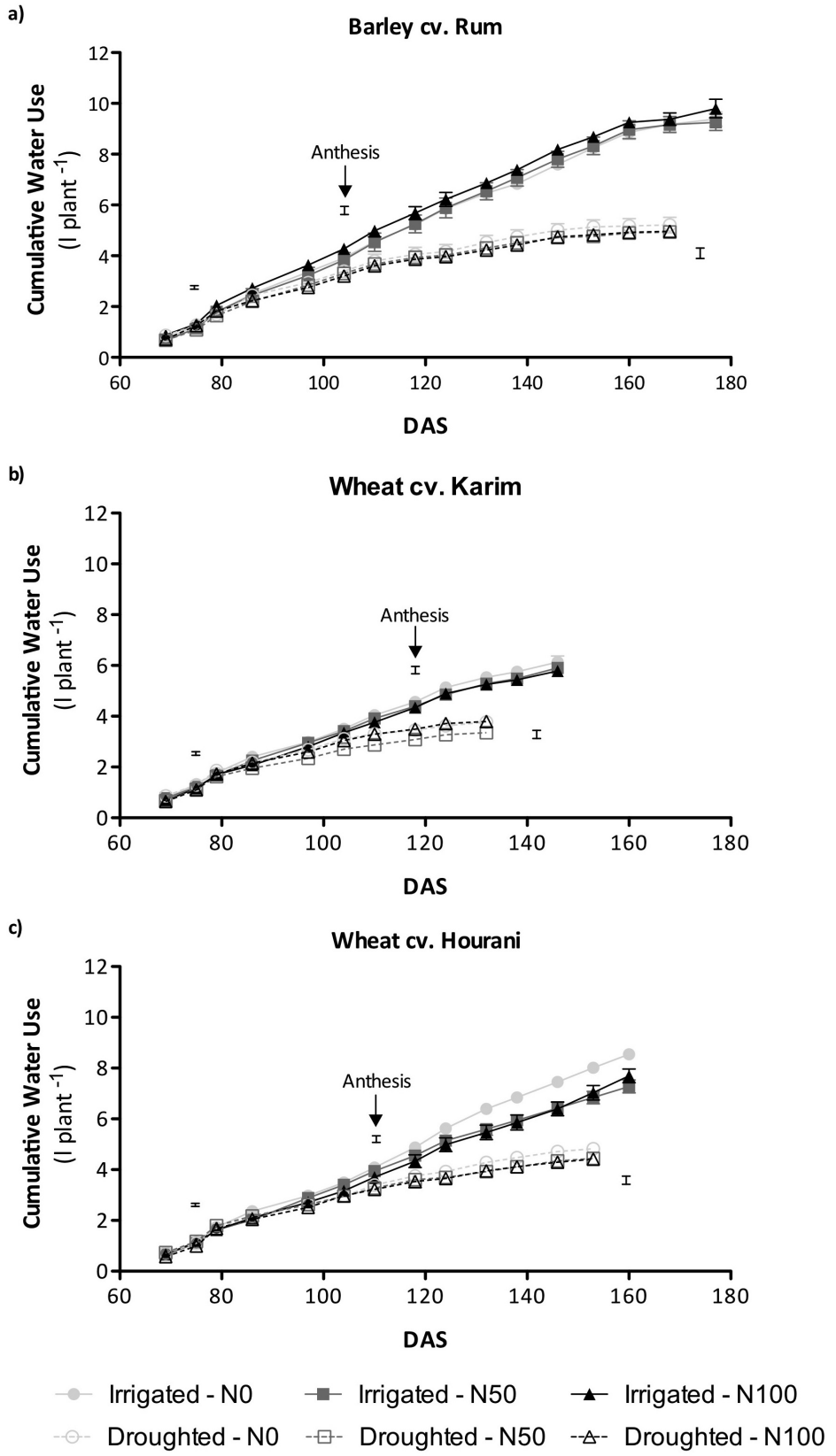

Figure 6.7 Cumulative water use per plant from 57 DAS in 2007 experiment for: **a)** barley cv. Rum, **b)** durum wheat cv. Karim and **c)** durum wheat cv. Hourani in 2007, subjected to fully irrigated (closed symbols and full lines) and droughted (open symbol and broken lines) treatments at three levels of N fertilizer: 0 kg N ha^{-1} (N0), 50 kg N ha^{-1} (N50), and 100 kg N ha^{-1} (N100), equivalents. Error bars represent SE of the mean and SED for irrigation x nitrogen (df = 20).

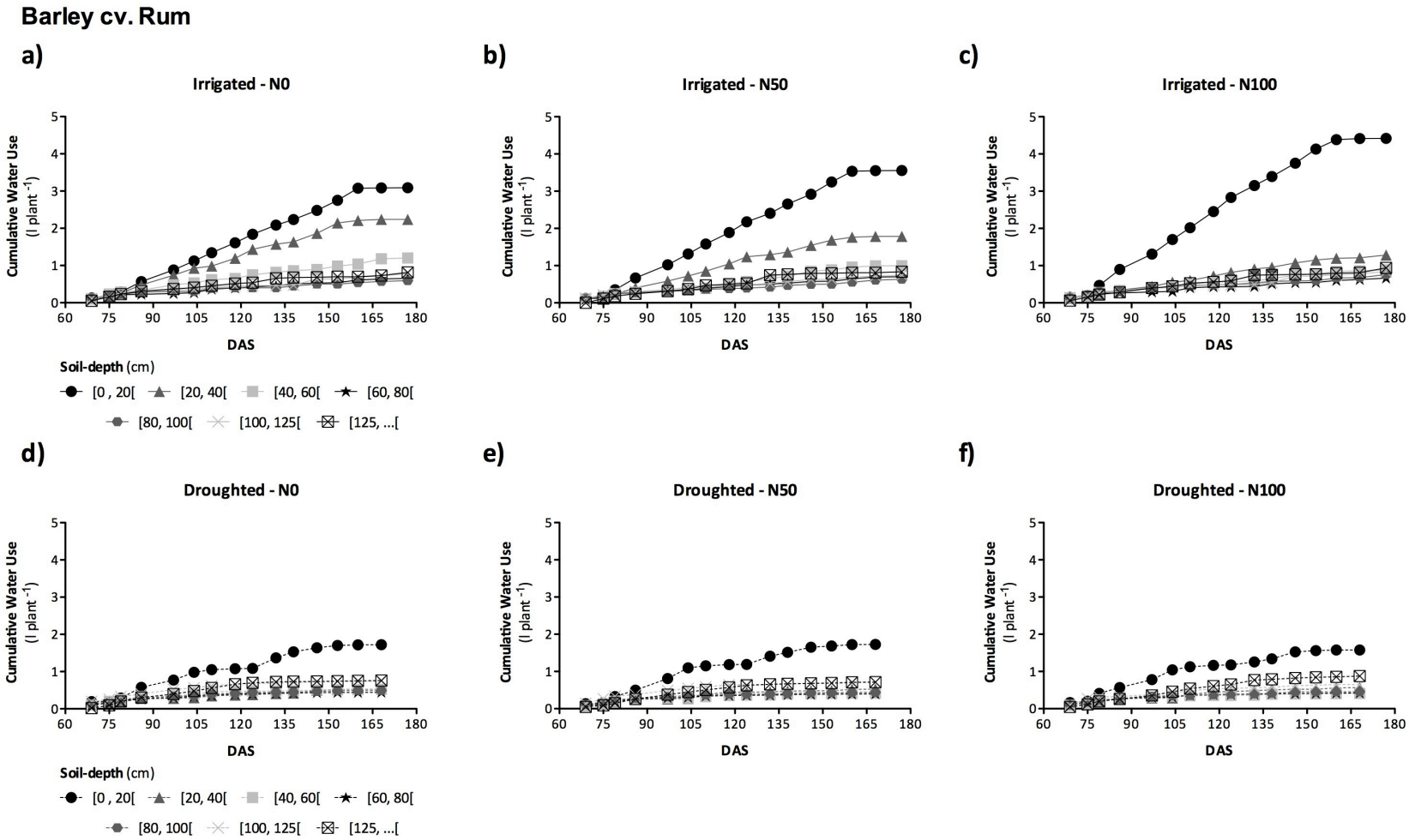

Figure 6.8 Cumulative water uptake through time for different soil-depth layers per soil column, from 57 DAS to harvest during the 2007 experiment for barley cv. Rum, under fully irrigated (full lines) and droughted (broken lines) at three levels of N fertilizer: 0 kg N ha^{-1} (N0 – **a** and **d**), 50 kg N ha^{-1} (N50 – **b** and **e**), and 100 kg N ha^{-1} (N100 – **c** and **f**), equivalents.

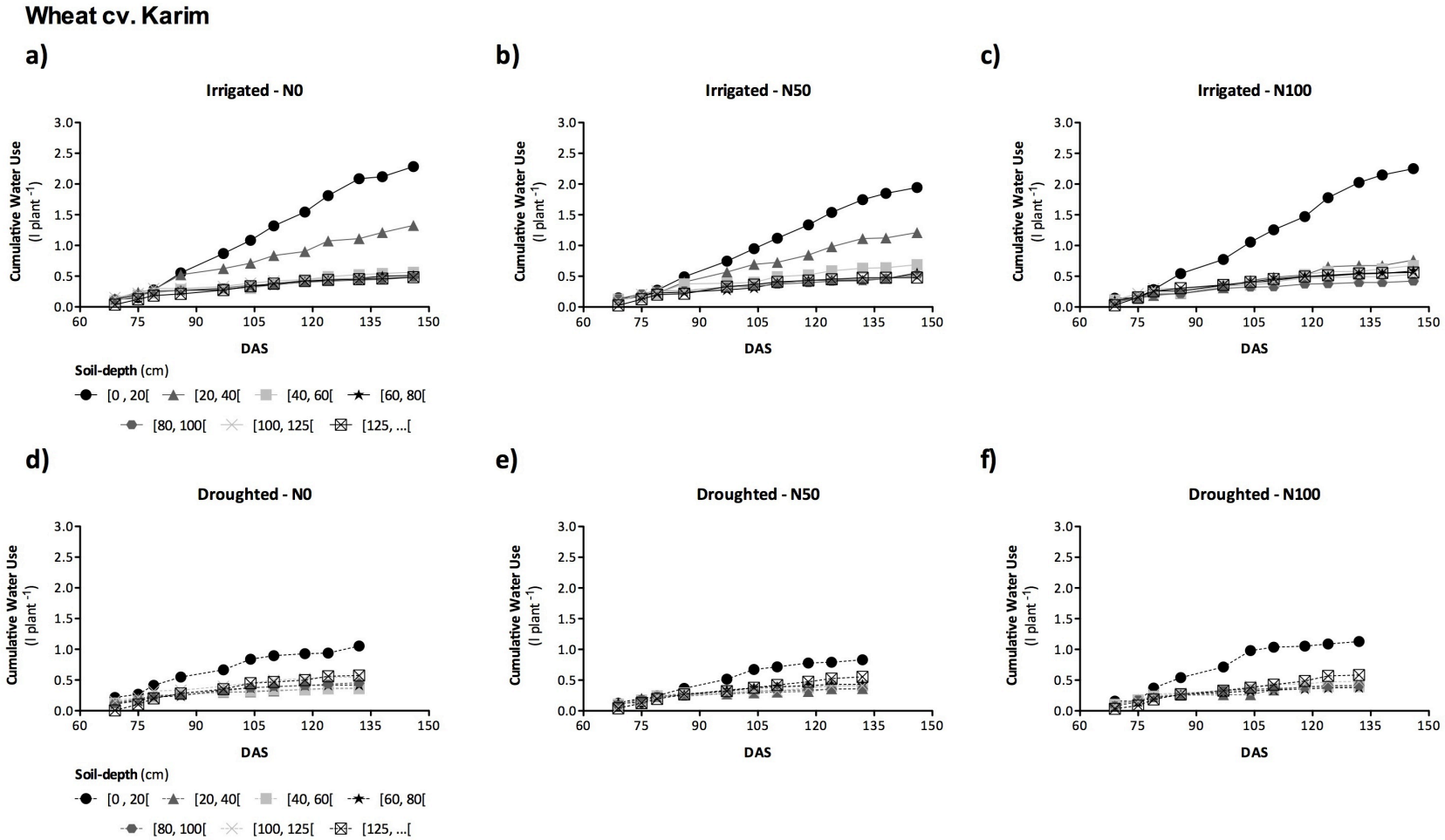

Figure 6.9 Cumulative water uptake through time for different soil-depth layers per soil column, from 57 DAS to harvest during the 2007 experiment for durum wheat cv. Karim, under fully irrigated (full lines) and droughted (broken lines) at three levels of N fertilizer: 0 kg N ha^{-1} (N0 – **a** and **d**), 50 kg N ha^{-1} (N50 – **b** and **e**), and 100 kg N ha^{-1} (N100 – **c** and **f**), equivalents.

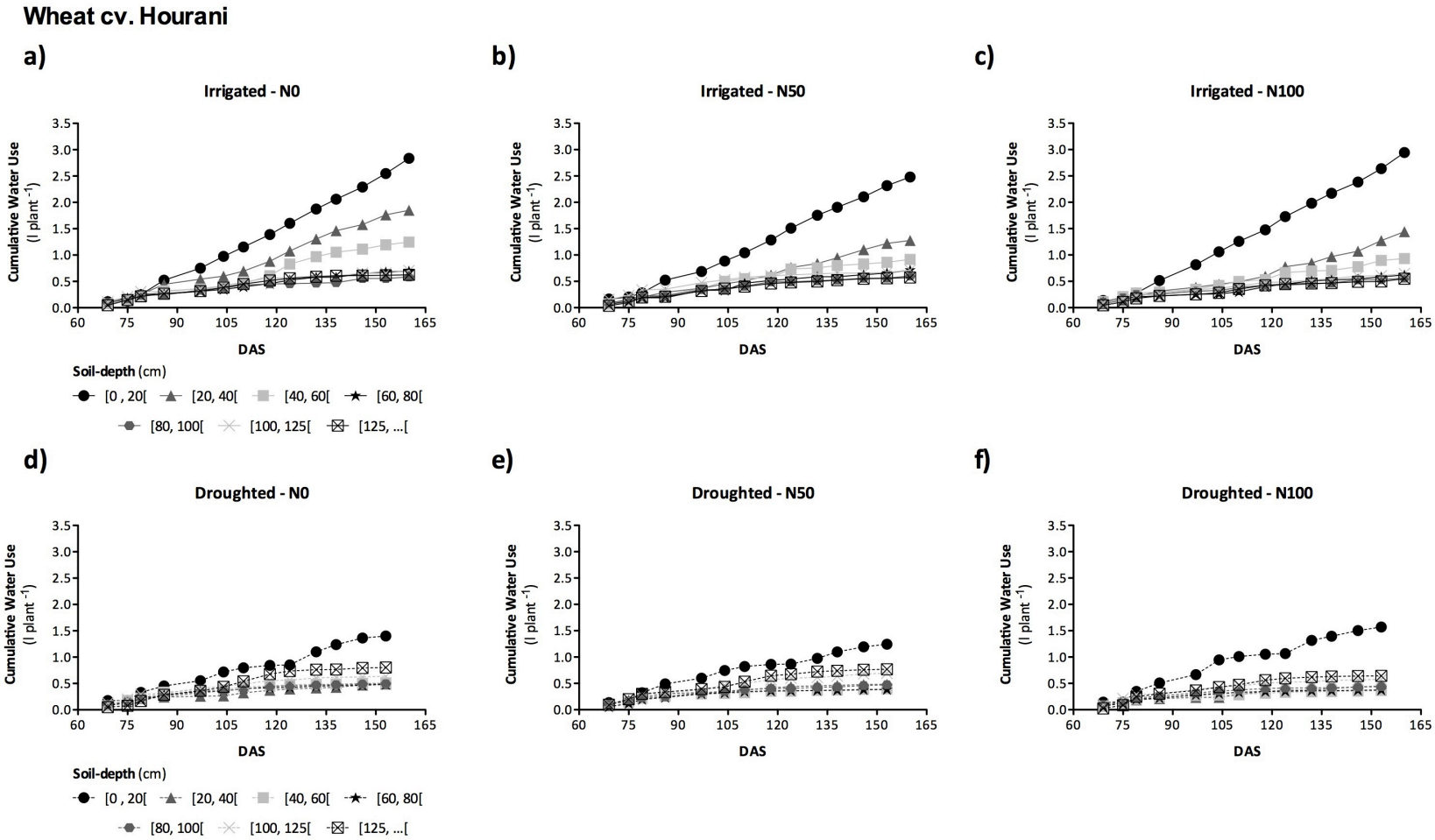

Figure 6.10 Cumulative water uptake through time for different soil-depth layers per soil column, from 57 DAS to harvest during the 2007 experiment for durum wheat cv. Hourani, under fully irrigated (full lines) and droughted (broken lines) at three levels of N fertilizer: 0 kg N ha^{-1} (N0 – **a** and **d**), 50 kg N ha^{-1} (N50 – **b** and **e**), and 100 kg N ha^{-1} (N100 – **c** and **f**), equivalents.

Table 6.1 Cumulative water uptake for 0 – 80 and > 80 cm soil-depth layers per soil column, at anthesis and harvest in the 2007 experiment for barley cv. Rum and durum wheat cv. Karim and Hourani under irrigation and droughted treatments, at three levels of N fertilizer (0, 50 and 100 kg N ha^{-1}, equivalents).

Irrigation	Fertilizer N (kg N ha^{-1})	% Cumulative Water Uptake											
		Barley cv. Rum				Wheat cv. Karim				Wheat cv. Hourani			
		Anthesis		Harvest		Anthesis		Harvest		Anthesis		Harvest	
		0 - 80 cm	> 80 cm	0 - 80 cm	> 80 cm	0 - 80 cm	> 80 cm	0 - 80 cm	> 80 cm	0 - 80 cm	> 80 cm	0 - 80 cm	> 80 cm
Irrigated	**0**	73.0	27.0	76.7	23.3	72.3	27.7	76.3	23.7	66.4	33.6	77.6	22.4
	50	71.0	29.0	76.1	23.9	71.5	28.5	74.6	25.4	65.0	35.0	74.0	26.0
	100	70.5	29.5	74.3	25.7	69.2	30.8	73.8	26.2	69.0	31.0	77.2	22.8
	Mean	*71.5*	*28.5*	*75.7*	*24.3*	*71.0*	*29.0*	*74.9*	*25.1*	*66.8*	*33.2*	*76.3*	*23.7*
Droughted	**0**	58.8	41.2	61.6	38.4	58.3	41.7	57.9	42.1	58.0	42.0	59.8	40.2
	50	60.0	40.0	62.4	37.6	61.8	38.2	60.8	39.2	56.9	43.1	56.6	43.4
	100	61.4	38.6	60.2	39.8	62.6	37.4	61.2	38.9	59.6	40.4	62.5	37.5
	Mean	*60.1*	*39.9*	*61.4*	*38.6*	*60.9*	*39.1*	*60.0*	*40.0*	*58.2*	*41.8*	*59.6*	*40.4*
	SED (df)												
	Irrigation (20)	1.57^{***}	1.57^{***}	1.22^{***}	1.22^{***}	1.07^{***}	1.07^{***}	0.70^{***}	0.70^{***}	0.98^{***}	0.98^{***}	0.96^{***}	0.96^{***}
	Nitrogen (20)	1.92^{ns}	1.92^{ns}	1.49^{ns}	1.49^{ns}	1.31^{ns}	1.31^{ns}	0.85^{ns}	0.85^{ns}	1.20^{*}	1.20^{*}	1.17^{**}	1.17^{**}
	*Irrigation*Nitrogen (20)*	2.72^{ns}	2.72^{ns}	2.11^{ns}	2.11^{ns}	1.85^{*}	1.85^{*}	1.21^{**}	1.21^{**}	1.69^{ns}	1.69^{ns}	1.66^{ns}	1.66^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and *ns* for a non significant result for the ANOVA test.

6.2.2.3 2008

In 2008 for barley cv. Rum, drought decreased WU by 44% at anthesis and by 71% at harvest ($p \leq 0.001$; Figure 6.11). As in 2007 most of the WU occurred in the upper 20 cm of the soil profile, representing 24% of the total WU at anthesis and 22% at harvest under irrigation; and 42 and 38%, respectively, under water limitation (Figure 6.12). For the irrigated plants the soil-depth >125 cm was where least percentage of WU occurred; here water captured represented only 4% of the total water used at anthesis and harvest (Figure 6.12 a), contrasting with 7% and 10%, respectively, under drought (Figure 6.12 b).

With regard to the percentage WU between 0 – 80 and > 80 cm soil-depths, no statistically significant differences were found between irrigation treatments (Table 6.2).

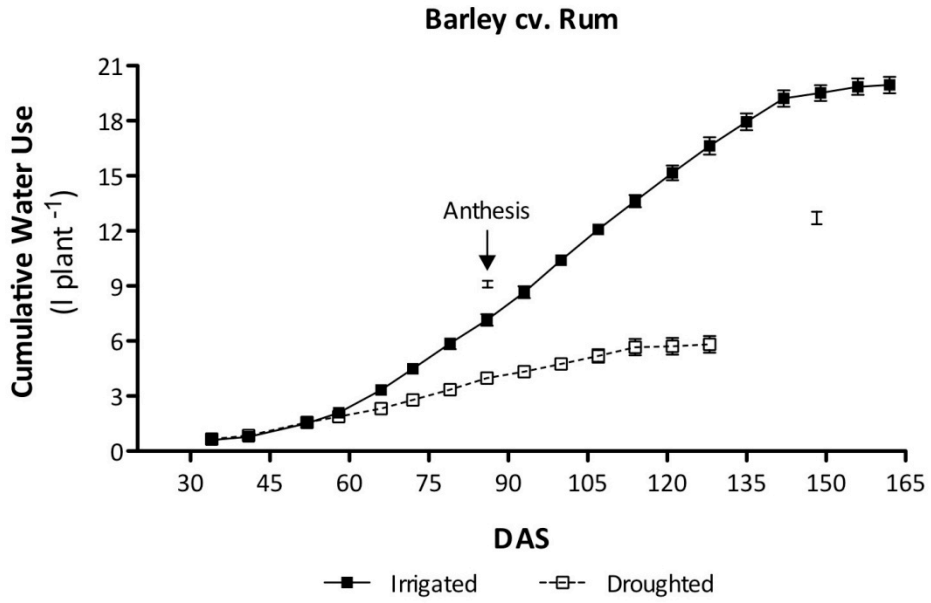

Figure 6.11 Cumulative water use per plant from 28 DAS during the 2008 experiment, for barley cv. Rum subjected to fully irrigated (closed symbols and full line) and droughted (open symbols and broken line) treatments. Error bars represent SE of the mean and SED for irrigation (df = 6).

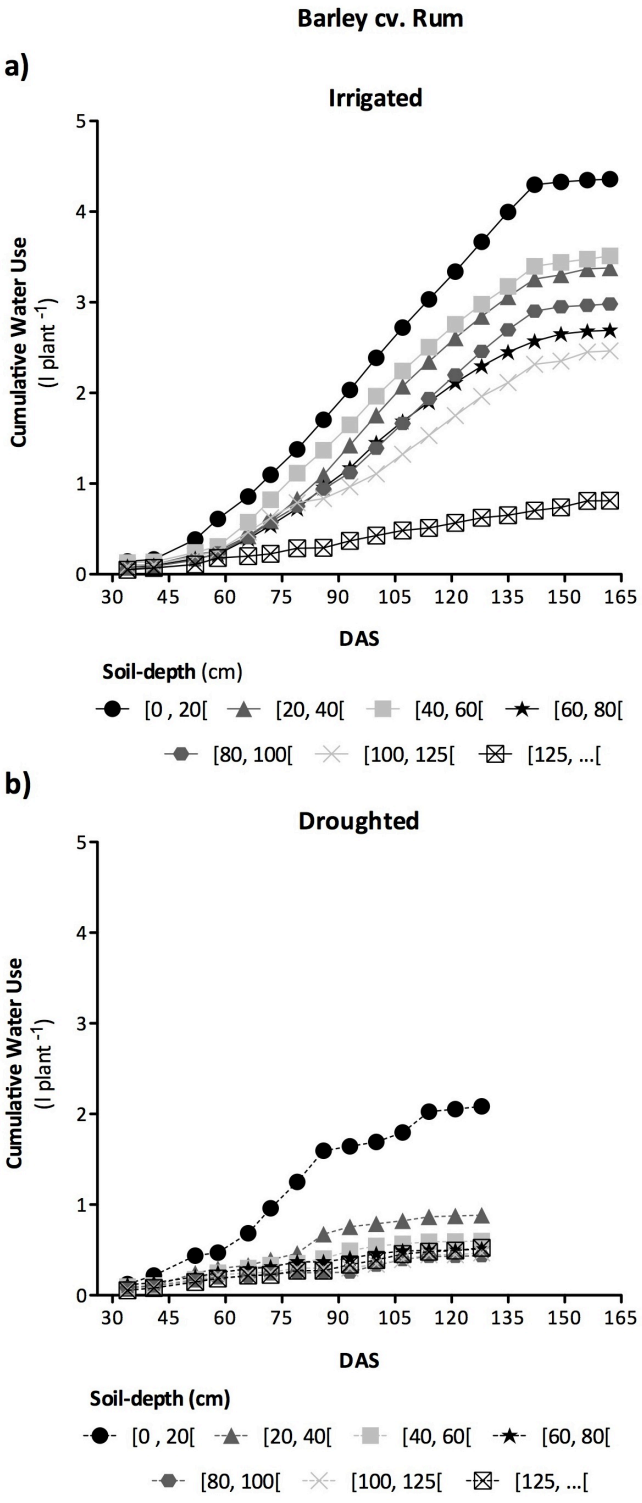

Figure 6.12 Cumulative water uptake through time for different soil-depth layers per soil column, from 27 DAS to harvest during the 2008 experiment for durum barley cv. Rum subjected to **a)** fully irrigated and **b**) droughted treatments.

Table 6.2 Cumulative water uptake for 0 – 80 and > 80 cm soil-depth layers per soil column, at anthesis and harvest in the 2008 experiment for barley cv. Rum subjected to fully irrigated and droughted treatments.

Irrigation	Barley cv. Rum			
	% Cumulative Water Uptake			
	Anthesis		Harvest	
	0 - 80 cm	> 80 cm	0 - 80 cm	> 80 cm
Irrigated	71.7	28.3	69.1	30.9
Droughted	78.9	21.1	74.0	26.0
SED (df)				
Irrigation (6)	4.19^{ns}	4.19^{ns}	4.14^{ns}	4.14^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and *ns* for a non significant result for the ANOVA test.

6.2.3 Relationship between water uptake and root length and root volume density

6.2.3.1 2007

Under full irrigation, statistically significant exponential regressions between ϕ for water and RLD were found for wheat cv. Karim (Figure 6.13 b, e) with an average k_{RLD} value across N treatments of 5.60 cm^2 contrasting with a k_{RLD} value of 3.58 cm^2 under drought (Figure 6.13 c, f and Table 6.3), resulting in a C_{RLD} of 0.41 and 0.64 cm cm^{-3}, respectively. Corresponding regressions for wheat cv. Hourani were not significant. Under drought, a significant regression was found for barley cv. Rum at N50, (R^2 = 0.45, $p \leq 0.01$) resulting in a k_{RLD} value of 2.38 cm^2 (Figure 6.13, d) and a C_{RLD} of 0.97 cm cm^{-3} (Table 6.3).

In general a slightly better relationship was found between ϕ and RVD than for RLD (Figure 6.14). Averaged across N treatments, k_{RVD} for barley cv. Rum was 5.13 under full irrigation and of 4.45 under drought (Figure 6.14 a, d), resulted in C_{RVD} values of 0.45 and 0.52 cm^3 cm^{-3}, respectively. However, values did not statistically differ (Table 6.4). The k_{RVD} values obtained for wheat cv. Karim were statistically higher than those for barley cv. Rum: 10.04 under irrigation and 5.86 under drought, corresponding to

C_{RVD} values of 0.23 and 0.39 cm^3 cm^{-3}, respectively (Figure 6.14 b, e, and Table 6.4). The fitted regressions between ϕ and RVD for wheat cv. Hourani resulted in k_{RVD} values similar to those obtained for barley cv. Rum (Figure 6.14 a, c, d, f). When calculated pooling data across N treatments, k_{RVD} under fully irrigation was significantly higher (5.0) than under drought (4.0; Figure 6.14 c, f) resulting in C_{RVD} values of 0.46 and 0.58, respectively (Table 6.4).

6.2.3.2 2008

The regressions obtained for ϕ and rooting traits, particularly RVD in 2007, gave successful fits and hence estimates of the critical values of root size for water capture (Figure 6.14). Unfortunately, the RLD and RVD values in the 2007 experiment were generally low and the critical values equivalent to 90% potential resource capture were therefore extrapolated beyond the points of the observed values (Figure 6.14). Thus, one of the main objectives of the 2008 experiment was to examine the relationship between ϕ for water capture across a wider range of RLD and consequently to obtain a more reliable estimate of the C_{RLD} and C_{RVD} values. In 2008, for the fully irrigated treatment, the regression between ϕ and both RLD and RVD was not significant (Figure 6.15), a fact that might be associated with irrigation later in the season not increasing WU as growth was already decreasing due to senescence. However, under drought, both regressions were significant. The regression was also significant when pooling the data across 2007 and 2008 for the N50 data (Figure 6.15 b, d). The k_{RLD} value in 2008 was 2.42 cm^2 corresponding to a C_{RLD} of 0.95 cm cm^{-3}. When using the pooled 2007 and 2008 data the k_{RLD} value slightly decreased to 2.40 cm^2 increasing the C_{RLD} to 0.96 cm cm^{-3}, whilst R^2 substantially increased from 0.77 to 0.91 (Figure 6.15, b). The regression between ϕ and RVD for 2008 resulted in a k_{RVD} value of 6.41 ($R^2 = 0.89$, $p \leq 0.01$) and a C_{RVD} of 0.36 cm^{-3}, but when using the pooled 2007 and 2008 data the k_{RVD} value was 5.21 ($R^2 = 0.94$, $p \leq 0.01$) and the critical C_{RVD} 0.44 cm^3cm^{-3}.

WU in 2006 was estimated gravimetrically for the entire column, with the objective of relating this to the RLD and RVD measurements at all soil-depths. Unfortunately, the RLD and RVD related to the WU for the entire column resulted in curve fitting that

failed to optimise, and incorporating that data would increase the noise in the analysis. Due to this fact it was decided not to incorporate the 2006 data in the present analysis of the relationship between RLD or RVD and ϕ.

Table 6.3 R^2, K_{RLD} and respective standard error of the mean (*se*) from fitting equation 5.1 to the proportional water captured (ϕ) by root length density (RLD) for 2007 (and 2008 for barley cv. Rum). For fitted curves see Figure 6.13 and Figure 6.15 a and b.

Species	Irrigation	R^2	K_{RLD} (cm^2)	*se*	C_{RLD} (cm cm^{-3})
Barley cv. Rum	**Irrigated**	*ns*	—	—	—
	Droughted	0.45**	2.38	0.27	0.97
	Droughted 2007/08	0.91**	2.40	0.18	0.96
Wheat cv. Karim	**Irrigated**	0.59**	5.60	0.58	0.41
	Droughted	0.40**	3.58	0.34	0.64
Wheat cv. Hourani	**Irrigated**	*ns*	—	—	—
	Droughted	*ns*	—	—	—

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and *ns* for a non significant fit.

Table 6.4 R^2, K_{RLD} and respective standard error of the mean (*se*) from fitting equation 5.1 to the proportional water captured (ϕ) by root length density (RLD) for 2007 (and 2008 for barley cv. Rum). For fitted curves see Figure 6.14 and Figure 6.15 c and d.

Species	Irrigation	R^2	K_{RVD}	*se*	C_{RVD} (cm^3 cm^{-3})
Barley cv. Rum	**Irrigated**	0.43**	5.13	0.68	0.45
	Droughted	0.61**	4.45	0.31	0.52
	Droughted 2007/08	0.94**	5.21	0.30	0.44
Wheat cv. Karim	**Irrigated**	0.92**	10.04	0.47	0.23
	Droughted	0.64**	5.86	0.43	0.39
Wheat cv. Hourani	**Irrigated**	0.61**	5.03	0.52	0.46
	Droughted	0.36*	4.00	0.31	0.58

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and *ns* for a non significant fit.

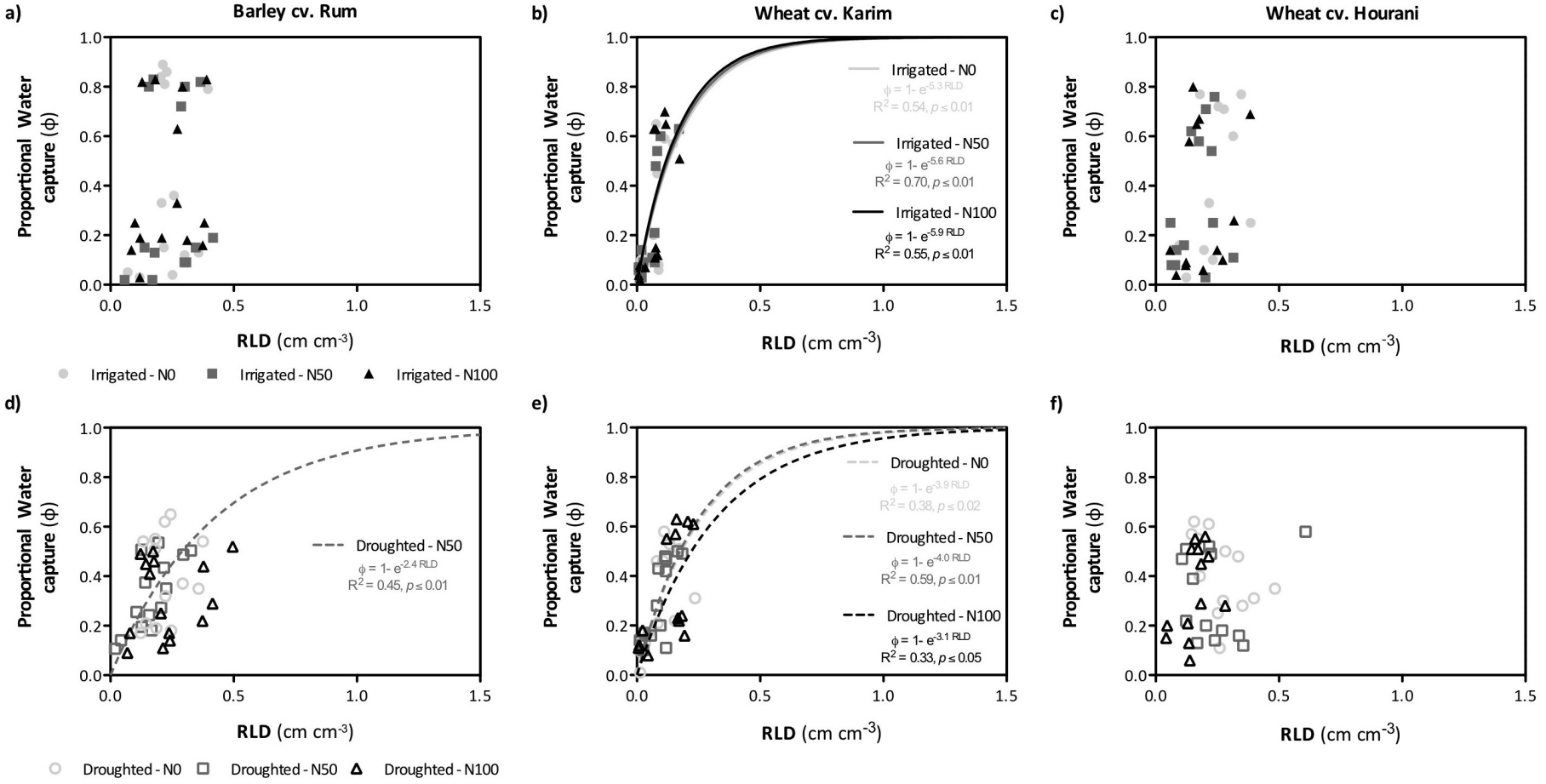

Figure 6.13 Proportional available water captured (ϕ) and root length density (RLD) for 2007, fitted with the equation, $\phi = 1 - e^{-k_{RLD}\,RLD}$ adapted from King *et al.* (2003), for barley cv. Rum, wheat cv. Karim and wheat cv. Hourani, subjected to irrigated **a)**, **b**) and **c)** (closed symbols and full lines) and drought treatments **d)**, **e)** and **f)** (open symbols and broken lines); and three levels of N fertilizer: 0 kg N ha^{-1} (N0), 50 kg N ha^{-1} (N50), and 100 kg N ha^{-1} (N100) equivalents. Only significant regressions are shown (df = 14).

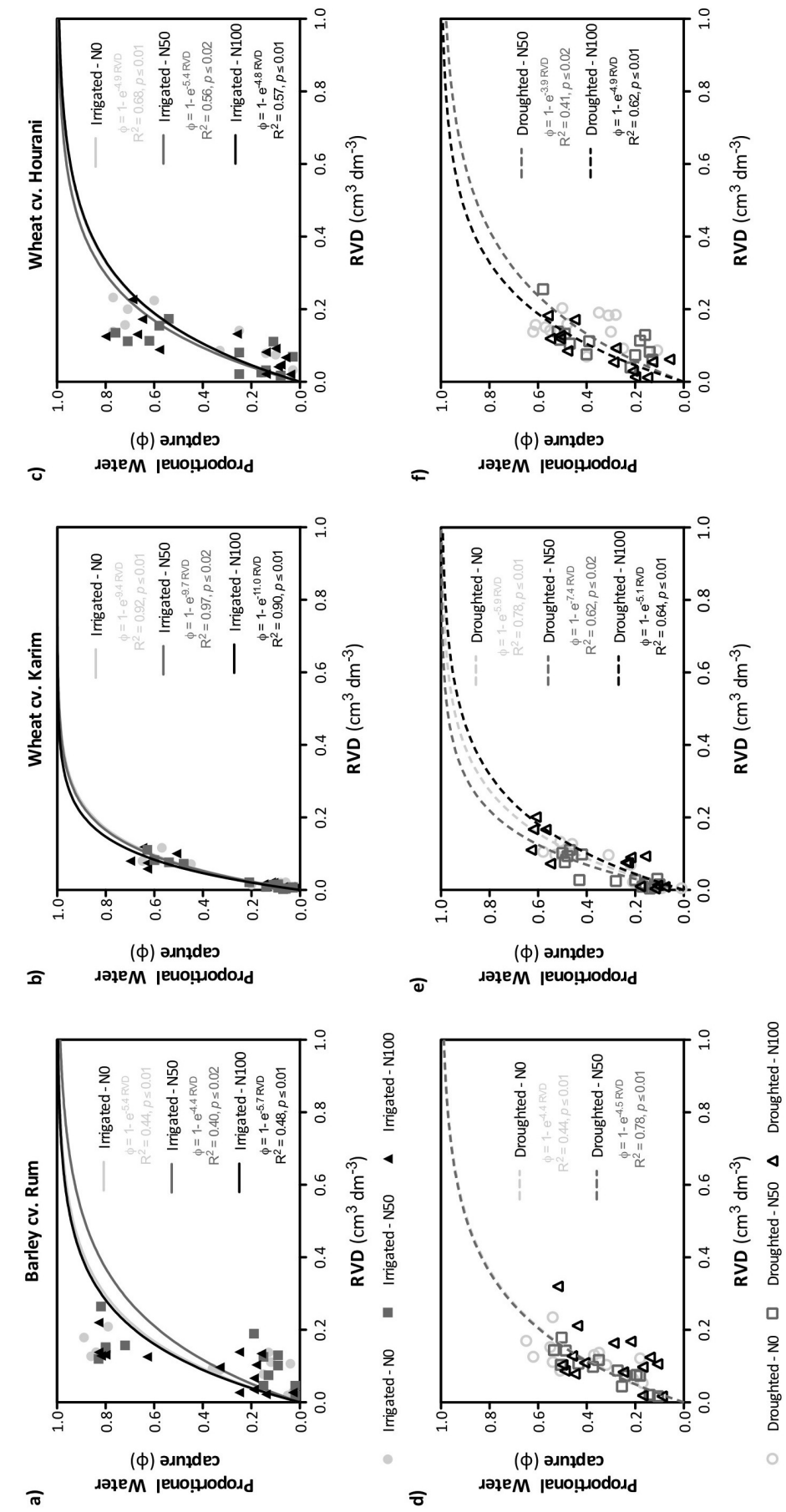

Figure 6.14 Proportional available water captured (ϕ) and root volume density (RVD) for 2007, fitted with the equation, $\phi = 1 - e^{-k_{RVD} \cdot RVD}$ adapted from King *et al.* (2003), for barley cv. Rum, wheat cv. Karim and wheat cv. Hourani, subjected to irrigated **a)**, **b)** and **c)** (closed symbols and full lines) and drought treatments **d)**, **e)** and **f)** (open symbols and broken lines); at three levels of N fertilizer: 0 kg N ha^{-1} (N0), 50 kg N ha^{-1} (N50), and 100 kg N ha^{-1} (N100) equivalents. Only significant regressions are shown (df = 14).

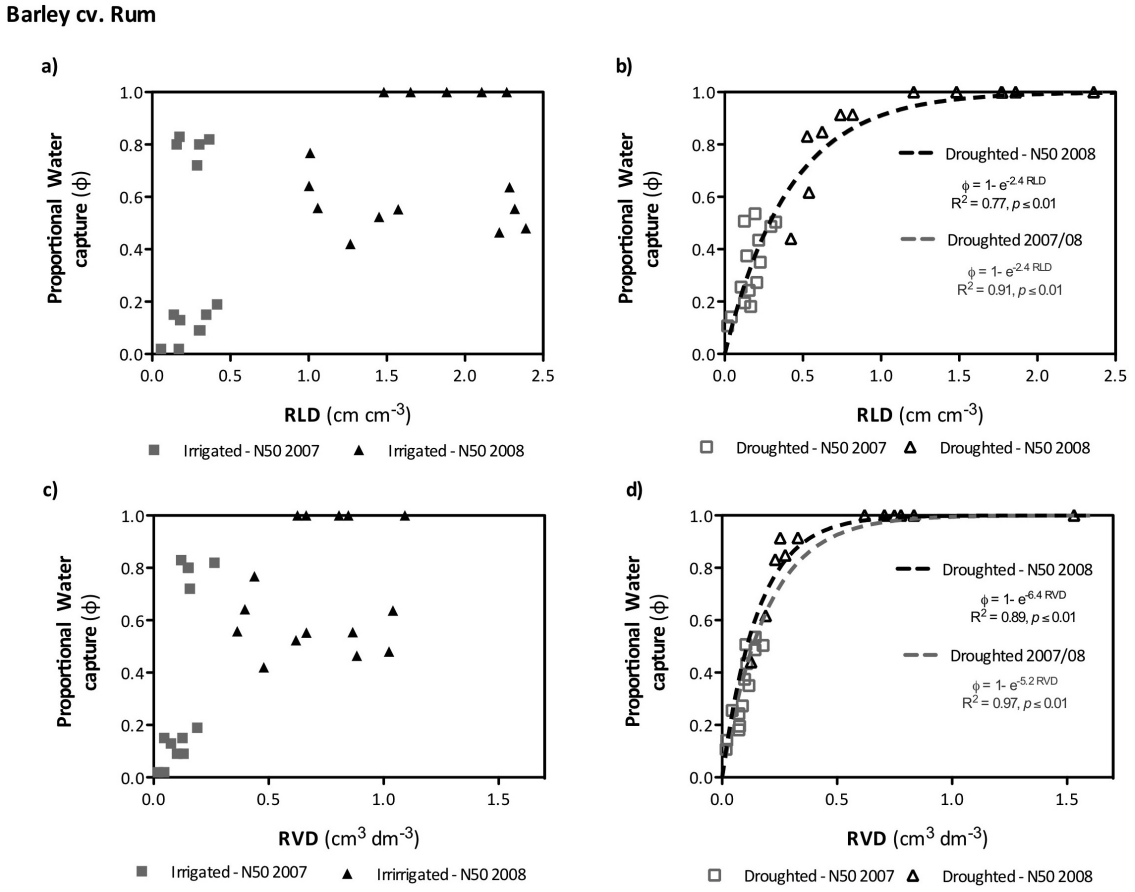

Figure 6.15 Proportion available water captured (ϕ) and root length density (RLD) under **a**) irrigated and **b**) drought treatments fitted with the equation, $\phi = 1 - e^{-k_{RLD}\ RLD}$ adapted from King *et al.* (2003); and proportion of available water captured (ϕ) and root volume density (RVD) under **c**) irrigated and **d**) drought treatments fitted with the equation, $\phi = 1 - e^{-k_{RVD}\ RVD}$ adapted from King *et al.* (2003), for barley cv. Rum in the 2007/08 experiments under 50 kg N ha^{-1} equivalent.

6.2.4 Nitrogen uptake (Nup)

6.2.4.1 2006

For barley cv. Rum at 67 DAS N uptake per plant (Nup) was 29% higher ($p \leq 0.001$) than for wheat cv. Hourani (Figure 6.16). At 102 DAS (GS61) drought decreased Nup by 18% (Figure 6.16; $p \leq 0.05$), but no effect of N application was found.

From 67 DAS to 123 DAS Nup increased by 37 and 23% for barley cv. Rum (GS71) with and without irrigation, respectively, and 18 and 17% for wheat cv. Hourani (GS61; Figure 6.16). At 123 DAS overall N uptake for wheat cv. Hourani was 54% lower ($p \leq$

0.001) than for barley cv. Rum (Figure 6.16). Irrigation did not significantly affect Nup of barley at N0, but irrigation increased Nup by 44% with N50 and 57% with N100 for barley; there were no statistically significant effects of N for wheat cv. Hourani at this stage (species x irrigation x nitrogen, $p \leq 0.001$) (Figure 6.16). At 123 DAS neither N or irrigation or any irrigation x N combinations significantly affected Nup for wheat cv. Hourani (Figure 6.16).

At harvest barley cv. Rum had an average Nup across irrigation an N treatments of 0.62 g plant^{-1} contrasting with the 0.29 g plant^{-1} for wheat cv. Hourani ($p \leq 0.001$) (Figure 6.16). At harvest, there was a species x irrigation interaction ($p \leq 0.01$), with drought decreasing Nup for barley cv. Rum by 48% (Figure 6.16 a) but only by 17% for wheat cv. Hourani (Figure 6.16 b). For both species at harvest, there was a trend for Nup to be larger at N50 compared to N0 ($p \leq 0.07$). However, at N100 Nup was either similar or slightly smaller compared to N0 for wheat cv. Hourani and barley cv. Rum, respectively (Figure 6.16).

6.2.4.2 2007

Overall average Nup values at harvest for barley cv. Rum were 167% (214 mg) of those found for durum wheat cv. Hourani (128 mg) and 284% of the durum wheat cv. Karim values (75 mg). Averaging across N treatments drought decreased Nup for both barley cv. Rum and wheat cv. Hourani ($p \leq 0.01$); however, not significantly for wheat cv. Karim. N fertilizer application decreased Nup at harvest for wheat cv. Hourani, but effects were not statistically different for barley cv. Rum and wheat cv. Karim.

For barley cv. Rum from 75 DAS to anthesis Nup overall increased by 90 mg plant^{-1} (Figure 6.17, a). Drought decreased Nup by 17% at anthesis and by 44% at harvest ($p \leq 0.01$ and $p \leq 0.001$, respectively), though N application had no significant effect on Nup (Figure 6.17 a). For wheat cv. Karim (Figure 6.17 b), neither water nor nitrogen had a significant effect on the Nup at anthesis or harvest. In contrast, for wheat cv. Hourani drought decreased Nup by 30 mg plant^{-1} at harvest ($p \leq 0.05$); and N application actually decreased Nup by 20 and 27% with N50 and N100, respectively, compared to N0 ($p \leq 0.05$; Figure 6.17 b).

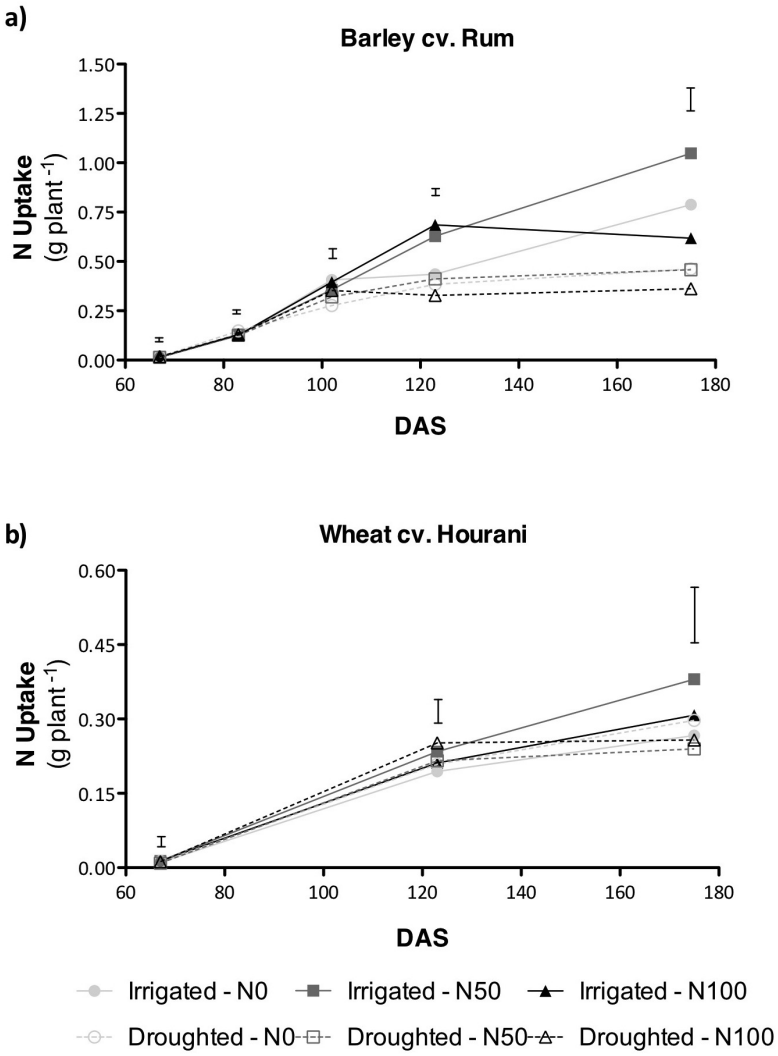

Figure 6.16 Total N uptake from 53 DAS during the 2006 experiment for **a)** barley cv. Rum and **b)** durum wheat cv. Hourani subjected to fully irrigated (closed symbols and full lines) and droughted (closed symbols and broken lines) treatments, at three levels of N fertilizer: 0 kg N ha^{-1} (N0), 50 kg N ha^{-1} (N50), and 100 kg N ha^{-1} (N100), equivalents. Error bars represent SED for species x irrigation x nitrogen (df = 22).

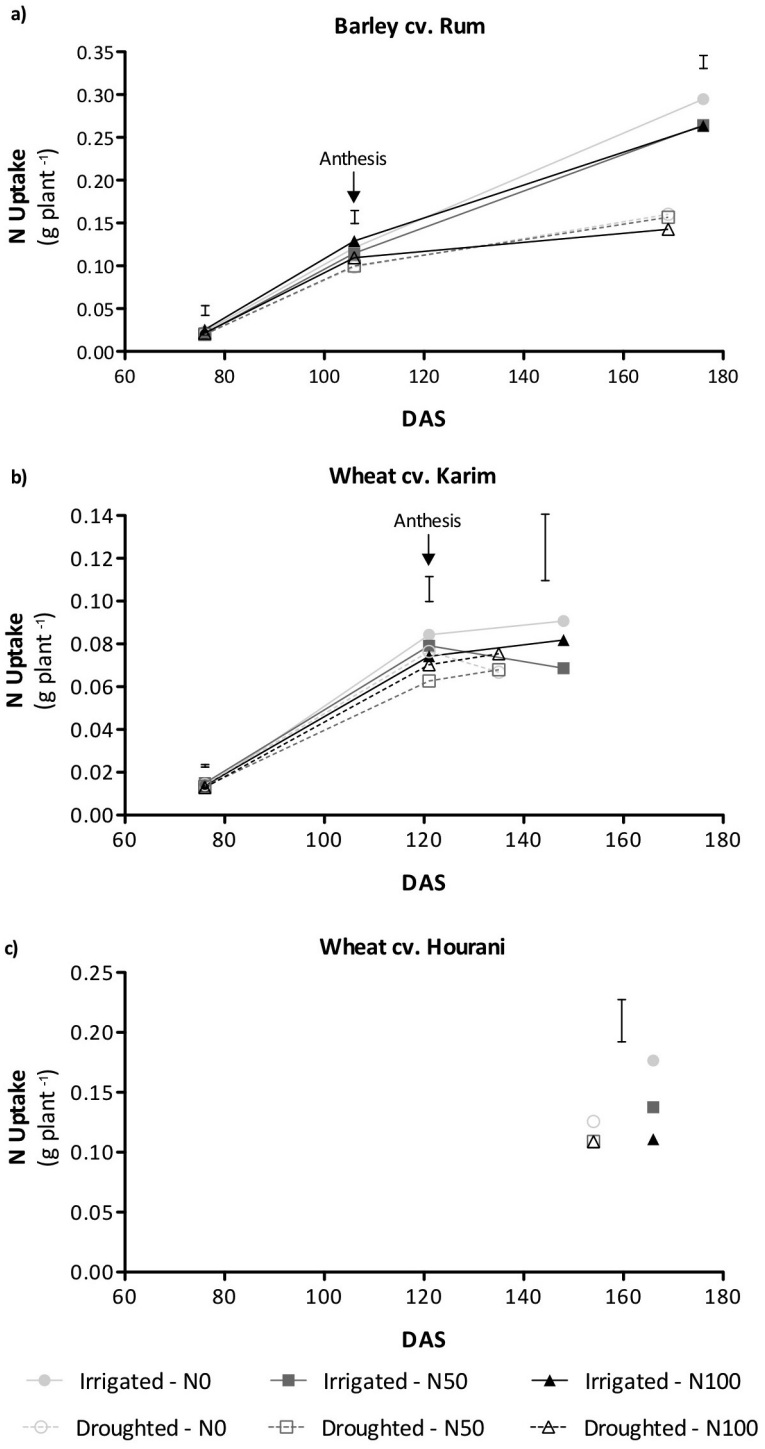

Figure 6.17 Total N uptake per plant from 57 DAS in the 2007 experiment for **a**) barley cv. Rum, **b**) durum wheat cv. Karim and **c**) durum wheat cv. Hourani, in 2007, subjected to fully irrigated (closed symbols and full lines) and droughted (open symbol and broken lines) treatments and three levels of N fertilizer: 0 kg N ha^{-1} (N0), 50 kg N ha^{-1} (N50), and 100 kg N ha^{-1} (N100), equivalents. Error bars represent SED for irrigation x nitrogen (df = 20).

6.2.4.3 2008

In 2008 for barley cv. Rum drought had no significant effect on Nup at anthesis but at harvest drought decreased ($p \leq 0.01$) uptake by 230 mg plant^{-1}.

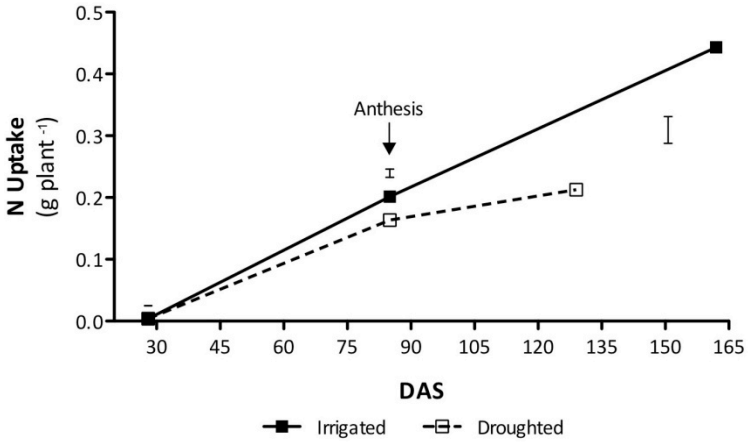

Figure 6.18 Total N uptake per plant in the 2008 experiment, for barley cv. Rum subjected to fully irrigated (closed symbols and full line) and drought (open symbols and broken line) treatments. Errors bars represent SED for irrigation (df = 6).

6.2.5 Soil nitrogen content at harvest

6.2.5.1 2007

At harvest under drought the N remaining in the top 20 cm of the soil profile, though a relatively high amount of roots are present in that layer, is relatively high due to lack of water and less contact of root with the soil. Whereas under irrigation, data shows evidence for leaching, so that N was moved to deeper-layers in the soil profile, probably earlier in the season, so when the aboveground crop demanded more N uptake, the RLD/ RVD deeper in soil-depths was still too low for an effective uptake.

In 2007 the residual soil N at harvest was measured in samples bulked across 5 replicates of each treatment, for the 0 – 20, 60 – 80 and > 125 cm soil-depths, for barley

cv. Rum and wheat cv. Karim. Due to this fact statistical analyses were not possible and only trends can be identified (Figure 6.19 and Figure 6.20).

For both barley cv. Rum and wheat cv. Karim under drought conditions, relatively more of the residual soil N was located in the upper 20 cm of the soil profile (Figure 6.19 c, d), whereas under well watered conditions most of the residual N was distributed deeper in the soil profile (Figure 6.19 a, b).

Under drought for barley cv. Rum and wheat cv. Karim, N applied tended to increase the total residual N at harvest, but under irrigation this was not observed (Figure 6.20). For the N0 treatment, irrigation tended to increase the residual N for both genotypes, but the reverse was observed under N50 and N100 for wheat cv. Karim or else no effect for barley cv. Rum (Figure 6.20).

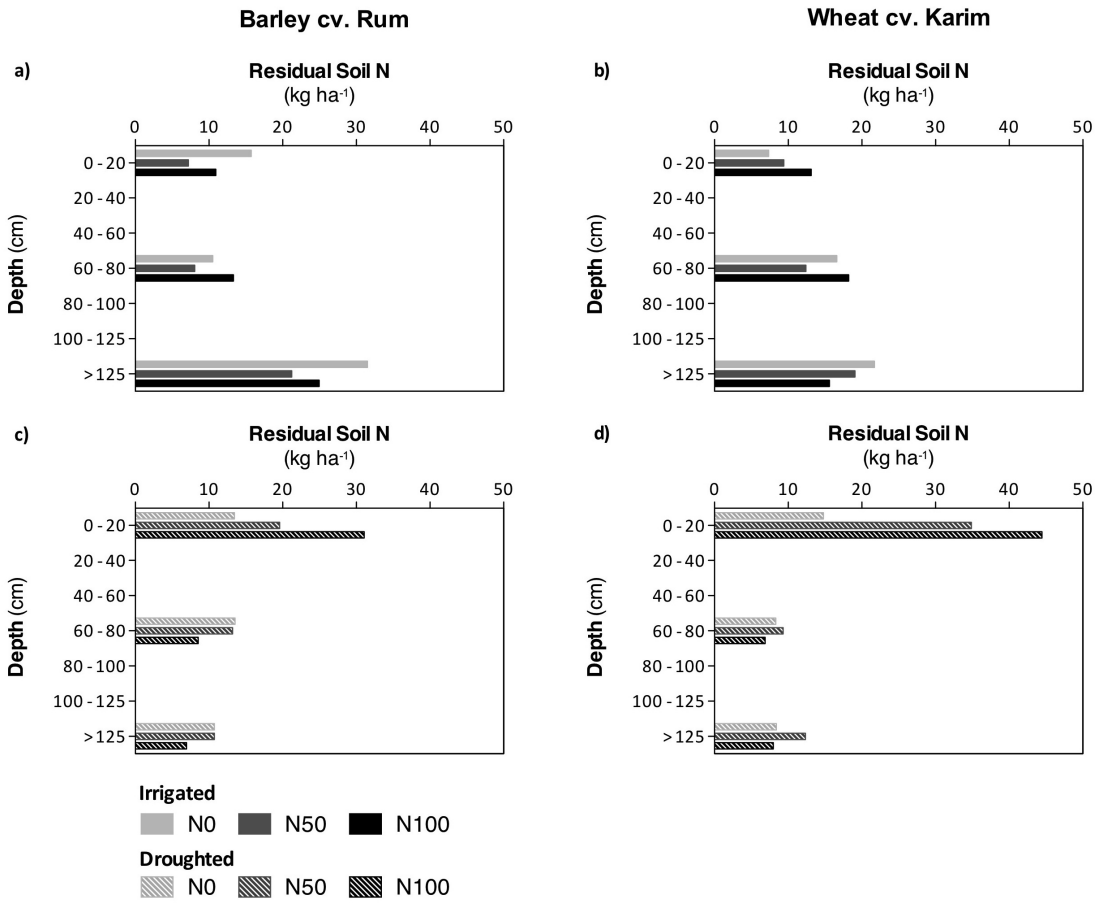

Figure 6.19 Residual mineral soil N at harvest in 2007for different soil-depth layers for barley cv. Rum (**a** and **c**) and wheat cv. Karim (**b** and **d**) subjected to fully irrigated (solid bars) and droughted (striated bars) treatments, at three levels of N fertilizer: 0 kg N ha^{-1} (N0), 50 kg N ha^{-1} (N50), and 100 kg N ha^{-1} (N100), equivalents.

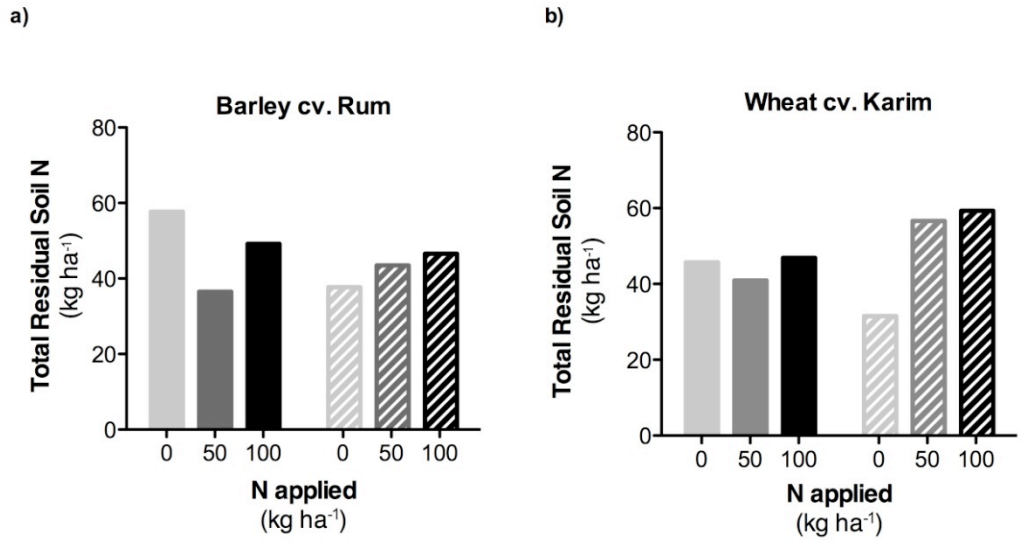

Figure 6.20 Total mineral soil N per column in 2007 at harvest (as sum of the residual N at 0 – 20, 60 – 80 and > 125 cm soil-depths) for **a**) barley cv. Rum **b**) and wheat cv. Karim subjected to fully irrigated (solid bars) and droughted (striated bars) treatments, at three levels of N fertilizer: 0 kg N ha^{-1}, 50 kg N ha^{-1}, and 100 kg N ha^{-1}, equivalents.

6.2.5.2 2008

For barley cv. Rum in 2008 drought increased ($p \leq 0.01$) the residual N at harvest for the 0 – 20 and 60 – 80 cm soil-depth layers (Figure 6.21), increasing the total residual N remaining in the soil (Figure 6.22).

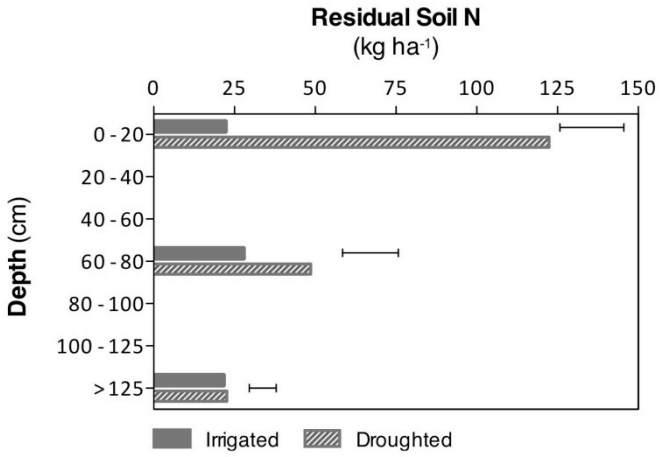

Figure 6.21 Residual mineral soil N at harvest for different soil-depth layers for barley cv. Rum subjected to fully irrigated (solid bars) and droughted (striated bars) treatments in 2008. Error bars represent SED for irrigation (df = 6).

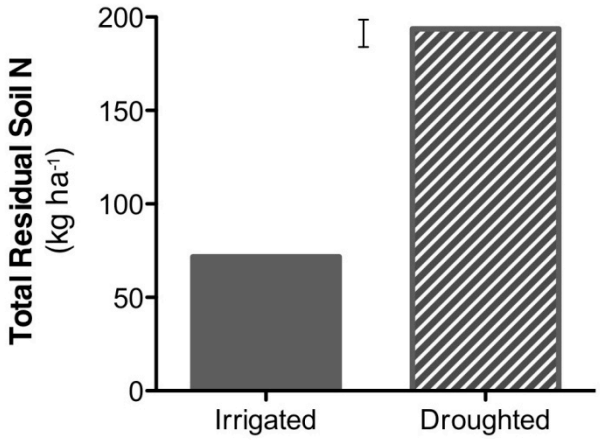

Figure 6.22 Total mineral soil N per column at harvest (as sum of the residual N at 0 – 20, 60 – 80 and > 125 cm soil-depths) at harvest for barley cv. Rum subjected to irrigated (solid bars) and droughted (striated bars) treatments in 2008. Error bars represent SED for irrigation (df = 6).

6.3 DISCUSSION

This discussion aims to examine the physiological basis of the differences in below-ground resource capture observed in the different irrigation treatments and/ or N applications in spring barley and durum wheat in the present study. Effects of experimental treatments on water and N capture will be discussed and when possible qualitatively related to the distributions of length and volume with depth and to the results of previous investigations. The implications of the findings for modelling studies will also be discussed.

6.3.1 Water and N uptake

This investigation consisted of three experiments in different years using very different soil media (*vide* 3.2). In 2006 a sandy loam soil from the field was used (FC = 0.38 m^3 m^{-3}), in 2007 a mixture of 20% sandy loam soil and 80% of commercial washed sand (FC = 0.15 m^3 m^{-3}), and in 2008 a similar mixture as in 2007 was used, though the ratios were 40% cf. and 60% respectively (FC = 0.25 m^3 m^{-3}). The use of soils with different FC and bulk density values (1.63 g cm^{-3} in 2006, 1.85 g cm^{-3} in 2007 and 1.73 g cm^{-3} in 2008) potentially affected root growth and the water and N distribution in the soil. The WU for both barley and durum wheat varieties was higher in 2006 than 2007

or 2008 (for barley cv. Rum), associated with higher water storage capacity of the soil used in 2006.

Barley had a higher water uptake across years and treatments than the durum wheat varieties in the study, though more significantly so under irrigation, probably in part due to its more extensive root system. According to field experiments in Jordan reported by Ebrahim (2008), with similar treatments to those presented in this work, the overall AGDW at harvest did not differ much between barley cv. Rum and wheat cv. Hourani. However in the present experiments the AGDW (*vide* section 4.2.5) for barley was 230% (2006) or 130% (2007) of that found for durum wheat cv. Hourani and 202% for cv. Karim (2007). The smaller growth and smaller size of the root system of durum wheat may be related to restricted tillering due to the sensitivity of the Jordanian durum wheat cultivars to the growing conditions in the UK glasshouses. Higher sensitivity to long days (Peltonen-Sainio *et al.*, 2009) or less capacity to penetrate soil in the high soil bulk density in the columns (Atwell, 1993) may have contributed to these effects. Nevertheless, the relationship between RLD or RVD and water capture as well as other aspects of root function may still be analysed, and compared between barley and durum wheat in the present study. Barley cv. Rum was also more responsive to irrigation than durum wheat, increasing water uptake with irrigation by 417 and 188% in 2006 and 2007, respectively, cf. 287 and 172%, respectively, for wheat cv. Hourani. The application of 50 kg N ha^{-1} (equivalent) increased total water use in 2006 for both barley cv. Rum and wheat cv. Hourani. However, N effects were not consistent across years. Thus, no effect of applied N on water use was observed for either barley or durum wheat genotypes in 2007.

Barley reached anthesis consistently earlier than both durum wheat varieties used in this study. For wheat cv. Hourani and wheat cv. Karim plant growth seems to reach a plateau shortly after anthesis for both irrigated and drought treatments, while for barley it continues to grow well beyond that point provided water is available (*vide* section 4.2.5). Therefore, while WU and especially Nup seem to cease shortly after anthesis for durum wheat, for barley particularly when irrigated, they continued to increase till harvest. This was associated with the observation that irrigated barley cv. Rum showed an increase in the number of tillers after anthesis.

Most of the water uptake occurred from the upper 20 cm of the soil profile, which contributed, under irrigation, with 39% of the total water uptake for barley cv. Rum, and 35-36% for wheat cvs. Karim and Hourani. At the soil-depth > 125 cm, the amount of roots was relatively low, but they contributed significantly with around 8 to 10% of the total water uptake under irrigation, and 15 to 17% under drought (2007).

N application increased WU in the top layer of the soil profile from 3.1 l with N0, to 3.6 l with N50 and 4.4 l with N100; however RLD or RVD in that layer did not differ amongst N treatments (*vide* sections 5.2.10.2 and 5.2.14.2). There was a consistent increase in the proportion of water uptake deeper in the soil profile with drought for all genotypes, with the soil below 80 cm accounting for 39 – 40% of uptake under drought compared to 24 – 25% under well water conditions. This was associated with an increase in the proportion of roots deeper in the soil profile (higher β_L and β_V *vide* 5.2.11 and 5.2.15, respectively) under drought. Compensatory RLD growth deeper in the profile in order to acquire water was previously described for winter wheat by Barraclough *et al.* (1989).

N application had no effect on the proportional water uptake between 0 – 80 and > 80 cm soil depth for barley cv. Rum, though it increased water captured deeper in the profile with N50 for wheat cv. Hourani compared to N0; for wheat cv. Karim N application increased water uptake deeper in the profile under irrigation but decreased it under drought.

N uptake and water availability are closely related. Water shortage can decrease N uptake by limiting the crop growth and therefore crop N demand, or by diminishing the N available due to soil water deficits (Hoad *et al.*, 2001; Lemaire & Gastal, 2009). Most N (nitrate) uptake occurs by mass flow in the transpiration stream, and N is a mobile element (Tinker & Nye, 2000), so it was expected that effects of roots on water uptake would translate into N uptake (King *et al.*, 2003). If water is in excess, due to intense rainfall or excess irrigation, leaching (Mengel & Kirkby, 2001; Dunbabin *et al.*, 2003) might occur (particularly in well drained sandy soils) decreasing the N available and therefore decreasing Nup.

Barley cv. Rum had higher Nup than durum wheat associated with its higher growth and more extensive root system. In 2006 for both barley cv. Rum and wheat cv. Hourani total Nup at harvest increased with irrigation, though to a larger extent for barley. N50

application tended to increase Nup for wheat cv. Hourani and barley cv. Rum compared to N0 but only under irrigation. A similar water availability x N interaction has been observed previously for winter wheat experiments in glasshouse conditions (Karrou & Maranville, 1994a).

In 2007 N applied had no effect on barley cv. Rum and had a negative effect on wheat cv. Hourani and for wheat cv. Karim; none of the treatments had a significant effect on Nup. This lack of effect might be related to two factors: N leaching and/or high residual N availability in the soil medium. The high temperatures incurred in the glasshouse combined with high soil moisture content will have favoured high soil N mineralization. In 2007/08, the soil used had a very high percentage of sand so was very susceptible to leaching, demonstrated by the residual soil N remaining deeper in the soil profile under irrigation, where the roots were too few to achieve effective resource uptake. Under drought, the opposite occurred, with the majority of the residual N distributed in the upper 20 cm of the soil profile; this was not available to the plants due to the very high water deficit imposed in this layer.

6.3.2 Proportional resource capture (water) and rooting traits (RLD *vs* RVD)

According to the theoretical model developed by van Noordwijk (1983), the most appropriate rooting trait to predict resource uptake depends on the rate-limiting factor for the transport of the soil resource to the plant. If the limiting factor is the movement in soil towards the root – root length should be considered; if it is the soil-root interface (transport from rhizosphere to root apoplast) – root surface area will be more appropriate; and finally, if it is the internal transport (root apoplast to root symplast) – root volume should be used. Furthermore, that author concluded that RLD should be used when estimating proportional resource uptake. From this model, a RLD value of 1 – 5 cm cm^{-3} would be required to capture the potentially available water. This predicted critical range for RLD was then supported by field data sets of barley grown on stored water in Syria indicating a RLD value of 1 cm cm^{-3} for 90% of extraction of available water and ≈ 2 cm cm^{-3} for complete extraction (Gregory & Brown, 1989). Barraclough

et al. (1989) concluded in field experiments with winter wheat growing under field conditions in the UK that a RLD of 1cm cm^{-3} would be necessary to extract all the water available in the soil; and more recently Zhang *et al.* (2004) found that for RLD values below 0.8 cm cm^{-3} water uptake would be considerably limited. In addition, Brown *et al.* (1987a) found that above a RLD of 1 cm cm^{-3} for barley the rate of water extraction (mm day^{-1}) would not increase. King *et al.* (2003) summarized these concepts in a simple root system model relating RLD and proportional water and nitrogen capture during grain filling (Equation 5.1). The King *et al.* (2003) model (and the modification to RVD – Equation 5.2) was presently used to calculate the k_{RLD} and k_{RVD} and estimate the C_{RLD} and C_{RVD}.

When applying Equation 5.1 to relate ϕ to RLD statistically significant regressions were only fitted in 2007 for wheat cv. Karim and barley cv. Rum (droughted – N50). Since there were no differences amongst N treatments, one curve was fitted to the pooled data across N treatments for each of the irrigated and droughted treatments of wheat cv. Karim, resulting in a k_{RLD} of 5.6 cm^2 under irrigation and 3.6 cm^2 under drought. This means that under drought a higher RLD is needed to acquire the same proportion of available water as in well-watered conditions, with a C_{RLD} of 0.64 and 0.41 cm cm^{-3}, respectively. However, these results should be used with caution, since the RLD and ϕ values were low and calculations of critical values were interpolated far beyond the values measured. However, combining the 2007 and 2008 datasets for barley cv. Rum under drought at N50 a single curve fitted all the data ($R^2 = 0.91$) with a k_{RLD} of 2.4 cm^2 and a C_{RLD} of 0.96 cm cm^{-3} comparable to the value of 1 cm cm^{-3} described in the literature. However, no statistically significant regression was found for the barley cv. Rum N50 treatment under irrigation, and so it is not possible to confirm for barley the observed lower C_{RLD} value under well watered than under drought conditions observed for wheat cv. Karim. This lack of fit between the ϕ and RLD under irrigation was associated with high values for RLD deeper in the profile and irrigation continuing almost to harvest which did not therefore allow sufficient time for the soil water to be depleted significantly below FC.

Though the model described above is relatively simple, defining the exact time period over which the proportional resource capture should be calculated can be complicated. In the literature, net DM root growth is usually considered to cease at anthesis (Gregory

et al., 1978b; Barraclough & Leigh, 1984; Gregory *et al.*, 1992), so one could consider that measuring the proportional water captured from anthesis to harvest would be most appropriate, though in our experiments RLD and RVD significantly changed from anthesis to harvest. The lack of fit between proportional water captured and RLD for wheat cv. Hourani and barley cv. Rum under irrigation might be associated with the few points across a very small range of low ϕ, due to only 3 layers of the soil profile having been analysed.

Regarding the relationship between rooting traits and ϕ, present data suggest that RVD is a slightly better descriptor of the potential water captured. The C_{RVD} was also calculated for the pooled 2007 and 2008 data for barley cv. Rum under drought with N50; the K_{RVD} was 5.21 representing a C_{RVD} of 0.44 cm^3 cm^{-3}. Furthermore, critical values of RVD were higher under drought suggesting than when breeding for RLD and RVD one must take into account the effect of environment on RLD [e.g. exact region and agricultural system (rainfed or irrigated)], since selection cannot be done having in mind a single value of C_{RVD} or C_{RVD}.

RVD was slightly better related to proportional water captured than RLD. Therefore this suggests that this trait could be a better predictor of potential soil resource uptake for use in modelling resource acquisition and/or ideotype analysis for breeding purposes. Although, it is concluded that the functional aspects of RLD and RVD in this experiment were representative of those in field conditions, extrapolation of these findings to the field crop level should be done with caution. Quite similar values of C_{RVD} for barley cv. Rum and wheat cv. Hourani around ≈ 0.45 cm^3 cm^{-3} under irrigation and 0.52 and 0.58 cm^3 cm^{-3}, respectively, under drought were observed. Both RLD and RVD data suggests that higher critical values (C_{RLD} and $C_{RVD)}$ were found under drought.

6.3.3 Contributions to crop models and breeding strategies

The use of crop models is an undoubtedly important tool to analyze the performance of cropping systems under variable climate (Wang & Smith, 2004). They can be used to predict yields in stress environments, or as decision tools to prioritise traits in crop

ideotypes for breeding (Baburai Nagesh, 2006), or to develop management strategies to cope with stress environments. The most used models for calculating N demand and distribution in wheat are, according to Foulkes *et al.* (2009): SIRIUS, CERES, APSIM; however, they are not currently genotype specific for rooting parameters or N allocation parameters. A promising new model regarding water uptake is the new AQUACROP model from FAO (Steduto *et al.*, 2009). However, it is based on simplicity and estimations of genotype x environment interactions (G x E) might fail due to oversimplification. A more physiological crop model that attempts specifically to address G x E interactions (G x E) is the University of Wageningen GECROS model (Xinyou & Laar, 2005). Usually models tend to over simplify the root sub-routine, assuming plants are uniformly distributed in homogenous soil layers, or that all roots have the same uptake ability, or that plant root length is always sufficient for resource uptake in rooted layers (Wang & Smith, 2004). However, it is well known that the interactions between roots, nutrients, water and soil are large, and simplification is therefore needed. Nevertheless, some parameters seem essential to be included. The King *et al.* (2003) approach its elegant and simple, and can be easily implemented in a running model, as it was recently done in GECROS assisted by the input of the current work within the EU Framework 6 WattNitMed project (INCO-CT-2004-509107).

However the findings of this work demand a more robust approach, especially regarding G x E. They raise the following specific points:

(i) RVD could possibly be used as a better predictor of potential resource uptake than RLD (although the improvement was only slight according to present results);

(ii) The β should be properly defined as a variable in models, since it is found generally to increase with drought and decrease with mechanical impedance;

(iii) k should be genotype specific, but not constant, as it might change with drought (and possibly with N availability and other environmental factors);

(iv) k for phosphorous (P) should be higher than for N or water, hence the C_{RLD} and C_{RVD}, will depend on the limiting nutrient to be considered in a specific environment. In the particular case of the South Mediterranean, a k for N and water would probably be the most useful;

(v) Other aspects should also be considered; the approach of most models is to define the root weight as function of aboveground weight, defining a R:S coefficient that

will decrease with time, and in the specific case of AQUACROP, increase with water stress. Although the results of the present work showed a good correlation between TRL and R:S for all species, depending on the genotype considering SRL or rV:rW, might be relevantly important. The present work gives some clues on values of β's; k's and C_{RXD}'s to be considered for spring barley and durum wheat. It also describes the relationship between TRL and TRV and the specific sub-traits thought to be considered in a simple root model (Figure 6.23). However, further field and CE work has to be done to support the present findings.

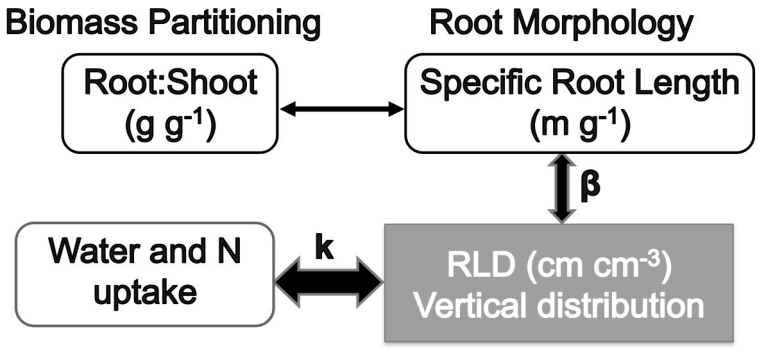

Figure 6.23 Relationship between RLD and root traits suggested being included in a simple root model.

In this work the C_{RLD} was determined to be close to 1 cm cm^{-3}. Furthermore various works showed that for wheat and barley grown in field conditions generally at anthesis RLD in the top 20 cm of the soil profile exceeds the 1 cm cm^{-3}, while deeper in the soil profile its bellow that value (Barraclough *et al.*, 1989; Gregory & Brown, 1989; Siddique *et al.*, 1990; Miralles *et al.*, 1997), and so the water and N in those layers will not be 'totally' available to the plant. For example, for barley growing under non-limiting conditions in the Mediterranean, RLD during grain filling in the top 15 cm of soil-depth was near 3 cm cm^{-3}, while at a depth of 45 cm was near 0.9 cm cm^{-3} and at 75 cm was only ca. 0.5 cm cm^{-3} (Gregory & Brown, 1989). Considering that wheat and barley root systems can extend to 2 m depth, it is therefore apparent that the amount of resources, especially water in dry environments, that might be lost due to an inefficient RLD distribution with depth may be relatively large. It is possible that a larger investment in roots at depth in the soil and less proliferation of roots in surface layers, larger β, would improve water and N uptake and hence yields in rain-fed environments, including those Mediterranean environments with moderate to high winter rainfall, by accessing extra resources. Selecting for higher β seems therefore a beneficial strategy

for Mediterranean rain-fed soils. A recent field investigation from the International Maize and Wheat Improvement Centre (CIMMYT, Mexico) with synthetic-derived wheat (SYN-DER) showed that SYN-DER lines have a relatively deeper distribution of roots when compared to the parental lines (Reynolds *et al*., 2007). The increase in roots observed deeper in the profile was not connected to a higher investment in root weight, but was associated with an increased partitioning of root mass to deeper soil layers potentially increasing the depth at which the C_{RLD} for water and N capture occurred. These SYN-DER lines seem, therefore, promising genetic resources for breeders, since they possibly may maximize the below-ground resource uptake without sacrificing the partitioning of assimilate to the aboveground yield-forming plant components in the pre-anthesis phase.

6.4 CONCLUSIONS

Referring in turn to the hypotheses stated in the beginning of the chapter:

1. The percentage of cumulative WU deeper in the profile increased with drought, which was related with a higher proportion of roots distributed deeper (> 125 cm) in the soil profile (higher β_W, β_L and β_V).

2. Increasing water availability increased water seasonal uptake (WU) and nitrogen uptake (Nup), but for a higher proportion for barley when compared to durum wheat.

3. N50 application increased seasonal water use in 2006, and in a higher proportion for barley (42%) when compared to durum wheat (16%).

4. A resource capture coefficient (k_{RLD}) of 2.4 cm^{-2} was defined for barley cv. Rum under drought (2007-08) resulting in a C_{RLD} of 0.97 cm cm^{-3}. For durum wheat cv. Karim a K_{RLD} of 0.59 cm^{-2}, was found under irrigation and 0.40 cm^{-2} under drought (2007); corresponding to C_{RLD} values of 0.41 and 0.64 cm cm^{-3}.

7 GENERAL DISCUSSION

7.1 INTRODUCTION

The present work aimed to quantify responses of spring barley and durum wheat roots, water and N capture to water and/or N stresses, in order to identify rooting traits or combination of traits determining resource capture. Detailed analysis on the aboveground growth, partitioning, yield, root growth and morphology, water and nitrogen uptake and use efficiency were performed as previously described. This chapter aims to integrate the main findings of the present study, regarding the initial hypotheses and relevant findings previously reported in the literature. Rooting results were summarized with the framework described by King *et al*. (2003); defining: β - that describes the root distribution (weight, length or volume) with depth and k - the resource capture coefficient, that determines the amount of roots (length or volume) necessary to effectively deplete the available water and nitrogen on a given soil volume [critical root length (C_{RLD}) and volume (C_{RVD}) densities].

The relationship of sub-traits defining root length density was analysed according to:

RLD_x = AGDW x R:S x SRL x β_L

and a similar approach was taken to root volume density (RVD).

Differences between spring barley and durum wheat regarding C_{RLD} and C_{RVD} and the sub-traits defining RLD and RVD are discussed. Implications of these findings to root models and application in breeding and agronomic management strategies in Mediterranean rain-fed systems are then considered.

Across experiments effects of N fertilizer applications on the aboveground and root variables considered were not consistent, and they were sometimes contradictory to previous reports in the literature. The generally inconsistent responses to the N fertilizer treatment might be related to two factors: high residual N availability in the soil medium (at the start of the experiment + mineralization through the season) and/or N leaching. High temperatures incurred in the glasshouse, combined with high soil moisture content initially in the season, will have favoured high soil N mineralization, therefore N available might have been relatively more than the initial amount measured. Also in

2007 the soil used had a very high percentage of sand, hence susceptible to leaching. So the N treatment effects were inconsistent most likely due to a high N available in 2006 and high leaching in the fully irrigated treatments in 2007. Therefore significant N treatment effects were interpreted with caution and only considered when highly significant and consistent.

The temperatures in the glasshouse were excessive at times, particularly in 2006 and 2007, with peaks exceeding 50 ºC. This is recognised as being inhibitory to plant growth and development. Wheat and barley roots, in the field, usually experience much lower temperatures below ground. However in these experiments roots were subjected the same high temperatures as shoots, this would have had a major impact on the observed root distributions. Furthermore soil columns in this work presented very high bulk densities, with average values as high as 1.85 g cm^{-3}, these are known to be limiting to root and shoot growth (Bowen, 1981). Durum wheat seemed to be more susceptible to these limiting factors than barley.

In field cropping inter-competition caused by plant density is known to influence the development of plant organs and grain yield (Satorre, 1999; Turner, 2004). In Mediterranean type environments, high plant densities were found to promote phenological development in barley (Fukai *et al.*, 1990); and low plant densities were found to decrease plant yield in wheat when water deficits occur (Turner *et al.*, 1994). However that does not happen when water is available, due to the higher tiller production by low plant populations (Turner *et al.*, 1994; Satorre, 1999; Turner, 2004). Total root dry mass of barley plants tend to increase in response to plant density (Kirby & Rackham, 1971), due to the increase competition for soil resources (Hoad *et al.*, 2001). However the diameter and strength of secondary roots, which are important determinants of lodging susceptibility, tends to decrease (Easson *et al.*, 1995; Hoad *et al.*, 2001). In the Mediterranean type ecosystems plant densities for durum wheat and barley are usually between 100 to 300 plants m^{-2} (Hafid *et al.*, 1998; Albrizio & Steduto, 2005; Moragues *et al.*, 2006; Ebrahim, 2008; Milroy *et al.*, 2008). Though, in the present work, to avoid root growth in the edges of the soil column, only one plant was sown per column, representing a plant density of about 57 plants m^{-2}. Therefore root densities might not be representative of those found in the field grown crops, and hence the results presented here have to be taken cautiously.

7.2 YIELD UNDER WATER AND/ OR NITROGEN DEFICITS

Yield limitations due to water scarcity in the rainfed farming system of the Mediterranean are well known, and are expected to increase due to the difficulty of ensuring supplies of fresh water (Araus *et al.*, 2003a). Furthermore, some climate change scenarios even predict scarcer and more erratic precipitations. Yields in dry areas are quite well correlated with the Passioura (1977) equation: Y = WU x WUE x HI.

Across years barley cv. Rum showed the higher yields of the three genotypes, but that difference was higher under irrigation. Agreeing with field experiments in Spain that showed, against common sense, that barley had in fact no advantage in relation to wheat when grown under drought conditions (Cossani *et al.*, 2009). Furthermore Y across genotypes, years, N and irrigation treatments, was highly correlated with grain (R^2 = 0.97) and fertile shoot number (R^2 = 0.76), due to a high post-anthesis growth for barley as was seen by Cossani *et al*. (2009). Consequently to secure yields in barley an adequate irrigation post-anthesis is required. N50 application in 2006 showed a consistent increase in Y for barley and durum wheat, but only when irrigated.

7.3 ROOT GROWTH AND MORPHOLOGY

Maximum rooting depth significantly varies between genotypes. Data reviewed by Hoad *et al.* (2001) showed values of maximum root depth for spring barley of about 1.3 and 1.6 m for spring wheat, when growing in the field in loam soil texture. Although root depth seems to differ between species, in the field it is largely dependent on the soil conditions (Gregory, 1994b). In the present experiment both species had a similar rooting depth pattern. Periodic analyses in 2006 revealed that both barley and durum wheat reached the 1 m soil-depth at 83 DAS and > 1.25 m at 102 DAS.

In the present work values of root weight density (RWD) and root length density (RLD) found in 2006 at anthesis for barley cv. Rum were comparable to those found under Mediterranean field conditions (Ebrahim, 2008). In contrast, durum wheat cvs Hourani and Karim had a relatively poor root growth. The difference in root growth was associated with a general plant growth restriction in the CE in the UK exacerbated, in particular for wheat cv. Karim, by a high soil bulk density (Young *et al.*, 1997; Price, 2009). Although the plant growth might have been reduced, and not quantitatively representative of field conditions, plant responses to water and N treatments in terms of root function should operate in the same way as in the field. Therefore the comparison of the relationship between root morphology and resource capture in the treatments applied for the different genotypes is still valid.

Root to shoot ratio values found for both durum wheat and barley in the present work were relatively lower than those usually described in the literature (Siddique *et al.*, 1990; Karrou & Maranville, 1994a). This may have been in part due to the high bulk density (BD) and temperatures in the soil. Values of BD in the first 20 cm of the soil profile ranged from 1.61 to 1.85 g cm^{-3}, reaching a maximum of 1.86 to 1.99 g cm^{-3} in the bottom layer of the soil profile. Average values of BD found in this work fit quite well with the critical values of BD described by Bowen (1981) for clay loam and sandy loamy soils, 1.55 and 1.85 g cm^{-3}, respectively.

N application had no effect on R:S of both durum wheat and barley, as was found for the same cultivars by Ebrahim (2008). The well described increase in R:S with water deficits (Tinker & Nye, 2000; Hoad *et al.*, 2001) was observed for all genotypes; however, to a higher extent for durum wheat. So that under irrigation R:S was broadly similar between species, but under drought was relatively higher for durum wheat. Overall the total root weight (TRW) decreased with drought for barley, but for durum wheat it increased under water limitations.

The TRW for durum wheat increase resulted in a higher total root length (TRL) and volume (TRV) under drought, when compared to the full irrigation treatment, while for barley there was a decrease for the same variables. This was probably related to differences in plant development. Barley cv. Rum has a shorter cycle to anthesis than durum wheat, therefore in Mediterranean conditions the late-season drought usually

occurs after anthesis (Ebrahim, 2008). This is what we tried to simulate in the present work. So the most severe level of water restriction (25% AW_{FC}) was imposed at GS61 for barley, when the root growth is generally determined, while for durum wheat it corresponds to ca. GS53. Hence droughted wheat plants were able to better adapt their roots to water deficits when compared to barley. This root adaptation in wheat seemed to be beneficial, since the differences in water and N uptake (WU, Nup), aboveground dry weight (AGDW) and yields (Y) between droughted and full irrigated plants of wheat, were less than that for barley. According to Blum *et al.* (1983) this type of root response is common in 'drought adapted' durum wheat cultivars.

Although N application is usually reported to increase TRW in durum wheat and spring barley and consequently TRV and TRL (Brown *et al.*, 1987b; Hamblin *et al.*, 1990; Ebrahim, 2008), the present results did not show this. Recent works by Zhang *et al.* (1999; 2000) and Linkohr *et al.* (2002) with *Arabidopsis* showed that when roots grow in a soil medium with homogeneous high concentration of nitrate, lateral root (LR) elongation is inhibited and lateral roots with abnormal morphology are induced. Since the soil in the column is relatively homogeneous and, as mentioned previously, highly susceptible to mineralization, this system might mimic the observations mentioned above but on a larger scale. If so, experiments in soil columns with the objective of evaluating similar effects in wheat and barley to those described to *Arabidopsis* will be of future interest.

The increase of TRW (higher R:S) with drought was allocated deeper in the soil profile (higher β_W), resulting in a increase in RLD for those layers, in agreement with Barraclough *et al.* (1989). This was observed for all genotypes; however not in the bottom layer of the soil column for wheat cv. Karim, due to its susceptibility to soil mechanical impedance (relatively lower β_W when compared to barley cv. Rum and wheat cv. Hourani). The increase in RLD deeper in the soil profile, from anthesis to harvest, due to the increased intensity of drought stress imposed (25% AW_{FC}) resulted in a more uniform root system distribution with depth (higher β_L) for all genotypes. However, this compensatory growth proved to be higher for wheat cv. Hourani, with almost a complete inversion of the usual exponential decrease of RLD with depth to an increase, as observed for cotton plants by Kramer and Boyer (1995). TRL and TRV are well correlated (vide Appendix I, Aggarwal *et al.*, 2006). Therefore, effects for RVD

and its distribution with depth (β_V), followed similar patterns as the ones described for RLD and β_L.

Roots were only analysed from three depth sections, and not the whole soil column profile. This partial analysis can result in different distributions with depth as expressed in the shape coefficient (β_W, β_L and β_V) compared with a full analysis. Consequently, and though the relative response of root growth to water and N deficits using the β coefficients being valid, the absolute values here presented should be taken cautiously.

If RLD (and possibly RVD) measures the potential resource acquisition (King *et al.*, 2003), the specific root length (SRL) evaluates the: "economical aspects of a root system stating the costs – mass, per potential return – root length" (Ryser, 2006). Specific root length is a complex trait, including the combined information for root diameter (RD) and tissue density. Of all the genotypes wheat cv. Hourani was the one showing highest SRL, probably explaining its compensatory RLD increase under drought conditions, followed by barley cv. Rum and wheat cv. Hourani.

Responses of SRL to drought differed between genotypes. Barley cv. Rum had a more plastic response, decreasing SRL with water deficits at harvest in 2006 and 2008 due to a combination of increasing mean root diameter (RD) and tissue density (low root volume root weigh ratio – rV:rW). However, in 2007 SRL for barley increased due to a steeper decrease in tissue density while still increasing RD. This different response for different years might be associated with the type of soil and respective available water. In 2006 and 2008 the soil was able to store more water (higher FC), so the water stress was imposed more slowly and plants invested in root longevity (higher tissue density) rather than growth. While in 2007 the sandy soil had a very low FC value, so the plants rapidly responded in producing length by decreasing their root tissue density; similarly response was found for wheat cv. Karim (but with no change in RD). Wheat cv. Hourani showed a relatively constant tissue density and the decrease in SRL was mainly caused by an increase in RD. The observed increase in RD for barley cv. Rum and wheat cv. Hourani would probably benefit soil penetration and improve water conductance under dry conditions (Ryser, 1998).

Improving soil resource capture can be achieved by a combination of: increasing TRL and/ or better distribution of RLD with depth, increasing β_L. The analysis of the sub-

traits that can possibly increase TRL, according to: TRL = AGDW x R:S x SRL, revealed differences between genotypes. While increases in TRL for durum wheat were mainly associated with increases in TRW and R:S. For barley changes in SRL explained a high percentage of the variation, showing it as a promising trait for breeding, to increase RLD at depth whilst maintaining AGDW. However similar studies as the present one, covering a wider range of N and water treatments, as well as soil conditions, are necessary for a more detailed analysis of the determinant sub-traits influencing root length and its distribution with depth.

7.4 ROOT FUNCTION AND WATER AND NITROGEN UPTAKE AND USE EFFICIENCY

Root length density has been proved to be quite well correlated with proportional resource capture (van Noordwijk, 1983; King *et al.*, 2003), and that a RLD value of 1 cm cm^{-3}, is necessary for an effective extraction of water and nitrogen in the soil (Barraclough *et al.*, 1989; Gregory & Brown, 1989). Below this value roots are considered insufficient to extract all the water and N in the soil, and above this value there is an excess of roots and intra-competition occurs, therefore this value is often called the critical root length density (C_{RLD}). In field conditions the RLD in the top layers of the soil profile is usually relatively higher than the C_{RLD}. However below ca. 60 cm they are usually lower than 1 cm cm^{-3} (Brown *et al.*, 1987b; Gregory & Brown, 1989; Siddique *et al.*, 1990). Furthermore according to the model developed by King *et al*. (2003) distributing roots relatively deeper in the soil profile and increasing SRL would increase water and N capture, and possibly increase yields under water and N deficits. The concepts in King *et al.* can therefore be summarized by:

RLD_x = AGDW x R:S x SRL x β_L (equation 4.5).

In the present study barley was able to achieve RLD values above C_{RLD} at anthesis, in 2006 and 2008, to a depth of ca. 80 cm, while for durum wheat those values were always below 1 cm cm^{-3}. In 2007 the RLD values were extremely low to all genotypes, therefore relatively lower WU was expected.

Fitting the King *et al.* (2003) equation to the RLD data and ϕ for water, a k_{RLD} of 2.4 cm^{-2} was found for barley cv. Rum under drought (2007-08), resulting in a C_{RLD} of 0.97

cm cm^{-3} in agreement with previous findings (Gregory & Brown, 1989). For durum wheat cv. Karim relatively higher values of k_{RLD}, were found: 5.60 and 3.58 cm^{-2}, respectively under irrigation and drought (2007); corresponding to C_{RLD} values of 0.41 and 0.64 cm cm^{-3}. Overall results indicated that under drought C_{RLD} are higher than under irrigation, and that possibly k_{RLD} and therefore C_{RLD}, might be lower for durum wheat. However, estimations for wheat cv. Karim were done in a very small range of values and therefore, by the nature of the exponential curve, a higher k would be expected (King *et al.*, 2003).

When fitting the adapted King *et al.* (2003) equation to RVD for water uptake, a more consistent relationship was found (than for k_{RLD} *vs* ϕ). Similar values of k_{RVD} were observed for barley cv. Rum and wheat cv. Hourani, averaging 5.1 under irrigation and 4.1 under drought. Although for wheat cv. Karim the values were relatively higher, 10.0 cf. and 5.9 respectively. Therefore, C_{RVD}, for wheat cv. Karim were relatively lower when compared with the other two genotypes. C_{RVD} = 0.23 and 0.39, under irrigation and drought for wheat cv. Karim, compared to 0.46 cf. and 0.55, when averaged for both barley cv. Rum and wheat cv. Hourani. Drought k_{RVD} values were lower than those found for irrigation, meaning higher C_{RVD} under water deficits. Although these values should be interpreted with caution, there is actual evidence for higher k values for wheat cv. Karim. In 2007 wheat cv. Karim besides having a RLD at > 125 cm of only 10%, of that found for wheat cv. Hourani, it was able to extract as much as 70% of the water extracted by the former.

In the present experiments barley cv. Rum had higher water (WU) and N uptake (Nup) than durum wheat, associated with its higher growth and more extensive root system. Drought decreased WU, but differences only began to be remarkably different after anthesis when the drought stress was increased from 50% to 25% AW_{FC}. As expected Nup proved to be well correlated with WU as described in the literature (Tinker & Nye, 2000; Mengel & Kirkby, 2001), therefore this suggests that findings for the relationship between RLD or RVD and proportional water uptake can be extrapolated to N (King *et al.*, 2003).

Differences in WU and Nup between irrigated and droughted treatments were relatively higher for barley cv. Rum than the durum wheat varieties. This is related with the fact

that under drought TRL decreased for barley, while increased for durum wheat. Allocation of roots deeper in the soil (higher β values) proved to be crucial for the droughted plants, where the roots at > 125 cm soil-depth contributed with ca. 16% of the total water uptake across genotypes, contrasting with only 8% for the irrigated plants. Percentage of cumulative WU deeper in the soil profile was remarkably similar between genotypes, with ca. 40% of WU coming from soil-depths > 80 cm for the droughted plants and only ca. 24% for the irrigated plants.

In 2006 N50 application increased total WU for wheat cv. Hourani and barley cv. Rum compared to N0 but only under irrigation. Similar responses have been described for field-grown barley in Syria (Cooper *et al.*, 1987). This increase in WU was not associated with higher a RLD, but instead associated with a more uniform RLD with depth for barley cv. Rum and wheat cv. Hourani (β_L) under irrigation at N50, confirming theoretical predictions that a more uniform RLD would favour WU (King *et al.*, 2003).

Present results therefore suggest that manipulating root systems to distribute root length density more uniformly with depth could lead to improved capture of water and N under dry conditions. This could potentially be achieved through either improved agronomy or through plant breeding. The agronomic options to boost RLD in the sub-soil may include earlier sowing, provided this does not lead to increased frost risk, or the application of plant growth regulators, or optimising the timing of N inputs. Optimising timing of N applications to favour the survival of the earliest tillers may be associated with relatively deeper roots. However, the best long-terms prospects for increasing β_L may be through the application of breeding. Further development of synthetic wheats may be one option here, since synthetic wheat derivatives incorporating genes from the diploid wild species *T. tauschii* (D genome) had similar root dry weight compared to check cultivars in Mexico, but roots were distributed relatively deeper in the soil profile (Reynolds *et al.*, 2007). Also the development of high-throughput screens that are well correlated with field expression of rooting traits will be crucial, and this area is discussed further in section 7.5.

In this work, WUE was measured in four different ways: (i) as the AGDW (g) at harvest divided by the actual water (l) used by the plant from transplantation to harvest; (ii) the slope of the linear regression forced through the origin of the cumulative AGDW and

the cumulative water used with time; (iii) the grain yield (Y, g) at harvest divided by the actual water - WUE_{grain} (l) used by the plant from transplantation to harvest; and (iv) by $\Delta^{13}C$ on grain at harvest. Besides having higher WU, barley cv. Rum proved also to have higher WUE than durum wheat, when measured as (i) or (ii); this is in agreement with previous works and was associated with a higher chlorophyll content for the barley cv. Rum (Araus *et al.*, 2003b). WUE_{grain}, was also higher for barley cv. Rum in 2006 than wheat cv. Hourani, though no differences between genotypes were found in 2007. Using $\Delta^{13}C$ in the grain as a surrogate for WUE, however, failed to detect differences between genotypes. As expected across years and genotypes irrigation reduced WUE, WUE_{grain} (Foulkes *et al.*, 2001) and occasionally increased $\Delta^{13}C$. N application contrary to reports in the literature failed to increase WUE for all genotypes (Cabrera-Bosquet *et al.*, 2007; Ebrahim, 2008; Katerji *et al.*, 2008). WUE was higher for barley than durum wheat, therefore if supplemental irrigation is limited possibly the best option would be to irrigate the former, since the farmer would overall derive the best benefits from such a scarce resource. Nevertheless, in the Mediterranean areas the opposite practice is usually observed (Thabet *et al.*, 2009).

Nitrogen-use efficiency is the grain dry matter yield (Y) per unit of N available (soil + fertilizer) and is divided into two components: (i) N uptake efficiency (crop N uptake / N available; NupE) and (ii) N-utilization efficiency (grain dry matter yield / crop N uptake; NutE) (Moll *et al.*, 1982). Overall barley cv. Rum showed higher values of NUE when compared to both durum wheat varieties in study, and out of the wheat cultivars cv. Karim was the less efficient. For all genotypes irrigation decreased NutE. However NupE increased to a greater extent, and hence NUE was consistently higher under irrigation. Furthermore, of the components that constitute NUE, NupE was the most relevant, explaining 95% of the variation found for NUE, across year, experiments, irrigation and N treatments, consistent with the findings of Muurinen *et al* (2006). Hence our results demonstrate that optimising NupE is where most of the benefits will be obtained, and therefore root optimization to increase N uptake should be considered. The data obtained in this work in the 2006 experiment show that N fertilization will result in the maximum benefit if combined with irrigation. However, irrigation has to be judiciously applied to avoid losses by leaching.

7.5 PHENOTYPING AND DEVELOPMENT OF SCREENS FOR ROOTING TRAITS IN BREEDING FOR WATER AND N UPTAKE

In the present work a C_{RLD} of ca. 1 cm cm^{-3} was found for barley, consistent with the investigation of Gregory & Brown (1989). It was also suggested that RVD is well correlated to ϕ. Consequently more work will be needed to determine if RVD, and k_{RVD} would be better indicators of the potential resource uptake. Furthermore, it could be inferred that species with higher root penetration capability would be advantageous, not only because soil strength increases with the dryness of the profile, but also because plants may require longer main root axes to access water stored deep in the soil profile (Bengough *et al.*, 2006). According to the framework previously described, a high R:S ratio in dry environments will increase the plant scavenging efficiency (Palta & Watt, 2009). Increasing SRL is also beneficial in order to increase length with the same biomass being allocated to roots (King *et al.*, 2003). However, in water deficit conditions increases in SRL should be better gained with a decrease in mean root diameter (RD), instead of decreases in tissue density, since roots with low tissue densities are more prone to root death particularly in dry soils (Fitter, 1987; Fitter, 1996). More uniform RLD densities with depth (higher β) will permit a better acquisition of the resources distributed deeper in the soil profile. However if phosphorous is also limiting, long root hairs as well as a higher distribution deeper in the profile would have to be taken in consideration (Palta & Watt, 2009). The aforementioned rooting traits seem to be the most appropriate to be considered in breeding programs aiming to improve WU and Nup.

The soil column system combined with the ThetaProbe was shown to be a valuable tool to evaluate the periodic water uptake in a simple and quick way. The ThetaProbe calibration via access apertures in the soil column showed a good calibration with the gravimetric measurement, it was a good method to reliably measure evapotranspiration. Furthermore 15 cm diameter by 150 cm depth seemed to be the best size of column system to be used in wheat and barley experiments in CE, since it minimizes as much as possible the root damage. Though having benefits, growing conditions in soil columns are difficult to control, particularly soil bulk density and temperatures. With benefit of

hindsight, soil columns should be filled as soon as possible before starting an experiment and tested for soil bulk density, so, if needed, the soil medium could be change in time. Furthermore to avoid mechanical impedance sand in the soil medium should not exceed 60%. Temperatures in soil columns could be controlled using white soil tubes or kitchen foil. Increasing the number of plants to 4/ 5 per column (226/ 283 plants m^{-2}), would be a better representation of the plant densities found in Mediterranean cropping systems. So if using cautiously soil columns, though not perfect, can be good surrogate of field conditions. However, due to the large amount of soil need to be analysed, soil columns would only be useful to screen parental or specific lines. For larger high-throughput screens other Phenotyping tools would be more applicable. On field-grown crops the soil core method is a valid and widely used phenotyping tool applicable to limited numbers of plots, combined with root image digital analyzer software like: WinRhizo (Regent Instruments Inc., Quebec, Canada) or the Delta-T (Scan Image Analysis System – DTS, Delta T Devices, Cambridge, UK). Other more rapid methods would be measuring the root angle, in seedlings, that was proved to be well related with root distribution with depth or the wax layer method, that can be used to measure the penetrability capacity of a root system (Manske *et al.*, 2001).

7.6 OVERALL CONCLUSIONS

Addressing the specific hypothesis stated in the end of the Chapter 2, one can therefore conclude:

1. Barley had a relatively larger TRL, TRV and TRW than that of durum wheat;

2. Similar distribution of root morphological traits with soil-depth (RWD, RLD, RVD and RD) was found between barley cv. Rum and wheat cv. Hourani, however wheat cv. Karim showed fewer roots deeper in the profile, possibly due to a high susceptibility to mechanical impedance.

3. Contrasting responses of rooting traits to water deficits between barley and durum wheat varieties were observed. TRW decreased for barley cv. Rum with water limitations, whereas it increased for durum wheat. Corresponding effects were found for TRL and TRV. N application generally decreased TRW, TRV and TRL for durum wheat cultivars. While for barley cv. Rum it increased TRW, TRL and TRV, at anthesis.

4. Effects of N on TRW were similar under irrigated and droughted treatments.

5. R:S was found to increase with drought for all genotypes, though more strongly for durum wheat cultivars, whilst N application had no significant effect.

6. RD was broadly similar between genotypes, increasing with water deficits though generally unaffected by N applications.

7. Barley cv. Rum revealed a high plasticity in its response to drought in terms of SRL and rV:rW: decreasing (2006), increasing (2007) or not being affected (2008) by water deficits. While tissue density (here accessed by rV:rW) for wheat cv. Hourani was generally constant and only in one experiment SRL decreased with drought (2006). SRL for wheat cv. Karim tended to increase with drought and N application, due to an decrease in tissue density (higher rV:rW).

8. Proportion of root weight (β_W), length (β_L) and volume (β_W) deeper in the profile consistently increased with drought. N had generally no effect on β values. Similar proportion of roots deeper in the profile for barley cv. Rum (higher β_W) and wheat cv. Hourani. However β_W values for wheat cv. Karim were relatively low demonstrating a lower penetration capability.

9. The percentage of cumulative WU deeper in the soil profile increased with drought, which was related to a higher proportion of roots distributed deeper (> 125 cm) in the profile (higher β_W, β_L and β_V).

10. Increasing water availability increased water seasonal uptake (WU) and nitrogen uptake (Nup), but to a greater extent for barley than durum wheat.

11. N50 application increased seasonal water use in 2006, but in a higher proportion for barley (42%) when compared to durum wheat (16%).

12. A resource capture coefficient (k_{RLD}) of 2.4 cm^{-2} was defined for barley cv. Rum under drought (2007-08) resulting in a C_{RLD} of 0.97 cm cm^{-3}. For durum wheat cv. Karim a k_{RLD} of 5.60 cm^{-2}, was found under irrigation and 3.58 cm^{-2} under drought (2007); corresponding to C_{RLD} values of 0.41 and 0.64 cm cm^{-3}.

13. In contrast to field experiments in Mediterranean conditions the AGDW and yields for barley cv. Rum were higher than for the durum wheat varieties in this study. Y and AGDW decreased with water deficits but to a greater extent for barley. In 2006 the N50 treatment increased fertile shoot number, AGDW and Y for both barley and wheat.

14. WUE and WUE_{grain} values were higher for barley cv. Rum when compared to durum wheat. Drought had a positive impact on both variables for all genotypes.

15. Grain $\Delta^{13}C$ increased with water supply for barley cv. Rum (2006 and 2008), wheat cv. Hourani (2006) and wheat cv. Karim (2007). N application had no significant effect on $\Delta^{13}C$.

16. NUE was higher for barley cv. Rum than the durum wheat varieties. NUE for all genotypes decreased with N application and drought, due to differences in NupE.

Drought consistently increases NutE for barley cv. Rum, had no effect for wheat cv. Karim, and had no effect for wheat cv. Hourani in 2006 but increased in 2007.

The main aim of this work was a glasshouse comparison of the responses of durum wheat and barley roots and shoots, to water and nitrogen deficits under simulated Mediterranean conditions. And, although responses to water deficits were observed, this objective was only partily achieved. Because there were no consistence responses to N application; due to the very high soil N availability at the start of the experiments and/ or mineralization during the plant growing season.

The simulation of Mediterranean environmet was also impossible to achieve, since the available glasshouse had no temperature or vapour pressure control deficit. Consequently, excessive and inhibitory temperatures to plant growth and development were felt, with peaks exceeding 50 ºC. Moreover, due to the nature of the soil column system, those temperatures were also felt by roots, possibly affecting both root growth and distribution in the soil column. These factors were agraveted by an extreamly high mechanical impedance, known to be inhibitory to shoot growth, root elongation and distribution with depth; caused by the elevated bulk density values in the soil columns.

The fact that the plants grown isolated, and therefore without inter-competition, might have contributed for the low RLD and RWD observed in these experiments.

With the benefit of hindsight, it is suggested to use white soil columns, or cover them with kitchen foil to avoid the increase in temperature in the soil. The use of high percentage of sand facilitated, to some extent, the root washing, however it dramatically increased the bulk density, therefore it is suggested not to use more than 60% of sand. The increase of the number of plants to 4 or 5 per column (226/ 283 plants m^{-2}), would be a better representation of the plant densities found in Mediterranean cropping systems, are therefore is suggested.

Root morphology results were measured only partially, in the top, middle and bottom 20 cm of the root system distribution in the soil profile. This incomplete dataset was used to estimate the shape coefficients (β) of the distribution of weight, length and volume, however if all the root system was analysed a different shape could be obtained. Moreover the β_W was used to estimate R:S.

The results obtained in these experiments were acquired under particular environmental and soil conditions. Hence, extrapolation of these datasets to field grown wheat and barley in Mediterranean type environments should be made cautiously.

7.7 FUTURE WORK

The present work was successful in characterizing wheat and barley root systems in terms of growth, morphology and function. Interesting findings were found regarding their strategies to search for water (increase RLD) and the importance of SRL for barley *vs* the high allocation of biomass to roots of wheat. Some of the more interesting findings were the confirmation of the well establish C_{RLD}, and the possibility of using RVD and C_{RVD} to predict the potential water uptake. β was estimated and was successful in summarizing the distribution of weight, length and volume in the soil profile. However β values were calculated using partial root data (only 3 soil depths were analysed), this incomplete analysis can result in different root distributions when compared to a full analysis. Therefore, further experiments to determine β coefficients in response to water deficits and N application in all plant root system are needed. A simple framework summarizing the concepts and traits was found to be relevant in this work and suggested.

The more immediate application of the current work is helping in the development of crop model root sub-routines. Initial findings of this work were already incorporated in the GECROS model (University of Wageningen), as partners in the EUFP6 "Management Improvements of WUE and NUE of Mediterranean Strategic Crops (wheat and barley)" (WatNitMed - no. 509107) consortium; that will be used to construct a set of management strategies to improve capture and/or use efficiency of nitrogen and water in the Mediterranean region. The inclusion of the concepts described by King *et al.* (2003) was already done. Although, further developments have to include traits like SRL, and a non-constant β, since they were found to change with drought and for e.g. mechanical impedance. k is another trait that needs to be addressed in future studies. Is k fixed for one particular nutrient? Does it change with drought? And more

important, is it different between genotypes? Should we use RVD instead of RLD? Those are some of the questions that were raised by this work.

Other short-term implications of the present work would be in the development of agronomic and breeding strategies, optimising roots for water- and N- use and uptake efficiency.

Agronomic strategies, aimed at a more uniform root distribution with depth, would definitely benefit crops growing in rainfed Mediterranean type ecosystems. Sowing the crop earlier in order to have a higher stem elongation phase and hence grow longer roots, in such a way that would be able to uptake stored water later in the season has been suggested. N application should be done not only accordingly to crop growth stage, but also taking account of weather information. Conservation or no tillage farm systems can also be applied to avoid soil compaction. Water harvesting systems like diked furrows can also be utilized. If water is available, deficit irrigation (DI) or partial root dry zone irrigation (PRD) adapted to cereals via trickle irrigation may also improve water savings, and even increase yields. Phenotyping existing variation in existing cultivars or landraces, for high β, in order to be used in breeding programs, can be proposed.

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9 APPENDICES

9.1 APPENDIX I

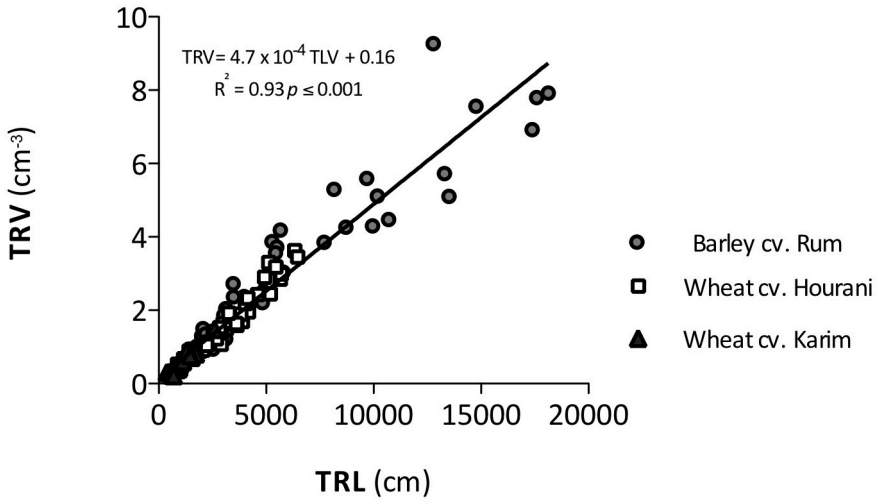

Figure 9.1 Simple linear regression between total root volume (TRV) and total root length (TRL measured) at harvest in 3 soil-depths layers (0-20, 60-80 and > 125 cm), for barley cv. Rum (2006/07/08), wheat cv. Hourani (2006/07) and Karim (2007) plants. Data includes full irrigation and drought treatments, as well as N application treatments (0, 50 and 100 kg N ha^{-1}, equivalents).

9.2 APPENDIX II

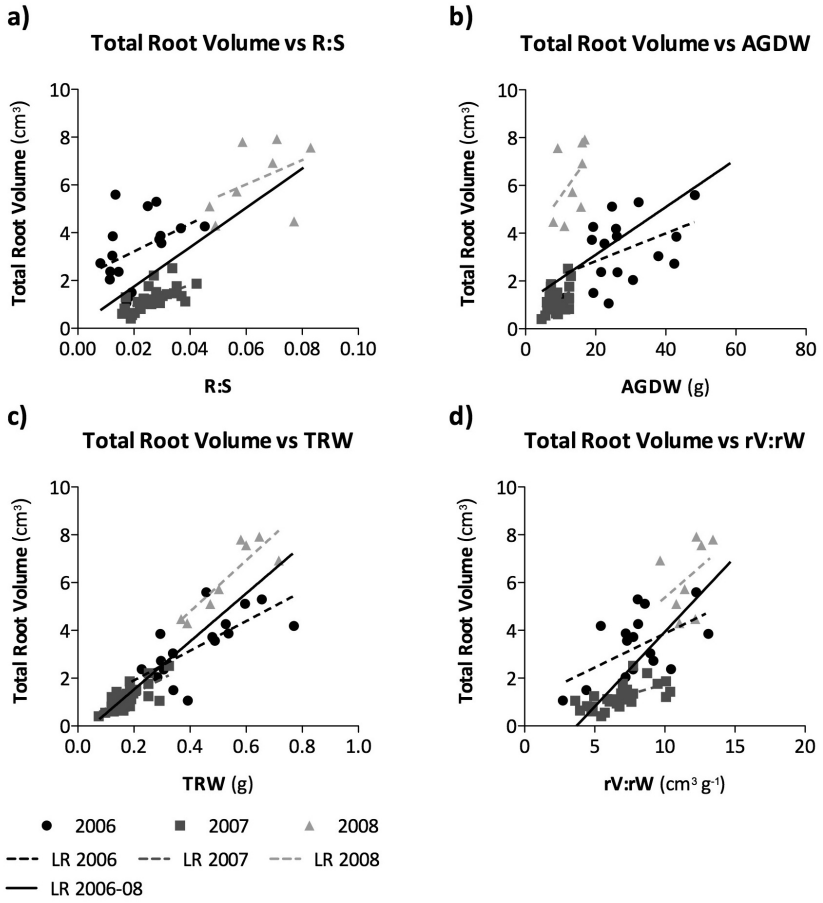

Figure 9.2 Simple linear regression (LR) between total root volume measured in 3 soil-depths layers (0-20, 60-80 and > 125 cm) and: **a**) R:S, **b**) AGDW, **c**) TRW and **d**) SRL at harvest for barley cv. Rum plants analysed in the 2006, 2007 and 2008 experiments. Data includes full irrigation and drought treatments, as well as N application treatments (0, 50 and 100 kg N ha^{-1}, equivalents). Details for the simple linear regression curves is presented in the Table 9.1.

Table 9.1 Simple linear regression between total root volume (TRV) measured in 3 soil-depths layers (0-20, 60-80 and > 125 cm) and: R:S, AGDW, TRW and SRL at harvest for barley cv. Rum plants analysed in the 2006, 2007 and 2008 experiments. Data includes full irrigation and drought treatments, as well as N application treatments (0, 50 and 100 kg N ha^{-1}, equivalents). To fitted regressions see Figure 9.1.

TRV vs	Barley cv. Rum							
	2006 (*df = 16*)		**2007** (*df = 28*)		**2008** *(df = 6)*		**2006-08** (*df = 54*)	
	Equation	**R^2**	**Equation**	**R^2**	**Equation**	**R^2**	**Equation**	**R^2**
R:S	y=58.0x+2.05	0.19^{ns}	y=43.4x+0.08	0.41^{***}	y=50.69x+2.98	0.20^{ns}	y=77.8x+0.37	0.35^{***}
AGDW	y=0.058x+1.67	0.17^{ns}	y=0.082x+0.51	0.16^{*}	y=0.21x+3.48	0.23^{ns}	y=0.100x+1.10	0.29^{***}
TRW	y=6.20x+0.67	0.51^{***}	y=6.16x+0.12	0.51^{***}	y=10.71x+0.50	0.76^{**}	y=10.64x-0.61	0.78^{***}
SRL	y=0.28x+1.02	0.27^{*}	y=0.17x+0.07	0.39^{***}	y=0.51x+0.24	0.16^{ns}	y=0.63x-2.31	0.58^{***}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the simple linear regression.

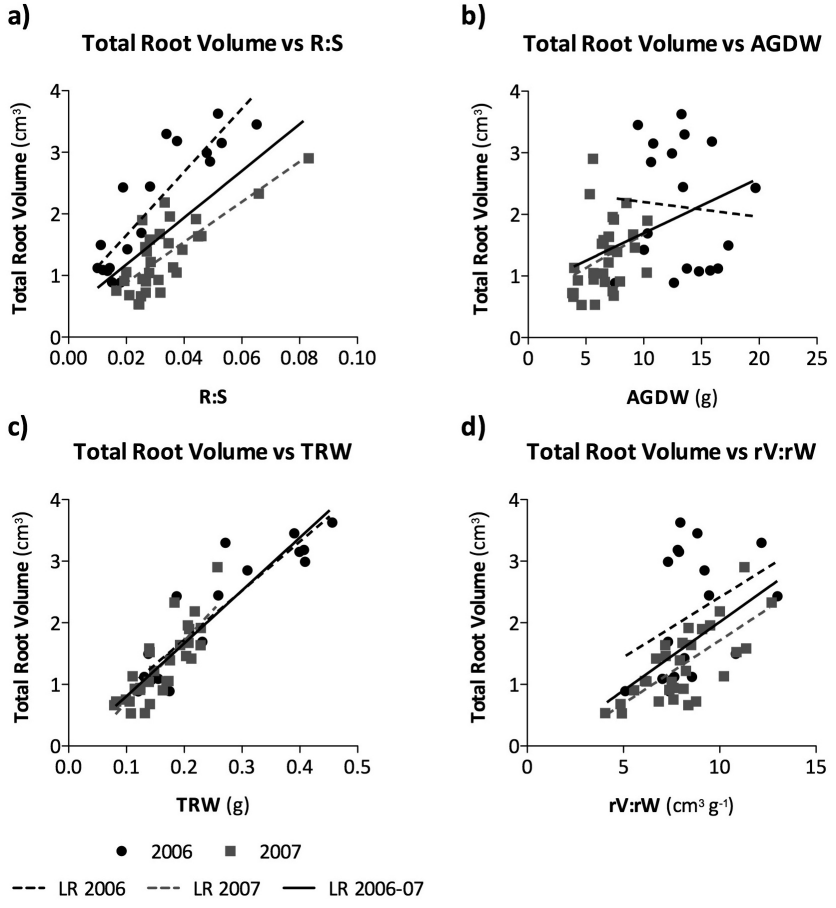

Figure 9.3 Simple linear regression (LR) between total root volume measured in 3 soil-depths layers (0-20, 60-80 and > 125 cm) and: **a**) R:S, **b**) AGDW, **c**) TRW and **d**) SRL at harvest for durum wheat cv. Hourani plants analysed in the 2006 and 2007 experiments. Data includes full irrigation and drought treatments, as well as N application treatments (0, 50 and 100 kg N ha^{-1}, equivalents). Details for the simple linear regression curves is presented in the Table 9.2.

Table 9.2 Simple linear regression between total root volume (TRV) measured in 3 soil-depths layers (0-20, 60-80 and > 125 cm) and: R:S, AGDW, TRW and SRL at harvest for durum wheat cv. Hourani plants analysed in the 2006 and 2007 experiments. Data includes full irrigation and drought treatments, as well as N application treatments (0, 50 and 100 kg N ha^{-1}, equivalents). To fitted regressions see Figura 9.2.

TRV vs	Wheat cv. Hourani					
	2006 (*df = 16*)		**2007** (*df = 28*)		**2006-07** (*df = 46*)	
	Equation	**R^2**	**Equation**	**R^2**	**Equation**	**R^2**
R:S	y=51.4x+0.63	0.79^{***}	y=32.68x+0.23	0.59^{***}	y=38.0x+0.42	0.45^{***}
AGDW	y=-0.02x+2.44	0.01^{ns}	y=0.11x+0.58	0.11^{ns}	y=0.09x+0.80	0.17^{**}
TRW	y=7.97x+0.13	0.84^{***}	y=10.04x-0.30	0.69^{***}	y=8.58x-0.05	0.82^{***}
SRL	y=0.19x+0.47	0.13^{ns}	y=0.21x-0.34	0.51^{***}	y=0.22x-0.21	0.26^{***}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the simple linear regression.

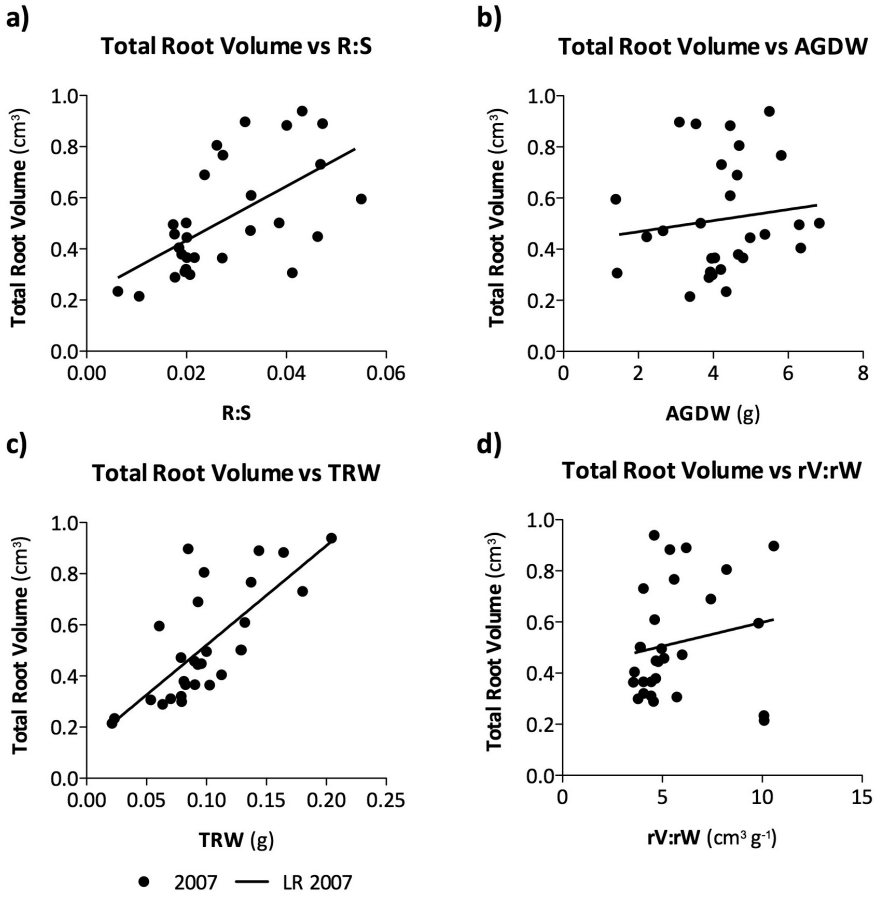

Figure 9.4 Simple linear regression (LR) between total root volume measured in 3 soil-depths layers (0-20, 60-80 and > 125 cm) and: **a**) R:S, **b**) AGDW, **c**) TRW and **d**) SRL at harvest for durum wheat cv. Karim plants analysed in the 2007 experiment. Data includes full irrigation and drought treatments, as well as N application treatments (0, 50 and 100 kg N ha^{-1}, equivalents). Details for the simple linear regression curves is presented in the Table 9.3.

Table 9.3 Simple linear regression between total root volume (TRV) measured in 3 soil-depths layers (0-20, 60-80 and > 125 cm) and: R:S, AGDW, TRW and SRL at harvest for durum wheat cv. Karim plants analysed in 2007 experiment. Data includes full irrigation and drought treatments, as well as N application treatments (0, 50 and 100 kg N ha^{-1}, equivalents). To fitted regressions see Figure 9.3.

TRV vs	**Wheat cv. Karim 2007** (*df=28*)	
	Equation	**R^2**
R:S	y=10.61x+0.22	0.35^{***}
AGDW	y=0.022x+0.42	0.02^{ns}
TRW	y=3.89x+0.13	0.54^{***}
SRL	y=0.019x+0.41	0.03^{ns}

* for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$ and ^{ns} for a non significant result for the simple linear regression.