THE EFFECTS OF PROCHLORAZ ON THE GROWTH AND YIELD OF OILSEED RAPE

by

Judith Anne Stafford

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TABLE OF CONTENTS

ABSTRACT

Yield production was investigated in the winter oilseed rape variety Capricorn by comparing crops grown under standard husbandry conditions in three seasons (1991, 1992 and 1993 harvest years). Also investigated were the effects of the phytotonic imidazole fungicide prochloraz on the physiology of yield production. Prochloraz was applied in autumn, spring and summer in all possible combinations (eight treatments), except in the second season (1992), when the autumn application was omitted. Crop growth and development were studied in detail using stratified sampling in 20 cm layers. Detailed growth analysis between flowering and final harvest was restricted to untreated controls and plots receiving all three prochloraz applications. Solar radiation interception was measured using tube solarimeters arranged to correspond with layers of the profile obtained in sampling.

The qualitative pattern of growth and development was the same in all three seasons regardless of variations in environmental conditions, and could be divided into the four distinct but overlapping stages described in previous studies. Potential yield (pod number) was determined at flowering and was almost constant between seasons. It did not limit final yield and can never be fully realised. Final seed yield was dependent upon the amount of solar radiation intercepted in Stage IV (seed development), and was manifested in the extent of pod and seed losses and seed growth during this period. The efficiency of radiation use varied between seasons.

The main role of leaves was the development of the reproductive framework, and rapid leaf senescence occurred at flowering, particularly in Stage III (pod development). Losses of potential pods and seeds were continuous from flowering onwards but were severe in Stage III. Pod retention was determined by the availability of assimilates which depended on radiation interception and intra-plant competition for assimilates. Regulation of this was probably under hormonal control. Dry matter production was unaffected by the flower canopy except when radiation levels were unusually low during Stage III. Final yield was not affected by such effects. Seed number per pod is determined genetically, but modified during

development by assimilate availability according to position in the canopy and the number of competing pods.

Seed growth occurred mainly in Stage IV and depended upon the extent of photosynthesis, largely in pods and branches. Seed yield was independent of growth up to flowering, and no remobilisation of dry matter occurred to support seed-filling. When open canopies were produced, leaf retention (largely at the base of the pod canopy), radiation interception by leaf, and therefore, assimilation by leaf, were all increased. Under such circumstances, assimilate production by leaf at the base of the pod canopy may have contributed up to 20% of the dry matter (seed) produced in Stage IV. Pod and seed retention were improved throughout, but particularly higher in the canopy, because seeds that were growing well were more likely to be retained.

Disease development in all treatments was monitored using detailed assessments throughout each season. The main fungicidal effects of prochloraz were on light leaf and pod spot and stem canker. Disease incidence was reduced in all seasons, but severity was reduced only in 1993. However, disease severities were generally very low, and these fungicidal effects probably had little or no effect on yield. Large losses of potential yield were caused by severe sclerotinia infection combined with high temperatures, a high soil moisture deficit, and possibly lodging (1992). Sclerotinia was controlled by iprodione in 1993. Disease data were used to form a model to estimate the expected yield losses caused by sclerotinia infection. Heavy infections of stem canker in 1993 did not seriously affect yield.

Prochloraz increased seed yield by up to 16% in 1991 through increased pod numbers largely in the upper and middle regions of the pod canopy. Seed number per pod was increased slightly, largely due to higher retention in lower pods, while 1000-seed weight was not affected. Effects were negative in 1992 and inconclusive in 1993. Prochloraz increased crop growth from March onwards in 1991, and the differences in green area and dry matter components were maintained to final harvest. There was no effect on harvest index. Leaf senescence was delayed by prochloraz so that during Stage IV (seed development), leaf area index in the pod canopy and just below was

greater in treated plots, and the proportion of radiation intercepted by leaf was slightly increased. Total radiation interception was increased due to the increased green area index mainly due to increased pod and stem areas in the top and middle of the canopy. Prochloraz delayed crop senescence and therefore reduced the decline in efficiency in late Stage IV. Total assimilate production in Stage IV was increased partly because of continued assimilate production for longer in all organs including retained leaf. This enabled more pods to be supported throughout the canopy. By prolonging assimilatory activity in the organs at the base of the canopy, prochloraz probably modified the pattern of assimilate movement between layers of the canopy. Seed numbers per pod in lower pods and pods higher in the canopy would, therefore, have been maintained. Reasons for the failure of prochloraz to elicit a similar response in 1992 and 1993, and the nature of the phytotonic effect are discussed.

The findings are discussed in relation to the development of an oilseed rape ideotype for maximising yield production.

LIST OF FIGURES

LIST OF TABLES

ABBREVIATIONS

ADAS	Agricultural Development and Advisory Service
°C	Degrees Celsius
cm	Centimetre
df	Degrees of freedom
DM	Dry matter
E	Efficiency of radiation use (derived from DM data)
FAO	Food and Agriculture Organization of the United Nations
g	Gramme
GAI	Green area index
ha	Hectare
k	Radiation extinction coefficient
kg	Kilogramme
LAI	Leaf area index
LLPS	Light leaf and pod spot (= LLS, light leaf spot)
m	Metre
m^{-2}	Per square metre
MJ	Megajoules
MT	Million tonnes
NFU	National Farmers Union
P	Probability
PAI	Pod area index
PBI	Plant Breeding International
PGR	Plant growth regulator
r^2	Correlation coefficient
R_i	Intercepted solar radiation
R_T	Total solar radiation
SAI	Stem area index
SED	Standard error of the difference
SMD	Soil moisture deficit
S1-S3	Seasons 1 - 3
t	Tonne
vs.	Versus
%	Per cent
<	Less than
>	Greater than

PUBLICATIONS

Data from this thesis have appeared in the following publications which are presented in Appendix VIII:

McWILLIAM, S.C., STAFFORD, J.A., SCOTT, R.K., NORTON, G., STOKES, D.T. & SYLVESTER-BRADLEY, R. (1995). The relationship between canopy structure and yield in oilseed rape. *Proceedings of the ninth International Rapeseed Congress, Cambridge*, 491-493.

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Section 1: INTRODUCTION AND LITERATURE REVIEW

1.1. INTRODUCTION

Growth-regulatory properties of fungicides, particularly the azoles, have been demonstrated in a wide variety of crops including cereals, ryegrass and brassicas. Most of the documented evidence relates to the triazoles which are mainly used commercially as growth regulators and/or fungicides, although growth regulating-effects of imidazoles have also been reported (Kuck & Scheinpflug, 1986).

Many triazoles occur in different isomeric forms, which may differ in their fungicidal and growth-regulatory activities (Büchel, 1986; Lürssen, 1988). The response to the compound is related to the relative proportions of the isomers in the mixture. The fungicidal activity of triazoles is attributed to the inhibition of sterol biosynthesis, while the growth regulatory effect is the result of the inhibition of gibberellin biosynthesis, which prevents extension growth.

Prochloraz, which is one of the most important azole fungicides, is an imidazole with a fungicidal mode of action the same as that of triazoles (sterol biosynthesis inhibition). Prochloraz was developed in the late 1970s but still retains a large share of the fungicide market because of its effectiveness in disease control in cereals and oilseed rape. Experiments at Rothamsted Experimental Station, however, revealed that prochloraz significantly increased the yield of disease-free oilseed rape (Rawlinson, Doughty, Bock, Church, Milford & Fieldsend, 1989). The nature of the response of the plant to prochloraz remains unknown. The present study was initiated firstly to define the physiology of yield formation in oilseed rape and, secondly, to identify and quantify the physiological effects of prochloraz on this process.

The physiology of oilseed rape has been reviewed by Daniels, Scarisbrick & Smith (1986) and more recently by Mendham & Salisbury (1995). The following survey will be restricted to:

1. A consideration of the physiology of crop growth and development with particular emphasis on the processes determining yield production in oilseed rape.

2. The nature of the physiological response of oilseed rape to prochloraz in past experiments.
3. Oilseed rape diseases and the effects on these of prochloraz.

1.2. THE PHYSIOLOGY OF OILSEED RAPE

1.2.1. **Introduction**

Oilseed rape production is favoured by the climate in the UK (Bunting, 1986), and yields are generally high compared with those in most of Europe. The average yield in the UK in 1994 was 2.70 t ha^{-1} compared with a European average of 2.45 t ha^{-1}, and a world average of only 1.35 t ha^{-1} (FAO, 1995). Oilseed rape has been grown in the UK since the seventeenth Century but following competition from imported oilseeds, it virtually disappeared in the nineteenth Century until 30 - 40 years ago, when it began to receive interest as a break crop in cereal production systems (Bunting, 1984, 1986; Scarisbrick, Atkinson & Asare, 1989). Oilseed rape remained a minority crop, however, until 1973, when the guarantee of price support following entry into the EEC triggered a rapid expansion in the UK rapeseed industry. By the mid 1980s, oilseed rape had become the most important combinable break crop in Northern Europe, and the third most important arable crop in the UK after barley and wheat (Scarisbrick & Daniels, 1984). In 1994, the area sown to rape in the UK was 490,000 ha compared with only 97,000 ha in 1979-81, and UK production accounted for 1,323,000 MT out of a total world production of 29,958,000 MT (FAO, 1995). Oilseed rape production in the UK came under scrutiny in the late 1980s because price support for oilseeds had become the third most costly commodity in the Common Agricultural Policy (Scarisbrick *et al.*, 1989). Changes in pricing arrangements and uncertainties over the increasing importance of seed quality led to a decrease in confidence among growers and in 1988, the area sown to oilseed rape fell (Scarisbrick *et al.*, 1989). A new pricing arrangement was introduced in 1992, in which world prices were supplemented by a subsidy paid per hectare rather than per tonne. Increasing seed and oil yields then became less important than improving seed quality.

By the mid 1980s, double-low varieties (O O-glucosinolate), had improved the quality (food value) of the oilseed rape crop. This was achieved by reducing the levels of

erucic acid, which had been implicated in heart problems in laboratory rats, and glucosinolates, which were associated with thyroid malfunction in non-ruminant animals (Rowan & Lawrence, 1982). Glucosinolates also reduced the palatability of feeds (Rowan & Lawrence, 1982), which further limited the inclusion of rapeseed meal in animal diets. Very low glucosinolate levels have been obtained in spring varieties (Inglis, Thearle & Isaacson, 1989). This fact, together with changes in the pricing scheme, and uncertainties over set-aside areas, diminished the advantages of winter rape over the spring crop. Since 1992, when the new pricing scheme was introduced, the national area sown to spring rape increased from around 5% of the UK total to approximately 20% in 1995/96, largely at the expense of the winter crop.

Improvements in seed quality have been achieved partly at the expense of yield, and average yields of oilseed rape in the UK at 2.70 t ha^{-1} (FAO, 1995) remain relatively low compared with the theoretical maximum of 7.56 t ha^{-1} proposed by Daniels *et al.* (1986). Higher seed yield remains a primary objective in most breeding programmes (Bowman, 1984). The ability to identify pathways for yield improvement has provided valuable information for breeding and crop manipulation strategies. This will be furthered by increasing understanding of the way in which yield is determined, and the degree to which this is manifested at final harvest. In previous studies, the identification of the major factors governing pod and seed losses (Bilsborrow & Norton, 1988) and the influence of these on final yield have been of particular importance in achieving this.

1.2.2. Crop growth and development

(a) Vegetative

Oilseed rape is normally sown in late August or early September in the UK, and in moist conditions, seeds germinate four to five days after sowing (Daniels *et al.*, 1986). Leaves initiate as small protuberances in a spiral arrangement around the apex (Daniels & Scarisbrick, 1983; Scarisbrick *et al.*, 1989), which determines the phyllotaxy. Rapid leaf production enables early ground cover to be achieved (Daniels & Scarisbrick, 1983), thereby maximising solar radiation interception. This facilitates the development of the tap root which stores reserves (carbohydrates) for utilisation

in early spring growth (Daniels *et al.*, 1982; Scarisbrick & Daniels, 1984). Rapid ground cover is also important for weed control, and for providing a buffer against winter-kill and pigeon damage (Daniels *et al.*, 1982).

When temperatures fall in the autumn, smaller leaves are produced at a lower rate and the overwintering rosette is formed (Daniels & Scarisbrick, 1983), which consists of approximately five true leaves and a well-developed root system (Tommey & Evans, 1988). Leaf development is confined to maintenance of leaf number only (Mendham, Shipway & Scott, 1981) and there is no net growth. Leaf formation is continuous from germination to the onset of reproductive development (Daniels *et al.*, 1986).

(b) Reproductive

In early November (for normal sowing dates), plants begin to initiate floral parts instead of leaves and axillary buds (Daniels *et al.*, 1982). The exact date and number of leaves is influenced by a number of factors including sowing date, variety, climate and geographical location but is mainly temperature-dependent (Scarisbrick & Daniels, 1984; Tommey & Evans, 1991). Floral initiation varies considerably between plants and, in the whole crop, it may take place over a 14 day period. (Scarisbrick *et al.*, 1989). Shipway (1981) considered the role of daylength in floral induction to be more important than temperature. Flower initiation has been found to be dependent upon a minimum developmental stage and vernalisation temperature (Tittonel, Chaput, Letoublon & Bonnot, 1988). Further, the date of commencement of spring growth appeared to be as dependent on autumn climatic conditions as on those in spring (Tittonel *et al.*, 1988). Mendham & Salisbury (1995) listed four main factors controlling initiation and flowering which were *(1)* a minimum number of leaf initials for the vernalisation response to occur, *(2)* the basic temperature response, *(3)* vernalisation responses, and *(4)* daylength responses.

Early floral development has been described by Smith & Scarisbrick (1990). Floral primordia appear acropetally from the domed apical meristem at regular intervals in a spiral pattern (Smith & Scarisbrick, 1990). The terminal raceme develops first and remains dominant throughout the life cycle (Daniels *et al.*, 1982). The distinct

hierarchical structure, with proximal parts more advanced than distal, is already present by mid-January (Scarisbrick *et al.*, 1989). Growth resumes in the spring when average temperatures rise and rapid stem extension raises the flower buds above the leaves (Scarisbrick *et al.*, 1989). Flowering in oilseed rape occurs acropetally on each branch beginning on the terminal raceme and then continuing with the primary branches in sequence. Therefore on any individual raceme, pods developing from the basal flowers are the most advanced (Addo-Quaye, Scarisbrick & Daniels, 1986). The process of branch formation is basipetal, since axillary buds on the mainstem develop into primary branches in sequence downwards (Mendham & Salisbury, 1995). Therefore upper branches are superior because they are initiated first (Addo-Quaye *et al.*, 1985). In glasshouse experiments with spring rape, Ancha & Morgan (1987) observed that the growth and development of branches was increasingly less advanced down the stem, and that the rate of stem elongation of the lower axillary branches increased during flowering.

Oilseed rape is essentially self- and wind-pollinated (Daniels & Scarisbrick, 1983). Following fertilisation of the ovary or potential pod, the petals abscise and pod growth ensues. In winter rape in the field, the pattern of growth for both pods and seeds is sigmoidal, with the former preceding the latter (Norton & Harris, 1975). In early pod development, seed dry matter (DM) accounted for only 20% of the total pod DM (Norton & Harris, 1975). When pod growth and hull (pod wall) DM achieved a maximum, seed DM accounted for 25% of the total pod DM (Norton & Harris, 1975). In field studies in Australia, Hocking & Mason (1993) found that by the time the pod walls had fully elongated, the seeds had accumulated around 35% of their mature dry matter.

Seeds of pot plants grown in controlled environments increased in size proportional to pod width (Pechan & Morgan, 1985). The increase in pod length and width resulted from the presence of developing seeds. Bilsborrow & Norton (1984) concluded from field investigations, however, that pod walls had to achieve a minimum size before appreciable seed development proceeded. After maximum hull DM was achieved it rapidly declined, while seed DM increased to achieve a maximum

of 60% of the final pod DM (Norton & Harris, 1975). The hull exported sugars from current photosynthesis to the growing seed (Norton & Harris, 1975). Hocking & Mason (1993) showed that DM redistributed from the hull was able to supply 11% of the DM of mature seeds in a pod.

1.2.3. **Yield determination**

Mendham & Salisbury (1995) concluded that the processes of pod and seed number determination largely coincided and were mainly governed by the assimilate supply. However, understanding of these processes is far from complete, and the aim of this section is to identify which areas require more investigation.

(a) Development of yield potential

The yield of oilseed rape is determined by the interaction of a number of factors, but ultimately it depends on the amount of solar radiation intercepted by the crop over the growing season, the efficiency of conversion of this radiation into DM, and the proportion of DM partitioned to usable yield (Jenkins, 1990). Variation in rapeseed yield between years is determined by interactions between the three main yield components: pod number, seed number per pod and individual seed weight. Potential yield is determined at flowering when maximum numbers of pods and seeds are determined (Mendham *et al.*, 1981; Bilsborrow & Norton, 1984). It is dependent upon the availability of assimilates during the vegetative stage, stem elongation and flowering (Bilsborrow & Norton, 1984), and Evans (1984) showed that stem and root reserves played an important role. Mendham *et al.* (1981) concluded that potential yield depended on crop size at flowering because this determined assimilate availability, but this proposal has not been resolved. Clearly the processes determining potential yield are not well understood.

(b) Final yield determination

Usually less than half the potential yield is realised at maturity (Mendham & Scott, 1975; Mendham *et al.*, 1981; Bilsborrow & Norton, 1984). Tommey & Evans (1988) considered final seed yield to be strongly influenced by the amount of growth made by the crop from the beginning of stem extension onwards, whereas Bilsborrow &

Norton (1988) concluded that it was determined by the photosynthetic capacity of the pods and pod-bearing branches during seed development. The main factors restricting full utilisation of yield potential were identified as sowing date, plant population density and nitrogen nutrition (Boelcke, Léon, Schulz, Schröder & Diepenbrock, 1991). The effects of such constraints were manifested through restricted radiation interception which resulted in limited assimilate supplies at critical stages in development (Bilsborrow & Norton, 1984; 1988).

Small numbers of potential pods may be lost due to frost damage to early-formed buds and flowers (Scott, Ogunremi, Ivins & Mendham, 1973b) and a failure of pollination and fertilisation due to cold and wet conditions at flowering (Shipway, 1981; Daniels *et al.*, 1986). However, more serious losses occur later and are probably due to restricted assimilate supplies which are considered to be critical in determining pod and seed survival. Limitations in the assimilate supply are a consequence of both internal competition and inadequate radiation availability due to shading, particularly towards the bottom of the canopy (Bilsborrow & Norton, 1984). Intense competition for assimilates between stems, branches, flowers, pods and seeds may arise because of the overlap of their growth and development (Ancha & Morgan, 1988). Mendham *et al.* (1981) identified the three-week period after full flowering as a major phase of pod losses. In Canadian spring rape, pod abortion occurred predominantly towards the end of flowering or after, and was severe on later-developing inflorescences (McGregor, 1981). Tayo & Morgan (1975) similarly showed in pot-grown spring rape plants that very few of the later-opening flowers contributed to yield. Mendham & Salisbury (1995) concluded that pod and seed number determination largely coincided in field-grown winter rape and most losses occurred within four weeks of full flower. However, Bilsborrow & Norton (1988) found that pod and seed numbers continued to decline throughout pod and seed development until maturity when, depending on season, only 40-60% of potential pods and 30% of potential seeds remained. The timing of the important phases of pod and seed losses would appear to merit further investigation.

Many experiments reported to demonstrate the importance of assimilate supply in

determining the size of the yield components have involved shading or removal of the assimilate source (leaf). The results were largely dependent upon the cultural conditions employed and on the development stage when treatments were imposed. In pot-grown spring rape plants, removal of lower branches was suggested to make more assimilates available to the upper inflorescences, which was most beneficial at the start of flowering and immediately afterwards, when pod and seed numbers were being determined (Ancha & Morgan, 1988; Kasa & Kondra, 1986). Pod number was reduced by leaf-shading or removal prior to mid-flowering (Clarke, 1978; Tayo & Morgan, 1979; Inanaga, Kumura, Etho & Tsunoda, 1986; Labana, Banga & Ghandi, 1988), while in field-grown winter rape, both pod numbers and seed numbers per pod were reduced by shading from shortly after mid-flowering (Shipway, 1981). When leaves from spring rape were removed at the end of flowering, yield and components were not affected (Clarke, 1978). Experiments involving leaf and branch removal impose unnatural stresses on the plants and Bilsborrow (1985) suggested that such results should be treated with caution. In general, however, these findings indicate that assimilate supply is the major determinant of pod number and plays an important role in the determination of seed number per pod, but the mechanisms restricting assimilate availability have not been investigated.

Inanaga & Kumura (1988) proposed that determination of seed number per pod involved the processes of pollination, fertilisation and seed growth. In winter rape in the UK, Mendham *et al.* (1981) attributed most variation in seed yield to variation in the number of seeds per unit area, and Jenkins & Leitch (1986) considered high seed retention to be essential for high yields. Early autumn sowings of winter oilseed rape normally produce large numbers of flowers and pods (Mendham *et al.*, 1981; Jenkins & Leitch, 1986), and severe competition between them may limit the number of seeds per pod. Mendham *et al.* (1981) considered the size of the assimilate source per pod to be a major determinant of seed retention. Inadequate crop growth at flowering was considered to be the main factor responsible for seed abortion in winter rape during drought conditions in Australia (Mendham *et al.*, 1984). However, Jenkins & Leitch (1986) considered current radiation availability (hence assimilate) to be a more important determinant of seed number per pod. Bouttier & Morgan (1992b)

questioned the involvement of hormonal factors but concluded that the primary cause of seed abortion was an inefficient assimilate supply during early pod development.

Norton & Harris (1975) showed that, in winter rape in the field, early rapid seed losses were due to the failure of embryos to develop, while the later, more gradual losses were associated with seeds ceasing to develop further and then disappearing. In spring rape plants grown in pots under controlled conditions, Pechan (1988) and Bouttier & Morgan (1992a) considered the failure of fertilisation to be a major factor limiting seed number per pod, and sufficient pollen on the stigma did not guarantee full seed-set (Pechan, 1988). Early seed abortion, which was associated with a failure in the events immediately subsequent to fertilisation, was found to be uncommon compared with actual failure of fertilisation and was not considered to be a major limitation (Pechan, 1988). However, Bouttier & Morgan (1992a) considered ovule sterility to be a major determinant of seed number per pod. Although insect activity increased the number of fertilised seeds per pod in field-grown winter rape, yields were not increased because pod number and seed size were reduced (Williams & Simpkins, 1989).

Yield component determination may be controlled by both nutritional and hormonal factors (de Bouille, Sotta, Miginiac & Merrien, 1989). Early pod development and pod number determination were shown to be under partial cytokinin control (de Bouille *et al.*, 1989). Apical flowers which would normally abort could be induced to attract assimilates and develop further by cytokinin application (Morgan, 1982). A role for auxins in the determination of both pod and seed number was also proposed. Through its involvement in regulating assimilate partitioning and the determination of sink strength, indole acetic acid might increase pod number by preventing flower or pod abortion (de Bouille *et al.*, 1989). Pod number was determined by assimilate supply whereas seed number per pod was not (Inanaga, Kumura, Etho & Tsunoda, 1986). Identification of the most important factors determining and controlling pod number and seed number per pod remains unresolved. Major areas requiring investigation include the factors causing fluctuations in the assimilate supply. The assimilate supply is dependent upon the photosynthetic

capacity of leaves, stems and pods, and evidence for this will be investigated in the following section.

(c) Sources of assimilate for yield determination

The previous sections have indicated that the formation of seed yield in oilseed rape is dependent upon the ability of the crop to maintain a sufficient supply of assimilates to the developing seeds. Bilsborrow & Norton (1988) estimated the gross photosynthetic capacity of the oilseed rape crop throughout reproductive development. The maximum rate of photosynthesis occurred before peak flowering, and by the end of the pod development stage, it had fallen to 55% of that maximum. At the end of seed development, it had decreased to 38% of the maximum. Throughout reproductive development, leaves, stems and pods act as the principal sources of photosynthate (Rood, Major & Charnetski, 1984b; Bilsborrow & Norton, 1988) and the role of each is determined by its contribution to the total crop dry weight at the time of assimilation (Rood *et al.*, 1984b; Bilsborrow & Norton, 1988).

(i) The role of leaves as sources of assimilate

Leaves are important in the determination of potential yield. Before flowering, photosynthates from the upper leaves of spring rape are mainly utilised in the development of the upper stem and buds (Brar & Thies, 1977; Rode, 1988). At the onset of flowering in winter rape, most of the initial fixation of $^{14}CO_2$ was carried out by leaves (58%) and stem (38%) (Chapman *et al.*, 1984; Scarisbrick *et al.*, 1989). Thus, leaf material was the major assimilate source at this time, while the most important sinks were the reproductive parts and, to a lesser extent, the developing stems and roots (Chapman *et al.*, 1984). Leaves played an important role in stem growth and reproductive development, but after the onset of flowering, loss of leaf resulted in a decrease in the assimilate supply from these organs (Addo-Quaye *et al.*, 1986).

In Canadian spring rape grown in pots, leaves had senesced when rapid pod growth was occurring, and Allen, Morgan & Ridgman (1971) concluded that leaves had little direct influence on pod growth. However, in similar experiments with a Canadian

spring cultivar, Brar and Thies (1977) showed that nearly 75% of the photosynthates from the topmost leaf were translocated to the pods and the relative contributions of assimilates for seed growth were 37%, 32% and 31% from leaf, pod and stem respectively. Photosynthates from the upper leaves were mainly utilised in the development of the upper stem and buds. To what extent the results of glasshouse experiments with spring rape can be applied to the field situation with winter rape is not clear. Pot-grown plants are devoid of all the inter-plant competition experienced by those in the field. Further, the growth and development patterns of the two types are different and when grown in pots, leaf retention is improved. Consequently, leaf photosynthesis would make a greater contribution to seed-filling in pot-grown rape. Also, Bilsborrow (1985) found that the relative contributions of different organs to total photosynthesis varied between seasons.

In spring rape, Major & Charnetski (1976) found no evidence of export of assimilates between leaves whereas Chapman *et al.* (1984) found that lower leaves of winter rape exported carbon assimilates to newly-formed higher leaves. Addo-Quaye *et al.* (1986) considered the topmost leaf to be important in seed growth, and Bilsborrow (1985) showed the small leaves high in the canopy to be very photosynthetically active. However, Chapman *et al.* (1984) concluded that since the well-illuminated leaves near the top of the canopy fixed little ^{14}C, they must make little contribution to seed growth.

(ii) The role of stem

Chapman *et al.* (1984) concluded that leaves provided assimilates mainly for stem development but little for reproductive growth. Photosynthates fixed by leaves and stem at the start of flowering were stored in the stem and remobilised into reproductive parts later in the season (Chapman *et al.*, 1984; Evans, 1984; Addo-Quaye, Daniels & Scarisbrick, 1985). Bilsborrow & Norton (1988), however, found no evidence for dry matter remobilisation from stems and branches during pod development or filling. They concluded that the assimilates for seed filling were provided by current photosynthesis of the pods and the pod-bearing branches.

Daniels *et al.* (1982) proposed the stem to be an important photosynthetic organ throughout pod and seed growth. During early flowering, stem material and pedicels fixed large amounts of $^{14}CO_2$ due to their favourable position for radiation interception. Stems were large sinks at the onset of flowering and imported ^{14}C, but later they became net exporters (Chapman *et al.*, 1984). Addo-Quaye *et al.* (1986) found that at the end of flowering and during rapid pod filling, stems and pedicels contributed little to the total amount of $^{14}CO_2$ fixed. Bilsborrow (1985) showed that pod-bearing branches made an important contribution to seed-filling, but the main stem did not because its photosynthetic activity was very low.

(iii) *Pods*

During flowering, the pods are small and can fix only small amounts of carbon. Therefore most of their requirements are met by imports. During seed growth, however, pods play a major role in carbon fixation (Chapman *et al.*, 1984). In defoliation and shading experiments, Labana *et al.* (1988) demonstrated that whereas pod number was influenced by the assimilate supply from leaves, seed development within was dependent upon pod photosynthesis. However, Clarke & Simpson (1978a) obtained a poor correlation between pod area and yield in spring rape in Canada which was attributed to a possible greater contribution to seed yield by leaves than by pods. Li & Wang (1988) found that pod area was positively correlated with leaf area at the end of flowering and with seed yield. Major & Charnetski (1976) observed that while leaves, stems and pods were all capable of assimilating $^{14}CO_2$, only leaves and stems exported assimilates. Pods exported assimilates to seeds contained within but not to other pods (Norton & Harris, 1975; Major, Bole & Charnetski, 1978). The contribution of seed photosynthesis to seed development was extremely small (Brar & Thies, 1977).

In summary, leaves are the major photosynthetic organs up to full flower. The stem becomes an important source of photosynthate for the developing pods because of progressive leaf senescence. During seed growth, the pods are largely responsible for their own filling (Bilsborrow & Norton, 1984; 1988) and pods and pod-bearing branches account for over 95% of crop photosynthesis. Bilsborrow & Norton (1988)

showed that, on a unit area basis, pod and stem photosynthesis was lower than that of leaf, even at this late stage. The extent to which pods are autonomous is unknown and the contribution of leaves to the later stages of yield determination has not been quantified. In addition, the role of DM remobilisation in seed-filling has not been resolved.

(d) Control of seed growth

Final yield is determined during the seed development phase by the extent of pod and seed survival and seed growth. This appears to be entirely dependent upon current events (Bilsborrow & Norton, 1988). Most published evidence for the control of seed growth comes from experiments on spring rape grown in controlled conditions, and the extent to which the physiology of source-sink management can be extrapolated to field-grown winter rape is unknown. Seeds act as strong sinks in attracting assimilates (Major & Charnetski, 1976; Labana *et al.*, 1988) and exert a controlling influence on the assimilate management of the source (Labana *et al*, 1988). Clarke & Simpson (1978a) suggested that a rapid increase in seed weight provided the high sink demand that in turn increased photosynthetic activity. The amount of assimilate translocated to the seed was related to the seed:total dry weight ratio, which increased with maturation, therefore making the seed a stronger sink (Rood *et al.*, 1984b; Major, Rood, Charnetski, Carefoot & Bole, 1985). The proximity of source to sink was considered to be important in rape in determining the availability and demand of assimilate (Major & Charnetski, 1976; Labana *et al.*, 1988). Assimilate movement through the phloem and down the mainstem to the roots was suggested to be easier than transport to the branches (Addo-Quaye *et al.*, 1986).

De Bouille *et al.* (1989) suggested that indole acetic acid synthesised in seeds enhanced assimilate accumulation in pods and controlled seed-filling as well as being involved in pod wall development. Abscisic acid accumulated during the seed maturation period and was also involved in seed-filling (de Bouille *et al*, 1989). Keiller & Morgan (1988a) related changes in floral sink strength to morphological and hormonal changes associated with flower development. When seed development started in the oldest pods, around 14 days after anthesis, the cessation of apical

development was attributed to a nutritional or hormonal mechanism or a combination of both. A time limit for flower and pod production was proposed which was associated with the onset of seed-filling in older pods (Keiller & Morgan, 1988b). These findings were obtained using spring rape grown in pots in the glasshouse, and to what extent they apply to field-grown material is unknown.

1.2.4. **The effect of crop morphology on yield production**

Pod and seed losses generally increase with depth in the canopy because of shading (Bilsborrow & Norton (1984). Mendham *et al.* (1981) concluded that there was little difference throughout the canopy in late-sown crops which had fewer pods. This was attributed to an improved distribution of solar radiation in the canopy, although the mechanisms involved are not fully understood. This section will review the current information available on the effect of crop structure on yield formation.

Competition for assimilates in indeterminate crops results in reduced assimilate supply to organs of low competing power (Labana *et al.*, 1988). Pod survival is influenced by its position in the canopy, since the availability of solar radiation for photosynthesis decreases with increasing depth, and seeds in the lowermost pods may be fewer and/or smaller. Pod age and position in the canopy affected carbon balance and reproductive development because those higher in the canopy were better positioned for radiation interception but had the disadvantage of smaller size because of their later initiation (Chapman *et al.*, 1984). Pods at the base of the terminal raceme which were oldest and developmentally most advanced were closer to sources of translocated assimilates from basal leaves and stem so they obtained water and nutrients from the vascular supply before pods in the upper parts of the canopy (Addo-Quaye *et al.*, 1986). The terminal raceme and uppermost branches had a higher sink capacity and hence a competitive advantage over lowermost branches (Addo-Quaye *et al.*, 1985).

The competitive advantage of flowers and pods at the base of the terminal raceme and topmost branches is lost in dense crops where the situation is modified and often reversed (Daniels *et al.*, 1986). Pods at the top of the canopy, on the terminal raceme and upper primary branches, receive high light intensity, while lower pods are

disadvantaged because of low light intensity. Daniels & Scarisbrick (1983) proposed that the larger size of lower branches required that more energy was expended in branch production with less being available for seed growth, resulting in lower seed weights on lower branches. This assumes that remobilisation of assimilates is important in seed-filling, because branch production and seed-filling do not coincide. Basally-positioned inflorescences were considered to be a drain on the assimilate resources of the plant (Ancha & Morgan, 1988; Tommey & Evans, 1992) and later-developing branches contributed very little to final yield. It is, therefore, an advantage to have high rates of pod- and seed-set on the terminal raceme and uppermost branches (Ancha & Morgan, 1988; Tommey & Evans, 1992).

Yield is stratified within the crop profile and even though the terminal raceme is dominant, and may support 2.5 times more pods than the first single side branch (Grosse & Geisler, 1988), there is usually a decline in productivity with increasing depth. In $^{14}CO_2$ tracer experiments, pods in intermediate positions in the canopy retained similar amounts to those fixed, while pods in upper and lower positions imported large amounts (Daniels *et al.*, 1986). Pods low in the canopy were in shade but contained well-developed seeds and continued to receive assimilate. The high sink demand of pods at the top of the canopy, where solar radiation was not limiting photosynthesis, was considered to be due to their relative immaturity and large numbers. Pods in the upper and middle regions of the terminal raceme were very photosynthetically active compared with basal ones (Daniels *et al.*, 1986).

This section has indicated the large extent to which seed yield production is influenced by position in the pod canopy. Canopy structure depends on many factors which interact to determine how much radiation is intercepted and where the most important sites of interception are. This can also be modified by the application of plant growth regulators (PGRs) which have been introduced for improving radiation distribution and utilisation within the canopy. The following section reviews previous work on the effects of PGRs on oilseed rape and forms a basis from which to investigate the effects of prochloraz.

1.2.5. Effects of plant growth regulators on oilseed rape

PGRs have been applied to oilseed rape in attempts to manipulate canopy structure, improve lodging resistance, and increase winter hardiness (Scarisbrick *et al.*, 1989). The anti-gibberellin effect usually produces a height reduction, but results are often conflicting and effects on crop yield inconsistent. Dawkins & Almond (1984) reviewed early experiments on oilseed rape and concluded that while some PGR effects were beneficial, others were deleterious. This is partly due to compensation between yield components (Scarisbrick *et al.*, 1989). For example, compensation following application of the triazole triapenthenol resulted in harvested yield increases being proportionately smaller than the increases in pod numbers (Eberhardt, 1988). In some experiments, this compound increased pod number per plant at the expense of pod-filling (Kübler & Aufhammer, 1990), but with no effect on seed weight (Lembrich, 1988). Foliar application of triapenthenol reduced crop height and lodging, leading to increased numbers of pods per plant and seed yield (Frank & Rola, 1987). However, profuse flowering promoted by paclobutrazol application increased the number of unproductive pods (Rao & Mendham, 1991). Plants were considered too small to support all their potential pods and seeds per pod which were substantially reduced (Rao & Mendham, 1991). Yield effects of PGRs are variable from year to year and with different cultivars. Furthermore, yield is only increased by PGRs if it is not limited by other factors such as climatic conditions (Lürssen, 1988).

Advantages of shorter rapeseed plants following triapenthenol application include improved access for crop machinery, a smaller amount of straw for disposal and reduced risk of early lodging (Naylor, Waldren & Connon, 1987). The latter is particularly important because lodging at early pod-fill reduces yield due to reduced radiation penetration (Baylis & Wright, 1990). Uneven pod maturation results which is confounded by the provision of an ideal micro-climate for the spread of fungal diseases. Triazole treatment may delay flowering, resulting in lighter racemes which, together with shorter stems, may reduce bending moments (Baylis & Wright, 1990). Shorter branches may provide a more compact canopy facilitating easier combining (Child, Evans, Hutcheon, Jordan & Stinchcombe, 1988). Daniels *et al.* (1982) claimed that smaller crops could be less demanding of nitrogen fertiliser, which may also be

used more efficiently (Rawlinson, Church & Duckney, 1986b).

Modifications to canopy structure are accompanied by changes in the incidence and severity of fungal diseases (Child *et al.*, 1988). Reducing crop height could increase infection, especially by splash-dispersed pathogens (Rawlinson *et al.*, 1986b). Scarisbrick *et al.* (1985) found that, following application of the triazole paclobutrazol, dwarf dense canopies were infected to a much greater extent with alternaria, although Baylis & Wright (1990) considered that the effects of such pathogens would be counteracted by fungicidal effects of the chemical.

The effects of PGRs are dependent upon the timing of applications (Daniels & Scarisbrick, 1983; Child *et al.*, 1985; Child, Butler, Sims, Johnson & Thorn, 1987; Child *et al.*, 1988). Triazoles such as paclobutrazol and triapenthenol are most effective prior to a period of rapid crop development such as the onset of spring growth (Scarisbrick *et al.*, 1985). This is because a build-up of precursor may occur, and after the anti-gibberellin has been metabolised, the precursor produces rapid gibberellin synthesis and growth (Daniels *et al.*, 1986). Therefore, triapenthenol application at the beginning of stem extension was most effective in shortening stems but a greater canopy density resulted from increased branching (Child *et al.*, 1987). Application at the end of stem extension shortened branches and resulted in a more open canopy with a more shallow pod layer, allowing increased radiation penetration to lower parts of the crop (Child *et al.*, 1987, 1988). Petal size and colour were also decreased (Child *et al.*, 1987), which was suggested to decrease the reflectivity of incident radiation.

Pod senescence was delayed in a more open canopy following triazole application at flowering (Luib, Kohle, Hoppner & Rademacher, 1987). Triapenthenol increased yield through increasing branch and pod numbers and enabling the crop to maintain more of the yield potential to maturity by increased and prolonged assimilate production by the less-shaded leaves (Child *et al.*, 1987). Reductions in the incidence of disease and delayed senescence resulted in a larger sink size and extended seed-filling period (Luib *et al.*, 1987).

By reducing plant size, triapenthenol application may reduce assimilate demands to the structural components which may divert assimilates into the yield components (Naylor *et al.*, 1987; Luib *et al*, 1987). Paclobutrazol increased the proportion of assimilate translocated to the uppermost branches but specifically the terminal raceme (Scarisbrick *et al.*, 1985). Increased yield could therefore ensue both from the modification in assimilate distribution and from the prevention of lodging (Addo-Quaye *et al.*, 1985; Baylis & Hutley-Bull, 1992). Luib *et al.* (1987) reported an increase in the uptake of ^{14}C-sucrose by detached whole pods following triazole application due to an increase in the sink strength of seeds. Child *et al.* (1987) suggested that triazole application (triapenthenol) might change the relative importance of pod and leaf photosynthesis after flowering, which could lead to increased assimilate production by the pods.

This section has reviewed previous studies on the effects of PGRs on oilseed rape physiology. The following section will introduce the fungicide prochloraz, review its development and properties, and discuss the evidence for phytotonic effects in oilseed rape in previous studies.

1.3. PROCHLORAZ

1.3.1. **Development of the chemical**

The synthesis of prochloraz in the early 1970s was the culmination of a research programme aimed primarily at the control of powdery mildew in cereals (Weighton, Rose & Wright, 1977; Birchmore, Brookes, Copping & Wells, 1977; Copping, Birchmore, Wright & Godson, 1984). In an attempt to maximise the fungicidal activity of imidazole-1-carboxamides, various derivatives were produced by successive insertions and substitutions in the imidazole ring and their activities were evaluated. Although the systemicity following root application was lost, fungicidal activity was greatly improved by the synthesis of alkyl/phenoxyalkyl derivatives, and it was from this group that prochloraz was derived (Copping *et al.*, 1984).

Prochloraz was found to have both high and broad-spectrum activity (Birchmore *et al.*, 1977). Very low application rates conferred high activity against cereal diseases and

seed-borne pathogens. For the first time, it enabled disease control over the whole season to be achieved with a single compound (Harris, Weighton, de St. Blanquat & Rose, 1979). An extensive evaluation programme in the late 1970s tested the efficacy of the compound against a wide range of cereal diseases (Harris *et al.*, 1979). The margin of crop safety was wide when applied at rates up to twice those needed for effective disease control. Some broad-leaved crops, however, were susceptible to foliar applications, and further development led to metallic complexes based on prochloraz which were less damaging (Birchmore, Wells & Copping, 1979). Gisi, Rimbach, Binder, Altweg & Hugelshofer (1986) suggested that the relatively low phytotoxicity of prochloraz was related to its lack of systemicity.

1.3.2. **Structure and mode of action**

Prochloraz is a nitrogen-containing heterocyclic substituted imidazole derivative (Copping *et al.*, 1984). Most other agriculturally important compounds with a similar mode of action to prochloraz are based on 1,2,4-triazole derivatives (Copping *et al.*, 1984). Prochloraz shares a functional relationship with triazoles, a number of which are used commercially as fungicides and PGRs. This section will explore the differences and similarities between these two chemical groups.

The activity of prochloraz appeared to be typical of a systemic fungicide (Cheah, Corbin & Hartill, 1981), giving both protective and eradicative action against a wide range of plant pathogens (Weighton *et al.*, 1977). Triazole derivatives are systemic in the transpiration stream but have little or no phloem mobility (Fletcher, Hofstra & Jian-Guo, 1986). Prochloraz and related compounds, however, are non-systemic following root application (Copping *et al.*, 1984). Nevertheless, the mode of action of prochloraz is similar to that of systemic triazole fungicides, with inhibition of sterol biosynthesis probably being the primary activity (Pappas & Fisher, 1979), although DNA and protein synthesis are also inhibited by prochloraz. Imidazole and triazole inhibitors of ergosterol biosynthesis inhibitors specifically inhibit the oxidative removal of sterol C(14) methyl groups by the cytochrome P-450 enzyme, resulting in the accumulation of several ergosterol intermediates (Schwinn, 1983). Differences exist, however, between prochloraz and triazoles with respect to uptake, movement,

accumulation at the site of action and degradation in both the pathogen and host plant (Copping *et al.*, 1984). These differences were attributed to the imidazole ring in prochloraz and its lack of systemicity (Copping *et al.*, 1984). Different substitutions within the triazoles, however, can lead to considerable differences in their effectiveness (Wainwright & Linke, 1987).

All triazole derivatives used as PGRs have fungitoxic properties (Fletcher *et al.*, 1986). Commercially available chemicals that interfere with the sterol biosynthesis, whether used as PGRs, fungicides, insecticides or herbicides, are suggested to be broad-spectrum biocides (Fletcher *et al.*, 1986). The ability of triazole compounds to behave as both fungicides and PGRs is dependent on the configuration of the carbon chain components (Fletcher *et al.*, 1986; Büchel, 1986; Lürssen, 1988). Different stereoisomers affect metabolism in different ways. For example, in the triazole triapenthenol, one isomer inhibits gibberellic acid biosynthesis resulting in growth inhibition, whereas the other inhibits sterol biosynthesis, causing a fungicidal effect. Different isomers may differ in their activities (Fletcher *et al.*, 1986), and compounds may be chemically optimised towards either fungicidal or growth regulatory activity (Lürssen, 1988). Krämer (1986) reported that most marketed and experimental azoles have at least one chiral carbon atom and therefore the commercial product may be a mixture of different isomeric forms, each possessing different biological activities. Prochloraz, however, does not exist in different isomeric forms (P.E. Russell, personal communication).

The imidazole fungicide, imazalil, has shown growth retarding effects in cereals when applied at high dose rates to seedlings (Kuck & Scheinpflug, 1986). The mode of action of this systemic fungicide in the plant is unknown, although it is transported mainly acropetally (Kuck & Scheinpflug, 1986). The growth regulatory effects of triazole chemicals are thought to be largely dependent on the inhibition of gibberellin biosynthesis, resulting in retarded growth, and the growth responses of some triazoles are greatest when uptake is via the roots (Child *et al.*, 1985). Root uptake of prochloraz is negligible, however, and the mode of action of prochloraz in the host plant is unknown.

1.3.3. **Fungicidal activity**

Prochloraz is particularly active against Ascomycetes and Fungi Imperfecti, but is less active against Basidiomycetes (Birchmore *et al.*, 1979). It provided protection against very high infection pressures from powdery mildew in cereals, and produced significant yield increases (Harris *et al.*, 1979). It also provided protection against all the early-season cereal diseases for up to six weeks after treatment (Harris *et al.*, 1979), although for curative control, a higher concentration was needed than for preventive control (Gisi *et al.*, 1986). Prochloraz increased crop vigour, improved photosynthesis and increased yields in oilseed rape (ADAS, 1983), and promoted a healthy green appearance in cereal crops (Weighton *et al.*, 1977). Light leaf spot was controlled on brassicas, yields were increased, and infection by both conidia and ascospores was prevented (Cheah *et al.*, 1981). Although prochloraz was particularly effective in inhibiting mycelial growth of *Botrytis cinerea* in liquid culture (Pappas & Fisher, 1979), foliar application on strawberries did not control this pathogen (Cooke, Pappas, Jordan & Western, 1979).

Since prochloraz is primarily a contact fungicide with negligible systemicity (Kuck & Scheinpflug, 1986), its effectiveness in disease control is difficult to explain. When prochloraz was applied to control eyespot in wheat, the effects of late autumn or early spring applications persisted until summer, but later applications gave good control only when applied to shoot bases (Bateman, 1987). This was due to the inability to penetrate the canopy effectively when sprayed conventionally (Bateman, 1987). When prochloraz was applied preventively to wheat, barley and rice, Gisi *et al.* (1986) reported that its activity had declined to zero after 13 days, but this was dependent upon temperature and relative humidity. Cooke, Jordan, Hislop & Western (1993) suggested that in wheat, control of eyespot by prochloraz was achieved by means of redistribution, particularly after heavy rain (Cooke, Hislop, Jordan, Western & Herrington, 1989). While the half-life of prochloraz on unweathered foliage was only about six days, deposits redistributed to stem bases changed little over two weeks (Cooke *et al.*, 1989). The fate of redistributed material was suggested to be more important than the amount (Cooke *et al.*, 1993). Daniels & Lucas (1990) noted that the number of penetration sites of the eyespot fungus on wheat coleoptiles was

sometimes increased by treatment with prochloraz, and suggested that the reduction of competition by prochloraz-sensitive microorganisms may have been responsible.

1.3.4. Uptake of prochloraz by the plant

The uptake of prochloraz by oilseed rape tissues involves a complex interaction of a number of factors including the leaf surface and the formulation of the chemical itself (Baker, Hunt & Stevens, 1983; Baker, Hayes & Butler, 1992). Relationships between the physicochemical properties of the chemical and the target cuticle were studied using ^{14}C-prochloraz labelled in the imidazole ring (Baker *et al.*, 1992). The distribution of a chemical over the leaf surface was dependent upon its formulation (Baker *et al.*, 1983) because the waxiness of the leaf produced a very large contact angle (Stevens, Baker & Anderson, 1988) and poor wettability (Baker *et al.*, 1992). Stevens & Baker (1987) proposed that the permeability and partitioning characteristics of the leaf surface were the major determinants of the absorption of prochloraz. Comparisons between the leaves of a number of species including rape, maize and strawberry revealed that the uptake of prochloraz was positively correlated with the amount of wax and inversely related to the contact angle, but not to leaf surface wetting (Stevens & Baker, 1987). Uptake into rape leaves was moderate (Stevens & Baker, 1987) and diffusion through the thick wax layer occurred gradually throughout a 72-hour period of observation (Baker *et al.*, 1992). The waxy surface of the rape leaf facilitated uptake of lipophilic chemicals, and allowed faster translocation rates (Baker *et al.*, 1983). Prochloraz may be metabolised rapidly in the leaf, thus maintaining a high concentration gradient across the cuticle (Stevens *et al.*, 1988). However, because of its high lipophilicity, little prochloraz moves from the wax into the leaf and the chemical is largely retained in the cuticle (Stevens *et al.*, 1988).

The aim of the present study was to determine the phytotonic effects of prochloraz on oilseed rape. In order to prove such effects unequivocally, it was important to identify any fungicidal effects of the chemical. The following section reviews the major diseases of oilseed rape, and the effects of prochloraz on oilseed rape pathology.

1.4. FUNGAL DISEASES OF OILSEED RAPE

1.4.1. **Introduction**

Several fungal diseases are of particular significance to oilseed rape. The marked increase in the area sown to winter rape since the early 1970s has been accompanied by changes in the importance of diseases affecting the crop (Davies, 1986). A survey in England and Wales from 1986 to 1988 showed disease incidence to be generally high, but severity low (Hardwick, Culshaw, Davies, Gladders, Hawkins & Slawson, 1989). Light leaf spot was the dominant disease of pod, stem and leaf, and of the stem diseases, stem canker and sclerotinia stem rot were at low severity. Alternaria, affecting mainly pods, was influenced by sowing date, with earlier-sown crops more severely affected. Species names used in this review are those stated in Davies (1986).

Different diseases vary in their effects and importance since the relative importance of different plant organs changes with time (Davies, 1986). Diseases may affect plants in different ways, but rape is capable of much compensatory growth, so yield loss is often difficult to access (Rawlinson, 1979). To achieve high yields, however, all photosynthetically active surfaces should be maintained free from disease. Disease incidence varies widely between cultivars and within the same cultivar grown at different sites (Rawlinson & Muthyalu, 1979), and may be the result of many interacting factors.

The most common source of disease inoculum is infected rape stubble from a previous crop, and infective agents may be carried short distances by rain-splash or longer distances by wind. Heavy rain may lead to increased disease infection through an effect of leaf surface wax, since the leaves of some susceptible cultivars are more wettable than those of resistant ones (Rawlinson, 1979). Since leaves become less waxy as they senesce, the dispersal of spores by rain-splash may be affected by age and position of infected leaves (Fitt, Dhua, Lacey & McCartney, 1989). Weather conditions are therefore of paramount importance in determining disease patterns, and an epidemic may result from a coincidence of favourable conditions.

1.4.2. Major diseases of oilseed rape

(a) Light leaf spot

Light leaf spot (= light leaf and pod spot) [*Cylindrosporium concentricum* (Grev.), the asexual stage of *Pyrenopeziza brassicae* (Sutton and Rawlinson sp.nov.)] is currently the most widespread, and probably the most damaging, pathogen of the oilseed rape crop in the UK. In commercial crops of susceptible cultivars, it can reduce yields by up to 20% (Rawlinson & Muthyalu, 1979; Rawlinson, Muthyalu & Cayley, 1984). The main sources of inoculum are infected plants, from which conidia may be transported by rain-splash, and infected rape stubble, but it can also be seed-borne (Rawlinson, 1979). Efficient germination of conidia and penetration into the leaf require wetting of the leaf surface (Rawlinson, Muthyalu & Turner, 1978).

Light leaf spot first becomes obvious on leaves in late autumn and winter (Rawlinson, 1979), although leaves and primordia can carry latent infection until the spring (Rawlinson, 1979). The beneficial effect of applied fungicides suggests that this latent infection may be damaging (Rawlinson & Muthyalu, 1985). The pathogen causes severe leaf scorch, distortion and stunting (Rawlinson, 1979), resulting in considerable reductions in leaf and pod area, stem length and yield (Davies, 1986). The extent of yield loss varies between cultivars (Jeffery, Jones & Jenkins, 1989), and is usually marked only when very susceptible cultivars are severely affected (Davies, 1986). The component most affected by light leaf spot was shown to be pod number per plant, which was largely a result of a reduction in branch number (Jeffery *et al.*, 1989), but probably also because flower buds may be killed and flower buds prevented from opening (Davies, 1986). Seed number per pod and mean seed size are also reduced (Jeffery *et al.*, 1989) and extensively affected pods ripen prematurely and split (Rawlinson, 1979; Davies, 1986).

(b) Alternaria dark leaf and pod spot

Alternaria dark leaf and pod spot [*Alternaria brassicae* (Berk.) Sacc. and *A. brassicicola* (Schw.) Wiltsh.] is mainly a late-season disease, and the most damaging phase is when pods are affected (Davies, 1986), which may cause significant yield losses (Ogilvey, 1984). Pod lesions, appearing as dark spots, reduce the

photosynthetic area (Ogilvey, 1984) so pods may be smaller, and as with light leaf spot infection, they ripen prematurely and shed seed before harvest (Cox, Swash & Paviot, 1981; Davies, 1986). In surveys, Hardwick *et al.* (1989) showed levels of light leaf spot to be consistently three to four times higher than those of alternaria, which suggests a possible interaction.

Seasonal factors are particularly important in the development of alternaria (Gladders, 1984) which is favoured by wet weather during flowering and pod-fill. During an epidemic in 1981, the disease appeared following lodging caused by heavy snow during early flowering in April, which brought developing pods into close contact with infected lower leaves (Ogilvey, 1984). This was exacerbated by wet weather in May (Gladders, 1982). Humpherson-Jones (1984) showed that the seed-borne phase of alternaria markedly reduced germination but Cox *et al.* (1981) reported it to have little effect on seedling emergence. The disease can be readily transmitted from crop infections to the seed (Humpherson-Jones, 1984), and from seed to seedling (Cox *et al.*, 1981). Dispersal of spores occurs mainly by wind, and following harvest, distribution can occur over a wide area (Humpherson-Jones & Maude, 1982).

(c) Sclerotinia stem rot

Development of stem rot [*Sclerotinia sclerotiorum* (Lib.) de Bary] is favoured by damp conditions at flowering (Davies, 1986). Moisture in April is essential for germination of the infective sclerotia to produce the apothecia from which spores are released. Spore discharge is again weather-dependent and requires dry, slightly windy conditions, but humid conditions are required for their germination. This occurs on dead petals which constitute an essential food source (Davies, 1986). Bowerman & Gladders (1993) showed that, in a high-risk season, when frequent rainfall in late April and early May favoured the production of apothecia, the best time of fungicide application for effective disease control was immediately before a dry period that would have favoured ascospore dispersal. Fungicide treatment at mid-late flowering is likely to be most effective (Davies, 1986).

Sclerotinia is potentially very damaging, and yield losses of 10 - 50% can occur

depending on the percentage of the plant population affected (Pope, Varney & Sweet, 1989). Infected plants may ripen prematurely and the stem may break at the site of infection where rotting occurs (Davies, 1986). Yield losses result from pod shattering and low seed weight (Davies, 1986; Pope *et al.*, 1989). Pope *et al.* (1989) found that there was no significant reduction in oil content. Infection of oilseed rape with sclerotinia may occur by air-borne ascospores from infected umbelliferous weeds (Hims, 1979). The infective agents of this pathogen are sclerotia, which have a long survival in soil (Jellis, Davies & Scott, 1984), and infection of a range of unrelated crops can occur. Peas have been suggested to be the crop most likely to interact with rape to give sclerotinia problems (Gladders, 1984). It is therefore important that the length of the rotation between successive rape crops should be as long as possible.

(d) Stem canker

Stem canker [*Leptosphaeria maculans* (Desm.) Ces. and de Not.; asexual stage *Phoma lingam* (Tode ex Schw.) Desm.] has generally remained at low levels although potentially it is a damaging disease (Davies, 1986), and occurs in all the major rape-growing areas (Humpherson-Jones, 1984). Although epidemics occurred in the late 1970s (Davies, 1986), which were particularly serious in France, the introduction of resistant varieties appeared to be the major factor reducing canker levels in the early 1980s (Gladders, 1984). The disease has caused considerable damage in Poland (Bonin & Fratczak, 1988) and has caused appreciable yield losses in Australia, where it limited expansion of the rapeseed industry (McGee & Emmett, 1977; Ballinger *et al*, 1988), and was responsible for almost eliminating oilseed rape from Western Australia (Mendham *et al.*, 1984). Calculations applied to assessments of stem canker in relation to yield indicated that even slight disease could be associated with a 13.6% yield loss (Rawlinson & Muthyalu, 1979).

Infected seed is the primary source of the pathogen in oilseed rape (Humpherson-Jones, 1984) but once the disease becomes established, infected rape stubbles are the main source of inoculum (Brown, Barbetti & Wood, 1976; Gladders & Musa, 1979, 1980; Gladders, 1982; Humpherson-Jones, 1984; Hammond & Lewis, 1986a), and air-borne ascospores are the major agents of dispersal (Brown *et al.*, 1976; Humpherson-

Jones, 1984). Disease severity was suggested to be related to the amount of ascospore inoculum (McGee & Emmett, 1977) and distance from the source was shown to be an important factor controlling disease development (Gladders & Musa, 1979, 1980; Hammond & Lewis, 1986a). A positive relationship between insect damage and stem canker has been reported (Newman, 1984; Davies, 1986), indicating that insect damage probably facilitates infection. Rawlinson & Muthyalu (1979) suggested that plants damaged by pigeon grazing might have been predisposed to infection and/or pigeons might have been responsible for additional spread of inoculum.

Leaf symptoms appear in early autumn and stem lesions in March, and there is a positive relationship between maximum incidence of phoma leaf spot infection in the autumn and the incidence of severe stem canker at final harvest (Gladders & Musa, 1979, 1980). Hammond & Lewis (1986a) showed that the timing of the early stages of disease development was important in determining the severity of subsequent cankers. Stem cankers appeared about 75 days after the onset of leaf lesion formation, this interval increasing with lower temperatures (Hammond & Lewis, 1986a). The probability of a severe epidemic was determined by the timing of leaf lesion formation, the speed with which the fungus travelled from the leaf lesion to the stem, and the differential effects of temperature on disease progression and leaf abscission. Gladders & Musa (1979) considered that rainfall distribution rather than temperature or wind direction was a major factor, and mild, wet autumns were likely to favour the development of severe stem canker infections. Rawlinson & Muthyalu (1979) suggested, however, that once established, disease incidence was less influenced by fluctuations in weather conditions. Gladders & Musa (1980) suggested that older plants were less susceptible to infection. Hammond & Lewis (1987b) detailed the host cell reactions associated with limitation of the lesion and the development of resistance (Hammond & Lewis, 1986b). Leaves became progressively resistant during development (Hammond & Lewis, 1987a).

Differences between environments may be attributable to variable pathogenicity (Humpherson-Jones, 1984). Virulent types cause severe stem canker and plant death, while non-virulent types produce only superficial lesions and do not affect plant

vigour (Humpherson-Jones, 1984). In addition, Hammond & Lewis (1987b) showed that oilseed rape cultivars differ in resistance to the stem canker phase and that, of the variables that influenced the establishment of the systemic phase, the genotypes of the host and pathogen had a predominant effect (Hammond & Lewis, 1987a).

(e) Other diseases

Both downy mildew [*Peronospora parasitica* (Pers. ex Pers. Fr.)] and botrytis (grey mould) [*Botrytis cinerea* (Pers ex Pers.)] are favoured by cool and damp weather, while powdery mildew [*Erysiphe cruciferarum* (Opiz ex 11 June)] requires warm conditions. Downy mildew mainly affects leaves in autumn and may also affect stems and pods (Bonin & Fratczak, 1988; Davies, 1986). Development of the pathogen is reduced in dry weather (Sadowski, 1988). In surveys of commercial crops in Hertfordshire and Bedfordshire between 1975 and 1978, downy mildew was usually the most prevalent disease (Rawlinson & Muthyalu, 1979). However, much of the damage was to lower leaves which senesced soon after flowering (Rawlinson & Muthyalu, 1979), and although severely affected plants may be stunted, downy mildew is not considered a serious problem (Davies 1986; Sadowski, 1988). Powdery mildew, which mainly affects pods and stems during the later stages of development, is also thought to have an insignificant effect on yield.

Botrytis affects leaves, stems and pods, usually developing on damaged tissue but, at present levels, is not damaging to yield. Surveys in the locality of Rothamsted Experimental Station between 1973 and 1978 showed a variable occurrence of botrytis and there was no discernible weather-related pattern, which was suggested to be because the pathogen was ubiquitous (Rawlinson & Muthyalu, 1979). Even when incidence was low, however, infection usually caused plant death or loss of the distal part of the inflorescence (Rawlinson & Muthyalu, 1979). During prolonged wet weather before harvest in 1987, botrytis colonised maturing pods and was not affected by previous fungicide applications (Rawlinson, Church, Inman & Wilson, 1988a). In Poland, its occurrence on pods was associated with damage by brassica pod midge (*Dasyneura brassicae)* and cabbage seed weevil (*Ceutorhynchus assimilis)* (Bonin & Fratczak, 1988). The pathogen may also develop secondarily to infection by other

pathogens such as sclerotinia.

1.4.3. **Effects of prochloraz on yield and disease control**

This section will review the results of experiments testing the efficacy of prochloraz against oilseed rape diseases and will demonstrate considerable variability. Prochloraz applications usually reduce disease and increase yield (eg. Rawlinson *et al.*, 1984, 1988c; Sutherland, Oxley, Brokenshire & Munro, 1990; Wakerley & Russell, 1987), but in some experiments, no significant effects on yield were detected (eg. ADAS, 1983; Rawlinson & Cayley, 1984; Mercer, Easson, McGimpsey & Ruddock, 1989). Furthermore, it is not always possible to link reductions in disease incidence and severity to yield improvements. When disease levels are low, yield responses are often not obtained (Evans, Bowerman & Giltrap, 1988). Also, even when disease levels are reduced, trials in the early 1980s (ADAS, 1983) showed that a yield response to prochloraz does not always result. For example, although alternaria was effectively reduced when prochloraz was applied shortly after petal-fall, yield was unaffected (ADAS, 1983). In another study (Child *et al.*, 1988), yields of cultivar Jet Neuf were increased significantly by the triazole triapenthenol, but not by an application of prochloraz that reduced the level of light leaf spot, although the significant lodging that occurred might have masked any effects.

In Poland, prochloraz applied to control downy mildew at low incidence promoted considerable yield increases (Sadowski, 1988). Since prochloraz is inactive against this disease, this must have resulted from the significant reduction in the incidence of other pathogens, including alternaria, botrytis and sclerotinia. Interestingly, prochloraz increased yield despite plants having more leaves infected with downy mildew than the control, although this may have been a consequence of increased leaf retention in prochloraz-treated plants. In the UK, Rawlinson, Church, Inman & Wilson (1988b) showed that when light leaf spot was particularly severe, autumn and spring applications of prochloraz produced an increased number of fully expanded leaves per plant in late April.

Yield increases obtained from application of prochloraz in experiments at Rothamsted

Experimental Station were the result of enhanced leaf and pod area (Rawlinson *et al.*, 1989; Rawlinson & Williams, 1990). Jeffery *et al.* (1989) reported increases in seed number per pod, but not seed weight. Trials at Rothamsted revealed increases in pod number per plant in some varieties (Rawlinson *et al.*, unpublished, 1990). Sweet, Knight, Pope & Sparks (1989) showed that yield increases in disease-resistant varieties resulted from either delayed pod ripening, which prolonged seed development, thereby increasing seed weight, or a fungicidal effect against a non-obvious infection. Rawlinson *et al.* (1989) also reported decreased seed shedding in cultivar Bienvenu following prochloraz treatment.

1.4.4. **Effects of timing and rate of prochloraz application on disease control**

Rawlinson & Cayley (1984) showed that, for effective disease control, the timing of spray applications was more important than the amount of active ingredient deposited on plants. This finding has been substantiated by several other trials. For example, in a variety susceptible to light leaf spot, good disease control and associated yield responses were achieved when prochloraz was applied shortly after symptoms first appeared (Rawlinson *et al.*, 1984; Giltrap, 1986). High yields were reported in Poland when prochloraz was applied at stem extension and early pod-fill (Bonin & Fratczak, 1988). Botrytis was reduced very significantly but incidences of stem rot, sclerotinia, and stem canker (phoma) were similar to the control. Evans *et al.* (1988) showed that autumn and spring applications of prochloraz reduced levels of phoma infection on both leaves and stems infected by cankers or lesions. Sometimes, disease severity was reduced but not incidence. In experiments in the early 1980s, prochloraz applied at stem extension and again at 95% petal-fall or mid-late flowering gave good disease control. Yield benefits of 14-30% were achieved from a two-spray programme when light leaf spot was the most important disease (Wakerley & Russell, 1987). When prochloraz was applied at full-flower in trials in Scotland aimed at the control of late-season diseases, effects were not consistent across years (Sutherland *et al.*, 1990). Both botrytis and alternaria were reduced in one year, but not the following year. The addition of very late prochloraz applications gave no further disease control (Sutherland *et al.*, 1990), and disease reductions did not consistently produce yield responses.

Chemical control of light leaf spot is most effective in the autumn, often before symptoms are expressed (Rawlinson *et al.*, 1988b; Jeffery *et al.*, 1989). Autumn application of prochloraz gave good control of light leaf spot until mid-April (Rawlinson & Cayley, 1984). An additional spring spray, while reducing severity slightly but not incidence, increased yield still further. In 1985, however, the April application gave good control, particularly of disease severity, but little increase in yield (Rawlinson & Muthyalu, 1985). The effect of the autumn prochloraz application was found to be still evident eight months later, even though there had not been any visible sign of infection when the treatment was applied (Rawlinson *et al.*, 1988b). When light leaf spot was the main pathogen, the best yields were obtained from plots sprayed with prochloraz in both autumn and spring (Rawlinson *et al.*, 1988b). Giltrap (1986) showed that, although further disease development occurred following prochloraz application in March, levels of leaf infection were lower than untreated controls five weeks later. Yield was significantly correlated with the severity of infection but the proportion of plants infected was not reduced.

Two-spray (autumn and spring) programmes of prochloraz application have been shown to control disease, but do not necessarily result in any yield response (Evans *et al.*, 1988). Scott & Rea (1986) showed that disease control from two applications was better than a single spray at either timing but there was no direct relationship with associated yield increases. Similarly, a two-spray programme applied at stem extension (spring) and mid-late flowering (summer) rarely produced better yields than controls (Marshall & Harris, 1984), although it was better for controlling light leaf spot than a single spray at either timing. A late autumn spray was much better than at stem extension when assessed three weeks after each application, but by July, the situation was reversed (Scott & Rea, 1986). Harris, Scott & Bush (1989) showed that spray programmes commencing in the late autumn always gave better control than single full-dose applications (500 g active ingredient (a.i.) ha^{-1}) at stem extension. Scott & Rea (1986) recommended that prochloraz should be applied when disease first appears in autumn or winter, followed by a second application if new infections appear from the onset of stem extension. Two critical times for disease control in commercial systems were identified as stem extension (primarily for light leaf spot),

and the flowering/pod formation period (for sclerotinia and alternaria). Since a third prochloraz application at the maximum rate (500 g a.i. ha^{-1}) would exceed safety limits, iprodione, which in any case, is more effective than prochloraz in controlling alternaria, is widely used in the summer.

1.5. OBJECTIVES

The first part of the preceding survey indicates that the mechanisms of yield production in oilseed rape are not well understood. Several areas have been identified where previous findings appear inconclusive or contradictory. The overall objective of the present study is to further elucidate the important factors involved in the determination of seed yield. This will be achieved by describing the processes of yield production in typical oilseed rape crops in defined growing conditions, and by investigating the effects on these processes of the phytotonic fungicide prochloraz. Important areas of focus will be the identification of the sites and timing of yield losses, the sources of assimilate for yield production, and the factors causing limitations to the assimilate supply. The findings will then be used to identify possible ways in which yields could be further increased by manipulating the crop using breeding and/or agronomic methods.

Section 2: MATERIALS AND METHODS

2.1. INTRODUCTION

Experiments were conducted in the 1991, 1992 and 1993 growing seasons in commercial crops of oilseed rape on the University of Nottingham Farms. The locations were as follows: 1990/91, Bunny Hall Farm, Nottinghamshire (52° 51.2' N, 1° 16' W), approximately 10 km from Sutton Bonington; 1991/92, Grove Farm, Clifton, Nottingham (52° 55.4' N, 1° 10.5' W), 12 km from Sutton Bonington; 1992/93, the University Farm, Sutton Bonington (52° 49.3' N, 1° 16' W), approximately 1 km from the local meteorological station situated on the campus.

The cultivar used was the double-low Capricorn because this gave a large yield response to prochloraz in experiments at Rothamsted Experimental Station (Rawlinson *et al*, 1989; Rawlinson & Williams, 1990). It is a relatively long-strawed cultivar and, with the exception of stem canker, has poor resistance to the more important pathogens of the rape crop, but with good management practice, it has been shown to be one of the highest-yielding cultivars available commercially (PBI, 1990).

Each experimental area was surrounded by wide margins of the commercial crop of the same variety. In Seasons 1 and 2 (1991 and 1992), the experimental area was chosen from the commercial crop after emergence, so that any area of poor establishment could be avoided. In Season 3 (1993), however, the experimental area was drilled with a separate seed-lot (Plant Breeding International, Cambridge) before the surrounding commercial crop was sown. This was to reduce pressure from sclerotinia stem rot following problems with farm-saved seed in previous years.

2.2. EXPERIMENTAL DESIGN

The experimental design was a replicated block (Appendix I). Treatments consisted of prochloraz (Sportak 45 [AgrEvo Limited, formerly Schering Agriculture]) application timings (*1*. two-five leaf stage [AUTUMN], *2*. green-bud stage [SPRING], and *3*. after petal-fall [SUMMER]) in all combinations in 1991 and 1993, but only two timings in 1992. The experiments in Seasons 1 and 3 were therefore arranged in a

2x2x2 multifactorial, giving eight possible treatments, while the experiment in Season 2 was restricted to a 2x2 design, with only four treatments. Within each block, treatments were allocated randomly. The second experiment received only two applications of prochloraz because the original trial, which had already received the first application, had to be abandoned following severe pigeon damage during the late winter. By the time the experiment was relocated, it was too late to apply the first spray.

Treatments were replicated in four blocks except in 1991, when one block was abandoned because of poor establishment and atypical growth (Appendix I, Figs. 1-3). Each plot was 35m long and 6m wide and the row width was approximately 18cm. In Season 3, however, the plot length was doubled, to allow an application of the fungicide iprodione to be made to half of each main plot. With the exception of fungicide applications, all the experiments received the same pre-drilling cultivations and crop protection measures as for the commercial crops (Table 2.1). Seedbed preparation consisted of turbo-tillering twice and rolling soon after harvesting of the previous crop. Immediately prior to drilling, the ground was spring-tine cultivated, and after drilling, it was rolled. Fertiliser applications differed between years in the dates on which they were made, and the rates used (Table 2.1).

2.3. FUNGICIDE TREATMENTS

2.3.1. **Prochloraz application**

The application rate for prochloraz was 500 g a.i. ha^{-1}. In commercial agriculture, it is normal to use two applications (autumn and spring) each of 500 g a.i. ha^{-1}. The maximum application over the season recommended by the manufacturers is 1.1 kg a.i. ha^{-1}. Therefore, plots receiving three applications of prochloraz exceeded this limit considerably. Details of application times and methods for all experiments are given in Table 2.2. Owing to poor weather and the unavailability of spraying equipment, prochloraz applications were delayed in the first and second seasons. Thus the spring applications were several weeks late (at flowering), while that in the summer in 1991 was almost four weeks late. Prochloraz applications were made either with a Drake and Fletcher knapsack sprayer with a 2.3 m boom or with a Lely 250 sprayer with an

Table 2.1. Agronomic details for rapeseed cultivations in three seasons

	SEASON 1 (90/91)	SEASON 2 (91/92)	SEASON 3 (92/93)
Sowing date	30 Aug	9 Sept	7 Sept
Seeding rate (kg ha^{-1})	8.0	7.5	7.5
Previous crop	Winter barley	Winter barley	Winter wheat
Soil type	Keuper marl	Alluvium	Alluvium
Aspect	South-west	Flat	Flat
Drill direction	East-west	East-west	East-west
Nitrogen fertiliser (kg ha^{-1})	100 (9 Oct)	37 (7 Dec)	
	68 (31 Jan)	46 (6 Feb)	48 (20 Feb)
		110 (9 April)	112 (19 Mar)
Seedbed fertiliser (kg ha^{-1})			
Phosphorus	211 (9 Aug)	205 (10 Aug)	130 (15 Aug)
Potassium	211 (9 Aug)	205 (10 Aug)	130 (15 Aug)
Pesticides* (active ingredients)	Cypermethrin; Deltamethrin; Alpha-cypermethrin	Cypermethrin	-
Herbicides* (active ingredients)	Fluazifop-P-butyl; Metazachlor; Benazolin + clopyralid; Clopyralid	Fluazifop-P-butyl; Metazachlor	Metazachlor; Benazolin + clopyralid; Sethoxydin
Pre-harvest treatment	Desiccant *Reglone* (6 Aug)	None	Desiccant *Reglone* (30 July)
Combine date	13 Aug	27 July	6-7 Aug

(* for the entire season)

18 m boom fitted with Lurmark F110-04 knozzles (Table 2.2). Knapsack applications were made with 168 l ha^{-1} water, and large sprayer applications with 300 l ha^{-1}. Spring applications with the knapsack sprayer resulted in considerable damage to the plots due to the operator walking through the plots at a relatively late stage of crop development. It was not always possible to avoid these areas when sampling for growth analysis.

Table 2.2. Prochloraz application dates, methods and spray rates used in the experimental programme

	Season 1 (1991)	Season 2 (1992)	Season 3 (1993)
AUTUMN	22 November[1]	-	30 October[1]
SPRING	23 April[1]	28 April[1]	2 April[2]
SUMMER	2 July[2]	10 June[2]	4 June[2]

[1] *knapsack sprayer*; [2] *Lely 250 sprayer*

2.3.2. **Application of iprodione in Season 3 (1993)**

In Season 3, half the area of each plot was sprayed with iprodione (Compass [Rhone-Poulenc]) to control sclerotinia stem rot which was a major problem in the previous seasons. Iprodione was applied during flowering at a rate of 3 l ha^{-1} in 300 l ha^{-1} water using a Lely 250 sprayer. Each subplot was 35m long. Sampling for growth analysis and disease assessment was from the unsprayed subplots until sclerotinia infection became evident in mid-June, when sampling was made from iprodione-sprayed subplots. Each subplot receiving iprodione was selected randomly.

2.4. DISEASE ASSESSMENT

2.4.1. **Sampling procedure**

Disease development was monitored by making assessments, normally four to five weeks after each prochloraz application, together with a post-winter check just before the spring application was made (Table 2.3).

In 1991, the plants in only one block were examined, except for the final assessment in July, when all blocks were used. In each case, all treatments were included. In 1992, assessments were made on all plots in all blocks. In 1993, the first two assessments, which were preceded only by the autumn prochloraz application, were made on a sub-set of plots consisting of control plots and plots receiving prochloraz only in the autumn, but in later assessments all plots in all blocks were sampled.

In the first two seasons, ten plants were taken at random from each plot at each assessment. At each assessment in Season 3, 20 plants were taken for each treatment (10 plants from each subplot including the future iprodione treatment). For assessments that preceded the application of iprodione in May, the samples from each subplot were pooled, but for the final assessment, at the end of June, all subplots were analysed separately.

For the late-autumn assessment, the whole plot area was sampled, but after stem extension had started, the sampling area was confined to a small area near the end of each plot, to avoid excessive damage by trampling. Plants were removed by cutting the stem at ground level, then placed in polythene bags and examined for disease following storage for two days at 3°C allowing visual symptoms to develop.

2.4.2. **Visual assessment of disease symptoms**

Disease assessments during the winter and early spring were made on vegetative plants, and involved inspection of leaf material only. Additional plant components were included in later assessments (Table 2.3). For vegetative plants (winter and early-spring assessments), all leaves were counted and examined except the smallest unexpanded ones. For plants post-flowering, only main-stem leaves were assessed. For each disease, leaf symptoms were recorded as lesion scores. Following removal of leaves, stems were examined, and finally a general assessment was made of all the pods.

The scoring systems used for each disease are shown in Table 2.4. The 0-3 scoring system for leaves and stems was based on the area infected (Rawlinson, 1979), in

which, for a leaf, a trace of the disease was indicated by a score of 0.1; score 1 = < 10% of area infected; score 2 = < 50%; score 3 = 50-100%. A 0-4 scale was used for botrytis and sclerotinia, with 1 indicating a trace of disease, 2 a superficial lesion, 3 a lesion girdling the stem, and 4 a dead plant. In the third season, basal stem cankers were far more common and severe, whereas in previous seasons, infection was mainly as main-stem lesions. Therefore in this season, a more detailed assessment method was used in which a transverse cut was made through the damaged stem base at the widest part, and a visual assessment of the extent of penetration of the lesion into the stem was made using a 0-6 scoring system (Gladders & Musa, 1979, 1981; Hammond & Lewis, 1986a). Pod diseases were normally assessed either as the number of pods infected or the percentage of the total pod area infected (Table 2.4).

Table 2.3. Disease assessment dates for each season (1-3). L (leaf), S (stem), and P (pod) indicate the organs assessed on each date

	Season 1	Season 2	Season 3
After AUTUMN prochloraz	18 December (L*)	-	27 November (L)
Early-spring	16 April (L)	20 March (L)	26 March (L)
After AUTUMN & SPRING prochloraz	25 May (L,S,P)	26 May (L,S,P)	29 April (L,S)
After AUTUMN, SPRING & SUMMER prochloraz	26 July (S,P)	10 July (S,P)	7 July (L,S,P)

2.4.3. **Presentation of data**

For each plot, totals were calculated: for lesion scores for each disease on each component; for numbers of leaves and numbers of infected leaves; and for numbers of infected plants. Lesion scores were expressed per leaf and per plant, either for infected leaves and plants only, or for total leaves and plants. The proportion of leaves infected was calculated for each disease. Stem and pod lesion scores were expressed either per infected plant or per plant. For each disease on each plant component, the proportion of plants infected was calculated.

Table 2.4. Disease assessment scoring used for each disease on each plant component

	LEAF	STEM	POD
Downy mildew	+/-	-	Number infected
Botrytis	+/-	0-4	Number infected
Light leaf and pod spot	0-3	0-3	% total pod area infected
Alternaria	0-3	-	% total pod area infected
Phoma/stem canker	Number of lesions	0-3*, 0-6#	Number infected
Sclerotinia	-	0-4	-
Powdery mildew	-	+/-	+/-

* Seasons 1 and 2, # Season 3

2.4.4. Assessment of pest damage

The extent of pest damage was assessed at the same time as disease assessments were made. Cabbage stem flea beetle (*Psylliodes chrysocephala*) feeds on oilseed rape throughout its life cycle; adult beetles make holes in leaf blades while larvae burrow inside the stem and leaf petioles. Damage by both adult beetles and larvae was assessed on leaves and stems, and expressed as numbers of lesions (in the same way as for diseases), the proportion of leaves affected and the proportion of plants. Pigeon (*Columba palumbus*) damage to leaves was assessed as the number of leaves affected per plant and also per damaged plant.

2.4.5. Analysis of data

Statistical treatment of data for assessments of both fungal diseases and pest damage involved analysis of variance, according to prochloraz treatment, using Genstat5. For each plot, each lesion score and calculated percentage was considered as a separate entity, and the variance for each was analysed accordingly. Prochloraz application times constituted factors.

2.4.6. Assessment for stem canker

During the summer of 1993, an exceptionally high incidence of stem canker occurred. This was monitored every two weeks by examining the plant material used for growth analysis. For control plots and those receiving three applications of prochloraz (AU+SP+SU), the extent of basal stem lesioning was assessed in the same way as for the regular disease assessments, for all the plants from a $1m^2$ sample. Lesion scores were used to calculate a mean severity score for each plot. The incidence of stem canker was calculated as the percentage of plants infected. In addition, the relative incidences of low, moderate and high disease severity were calculated by grouping lesion scores into categories. As for other disease data, statistical analysis involved analysis of variance using Genstat5.

2.5. CROP GROWTH AND DEVELOPMENT

2.5.1. Introduction

Visual observations of the development of the crop were made regularly from establishment onwards. Detailed destructive growth analysis was used to monitor crop growth and development throughout each growing season. In 1991, growth analysis began in late January, and continued at intervals until April, after which sampling was weekly until final harvest in August. In 1992, analysis started in March and continued after flowering at fortnightly intervals until final harvest. Samples were taken at similar intervals in 1993 after flowering, but in this particular season, sampling started in early November and continued throughout the winter. The interval between winter harvests varied between two and four weeks according to the rate of crop growth.

2.5.2. Harvesting procedure

A sample area of 1 m^2, i.e. 1 m x 1 m square, was used throughout. Sampling areas were taken from a corresponding area in each plot, beginning at one end of the plot and progressing along with each successive harvest. This method was used to eliminate bias in sampling associated with variations in visual appearance of the crop.

During vegetative growth and until the crop had reached a height above about 40 cm in the spring, whole plants were cut off at ground level from the designated area. In

Season 1, with the exception of the first harvest, in which only control and AU+SP+SU plots were used, all plots were sampled until shortly before flowering. In Season 2, when there was no application of prochloraz in the autumn, only one plot was sampled from each block prior to the spring prochloraz application. In Season 3, harvesting during the autumn and early spring was restricted to control plots and those receiving prochloraz only in the autumn.

When stem extension was in progress, and thereafter, a stratified sampling technique was used (Norton & Shipway, unpublished; Bilsborrow & Norton, 1984, 1988; Bilsborrow, 1985), in which the crop profile was harvested in 20 cm layers by means of a frame constructed within the crop (Plate 1). Two wooden runners, each approximately 140 cm long and 8 cm wide, with two metal sockets 1 m apart on the upper surface, were pushed along rows of the crop at ground level, 1 m apart. Aluminium rods were inserted into the sockets to form vertical uprights at the corners of a 1 m square. Shorter aluminium rods were then clamped to these to form horizontal squares at 20 cm intervals upwards from ground level. The positioning of the rods was such that those parallel to the crop rows were 1 cm lower than those at right angles to the rows. A moveable rod (1 cm diameter) was placed across these rods and this enabled accurate sampling to be made at exactly 20 cm intervals.

Harvesting proceeded from the top of the crop downwards. Successive layers were removed by aligning each plant or component with the top of the moveable rods and cutting with secateurs, proceeding from the edges inwards. Overhanging parts were aligned with the vertical plane and either included (inside the 1 m square), or discarded (outside the 1 m square). Stems in the lowest layer were cut off at ground level. Harvested plant material was collected in polythene bags and stored at 3°C until analysed.

From the onset of flowering onwards, only control and AU+SP+SU plots were harvested in Seasons 1 and 3, and only control and SP+SU plots in Season 2. The sampling procedure was extremely time-consuming. Consequently, it was only possible to harvest three plots for each treatment on each occasion.

Plate 1. Frame constructed within the crop for stratified sampling. Surrounding plants were removed to allow easier viewing.

At maturity, all plots in all blocks were harvested using the frame. Instead of harvesting in 20 cm layers, however, the profile was divided into only two sections: the pod canopy (removed first) and stem material remaining below this. In Seasons 1 and 2 (1991 and 1992), the pod canopy was above 80 cm, whereas in the third season (1993), when the crop was considerably shorter, it was above 60 cm. In 1991, control and AU+SP+SU plots were harvested several days before all the other plots (29 July) using the 20 cm layer sampling system and collected in polythene bags as previously. All other treatment plots were harvested either four or seven days later (2 and 5 August) in two sections (pod and stem). This material was collected in cotton sacks and placed on a drier prior to analysis. In later years, final harvest samples were collected in polythene bags, stored at 3°C and analysed fresh because drying was found to increase pod shattering.

2.5.3. **Growth analysis**

(a) Vegetative plants

Generally, the whole sample from the 1 m^2 area was used for growth analysis except in the first season, when a subsample of approximately 30% by fresh weight of the total vegetation was used. This was derived from the main sample after thorough mixing. Total, green and senescing leaf numbers were determined, and leaf numbers included only those expanded more than 50%. Projected areas of green leaves were determined using an area metre (Li-Cor Model 3100), and dry matter contents were determined following oven-drying to constant weight at 85°C, usually for 48 hours.

(b) Reproductive growth

Each 20 cm layer of the crop profile for each plot was divided into its component parts, enabling measurements to be made of leaf, stem and pod area as above, and dry matters following oven-drying at 85°C to constant weight (usually 48 hours). The photosynthetic green areas of stem and pod were calculated by multiplying values obtained from the area metre by $\pi/2$, assuming that these organs were cylindrical and that only half of the total area was capable of photosynthesis at any one time (Bilsborrow, 1985).

Pods were counted as soon as the petals had fallen from the first flowers. In 1991 and 1992, flowers, buds, pod stalks and aborted pods were grouped together so that their total together with that of fertile pods gave an estimate of potential pod numbers. In 1993, these categories were counted separately.

During early pod development, subsamples of 40 randomly selected pods preserved in ethanol/acetic acid (10/5 volume/volume) were used for the assay of seed numbers. In the first season, seed numbers in these small pods were determined following dissection under a binocular microscope, but in later years, seeds were counted *in situ* using a hand lens to view the pods against a light source.

In the later stages of pod development, when appreciable seed development had occurred, seeds were removed directly from a known number of pods, usually 100-200. Hull and seed dry weights were determined after oven-drying as for other plant material. Seed number per pod was determined by counting the seeds in a subsample of known weight from the dried seeds. Thousand-seed weight (1000-seed weight) was calculated by determining the weight of at least 1500 seeds.

Harvests late in the season included an additional category of split/shattered and diseased pods. This included pods that had shattered both before and after harvesting. Pods that shattered prior to harvesting were largely devoid of seed, whereas those that shattered post-harvesting were retained with seed. The number of pods that contributed to final yield was calculated from the known weight of shattered pods by subtracting pods that shattered before harvest. Both categories of shattered pods were added to the intact fertile pods to give a total pod number.

At final harvest in each season, the large samples from grouped layers were analysed in the same way as for previous harvests, for both fresh and dried material. Green area measurements were made only in 1991 (control and AU+SP+SU plots).

2.5.4. **Combine yields**

The undisturbed half-plots remaining after the final sampling for growth analysis were

combined following desiccation in 1991 and 1993, but combined direct in 1992, using a Walter & Wintersteiger Seedmaster Universal Hydrostatic combine with a 1.75m cut. Two strips of known length (approximately 12m) were taken through the centre of each plot in 1991 and 1992. In 1993, all subplots were combined but hand-harvesting was restricted to the iprodione-treated plots.

Seed samples were collected in paper sacks, cleaned and weighed. Moisture contents were determined as soon as possible after harvesting by oven-drying samples of approximately 150 g for one week at 85°C, and combine yields were corrected to 9% moisture. 1000-seed weight was determined for each plot by hand-counting about 1500 seeds in the same way as for hand-harvesting.

2.5.5. **Data analysis for growth and development**

(a) Introduction

For each season, the data for individual harvests were treated as discontinuous and were analysed separately. This also applied to final harvest data. In order to investigate the effect of season on the effects of prochloraz, a further analysis was made in which the final harvest data for all seasons were combined and analysed using season as an additional factor.

(b) Growth analysis through the season

For vegetative growth, green areas and dry weights of each type of organ (leaf/stem) were added to obtain values for total green area index (GAI) and dry matter (DM) for each plot. For reproductive plots, the components were combined for each layer, and layer values for all components were combined to give plot totals. All green area and DM data were expressed on a unit crop area basis (m^{-2}). For seed data, mean values of seed number per pod were calculated for each plot by weighting individual layer values according to the contribution made by each layer to the total seed DM.

Analyses of variance were performed for all the components. Until the final harvest, statistical analysis involved a comparison of only two treatments. For vegetative plants, autumn-treated plots were compared with non-treated, while for reproductive

plants, AU+SP+SU plots (SP+SU in 1992) were compared with controls. Analysis of variance was performed using prochloraz spray as a factor value with two levels.

When stratified sampling was initiated, each layer was treated as a separate value, and analysis of variance was applied to the spray x layer interaction. For seed and pod data, which were generally confined to the upper layers, and for leaf data following senescence in the lower layers, analyses were restricted to the relevant layers. Plot totals were analysed in the same way as for vegetative plots.

(c) Final harvest

Final harvest data (seed yields, components and DM) were analysed as the sum of all material in the sample. Analysis of variance was used to compare DM data and pod and seed numbers across all treatments by taking each prochloraz application (AUTUMN, SPRING and SUMMER) as a separate factor, each with two levels according to whether or not each was applied to a particular plot. This involved analysis of the interaction between all three prochloraz applications.

Combine harvest data were analysed in the same way as hand-harvested data with the exception of 1993. Since all subplots were involved in this season, an extra factor for the iprodione application was introduced to the analysis. Four different spray factors were then involved and, covering all possible treatment combinations, the analysis of variance analysed the interaction between them.

(d) Leaf number data (1993)

Numbers of leaves in each category were expressed on an area basis and on a per plant basis. Total leaf numbers were given by the sum of green leaves, senescing leaves and missing leaves (indicated by leaf scars). The sum of senescing and missing leaves was used as a measure of overall leaf senescence. Green area and DM data combined with leaf number data were used to calculate mean values for individual leaf size. Analysis of variance was performed on each leaf number component and derived leaf size components for prochloraz treatment.

2.6. MEASUREMENT OF SOLAR RADIATION INTERCEPTION IN THE CROP

Total radiation interception was measured by means of tube solarimeters positioned in the crop at successive 20 cm intervals from the ground upwards. In each season, measurements were confined to one untreated control plot and one AU+SP+SU plot (or SP+SU in 1991/92), which were taken as representative of the general pattern of growth and development over all the blocks. The area used for the placement of solarimeters was undisturbed by growth analysis and disease assessment sampling.

Each solarimeter was placed along plant rows, which were in an east-west direction. Solarimeters at successive height levels were placed in alternate rows (30-40 cm apart), with the lowest solarimeter in the southernmost row and successively higher tubes added northwards in order to exclude mutual shading. Measurements of radiation penetration into the crop were made by integrating over one day every week in 1991 and 1993, and every two weeks in 1992. Solarimeters were removed from the crop following each period of integration and replaced on each subsequent occasion. This avoided disruption of the natural structure of the profile since plant organs would have been supported by the solarimeters if left *in situ*.

Total incident radiation was measured using a solarimeter arranged in parallel to the others and placed above the crop. The total radiation received was assumed to be the same as that incident on the meteorological site at Sutton Bonington. Reflected radiation was measured by placing an inverted solarimeter approximately 30-40 cm above the crop (Yates & Steven, 1987), again positioned parallel to the other solarimeters.

Solarimeters were calibrated relative to the one measuring the total incident radiation, and the radiation incident at each 20 cm horizon was calculated as a percentage of the total. Absolute measurements of incident radiation were calculated as proportions of totals obtained from meteorological records for the Sutton Bonington site.

Section 3: YIELD PRODUCTION IN OILSEED RAPE

3.1. INTRODUCTION

Winter oilseed rape is sown in late August or early September in the UK and is generally harvested during July, according to environmental conditions. Standard growing practices recommend that growth in the autumn should be adequate to allow rapid resumption of growth in the spring, enabling the achievement of a minimum crop size at flowering so that potential yield is not limited. These recommendations assume that yield production is dependent on growth prior to flowering because crops need to be large in order to support their pods to maturity (Mendham *et al.*, 1981). Considerable pod losses occur after flowering regardless of the number produced (Mendham *et al.*, 1981) and seed losses are usually substantial (Norton & Harris, 1975). Bilsborrow & Norton (1988) studied the source and extent of these losses and proposed that the main phase of yield determination occurred during seed development and was determined by the photosynthetic capacity of the crop at this time. In the present study, the importance of pre-flowering growth in yield determination is examined and additional evidence is presented for seed yield being mainly determined by current assimilation during the seed-filling stage.

3.2. YIELD DETERMINATION IN THREE SEASONS

3.2.1. **Introduction**

The growth and development of winter oilseed rape have been described for older varieties by Mendham (1975) and Shipway (1981). These workers divided growth into autumn and spring phases described according to the accumulation of dry matter and changes in green area. Bilsborrow (1985) described growth and development as a sequence of events determining yield. Four interdependent but not completely distinct stages were proposed that described how different organs sequentially contributed to the production of final yield (Bilsborrow & Norton, 1984). These were:

I. Vegetative
II. Stem extension, development of the reproductive framework and flowering
III. Pod development
IV. Seed development.

Growth and development are interdependent processes ultimately controlled by radiation interception and temperature. A consideration of the interaction between the two has not been undertaken for oilseed rape, which, within a season in the field-grown crop, is complicated by the association of temperature and radiation with daylength. To elucidate this relationship, the process of yield formation has been examined over three contrasting seasons with respect to temperature and radiation patterns.

3.2.2. Crop growth and development in 1993

The general pattern of crop growth and development will be described for 1993 which represented a typical season for the plant densities used (80 plants m^{-2} in spring). On the basis of dry matter (DM) and green area changes with time, the developmental sequence in 1993 was defined in terms of the same four stages described by Bilsborrow (1985) rather than the three stages used by Mendham & Salisbury (1995) (Fig. 3.1). The sequence started with a vegetative phase in which leaf accounted for almost all the green area and provided all the assimilates for further growth (Stage I). In Stage II, the reproductive framework was developed, when leaf and stem together constituted most of the green area. In Stage III, the pod walls expanded to maximum area and weight and almost all the leaf disappeared. In the final stage (IV), pods and stem accounted for most of the green area and were largely responsible for the assimilation associated with seed development (Stage IV). The significance of each developmental stage will be examined in more detail for the 1993 season (Fig. 3.1).

I. The vegetative stage

The vegetative crop remained small from early November until mid-March with total DM averaging around 30 g m^{-2}. Throughout this phase the crop consisted mainly of leaf, and DM remained constant because of leaf turnover. The low overall growth rates from early November to early January and from early January to mid-March were 0.13 g m^{-2} day^{-1} and 0.32 g m^{-2} day^{-1} respectively (Table 3.1), indicating that the crop was changing little. DM accumulation was limited by low temperatures during the winter and did not increase with accumulated radiation until temperatures were rising in March (Fig. 3.2).

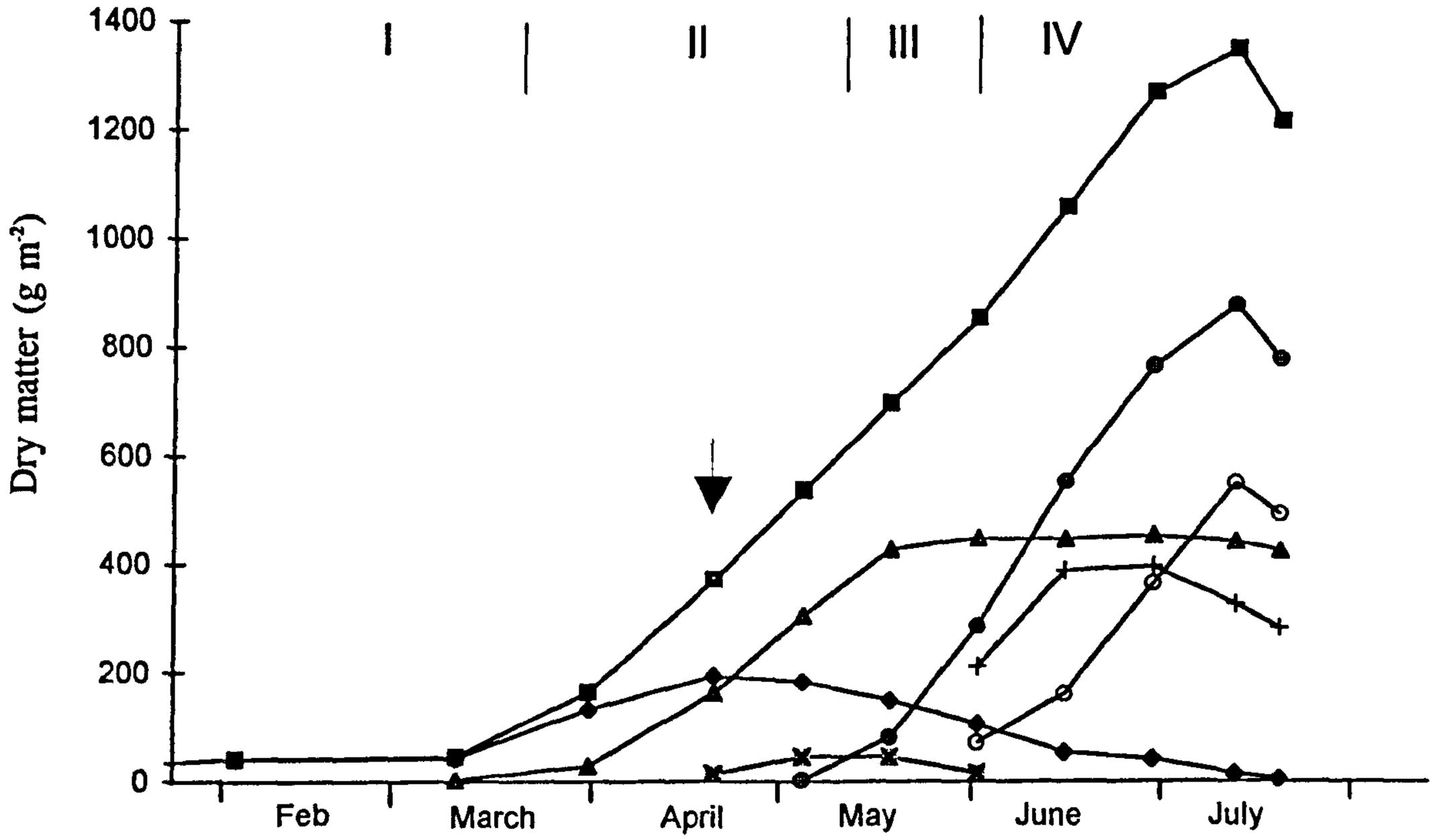
Fig. 3.1. Growth and development of oilseed rape in 1993: (a) Dry matter, (b) Green area index

♦	leaf	+	hull
▲	stem	○	seed
✖	flower	■	total
●	pod		

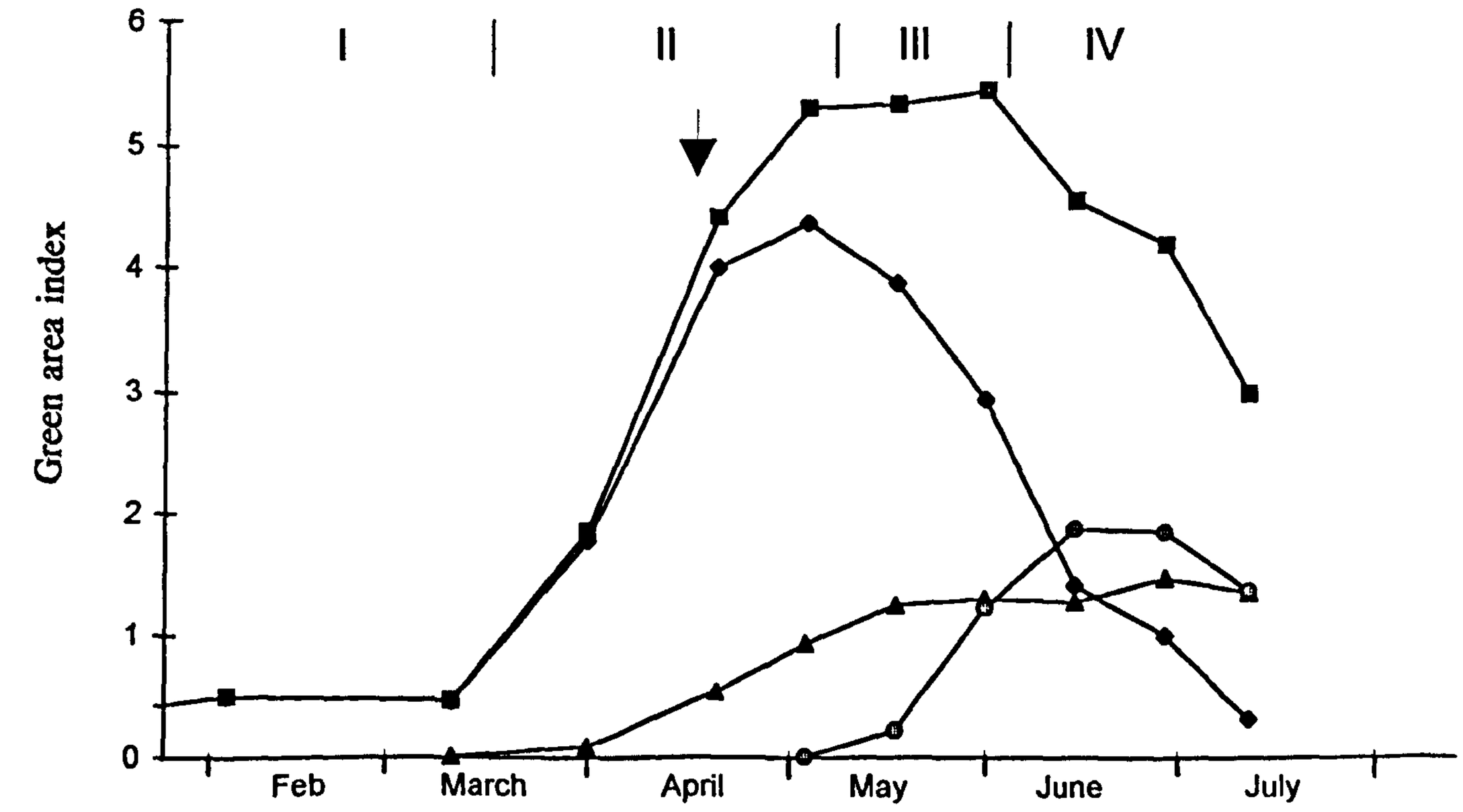
Arrows indicate onset of flowering

Developmental stages are indicated by Roman numerals

(a)


I
II
III
IV
Dry matter (g m-2)
1400
1200
1000
800
600
400
200
0
Feb
March
April
May
June
July

(b)


I
II
III
IV
Green area index
6
5
4
3
2
1
0
Feb
March
April
May
June
July

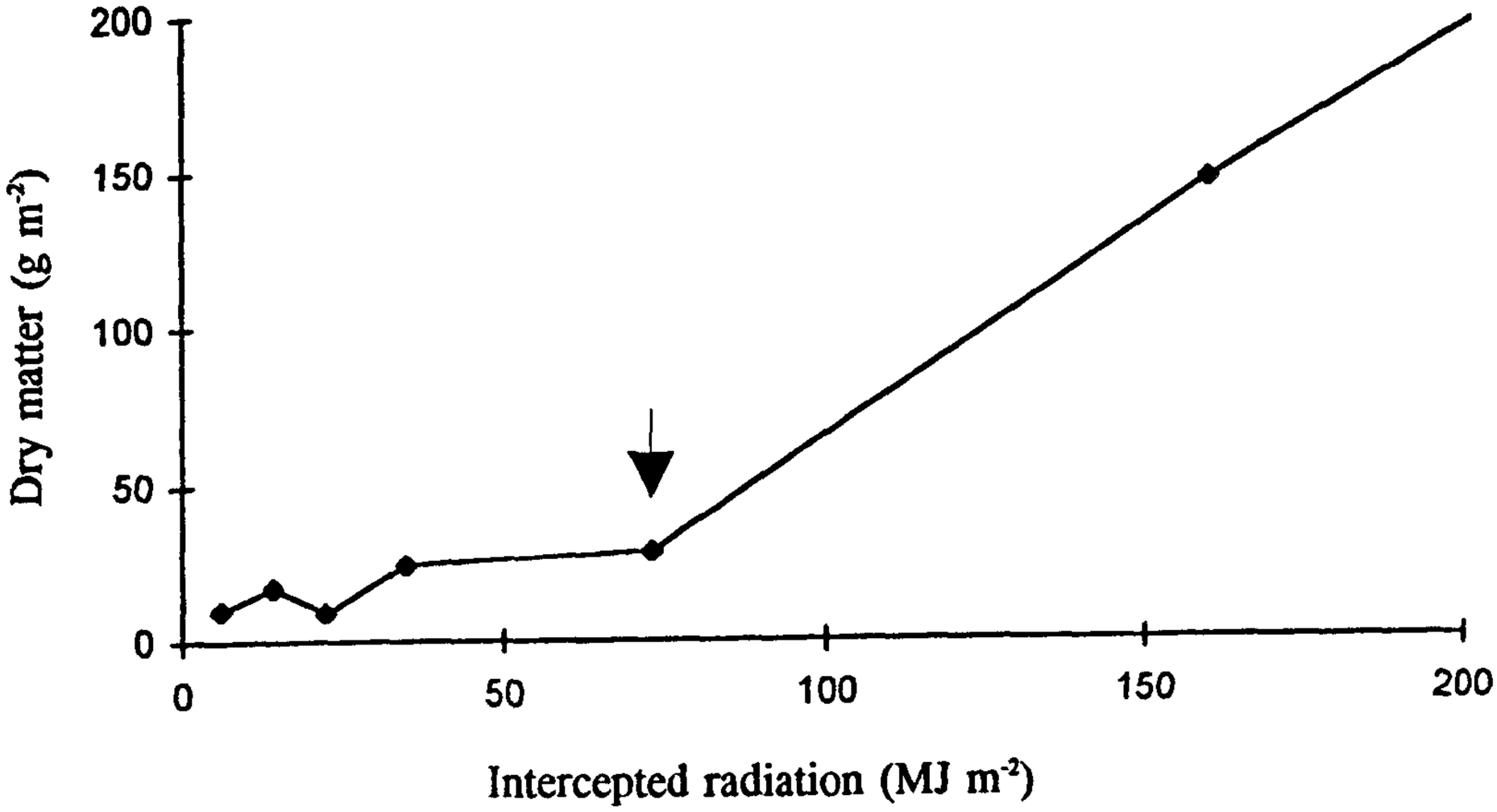


Fig. 3.2. The relationship between radiation interception and dry matter production during vegetative growth (Stage I) in 1993. Arrow indicates the date on which weekly average temperatures increased above 5°C (11 March).

Table 3.1. Rates of DM accumulation (g m^{-2} day^{-1}) during each developmental stage in three seasons

	1991	1992	1993
Vegetative (Stage I)	1.29[1]	-	0.13[1] 0.32[2]
Stem extension up to flowering (Stage IIa)	9.8	9.4	10.4
Flowering to full flower (Stage IIb)	12.5	13.7	11.6
Pod development (Stage III)	8.1	17.3	11.1
Seed development (Stage IV) (*June only**)	11.8	10.5	14.4

[1] Rate for November to January, [2] January to March.
** Rate calculated for June only to avoid DM losses due to pod-shattering*

II. Stem extension, development of the reproductive framework and flowering

The second stage started with a rapid increase in the rate of DM production (10.4 g m^{-2} day^{-1} in the first three weeks of April) (Table 3.1). This was largely due to the rapidly expanding leaf area which provided assimilates for the DM production for stem elongation and branch formation. Following the initial exponential growth phase in March, total DM increased linearly. During the first three weeks of flowering (defined as the date when 50% of plants had at least one open flower), the growth rate increased to 11.6 g m^{-2} day^{-1} (Table 3.1).

Shortly before flowering, the lowest leaves of all plants began to senesce, and with time this progressed up the profile. Thus leaf DM attained a maximum at the onset of flowering and thereafter it declined because senescence exceeded production. New leaves that developed higher up the profile on the flowering branches were small and bract-like. Leaf and stem DM contributed equally to total DM at flowering. Maximum leaf area index (LAI) was achieved two weeks later when stem DM and area were approximately two thirds of their maxima. Although leaf DM declined, total DM accumulation increased linearly due to stem and branch DM production (maximum on 11 May) and the initiation of pod growth.

At flowering (20 April), crop DM was 372 g m^{-2} but flowers accounted for only a

small proportion of the DM. Maximum stem DM (reproductive framework) coincided with the end of this stage, but flowering had not ceased. One of the main functions of the leaf during this period was the provision of assimilates for the development of the reproductive framework. When this was completed, leaf DM and area were 75% and 92% of their respective maxima and were declining rapidly. Leaf production ceased at the end of flowering and remaining leaf was located in and just below the developing pod canopy.

III. Pod development

Limited pod DM accumulation began during early flowering, but until maximum stem DM was attained, development from these first-formed flowers was restricted. The linear phase of pod DM accumulation began after maximum stem DM and flower numbers (and potential pod numbers) were attained in mid-May. Pod wall (hull) growth was almost completed during Stage III before attaining maximum DM and area early in Stage IV. Seed growth was restricted until maximum hull DM and area were attained. Leaf senescence proceeded up the profile until the remaining leaf material (bract-like leaves subtending the branches) was located only in the pod canopy. Despite leaf senescence, the rate of DM accumulation was essentially constant throughout Stages II and III (Table 3.1). Pod accounted for all the DM accumulated because while stem DM remained constant, that of leaf declined.

IV. Seed development

Rapid seed development began shortly before the attainment of maximum pod wall DM and area. An approximate date (5 June) was obtained by extrapolation of the linear part of the seed DM curve (Fig. 3.1). Maximum pod area was attained early in this stage (15 June). Throughout this period, DM accumulation was faster than in any other phase (Table 3.1). Seed DM amounted to approximately 25% of the total pod DM at the onset of seed development but on completion of this stage it accounted for 63% and 41% of the pod and total plant DM respectively. During this stage, the crop accumulated 33% of its total DM at maturity. Stem DM remained constant throughout Stage IV indicating that no remobilisation of stem and branch DM occurred. Hull DM declined mainly through continued pod losses. Throughout Stage

IV, seed growth accounted for all DM accumulation which must have been supported entirely by current assimilation in the pod walls, stems and branches together with a little from remaining leaves. Final biomass was 1220 g m^{-2} and the harvest index (hand-harvested) was 0.42 with final seed yields of 4.91 t ha^{-1} (hand-harvested) and 4.00 t ha^{-1} (combined).

Main features of seed yield development

Remobilisation of DM within the plant during Stages III and IV was minimal since stem DM remained constant during pod and seed development. It was concluded that yield formation (seed growth) was dependent upon current photosynthesis of pods, branches and stems, with a small contribution from remaining leaf throughout Stage IV. Therefore, although leaf supported the growth of the reproductive framework on which the yield was borne, it probably made only a limited contribution to seed growth.

3.2.3. Comparison of growth and development between seasons

The robustness of the general growth and development pattern will now be tested in contrasting seasons (1991 and 1992) with respect to radiation and temperature.

The effect of season

Meteorological data for all seasons are presented in Appendix VII. Since most growth occurred between April and July, mean temperatures and radiation for these months are compared with the long-term average (Table 3.2). Incident solar radiation levels and temperatures were low in 1991 and high in 1992, whereas in 1993, temperatures were low but radiation levels were higher than average. The length of developmental stages was largely determined by temperature accumulation and not solar radiation interception (Tables 3.3 and 3.4). Thus modifications due to seasonal conditions produced long and short growing seasons in 1991 and 1992 respectively.

Developmental sequence

Although the duration of the developmental stages was variable because of the response to temperature (Mendham & Salisbury, 1995), the qualitative patterns of

Table 3.2. Solar radiation receipts per day and mean monthly temperatures in May, June and July in three seasons with long-term averages (L.T.Av.)

	Solar radiation per day (MJ m^{-2} day^{-1})				Mean monthly temperature (°C)			
	1991	1992	1993	L.T.Av.*	1991	1992	1993	L.T.Av.#
April	11.0	11.5	10.9	11.1	7.9	8.7	9.5	7.0
May	12.5	19.0	16.0	14.9	11.0	13.4	11.4	12.8
June	13.0	18.0	17.5	16.5	12.1	15.9	14.7	14.9
July	8.5	15.0	17.0	15.5	17.4	16.2	15.3	17.1

Long-term averages * 1958-94; # 1921-94

Table 3.3. Growing degree days above 0°C in each developmental stage from stem extension to maturity in each season

	1991	1992	1993	Mean
II (stem extension, flowering)	489	489	455	478
IIa (stem extension to flowering)	*230*	*230*	*230*	*230*
IIb (flowering to full flower)	*259*	*259*	*225*	*248*
III (pod development)	286	324	311	307
IV (seed development)	536	445	463	481
Total	1311	1259	1229	1266

Table 3.4. Solar radiation (total incident and intercepted) in each developmental stage between stem extension and maturity in three seasons (MJ m^{-2})

			1991	1992	1993
Total	II	(a) Stem extension-flowering	318	280	315
		(b) Flowering-full flower	339	369	295
		Total	657	649	610
	III	Pod development	298	417	354
	IV	Seed development	469	657	755
	Total		1424	1723	1719
Intercepted	II	(a) Stem extension-flowering	282	225	259
		(b) Flowering-full flower	250	280	205
		Total	532	505	464
	III	Pod development	172	226	240
	IV	Seed development	386	599	669
	Total		1090	1330	1373

growth and development were the same in all three seasons. This developmental sequence is dependent on the specific functions of organs in each stage and, relating to the husbandry conditions employed, these are together responsible for the yield production.

Dry matter and seed yield production

The major features of growth and development in the three seasons are listed below with reference to Figs 3.1 and 3.3.

1. The rate of DM accumulation from the beginning of stem extension up to flowering (Table 3.1) was not related to the size of the vegetative crop (Table 3.5), nor to the total amount of radiation intercepted during this period (282, 225 and 259 MJ m^{-2} in 1991, 1992 and 1993 respectively; Table 3.4) because of the variation between seasons in solar radiation interception with time.
2. Leaf and stem DM and area increased exponentially in Stage II, with leaf preceding stem. Leaves were the major source of assimilate during the production of the potential yield.
3. Growth rates in Stage II increased at the onset of flowering (Table 3.1).
4. Leaf DM and area attained maxima during early flowering and then declined.
5. Stem DM and area remained constant after attaining maxima at the onset of Stage III (pod development), indicating that remobilisation of stem DM was minimal.
6. Pod DM and area increased linearly after maximum stem DM and area had been attained.
7. Seed DM increased almost linearly after attainment of maximum hull DM.
8. Total DM at final harvest was similar in all seasons but seed yield (and hence harvest index) was variable.
9. Harvest index was not an accurate measure of the partitioning of DM in oilseed rape crops in seasons when heavy pod-shattering led to large seed losses prior to harvest.
10. Seed yield was not related to crop DM at any time before or during flowering. The 1993 crop was much smaller during Stage I and at flowering than those in 1991 and 1992 (Table 3.5), but produced the greatest seed yield.
11. The 1993 crop was the smallest at the onset of Stage IV but went on to produce

the highest yield, thus supporting the view that the realisation of potential yield is determined by photosynthesis in Stage IV.

Table 3.5. Crop DM (g m^{-2}) at defined points during development, hand-harvested seed yield (g m^{-2}) and harvest index (%)

	1991	1992	1993
Stem extension (Stage II)	138	168	104.5
Flowering	472	429	372
Full flower (Stage III)	822	746	617
Seed development (Stage IV)	1007	1098	912
Final	1191	1246	1218
Seed yield	414	432	491
Harvest index	34.5	34.7	40.3

3.2.4. **Pre-flowering growth and development - Discussion**

LAI did not exceed 1.0 (theoretical complete ground cover) until relatively late in 1993 (early April). The onset of spring growth was probably delayed by low temperatures in late February and early March. The beginning of spring (date of rapid increase in accumulated day degrees above 5°C) (Scott, English, Wood & Unsworth, 1973a) occurred on 23 and 6 February in 1991 and 1992 respectively, and on 11 March in 1993. However, stem extension (Stage II) commenced at approximately the same time in all seasons, and consequently the 1993 crop was the smallest by the end of Stage I. Despite this an adequate leaf area was available to maximise radiation interception. Radiation levels were high in late March, which allowed a similar rate of growth up to flowering to the other seasons. Because the stem extension phase up to flowering was the same length in all seasons, the 1993 crop was considerably smaller at flowering. Heavy infection with phoma/stem canker (*Phoma lingam/Leptosphaeria maculans*) may also have contributed to the smaller growth in 1993 although this did not affect yield (see also Section 4). Ballinger, Salisbury, Dennis, Kollmorgen & Potter (1988) showed that stem canker can reduce plant height, and presumably the effects would be mediated prior to the end of stem extension.

Fig. 3.3. Growth and development of oilseed rape in 1991 and 1992:

(a) Dry matter in 1991

(b) Green area index in 1991

(c) Dry matter in 1992

(d) Green area index in 1992

♦	leaf	+	hull
▲	stem	○	seed
✖	flower	■	total
●	pod		

Arrows indicate onset of flowering

Developmental stages are indicated by Roman numerals

(a)

1991

I II III IV

Dry matter (g m^{-2})

1400
1200
1000
800
600
400
200
0

Feb March April May June July

(c)

1992

I II III IV

1400
1200
1000
800
600
400
200
0

Feb March April May June July

(b)

Green area index

7
6
5
4
3
2
1
0

Feb March April May June July

(d)

7
6
5
4
3
2
1
0

Feb March April May June July

The rate of development up to flowering (Stage IIa) was the same in all seasons despite differences in spring growth, which indicates that daylength may be more important than temperature in controlling the onset. Shipway (1981) proposed that daylength was the main factor determining the time between initiation and flowering, but suggested that temperature was also involved. Tittonel *et al.* (1988), however, attributed the consistent onset of stem extension entirely to the influence of daylength on flower development.

Main conclusions from three seasons

The overall pattern of development was consistent between seasons despite modification of growth (and hence yield) by environmental conditions. No evidence of DM remobilisation from stem to seeds was observed. It must be concluded that seed growth is dependent upon photosynthesis carried out by pods, branches, stems and remaining leaf during Stage IV over a final six-week period. Thus, provided potential yield (numbers of flowers/pods) is adequate, seed yield is independent of pre-flowering events and crop size at flowering. These findings will now be substantiated.

3.3. THE RELATIONSHIP BETWEEN PLANT SIZE AT FLOWERING AND SEED YIELD

In the previous section it was shown that final seed yield was determined by post-flowering events. This conclusion is in agreement with the findings of Bilsborrow & Norton (1984) who showed that ultimate seed yield was largely determined by photosynthetic capacity during Stages III and IV. Crop growth up to the end of Stage II was indirectly involved in yield determination since it provided the potential yield.

Mendham *et al.* (1981) proposed that in addition to setting the potential yield of oilseed rape crops sown late in the autumn, growth up to flowering determined

> "*the degree to which this potential is fulfilled during the subsequent stages as the yield components are determined.*"

Crop weight at full flower therefore

> "*closely reflects the photosynthetic capacity and/or seed-bearing capacity of the crop.*"

Early-sown crops in the same experimental series, however, did not show a similar relationship because the production of large pod numbers limited radiation distribution which resulted in large pod and seed losses (Mendham *et al.*, 1981).

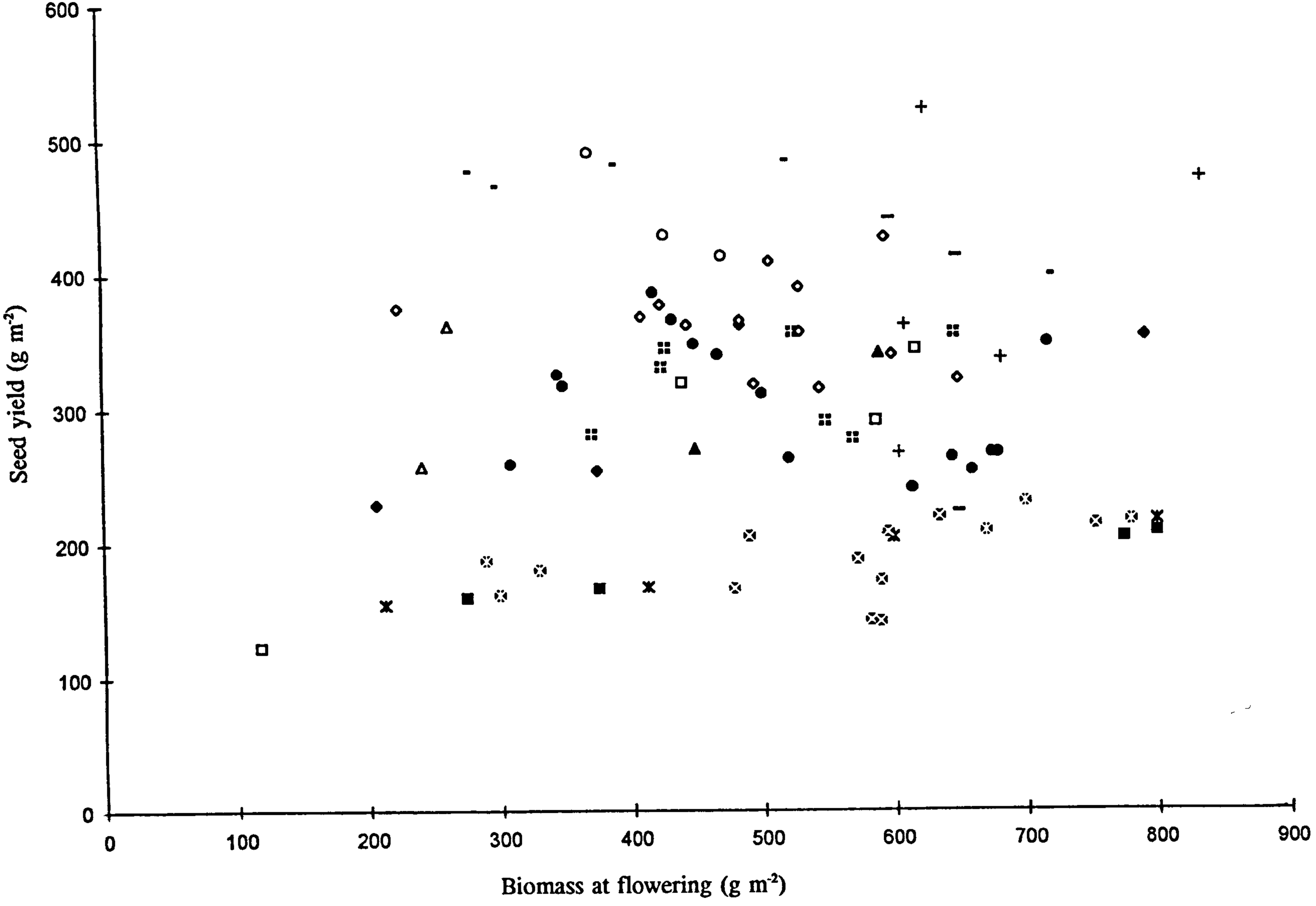
The relationship between crop size at full flowering and seed yield proposed by Mendham *et al.* (1981) was not observed in the present study. The relationship between crop size at first-flowering and ultimate yield has been examined here by use of all the appropriate data on winter rapeseed over the last 25 years, including published work, current work at Sutton Bonington and unpublished work. The considerable scatter of data points ($r^2 = 0.006$) clearly showed no overall relationship between biomass at first-flowering and seed yield (Fig. 3.4). Furthermore, when the data were divided into subsets for normal and late sowings, and for old and new varieties, no relationship was observed within these groups between biomass at flowering and seed yield (Table 3.6). Neither was there any relationship between plant density and seed yield.

Late sowing reduced biomass and yield considerably compared with normal sowing dates (Table 3.6). The ratio of seed yield:biomass was surprisingly constant: 0.59 and 0.57 for normal and late sowings respectively. Such ratios are considered to be coincidental and do not indicate a relationship between yield and biomass, as indicated in the regression analysis. Furthermore, the assimilatory organs in Stages III and IV in early- and late-sown crops are different because the growth pattern is different, e.g. greater leaf retention and contribution of leaf photosynthesis in late-sown crops. Seed yield/biomass (at flowering) ratios were considerably higher for the newly introduced varieties. This indicated a more efficient partitioning of assimilates for seed growth in the shorter-strawed new varieties, and reinforces the conclusion that post-flowering events are central to yield determination.

In conclusion, data from a number of other studies have verified the observations from the present study (1991, 1992 and 1993) that provided the yield potential is adequate, there is no advantage in producing a larger crop at flowering. Final seed yield was found to be entirely dependent on assimilation occurring during the seed development

Fig. 3.4. The relationship between seed yield and biomass at first-flowering for oilseed rape crops in the present and previous studies.

Sources: + Almond (1985); ▬ Bilsborrow (1985); - Jenkins & Leitch (1986); ◊ Leach *et al.* (1994); ● McWilliam, S.C. (unpublished, 1995); ♦ Mendham (1975); ▵ Mendham *et al.* (1984); ☐ Mendham *et al.* (1981a); ■ Mendham *et al.* (1981b); ▲ Norton, G. (1978, unpublished); ✖ ✪ ∷ ⊠ Shipway (1981); ○ present study.


Seed yield (g m-2)
600
500
400
300
200
100
0
0
100
200
300
400
500
600
700
800
900
Biomass at flowering (g m-2)

stage. Therefore, the greater yield potential of larger crops (1992) may be modified by crop and environmental factors during seed formation, while small crops (1993) may out-yield these if conditions are more favourable in Stage IV.

Table 3.6. Effect of biomass at first-flowering on seed yield. Mean values for each data set (g m^{-2}) (+ *standard deviation*), number of values (N), correlation coefficient (r^2) and ratio of seed yield to biomass at flowering

	Biomass	Yield	N	r^2	Ratio
All data	525.1 (*185.3*)	304.2 (*96.2*)	87	0.006	0.58
Normal sowing dates	575.5 (*142.7*)	338.7 (*83.3*)	45	0.092	0.59
Late sowing dates	463.6 (*151.1*)	262.7 (*97.5*)	39	0.006	0.57
Old varieties (normal sowing dates)	680.2 (*113.1*)	258.4 (*60.0*)	12	0.102	0.38
New varieties (normal sowing dates)	517.2 (*136.2*)	351.2 (*69.7*)	43	0.008	0.68

3.4. POTENTIAL YIELD DETERMINATION

3.4.1. **Introduction**

Daniels *et al.* (1986) estimated the theoretical maximum yield of a winter oilseed rape crop in the UK to be 7.56 t ha^{-1}. This yield was based on a consideration of the relationship between solar radiation interception and DM production. The average yield of winter oilseed rape crops in the UK in 1994 was 2.7 t ha^{-1} which clearly indicates considerable under-performance. In this section, potential yield is defined, its determination is outlined, and the causes of the loss of potential are examined.

3.4.2. **Potential yield**

Potential yield is determined at flowering by the number of flowers (potential pods) produced, which is dependent on preceding growth (Mendham *et al.*, 1981;

Bilsborrow, 1985). Potential pod numbers continued to increase beyond full flower in all seasons but not to the same extent. The maximum was attained only one week later in 1993 (18 May), but much later in 1991 (17 July) and 1992 (12 June) (Table 3.7). The continued increase into Stage IV in 1991 and 1992 was due to later flower development. Potential pod numbers were fairly consistent between seasons (approximately 15000 m^{-2}) and were not related to crop biomass (Table 3.7).

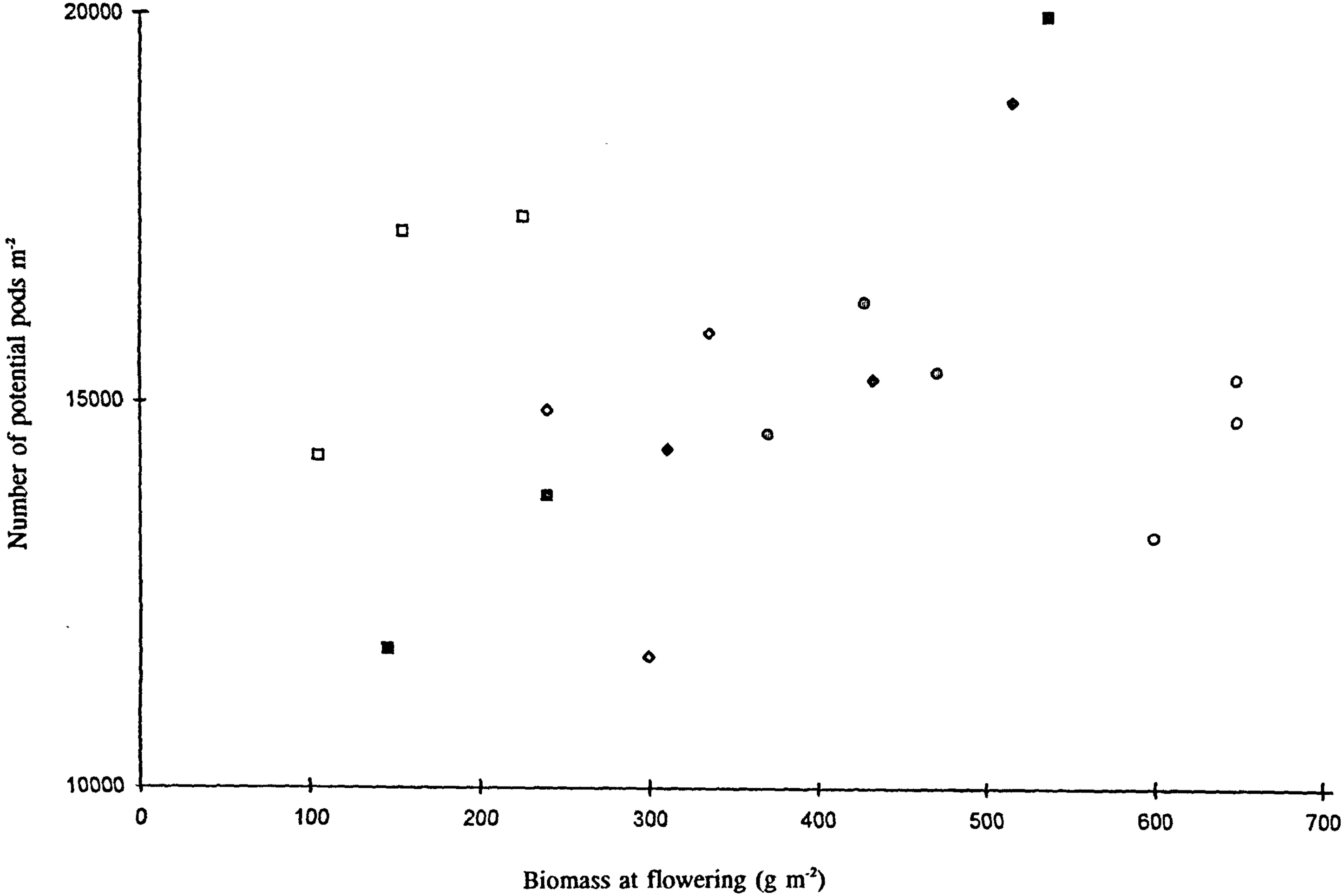
Table 3.7. Potential pod numbers in three seasons and crop biomass at flowering

	Potential pod number m^{-2}				Crop Biomass at flowering ($g\ m^{-2}$)		
	Full flower		Maximum		Onset	Full flower	Increase
1991	13800	21 May	15400	17 July	472	822	350
1992	14200	14 May	16300	12 June	429	746	317
1993	13800	11 May	14600	18 May	372	617	245

A survey of data for oilseed rape crops grown at Sutton Bonington in other studies under similar agronomic conditions confirmed that potential pod number m^{-2} was usually around 15000, and was independent of crop biomass ($r^2 = 0.07$) (Fig. 3.5). Although potential pod number will ultimately be under genetic control, it is moderated by growing conditions. Mendham *et al.* (1981) suggested that potential pod number was partly controlled by sowing date because this determined plant size at inflorescence initiation, and consequently leaf and ultimate branch number. Potential pod numbers in 1974-75 ranged from 24000 m^{-2} in early-sown to 5000 m^{-2} in late-sown crops (Mendham *et al.*, 1981). Some flexibility in pod number remained, however, because the number of pods produced per branch was not fixed, and branch and pod numbers were heavily dependent on plant density (Mendham *et al.*, 1981). McWilliam (1995b) also found wide variation about the general average 15000 m^{-2} (Fig. 3.5). These fluctuations, however, are likely to be determined by an interaction of plant density and the indeterminate growth habit of oilseed rape. The production

Fig. 3.5. The relationship between the number of potential pods and biomass at first-flowering for oilseed rape crops.

Sources: ○ Bilsborrow (1985); ■, □, ♦, ◊ McWilliam, S.C. (1995b, for early-sown 1993, late-sown 1992, late-sown 1993, and late-sown defoliated 1993 respectively); ● present study.


20000
15000
10000
0
100
200
300
400
500
600
700
Number of potential pods m-2
Biomass at flowering (g m-2)

of 12000-14000 flowers m^{-2} in low density treatments of 7 plants m^{-2} (McWilliam, 1995) indicated that individual plants are capable of producing 2000 or more flowers.

3.4.3. **Sources of assimilate during potential yield formation**

The main events in Stage II are the formation of the reproductive framework and determination of the potential yield. Bilsborrow (1985) showed that photosynthetic activity was closely correlated with green area index (GAI) and sites of assimilation were indicated by green areas of individual organs. At the onset of Stage II, leaf accounted for almost all of the assimilation (96% of GAI 0.47) (Fig. 3.1). As the leaf area increased, stem extension ensued so that with time, stem made an increasing contribution to total assimilation. When flowering commenced, leaf was still the major assimilatory organ (79% of GAI 5.1) but stem (21% of GAI and 50% of its maximum area) made a small contribution. Thereafter, leaf area declined while stem area increased. This resulted in proportional changes in contributions to assimilation. Maximum stem area was attained at the end of Stage II, when stem and leaf constituted 37% and 57% of the total green area respectively. These observations are consistent with those of Daniels *et al.* (1986) who showed that at the onset of flowering (mid-Stage II), most of the initial fixation of ^{14}C was by leaves (58%) and stem (38%). The contribution made by pods to assimilation at the end of Stage II would have been relatively small (3% GAI). This sequence is consistent with the work of Bilsborrow (1985) who showed that the photosynthetic contribution from leaves declined in Stage II (from almost 100% to 70%), while that from stem increased (up to a maximum of 40%).

3.4.4. **Realisation of potential yield**

Oilseed rape crops grown under standard agronomic conditions generally support around 6000 pods m^{-2} at harvest, while potential numbers are 2.5 times this. Under normal husbandry practices, final yield will never be restricted by insufficient potential pod numbers, and even when these are low, appreciable losses may still occur (Mendham *et al.*, 1981). Indeed Shipway (1981) considered it unlikely that yields were limited by low pod numbers. It may be concluded that potential yield is rarely limiting and is generally incompletely realised.

The maximum number of seeds per pod is determined by the number of ovules at anthesis which is controlled genetically and has been found to range between 25 and 30 ovules per ovary (Mendham, 1975; Shipway, 1981; Daniels *et al.*, 1986; Mendham & Salisbury, 1995). In the present study, some immature pods (immediately after shedding petals) contained up to 40 ovules, indicating a much higher potential seed number per pod. Under normal circumstances, therefore, it is unlikely that ultimate yield will be limited by the number of ovules per ovary.

3.4.5. Conclusions

1. Potential yield is determined at flowering by the extent of flower production.
2. Under standard growing conditions, potential pod number varies little between seasons.
3. Formation of the potential yield is initially fuelled mainly by leaf assimilation, with the contribution from stem increasing throughout.
4. Potential pod numbers and ovule numbers per ovary are unlikely to limit final yield.
5. Large pod (and seed) losses occur in all seasons and potential yield is never fully realised.

3.5. FINAL YIELD DETERMINATION

3.5.1. Introduction

The components of yield are pod number m^{-2}, seed number per pod and individual seed weight. In this section, the mechanism by which the potential yield is moderated to produce the final yield will be examined. Using data from three seasons (1991-93), it will be shown that, depending on season, both pod numbers m^{-2} and seed numbers per pod may decline continuously but not proportionately, from flowering to final harvest. These aspects will be considered with respect to the developmental stages. It will be shown that the inability of an oilseed rape crop to realise its full potential yield is due to an inability to maintain all its pods and seeds.

3.5.2. Pod and seed abscission in Stage II

Potential pod losses occurred simultaneously with flowering because of bud, flower

and pod abscission (Fig. 3.6). Detailed data on pod and seed losses in Stage II are available only for 1993 and these will be considered in this section. In 1993, 12% of the potential pods produced by 4 May (early flowering/late Stage II) had abscised. Two weeks later (18 May, early Stage III) this amounted to 23%. In early flowering (4 May), pod abscission was greatest in the top of the crop, but later (18 May), it was greatest in the lowest 20 cm layer of the canopy and decreased up the profile (Fig. 3.7). The effect of position in the pod canopy on pod abscission will be considered in more detail in Section 3.8.

In 1993, mean seed number per pod in late Stage II (4 May) was 22, indicating that a substantial loss of potential seeds had already occurred (Fig. 3.8). Seed numbers per pod were not constant throughout the profile and were higher towards the top of the crop (Fig. 3.8). This indicates that at least in this variety, ovule numbers per ovary must be in excess of 25-30. Generally the earliest-formed pods had fewer seeds per pod. Shipway (1981) also found that, throughout the flowering period, flowers in the middle and upper sections of the inflorescence tended to contain slightly more ovules per ovary than earlier-opening flowers lower down.

3.5.3. **Productivity in Stage II**

Overall DM production during Stage II was not directly related to the amount of solar radiation intercepted because of variation between seasons in the efficiency of radiation conversion. These were similar in 1992 and 1993 but higher in 1991 (Table 3.8), and may have been influenced by environmental conditions (although some inaccuracy may have resulted from the relatively short time periods involved). In the interval between flowering and full flower, DM production was related to radiation interception because there was little variation in efficiency between seasons, indicated by the calculated E values, but this was not the case in Stage IIb (Table 3.8). Efficiencies did not fall during this interval, indicating that the flower cover had no adverse effect on radiation use.

3.5.4. **Conclusions**

1. Many potential pods were lost during early flowering (as buds and flowers) before

maximum numbers were attained.

2. Losses of potential yield were relatively small in Stage II (in 1993) compared with the large losses that occurred later (in Stage III).
3. Earliest-formed pods which were eventually the lowest in the canopy had lower numbers of ovules per ovary than those developing later, higher in the canopy. This implies that the decline in seed number per pod down the canopy at the end of Stage II is genetically determined.
4. Overall DM production in Stage II was related to the amount of solar radiation intercepted. Relatively constant efficiencies in Stages IIa and IIb indicated that DM production was not affected by flower cover.
5. The early stages of final yield determination coincided with potential yield formation.

Table 3.8. DM produced (g m^{-2}), total radiation intercepted (R_i; MJ m^{-2}) and the efficiency of DM production (E; g MJ^{-1}) in the whole of Stage II, Stage IIa (stem extension - start of flowering) and Stage IIb (start of flowering - full flower)

	Stage II (Total)			Stage IIa			Stage IIb		
	DM	R_i	E	DM	R_i	E	DM	R_i	E
1991	684	532	1.29	334	282	1.18	350	250	1.40
1992	578	505	1.14	258	225	1.15	320	280	1.14
1993	530	464	1.14	285	259	1.10	245	205	1.20

3.6. EARLY POD DEVELOPMENT (STAGE III)

3.6.1. **Sources of assimilate during Stage III**

Leaf material still made a contribution to total assimilation during Stage III, but its relative contribution declined throughout due to continued leaf senescence (Figs. 3.1 & 3.3). Bilsborrow (1985) reported that by the end of Stage III, leaf made only a small contribution (20%) to total photosynthesis. In the present study, stem area attained a maximum at the end of Stage II and remained constant thereafter. Chapman

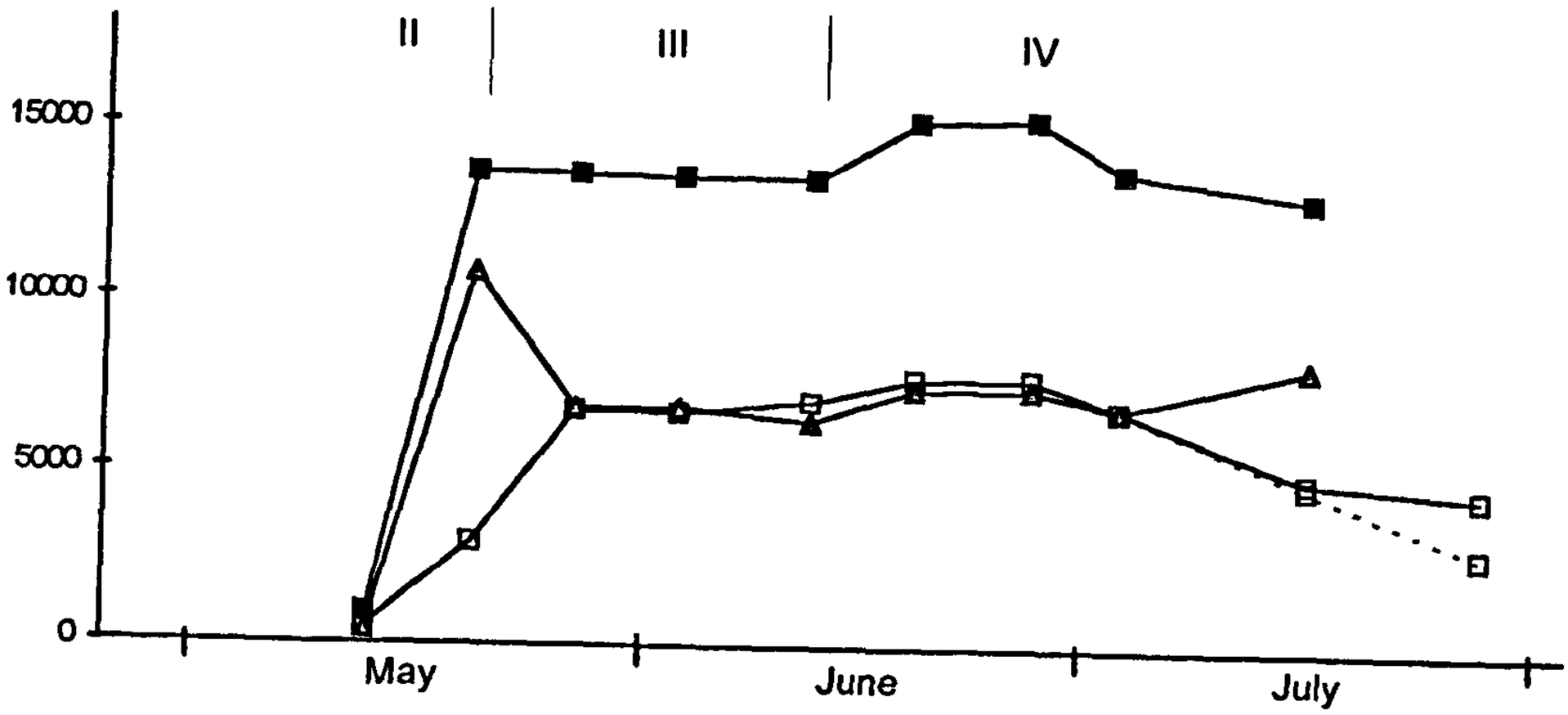
Fig. 3.6. The development of pod numbers in each season:

All seasons		1993 only	
□	Fertile	●	Buds
▲	Abscised[1]	✖	Flowers
■	Potential		

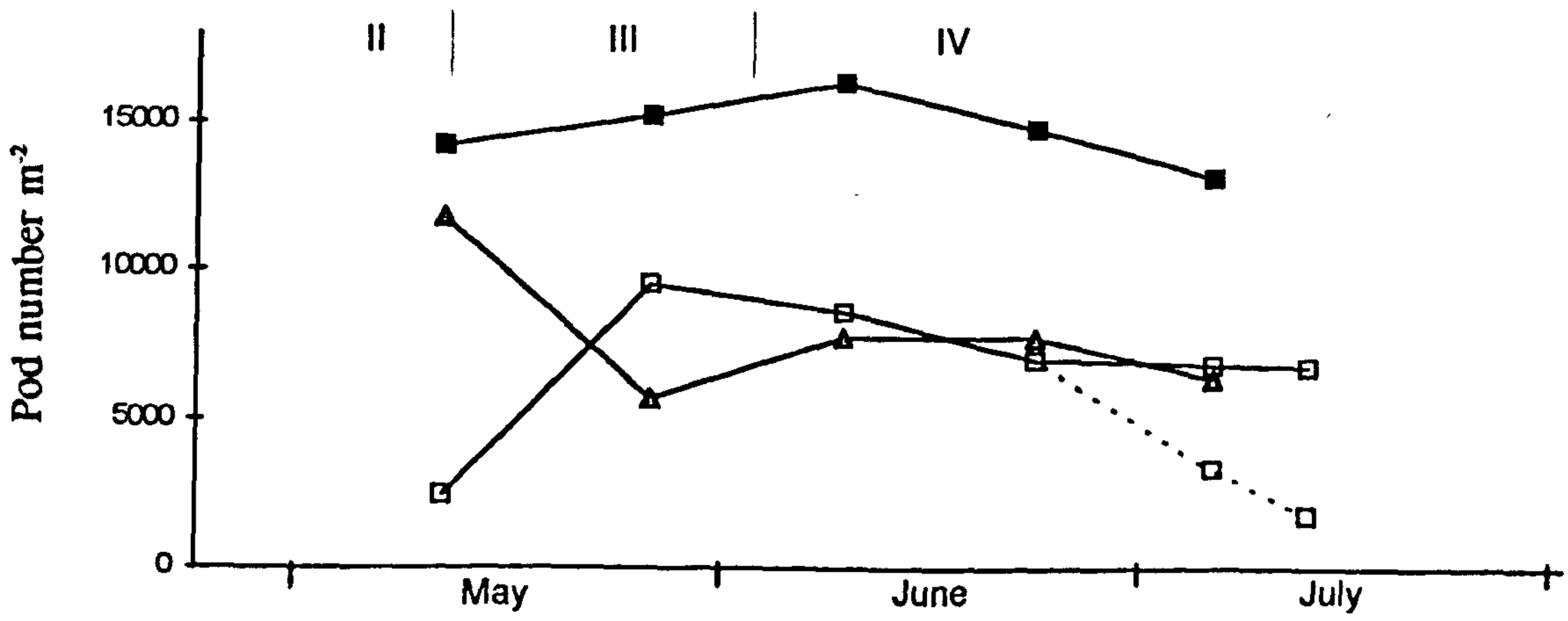
[1] includes flowers and buds in 1991 and 1992

Developmental stages are indicated by Roman numerals

1991



1992



1993

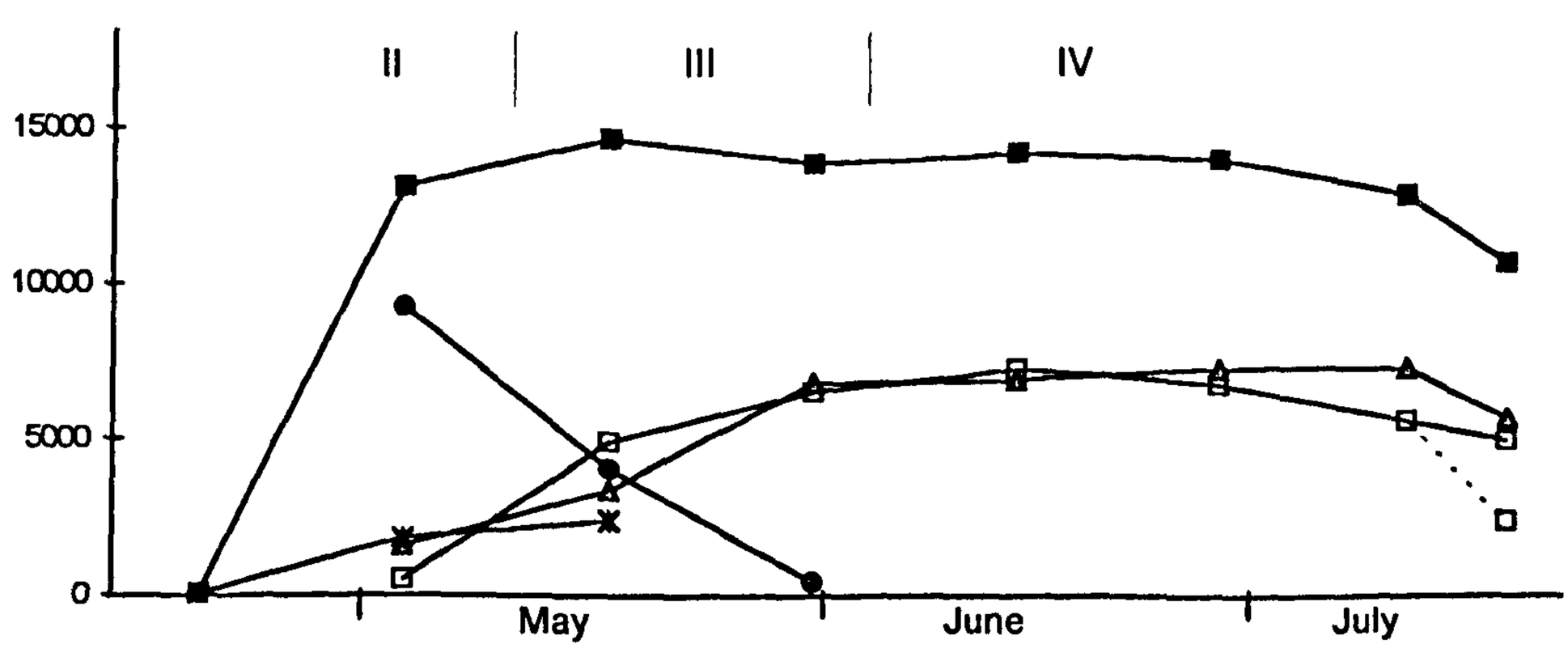


Fig. 3.7. The development of pod numbers in each layer of the pod canopy in each season:

All seasons		1993 only	
■	Fertile	●	Buds
▲	Abscised[1]	✖	Flowers
□	Potential		

[1] includes flowers and buds in 1991 and 1992

Developmental stages are indicated by Roman numerals

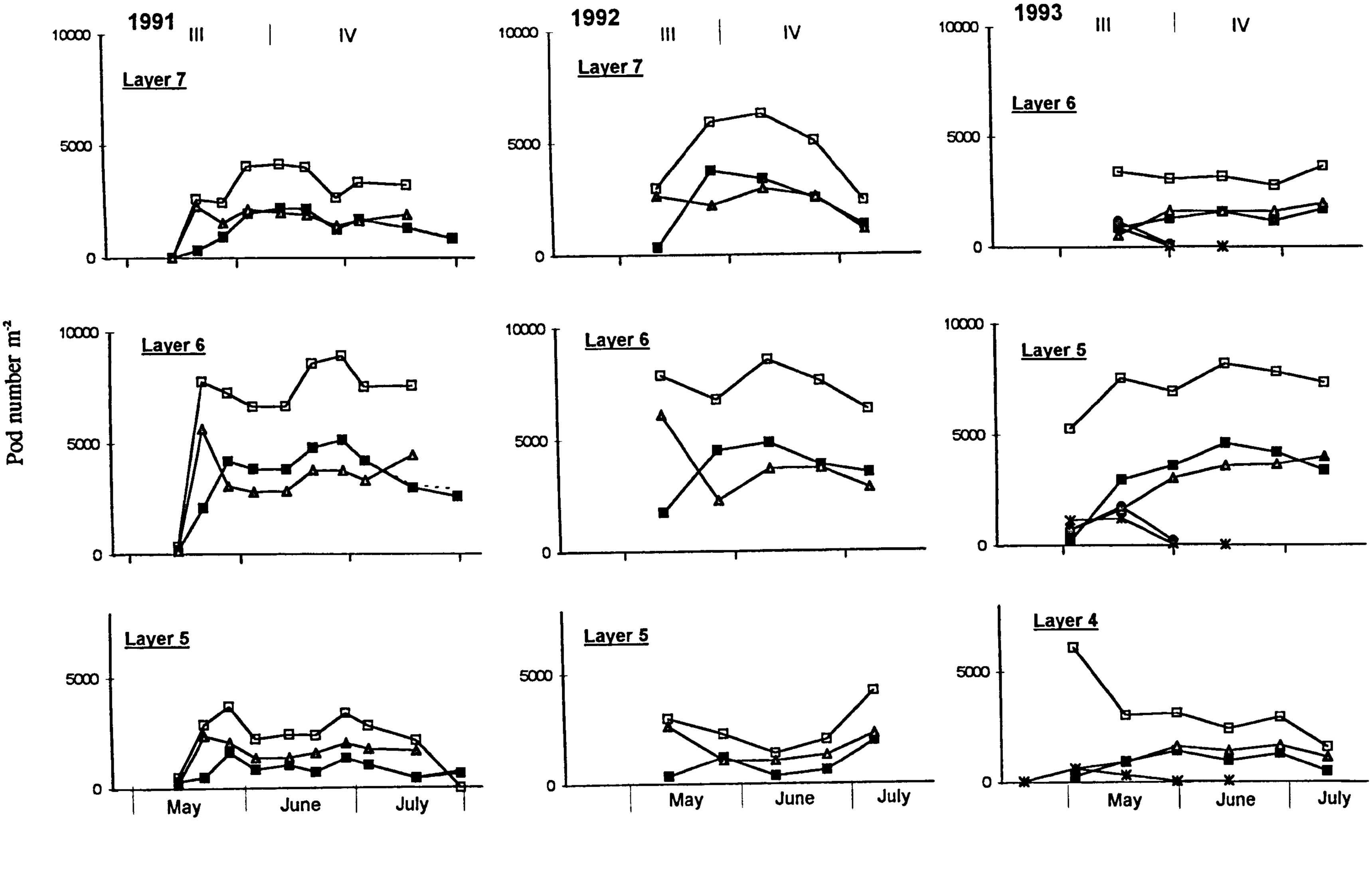

1991
III
IV
1992
III
IV
1993
III
IV
Layer 7
Layer 7
Layer 6
Layer 6
Layer 6
Layer 5
Layer 5
Layer 5
Layer 4
10000
5000
0
Pod number m-2
May
June
July

Fig. 3.8. The development of seed number per pod in each layer in each season:

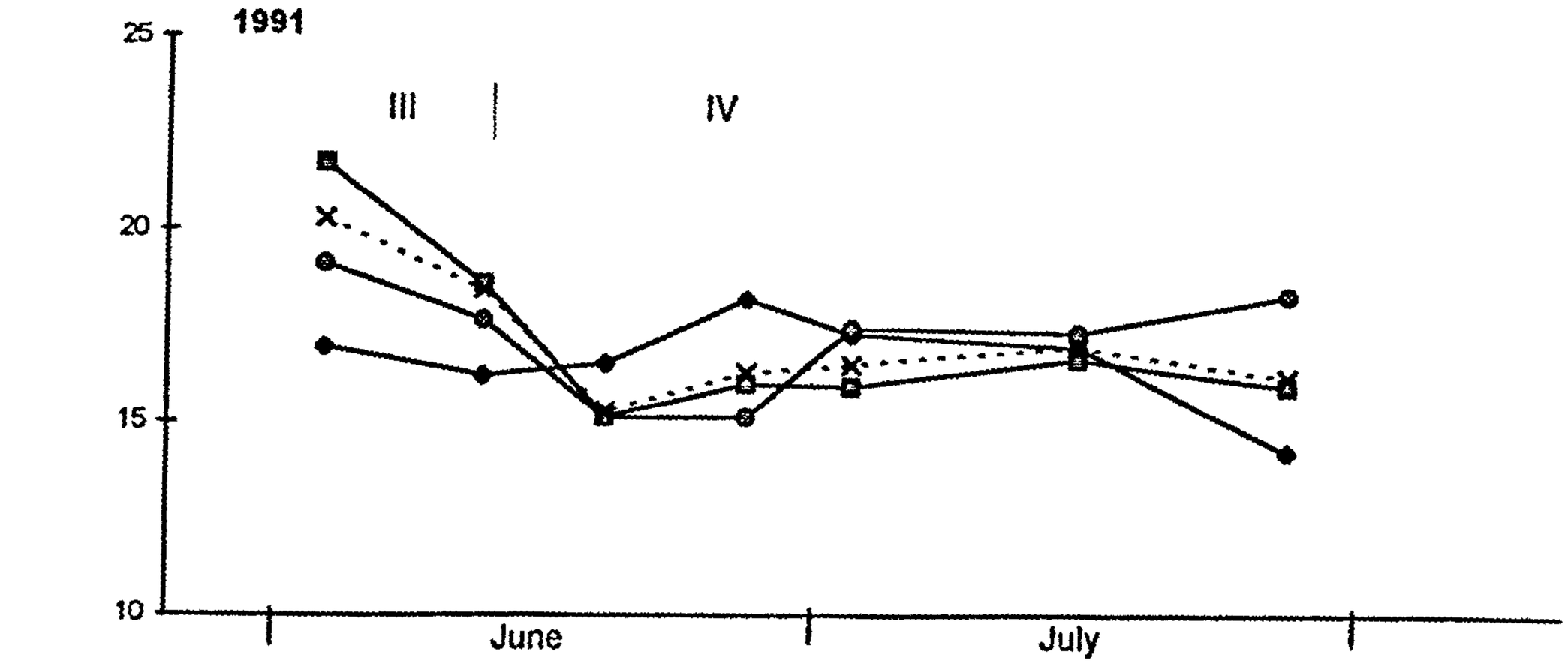
● Layer 7

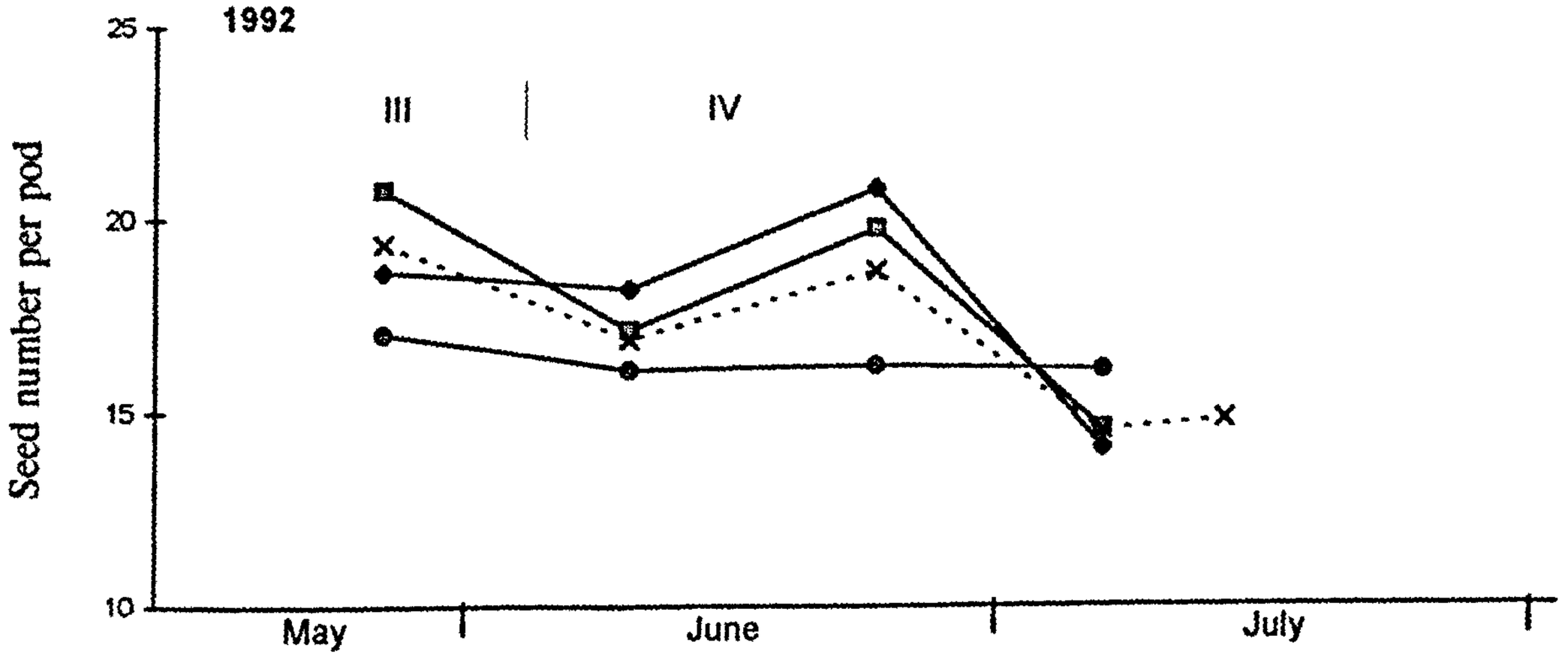
■ Layer 6

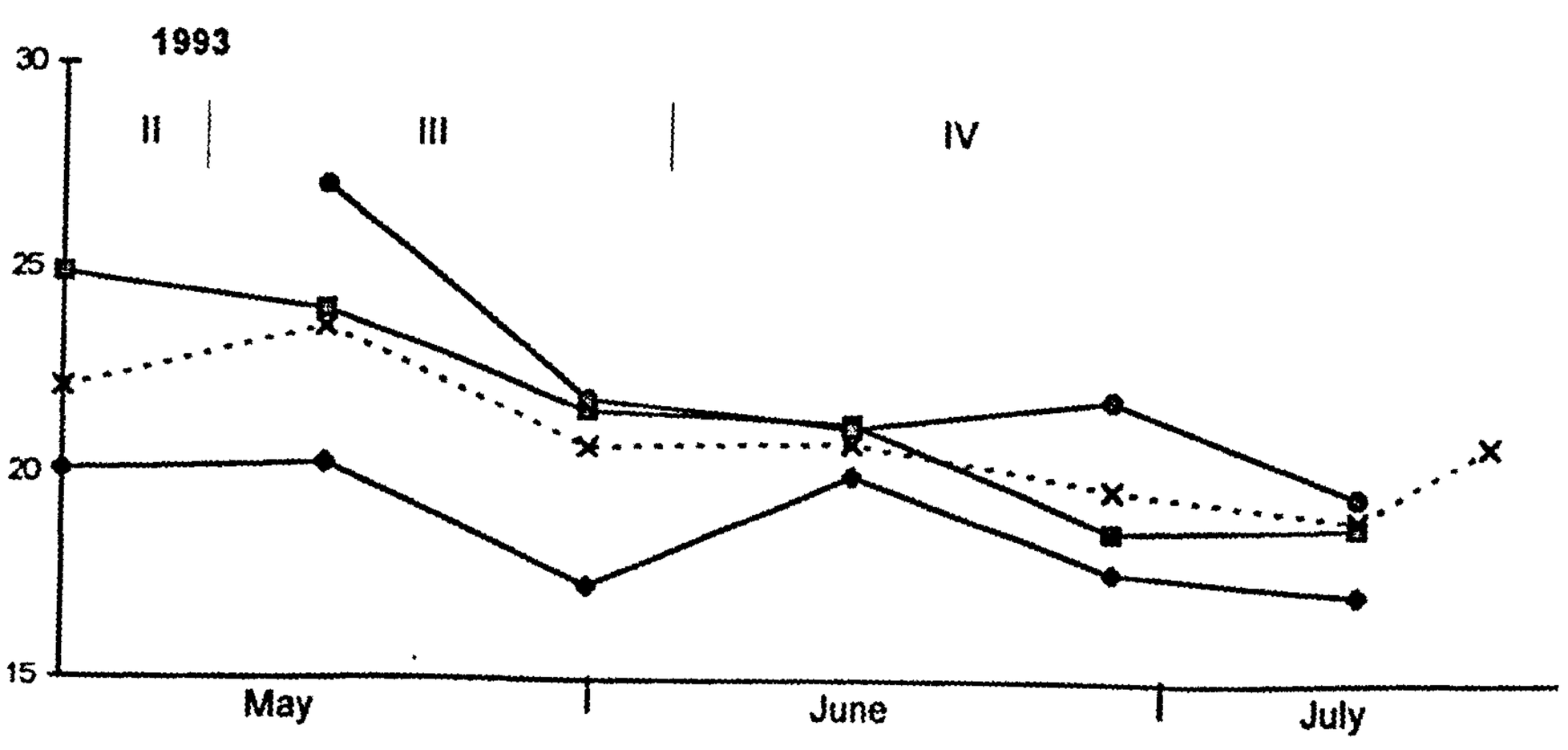
♦ Layer 5

x with broken line = weighted average of all pod layers

Developmental stages are indicated by Roman numerals


1991
25
20
15
10
III
IV
June
July


1992
25
20
15
10
III
IV
Seed number per pod
May
June
July


1993
30
25
20
15
II
III
IV
May
June
July

et al. (1984) showed that the main support stem made an important contribution to photosynthesis at this time. Bilsborrow (1985) found that the photosynthetic efficiency of the mainstem was low and that the major contribution of stem material (mainstem and branches) was due to its large area. Its main role is probably support of the plant and the flowering structures. Pod area increased throughout Stage III and attained a maximum at the beginning of Stage IV. Consequently the contribution of pods to assimilation would have increased throughout this period. These conclusions are in agreement with those of Bilsborrow (1985) who proposed that stem played a transitory role in maintaining crop photosynthesis at a time when leaves were declining and pods were increasing.

The onset of leaf senescence at flowering, beginning at the base of the crop profile, is usually attributed to shading by the flower canopy and then the pod canopy (Chapman *et al.*, 1984; Bilsborrow & Norton, 1984). However, in the present study, leaf senescence was already in progress by the onset of flowering. The rate of senescence varied between seasons, but always commenced with the oldest leaves which were lowest in the profile. Although initially high in 1991, the rate of senescence was generally higher in 1992. In addition to shading, the varied rate of leaf senescence between seasons may be linked to the amount of rainfall at flowering (Clarke & Simpson, 1978b). Leaves are particularly prone to senescence under conditions of stress (Rood & Major, 1984) and the 1992 crop may have suffered water stress (Section 3.9). Also, temperatures were high at this time in 1992, and faster growth rates associated with high temperatures may result in short leaf area duration (Morrison *et al.*, 1992). The persistence of well-illuminated leaf during pod development could provide a large increase in the assimilate supply which would influence yield component determination. This effect is most likely to occur in crops grown at low densities.

3.6.2. **Pod and seed losses in Stage III**

Pod retention at maturity was not related to the potential pod number because of environmental and crop factors operating during the later stages of development which varied between seasons. This was consistent with the findings of Mendham *et al.*

(1981) and Bilsborrow (1985). More pods were retained at the end of Stage III than were necessary to ensure a respectable yield was obtained. Many potential pods (33-56%) were lost as buds, flowers, and young pods during Stage III in all seasons (Fig. 3.6). Fertile pod numbers at the end of Stage III were considerably lower than the potential, and the proportion of pods set differed between seasons (Table 3.9).

Table 3.9. Fertile pod numbers m^{-2} at the end of Stage III (+ dates), maximum fertile pod numbers m^{-2}, and the percentage of potential pods at full flower retained to the end of Stage III

	Fertile pod number				% of potential
	End of Stage III		Maximum		
1991	6744	(4 June)	7826	(28 June)	49
1992	9506	(29 May)	9506	(29 May)	67
1993	6473	(1 June)	7199	(15 June)	44

At the onset of Stage III in 1993, seed number per pod declined down the pod canopy (Fig. 3.8). Data are not available for early Stage III in 1991 and 1992, but variation in seed number per pod down the profile was observed in late Stage III in both seasons. At the end of Stage III the variation in average seed number per pod between seasons was relatively small. However, the effect of position in the canopy on seed number per pod was not consistent between seasons. The determination of seed number per pod will be investigated further in relation to solar radiation interception in Section 3.8.

3.6.3. **Productivity in Stage III**

The rate of DM production in Stage III was much greater in 1992 (17.3 g $m^{-2}day^{-1}$) than in 1991 and 1993 (8.1 and 11.1 g m^{-2} day^{-1} respectively) (Table 3.1). This probably reflected greater assimilate production in this season, and was associated with much higher pod-set. The high growth rate indicated rapid pod growth, assimilates for which were largely supplied by leaves, particularly in early Stage III. The high

rate of assimilate production in 1992 would have been important in determining the size of the yield components (Morgan, 1982). Similarly, Kasa & Kondra (1986) showed that higher-yielding genotypes of summer rape developed more pods because they maintained a better assimilate supply to the pods when pod numbers were being determined. Higher growth rates have also been associated with higher pod numbers in *Vicia faba* (Stützel & Aufhammer, 1992).

Total radiation interception during Stage III was lowest in 1991 and highest in 1993 (Table 3.10), but radiation interception per day was highest in 1992, and development was faster in 1992 because of higher temperatures (Table 3.2; Appendix VII, Fig. VII.1). The efficiency of conversion was higher in 1992 (Table 3.10). The reason for this is unknown, but the high temperatures in this season may have been involved. Maximum pod area index in 1992 was much greater than in 1991 and 1993. This may have been a consequence of the high growth rate in 1992. Leaves tend to have larger areas when their expansion rates are high (Morrison *et al.*, 1989) and likewise, individual pods may attain larger size when their growth is rapid. This conclusion is supported by the larger pod area per pod in 1992 at the time when maximum pod areas were achieved (6.1×10^{-4} m^2 compared with 5.4×10^{-4} m^2 and 5.2×10^{-4} m^2 in 1991 and 1993 respectively). Maximum pod area index in all seasons approximated half that of the maximum LAI but in 1991 it was lower than expected. This was probably due to limitations in pod wall growth during Stage III in 1991 which resulted from a restricted assimilate supply in the low radiation environment.

Table 3.10. Total DM production (g m^{-2}), rate of DM production (g m^{-2} day^{-1}), total radiation intercepted (R_i; MJ m^{-2}), length of stage (Days), radiation intercepted per day (MJ m^{-2} day^{-1}) and the efficiency of DM production (g MJ^{-1}) during Stage III in three seasons

	Total DM production	Rate	R_i	Days	R_i day^{-1}	Efficiency
1991	185	8.1	172	24	7.2	1.08
1992	352	17.3	226	21	10.8	1.56
1993	295	11.1	240	25	9.6	1.23

The small variation between seasons in average seed number per pod at the end of Stage III appeared to be related to the total amount of radiation intercepted during this stage (Table 3.11). However, other factors must have been involved because the cessation of net DM production during Stage III in 1991 was not reflected in a large effect on seed number per pod. It is proposed that seed number per pod is a function of both the number of competing pods and total DM production, i.e. sink and source sizes. This conclusion is supported by the link between DM production per fertile pod in Stage III and seed number per pod at the end of Stage III (Table 3.11), and by the very weak negative correlation between pod number m^{-2} and seed number per pod (r^2 = -0.31; Appendix VI). Therefore assimilate availability and hence good radiation interception by leaf at this time, as in 1993 (Section 3.8), are important in seed number determination. In addition, assimilate availability in 1993 may have been promoted by the crop having far fewer flowers at any time than in 1991 and 1992, as this could have reduced competition between flowers for assimilate. Numbers of reproductive sites m^{-2} at full flowering (excluding fertile pods) were 10800, 11800 and 5700 in 1991, 1992 and 1993 respectively (of which 2400 were open flowers in 1993).

Table 3.11. Seed number per pod (average of pod layers) at the end of Stage III, total radiation interception in Stage III (MJ m^{-2}), total DM production in Stage III (g m^{-2}), fertile pod number m^{-2} and DM per pod (g pod^{-1}) at the end of Stage III

	Seed number per pod	Radiation intercepted	DM production	Fertile pod number	DM per pod
1991	18.5	172	185	6744	0.027
1992	19.4	226	352	9506	0.037
1993	20.7	240	295	6473	0.046

3.6.4. **Conclusions**

1. The main phase of pod and seed number determination occurred in Stage III.
2. The contribution of leaf to total assimilation declined in Stage III, the extent varying with season.

3. On the basis of green area, the contribution of pods to assimilation increased while that of stem remained constant in Stage III.
4. Pod retention was not related to potential pod number.
5. Pod retention depended on the rate of assimilate production and supply, which was reflected in the rate of DM production during the entire flowering period (Stages IIb & III). This was dependent upon incident radiation levels.
6. The distribution of pods in the canopy was a reflection of DM production with time, and was therefore determined by the rate of DM production which in turn depended on incident radiation.
7. Even when incident radiation in Stage III was low (1991), pod numbers were not limiting to yield. This indicates that radiation interception was not the critical factor in pod retention.
8. Large pod losses occurred at the end of flowering (end of Stage III) regardless of radiation interception (1993). This again indicates the involvement of other factors.
9. Fertile pod number was largely determined by the end of Stage III.

3.7. SEED DEVELOPMENT (STAGE IV)

Pod and seed losses continued throughout Stage IV while seed growth was occurring. This section examines how final yield is determined in this stage and is dependent upon the extent of photosynthesis.

3.7.1. **Final yield components**

Total pod numbers (fertile + shattered) per m^2 at final harvest and numbers of pods contributing to final yield (fertile pods + pods that shattered after harvesting) were higher in 1992 (Table 3.12), but seed number per pod and 1000-seed weight were lower in 1992 than the other seasons. Numbers of yield-forming pods (4000 m^{-2}) and 1000-seed weights (6.63 g and 6.53 g) were similar in 1991 and 1993, but seed numbers per pod were higher in 1993. Thus seed yield was highest in 1993 through the higher seed number. Total seed numbers m^{-2} were similar in 1992 and 1993 due to high pod numbers m^{-2} in 1992 and high seed numbers per pod in 1993, but the 1993 yield was higher due to the greater 1000-seed weight.

Table 3.12. Seed yield and yield components in three seasons (*S.E.D in parentheses*)

		1991	1992	1993
Seed yield (t ha^{-1})	(Hand-harvested)	4.1 (*0.12*)	4.3 (*0.42*)	4.9 (*0.52*)
Pod number m^{-2}	Total	4530 (*151*)	6713 (*663*)	4918 (*959*)
	Yield-forming *(A)*	4001 (*189*)	5243 (*148*)	4038 (*176*)
Seed number per pod *(B)*		16.1 (*0.96*)	14.8 (*1.17*)	20.7 (*3.90*)
1000-seed weight (g) *(C)*		6.63 (*0.20*)	5.86 (*0.25*)	6.53 (*0.56*)
Seed number per m^2 (1000s)		61.7 (*0.25*)	74.7 (*9.88*)	75.5 (*7.91*)
Seed yield calculated from yield components (*A x B x C/1000*) (t ha^{-1})		4.27	4.55	5.46

If seed yields are calculated from yield components, those in 1991 and 1992 are similar to actual yields, but not in 1993 (Table 3.12). Similar discrepancies were encountered and discussed by Mendham (1975) and could be accounted for by an over-estimation of one or more of the yield components. However, in the present study, errors were minimised by replication of large samples. The most likely source of error is the derived number of yield-forming pods which is probably an overestimate.

3.7.2. **Contribution of components to final yield**

In this section, the changes in the yield components that occurred during Stage IV (late May/early June to final harvest) will be considered. At the beginning of Stage IV (late May/ early June), fertile pod numbers were similar in 1991 and 1993 (7800 and 6800 m^{-2} respectively), but much higher in 1992 (9500 pods m^{-2}). Fertile pod numbers increased gradually during early Stage IV in 1991 and 1993 due to later-opening flowers but were already in decline in 1992 (Fig. 3.6). Most fertile pod losses occurred in early and late June in 1992 and 1991 respectively. Losses in 1993 were small (Fig. 3.6). Pod retention was greatest in the middle 20 cm layer of the pod canopy and lowest in the bottom layer irrespective of season (Fig. 3.7; Table 3.13). In 1993, the difference between the top and bottom layers was less. Pod survival will be considered in relation to solar radiation interception in Section 3.8. Pod losses later

in Stage IV were the result of pod shattering due to disease and moisture stress, particularly in 1992 (Section 3.9). At maturity, 12%, 22% and 18% of the total pods did not contribute to yield in 1991, 1992 and 1993 respectively due to pre-harvest shattering (calculated from figures in Table 3.12). Total shattering (pre- and post-harvest) increased down the pod canopy in all seasons as typified in 1991 when shattered pods as a percentage of total pods were 32%, 36% and 51% in layers 7, 6 and 5 respectively. This may have been due to earlier ripening of older, lower pods and/or increased disease on pods in the more moist environment lower in the canopy.

In 1991 and 1992 but not in 1993, seed number m^{-2} declined steadily during seed development as a result of both pod and seed losses (Fig. 3.9). Initial seed numbers per m^2 were very high in 1992 but, at final harvest, were similar to those in 1993 (75000 seeds m^{-2} compared with 62000 seeds m^{-2} in 1991). At the beginning of Stage IV, average seed numbers per pod were 18, 19 and 20 in 1991, 1992 and 1993 respectively (Fig. 3.8), but declined only in 1991 and 1992 to 16 and 15 respectively. At the onset of seed development, seed number per pod was lower in the lowest pod layer in 1991 and 1993, and in the top layer in 1992 (Fig. 3.8). In 1991 and 1992, seed losses increased down the profile but in 1993 seed number per pod remained almost constant throughout the canopy. Therefore during Stage IV in 1993, position in the canopy did not affect the number of seeds lost per pod, although seed number per pod still declined down the canopy at maturity.

Table 3.13. Pod retention (fertile number as a percentage of potential) in each layer of the pod canopy at the end of Stage III in each season

	1991	1992	1993
	14 June	29 May	1 June
Top	52	63	46
Middle	57	67	52
Bottom	42	53	42
Average*	52	63	47

**Averages are not the same as in Table 3.9 because there the potential at full flowering was used whereas here the potential at the start of Stage IV is used to avoid fluctuations between layers.*

Seed growth, indicated by the increase in 1000-seed weight, was exponential, but mainly linear over the period examined (Fig. 3.10). The average rate of seed growth (increase in 1000-seed weight) during seed development (linear phase) was 0.12 - 0.13 g day^{-1}. Final 1000-seed weights differed between seasons, and were 6.63, 5.86 and 6.53 g in 1991, 1992 and 1993 respectively. The effect of pod position in the canopy on seed growth was similar in all seasons. The largest seeds were located initially in the lower parts of the pod canopy but by maturity, these were in the top layer due to progressively lower growth rates down the canopy (Table 3.14).

Table 3.14. The effect of position in the pod canopy on 1000-seed weight (g) in early and late seed development (= final harvest in 1991 only) in three seasons (* mean at final harvest). Averages weighted according to seed DM m^{-2} per layer.

	1991		1992		1993	
Layer	Early	Late	Early	Late	Early	Late
Top	1.31	6.77	1.83	5.34	0.78	6.59
Middle	1.58	6.71	1.85	5.16	1.01	6.40
Bottom	1.73	6.40	1.98	5.04	1.11	5.65
Average	1.54	6.63	1.85	5.86*	1.00	6.53*

3.7.3. **Sources of assimilate during seed development**

Stem and pod area were maximal during Stage IV (Fig. 1.b) and must have been responsible for much of the assimilation as LAI had already declined rapidly in Stage III. Bilsborrow (1985) showed that the contribution of leaves to crop photosynthesis had fallen to below 20% at the onset of Stage IV. In the present study, however, leaf retention varied between seasons depending on both agronomic (canopy density) and environmental (temperature and solar radiation) factors (Figs. 3.1, 3.3 & 3.12 [where LAI is represented by heavily shaded areas]). In 1993, 67% of the maximum LAI (4.35) still remained at the onset of Stage IV but this declined to 32% (LAI = 1.4) in the first two weeks (Fig. 3.1). In 1992, LAI declined from 66% of the maximum (4.8) to 20% (LAI = 0.9) over the same period, and in 1991, from 29% of maximum (4.8) to 15% (LAI = 0.72). Therefore the smaller 1993 crop had a considerably greater LAI

Fig. 3.9. The development of seed number per m^2 in each season:

■ 1991

* 1992

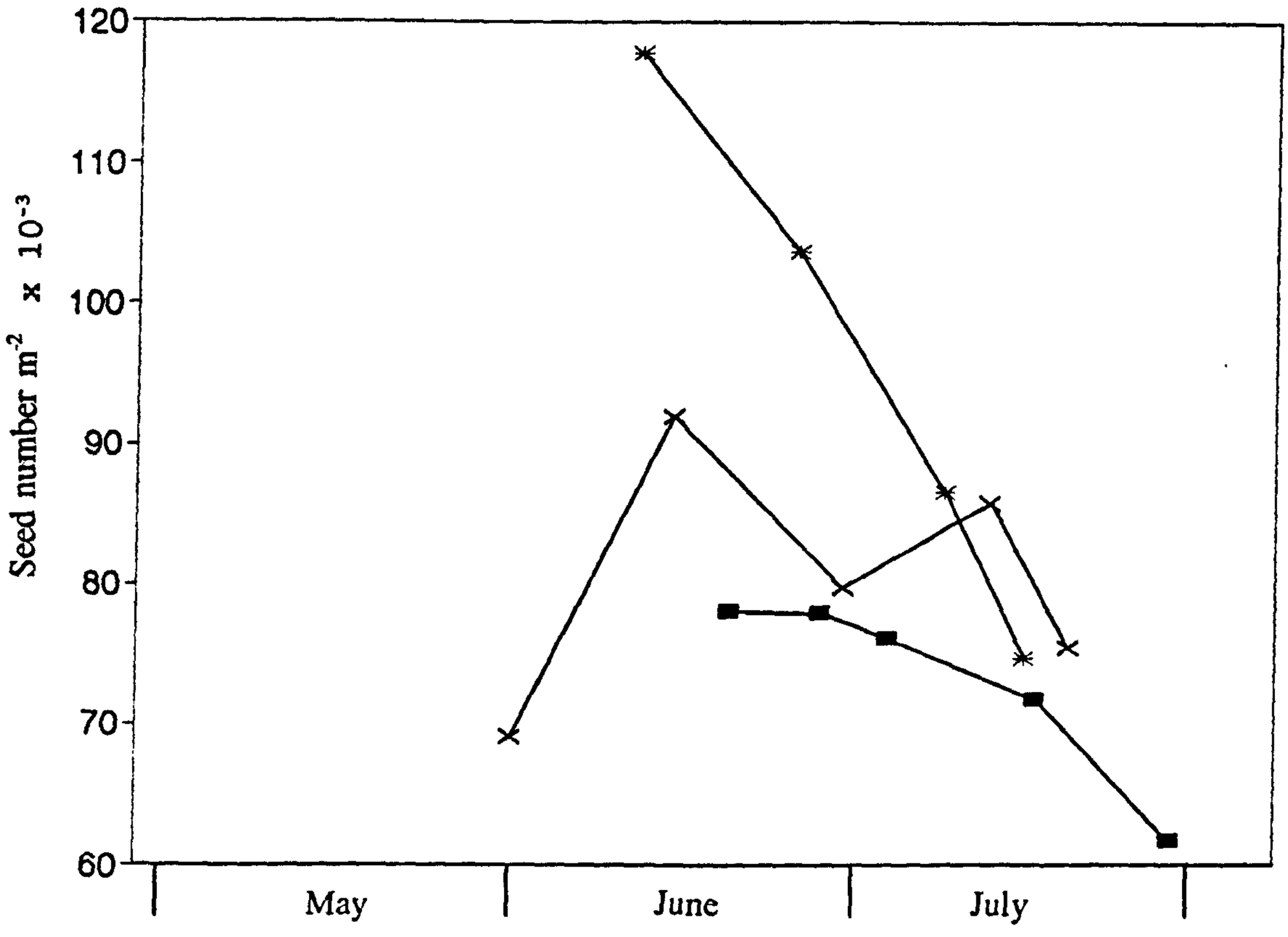
x 1993

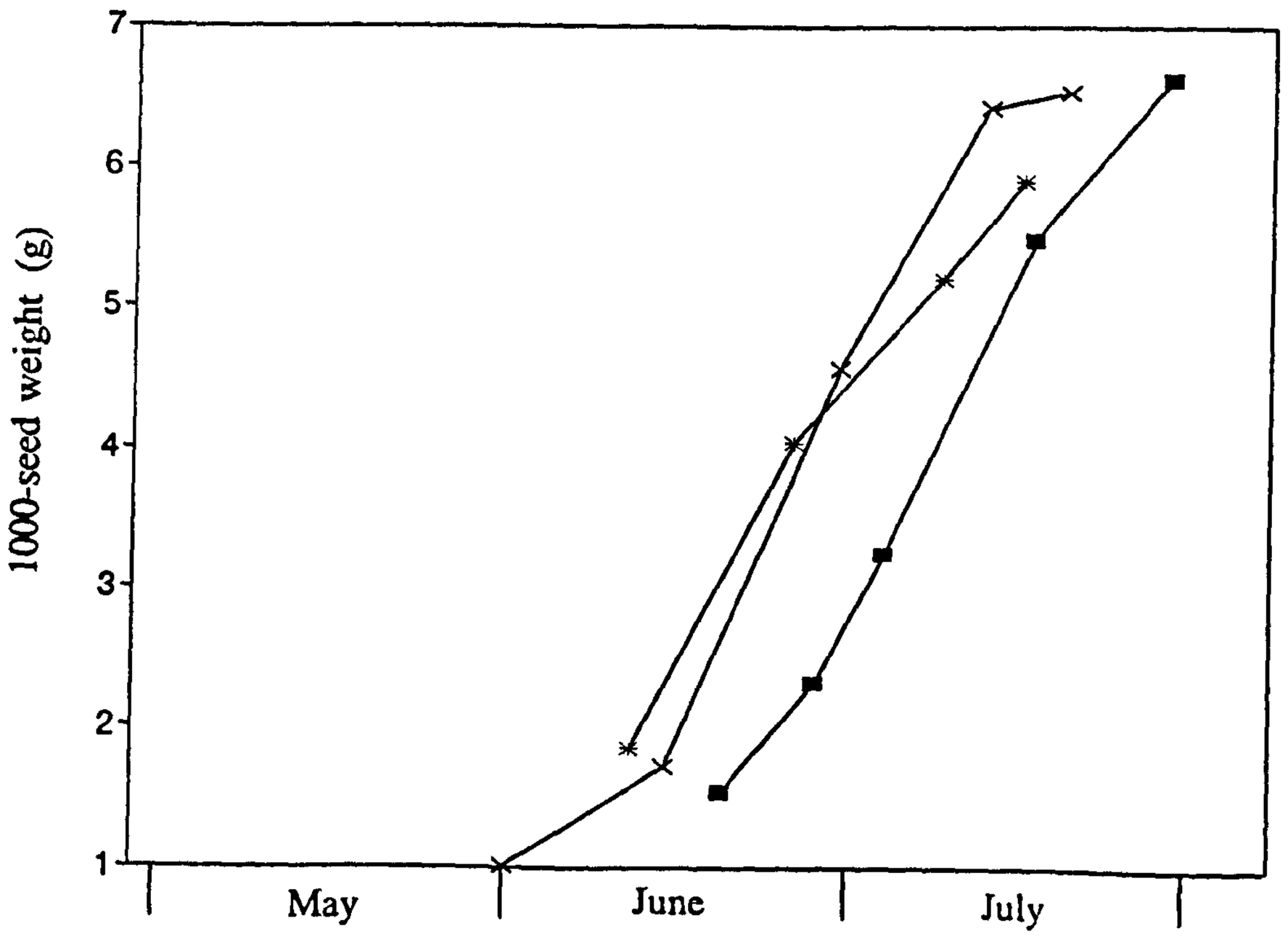
Fig. 3.10. The development of 1000-seed weight in each season:

■ 1991

* 1992

x 1993


120
110
100
90
80
70
60
Seed number m-2 x 10-3
May
June
July


7
6
5
4
3
2
1
1000-seed weight (g)
May
June
July

during Stage IV than the 1991 and 1992 crops. In view of its relatively small contribution to the total green area of the crop (18%, 11% and 23% on 1 July in 1991, 1992 and 1993 respectively), it must be concluded that the contribution of leaf to seed filling is small. This bract-like leaf material, however, was situated in the pod canopy (Fig. 3.12) and was shown by Bilsborrow (1985) to be highly efficient in photosynthesis. Bilsborrow (1985) concluded that these leaves would have provided some assimilates for seed growth. However, the main photosynthetic organs were pods, branches and stems which accounted for more than 95% of total assimilation in Stage IV (Bilsborrow, 1985). Seed growth was the product of current assimilation. Although the mobilisation of stem reserve materials for seed growth has been proposed (Daniels & Scarisbrick, 1983; Chapman *et al.*, 1984; Evans, 1984; Addo-Quaye *et al.*, 1986), no such mobilisation was detected in the present study (Section 3.2). This is consistent with the findings of Bilsborrow & Norton (1984) and Bilsborrow (1985). The sequence of green area development, and therefore assimilate supply, was the same in all three seasons (1991-93) (Figs 3.1 and 3.3).

3.7.4. Crop productivity in Stage IV

The end of Stage IV was taken to be the date when seeds stopped growing (Fig. 3.10). Gross DM production in Stage IV, which was entirely seed DM production (Section 3.2.2), was highest in 1993 and lowest in 1991 (Table 3.15). Energy receipts (total radiation interception) in Stage IV varied considerably between seasons due mainly to differences in incident radiation levels (Tables 3.2 and 3.4) and to small differences in fractional interception. Indeed incident and intercepted radiation in Stage IV in 1993 were respectively 61% and 73% more than in 1991. The proportion (%) of radiation intercepted by the whole crop was highest in 1993 and lowest in 1991. Over the whole of Stage IV, the efficiency of DM production per MJ intercepted radiation in 1991 was 48% higher than in 1992 and 1993.

To determine whether pod and seed losses late in the season had any marked effect on calculated efficiencies, seed DM production in Stage IV was plotted against intercepted radiation (Fig. 3.11). The efficiency (gradient) declined considerably with time throughout Stage IV in 1992, which may have been due to the heavy sclerotinia

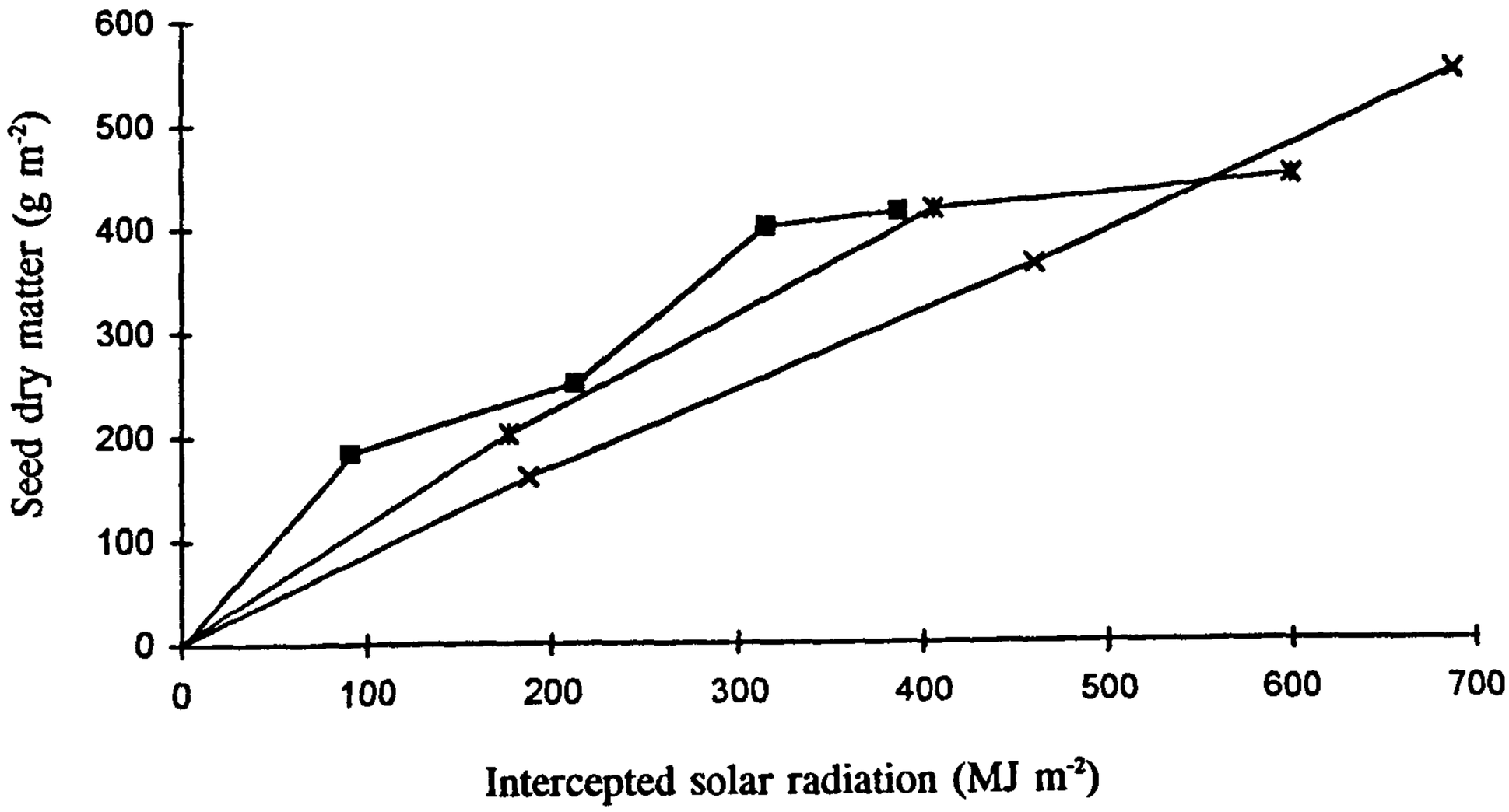


Fig. 3.11. The relationship between cumulative solar radiation and seed dry matter production during Stage IV (seed development) in each season

■ 1991

* 1992

x 1993

Points correspond to growth analysis harvests. Gradients indicate the efficiency of seed dry matter production. Note: such values are not strictly comparable with efficiency values calculated for Stages II and III because of the greatly increased energy requirements for oil production in the seed in Stage IV

infection (Section 4). In 1991, the efficiency declined in late Stage IV but in 1993, it remained constant throughout. These findings indicate that the greater seed DM production in 1993 was due to higher radiation interception than in 1991 and 1992. The relatively high efficiency in 1991 resulted in a much greater seed DM per MJ radiation intercepted than in 1992 and 1993. This suggests that the lower efficiencies in 1992 and 1993 may have been due to radiation saturation at the top of the crop. Radiation use by the pod canopy will be further investigated in Section 3.8.

Table 3.15. Radiation interception and DM production in Stage IV

	1991	1992	1993
Approximate start of stage*	13 June	29 May	1 June
Date of maturity	29 July	16 July	13 July
Total incident radiation (MJ m^{-2})	469	657	755
Fractional interception	0.82	0.91	0.89
Radiation intercepted in Stage IV	386	599	687
Gross DM production (g m^{-2}) (= seed yield)	414	432	491
Efficiency (g seed MJ^{-1})	1.07	0.72	0.71

* Sampling date nearest to the onset of Stage IV

3.7.5. **Conclusions**

The most important conclusion is that final yield was determined by the amount of radiation intercepted in Stage IV. This was a function of the total amount incident (MJ day^{-1} x days in Stage IV) and the proportion intercepted. Further findings from this section are listed below.

1. Pod numbers generally remained constant in Stage IV until late in the season when some shattering occurred.
2. Large pod losses occurred in early Stage IV in a season when high pod retention coincided with low incident radiation levels (1992), although this was complicated by the high incidence of sclerotinia.
3. Seed numbers continued to decline on a reduced scale in Stage IV.
4. Individual seed weight was determined in Stage IV.

5. Seed number per pod and 1000-seed weight decreased down the canopy in all seasons.
6. Pod and stem must be responsible for much of the assimilation in Stage IV but any remaining leaf would contribute to some extent depending on season.
7. Leaf remaining at the onset of Stage IV was located at the base of the pod canopy.
8. Radiation interception was increased by leaf retention.
9. In 1993, leaf was responsible for more of the total radiation interception and presumably therefore assimilation in Stage IV. This did not increase the efficiency of DM production relative to the other seasons.
10. Radiation use was more efficient in a low radiation environment (1991). This suggests a cut-off may occur above which other factors become limiting, eg. hormonal effects.

3.8. SOLAR RADIATION INTERCEPTION AND YIELD DETERMINATION

3.8.1. **Introduction**

Over the three seasons in the present study, different weather patterns interacted to produce canopy structures that varied widely. Following a very high growth rate during flowering (Stages IIb and III), the 1992 crop set many pods and a dense canopy resulted. Observations and measurements with solarimeters showed that penetration of solar radiation through to the lower regions of the profile was restricted. In contrast, the 1993 canopy was relatively sparse, while that in 1991 was intermediate. Therefore, the distribution of radiation through the crop profile differed between seasons. In this section, these differences will be examined in order to identify the major sites (and organs) of radiation interception in relation to the effects on yield production.

3.8.2. **Crop green area and solar radiation interception**

Linking the stratified green area measurements with solar radiation measurements in the crop profile should indicate the major sites of radiation interception and the organs involved. However, these two measurements were made in different areas of the plots. Variability within plots resulted in plant height and density differences and therefore, it was not always possible to relate green area measurements directly to

radiation data. This problem is illustrated in Appendix IV, where original data are presented with corresponding green areas. In order to overcome this, radiation data were corrected to fit GAI data by assuming the pod canopies for the two different crop areas were the same with respect to radiation interception (Appendix IV).

3.8.3. The effect of crop structure on solar radiation interception during yield production

Fig. 3.12 shows green area profiles for each season in relation to radiation interception, namely the proportion of the total incident radiation intercepted in each 20 cm layer of the crop together with absolute values intercepted in the intervals between successive sampling dates. This indicates the location of the major sites of radiation interception and therefore assimilation during yield production. Prior to Stage III, the majority of the GAI was leaf which was responsible for most of the radiation interception. During Stage III, leaf interception declined while pod interception increased as a consequence of leaf senescence, pod wall growth and the shading of leaf by developing pods. In Stage IV, a large proportion of incident radiation was intercepted by pod and stem material in the upper layers, while the amount of radiation available for leaf assimilation varied between seasons. High pod retention and the formation of a dense pod canopy resulted in shading down the profile which may have hastened leaf senescence. Penetration of radiation through a pod canopy was inversely related to the number of pods, and the extinction coefficient (k) was reduced in sparse canopies with low pod numbers (Appendix IV). The following sections will relate crop structure and radiation interception to the pod and seed losses described in Sections 3.5 - 3.7.

3.8.4. The effect of solar radiation interception on potential yield development (Stage II)

Detailed data relating radiation interception with pod losses in Stage II are available only for 1993, and this section refers to Fig. 3.12.c. On 4 May (late Stage II) in this season, crop growth was largely dependent on leaf photosynthesis, and radiation was intercepted by leaf throughout the profile. From 4-18 May, the top two layers (4+5) intercepted only 37 MJ m^{-2} (15%) of the total incident radiation (R_T), leaving 207 MJ

m^{-2} (85%) available to layer 3. At this time, 86% of the total LAI (0.6 GAI) was located in layers 1-3. Leaf assimilation would not have been limiting to growth, as reflected in the net rate of DM production which did not decline at flowering (11.6 g m^{-2} day^{-1} compared with 10.6 g m^{-2} day^{-1} in Stage IIa; Table 3.1). The proportion of potential pods that were set was 4% in both layers 4 and 5, and the proportions that had abscised were 10% and 13% in layers 4 and 5 respectively (Fig. 3.7). Most potential pods were still flowers or buds at this stage during potential yield determination. It may be concluded that potential yield development is not limited by solar radiation interception in the canopy.

3.8.5. **The effect of the flower canopy (Stages IIb and III)**

The proportion of R_T reflected during flowering was approximately 30% in 1991 and 1992, and 25% in 1993. Since proportions of radiation intercepted by the pod canopy were calculated for GAI only, the amount intercepted by flower petals cannot be directly determined. The maintenance of a constant growth rate (increase in DM) during flowering in 1992 and 1993 (Figs. 3.3 & 3.1) indicates that any limitations to radiation interception imposed under bright conditions were of little significance to growth. However, in 1991, when radiation levels and temperatures were low, the growth increment was reduced in Stage III (Fig. 3.3) because the rate of DM production was very low (Table 3.1). During the week when total DM declined in 1991 (28 May), 33 MJ m^{-2} were intercepted by the developing pod canopy and only 21 MJ m^{-2} by the two leaf layers below. In the corresponding week in 1993 (18 May), the same leaf layers intercepted 72 MJ m^{-2} while the pod canopy intercepted 23 MJ m-2. k values were reduced only marginally during flowering (Appendix IV), indicating that petals may have slightly reduced the penetration of radiation through the canopy. This was of little consequence, however, unless low incident radiation levels (1991) were exacerbated by reflection from the pod canopy.

The proportion of photosynthetically active radiation (PAR) reflected was not measured in the present study. Based on anecdotal evidence only, Mendham *et al.* (1981) considered reflection by flower petals to be a major source of loss of solar radiation. Bilsborrow (1985) observed that 19% of PAR was reflected at full flower,

(a) 1991

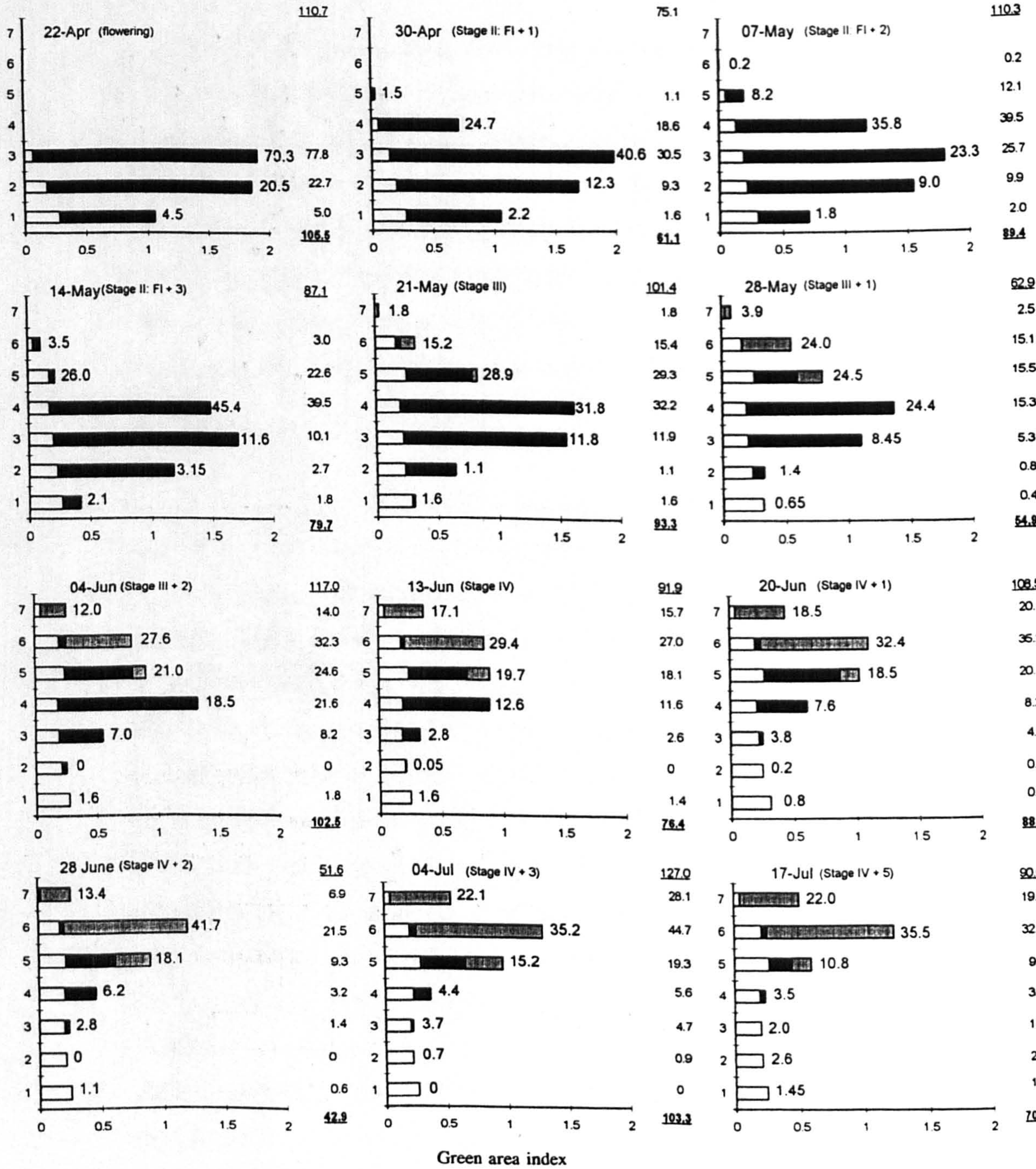
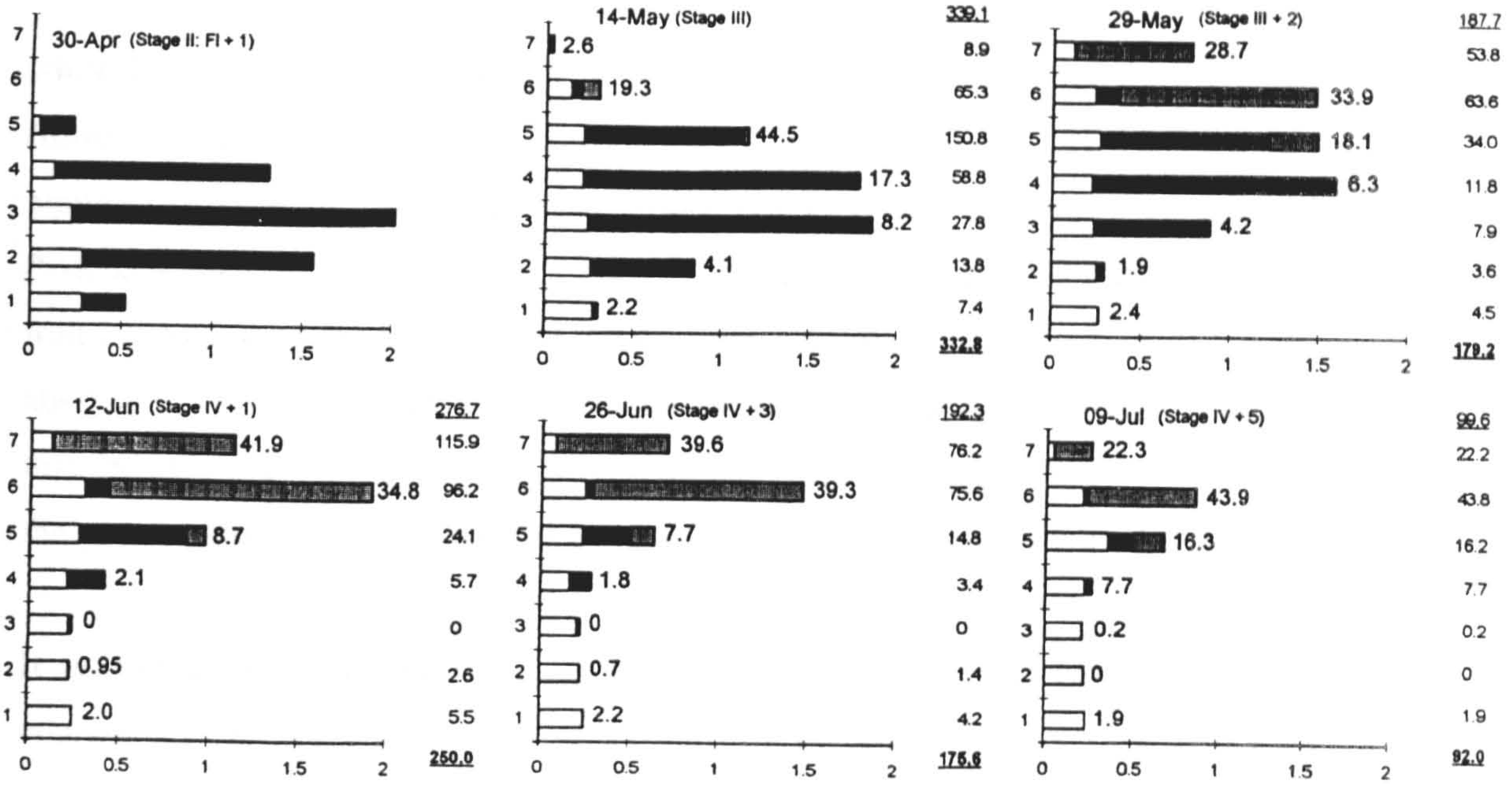
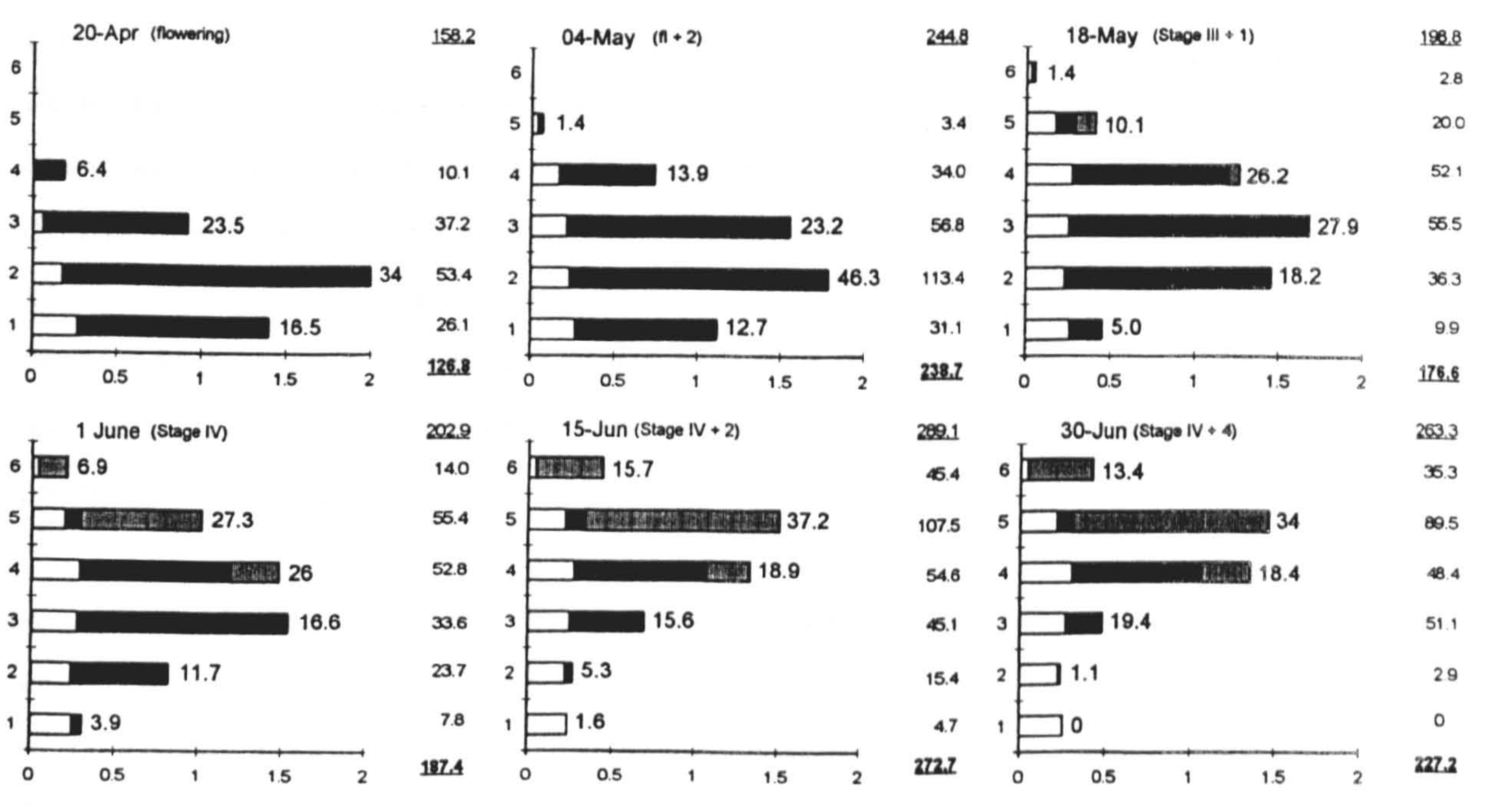


Fig. 3.12. Radiation interception in the crop profile in relation to green area index. Contents: GAI in each layer of the profile (bars: □ stem, ■ leaf, ▒ pod); % of total incident radiation intercepted in each layer (figures next to bars); total incident radiation (MJ m^{-2}) in intervals between sampling dates (top right in bold); radiation intercepted in each layer (MJ m^{-2}, column on

(b) 1992



(c) 1993



Green area index

right); and the total radiation intercepted in each interval (bottom right in box) for reproductive development in each season: (a) 1991, (b) 1992, and (c) 1993.

Developmental stages (in weeks) in parentheses.

Note: No radiation data are available for 30 April, 1992.

while Daniels *et al.* (1986) similarly obtained reflectances of 10-20% of PAR from flowering canopies. Yates & Steven (1988) showed that the presence of large numbers of flowers can substantially reduce (by 16% over a range of varieties) the PAR available for absorption by the leaves. A flower cover of 62% effected a 2.7-fold increase in reflection with the result that leaves absorbed only 41% of the PAR absorbed by a non-flowering canopy. Despite this, Yates & Steven (1987) concluded that the effect on final yield was only marginal. This is supported by the findings of the present study showing that final yield is dependent upon events in Stage IV.

It appears unlikely that, during Stage II, photosynthesis limited growth, a conclusion consistent with the observations of Bilsborrow (1985). However, the major and preferential sink for assimilates at this time was stem (Daniels *et al.*, 1986) which, during early flowering, was growing rapidly. Therefore, in Stage II, a proportion of pod and seed losses may have been caused by competition for assimilates within the plant. In CO_2 assimilation studies, Chapman *et al.* (1984) found that at early flowering (30 April), pods were responsible for 2% of the total assimilates initially fixed, and imported a further 5% within 24 hours. This relatively small assimilate demand contrasted markedly with stem which fixed 30% and then imported a further 13.5% (from leaf) over the same period. Other possible factors affecting yield production in Stage II include incomplete formation of vascular connections to pods and seeds, and the involvement of plant hormones or other factors, which may be produced by developing seeds and may influence sink demand (Daniels *et al.*, 1986).

Assimilate demands of the developing reproductive framework clearly take priority with respect to assimilate partitioning until Stage III when the growing pods become the major sink. Prior to this, stem development is dependent upon leaf photosynthesis. The ultimate control of stem growth is probably mediated by hormones associated with the onset of pod development because at the onset of Stage III, when stem growth ceases, pods are still weak sinks. Growth and yield potential are not limited, but pod survival is limited by assimilate availability. Consequently crops that produce less stem material (as in 1993) could be at an advantage with respect to assimilate availability for early pod development because, depending on the extent of overlap

between the stages, pod and/or seed survival in the earliest-formed pods could be enhanced.

Conclusions

1. The rate of DM production was not affected by the flower cover in Stage II. In Stage III, the rate of DM production was reduced only when incident radiation was low.
2. Pod survival in Stage II was determined by the availability of assimilates because flowers and developing pods were competing for these with the rapidly-growing stem.
3. The assimilate demands of the stem took priority until Stage III when its growth ceased.

3.8.6. The effect of radiation interception on yield component determination in Stage III

Section 3.8.3. indicated the considerable variation between seasons in the pattern of radiation interception down the profile (Fig. 3.12). In this section, Fig. 3.12 will be used to demonstrate that, in 1993, a greater proportion of the incident radiation was available lower in the profile for utilisation by leaf material. The effects of this on pod and seed retention will be examined.

At the onset of Stage III, crop growth was still largely dependent on assimilation by leaf but during this phase, the proportion of radiation intercepted by each layer of the crop profile changed rapidly, and leaf interception decreased while pod interception increased and that of stem was constant (Fig. 3.12). This was because the proportion of radiation available to the main leaf layers was reduced by pod growth in the upper layers. The important sites of radiation interception and assimilation were initially leaf in the base of the pod canopy and the layer below (Table 3.16; Fig. 3.12). Throughout Stage III in 1991 and 1992, the importance of these sites was in rapid decline while pods, stem and branches in the two upper layers became the major sites of interception. The decline in photosynthetic contribution from leaf was much slower in 1993. Consequently, the contribution of leaf to radiation interception and therefore assimilation was much greater (76%) than that of pod and stem (24%), while in 1991

and 1992, the contributions were approximately equal (Table 3.16). This would represent a significant advantage to the crop if, as considered by Bilsborrow (1985) leaves were more efficient than pods and stems. Since it was shown in Section 3.7.4., however, that the efficiency of the 1993 crop was not improved relative to the other seasons, any advantage of increased leaf interception during Stage IV was not manifested in an increased efficiency. The way in which it may have contributed to the higher seed yield in this season will be investigated in the following sections.

Table 3.16. Radiation interception in the profile in Stage III; layers are divided into leaf and pod/stem components according to green area; upper four layers only but totals include lower layers

		MJ m^{-2}			Proportion of total	
		Pod/stem	Leaf	Total	Pod/stem	Leaf
1991	Layer 7	18.3	0	18.3	100	0
	6	62.4	0.4	62.8	99	1
	5	28.6	40.8	69.4	41	59
	4	10.6	58.5	69.1	15	85
	Total	130.2	120.5	250.7	52	48
1992	Layer 7	35.5	0.3	35.8	99	1
	6	82.3	14.8	97.1	85	15
	5	39.3	128.5	167.8	23	77
	4	8.1	56.6	64.7	13	87
	Total	187.0	237.7	424.7	44	56
1993	Layer 6	2.8	0	2.8	100	0
	5	15.4	6.3	21.7	71	29
	4	18.2	50.9	69.1	26	74
	3	12.7	71.2	83.9	15	85
	Total	72.0	224.0	296.0	24	76

By Stage III, the maximum number of potential pods had already been determined (Section 3.4.2). Detailed data on early pod development are available only for 1993 while data for the end of this stage are available for all seasons. In 1993, fertile pods accounted for 31%, 39% and 26% of the potential pods in layers 4, 5 and 6 respectively on 18 May (Stage III + 1 week) (Fig. 3.7). As more flowers developed,

these increased to 42%, 52% and 46% in layers 4, 5 and 6 respectively by 1 June (Table 3.13). Pod retention (% of potential pods retained as fertile pods) was greatest in the middle layer in all seasons. Pods were most numerous in the middle of the canopy which would have created a high sink strength. Although located closer to the main assimilate source, pods in the lowest layer were fewer in number and would have had low sink strength. These pods would also have been shaded which would have resulted in limited photosynthesis. Pods at the top of the canopy were initially weak sinks because of their relative immaturity (Chapman *et al*, 1984). During Stage III in 1993, numbers of abscised pods increased in the lowest and middle pod layers by 81% and 88% respectively (Fig. 3.7). The increase in the top layer was much greater, however (213%). This represented a large loss of flower buds at the end of flowering. Total radiation availability to leaf and interception by leaf (188 MJ m^{-2}) remained high throughout this stage in 1993. The growth rate was fairly constant throughout the flowering period (Table 3.1), indicating that crop growth was not limited by assimilate supply. Pod retention was therefore determined by competition for assimilates within the plant, and large losses of potential pods occurred regardless of solar radiation levels. Other factors may exert overall control over this process. For instance, Keiller & Morgan (1988a, 1988b) suggested that there was limited time available for flower and pod production, and that when seed-filling commenced in the older pods, a hormonal and/or nutritional mechanism inhibited further development in apical regions.

At the onset of Stage III in 1993, seed number per pod declined down the pod canopy (Fig. 3.8). Evidence from Stage II (Section 3.5.2) suggests that this was either genetically or hormonally determined, and was not related to solar radiation levels. During Stage III, the decline in seed number per pod with time was greatest in the top layer (Fig. 3.8). Lower pods may have lost fewer seeds because they were more favourably positioned with respect to the source of assimilate. Seed numbers per pod were not investigated in Stage III in 1991 and 1992, but at the end of this stage, these were lowest in the bottom pod layer in 1991 and in the top layer in 1992. The low seed number per pod in upper pods in 1992 may be linked to competition between a large number of pods at a time when the crop was largely dependent on leaf

assimilation, because the assimilates would have been more readily available to lower pods. In Stage III in 1991, fewer pods were competing at any time for the assimilates supplied by the much larger LAI (Fig. 3.12). Rapid fluctuations in assimilate supply could affect seed number per pod through the effects of plant hormones. Levels of these can change very rapidly, especially during the first week of pod development (Rood *et al.*, 1989), and since assimilate partitioning is thought to be regulated by plant hormones (Morgan, 1982; Pechan & Morgan, 1985; Rood *et al.*, 1989), such changes could cause seed losses.

Determination of seed number per pod is largely dependent on the capacity of the crop to supply assimilates to its seeds during the flowering period, particularly in Stage III. Under similar growing conditions in the UK, Mendham *et al.* (1981) observed large seed losses to occur in the first two-three weeks after the onset of flowering, which would correspond approximately with Stage IIb. However, this coincided with rapid growth of pod walls (Mendham *et al.*, 1981) which, by definition, implies that this important phase was Stage III. Within the developing pod canopy, pods of different ages are developing simultaneously, so the process is prolonged for the crop as a whole compared with an individual pod.

When large numbers of pods are set (as in 1992), the number of seeds per pod may be limited by severe inter-pod competition for assimilates (Mendham *et al.*, 1981; Chapman *et al.*, 1984; Ancha & Morgan, 1988). However, Jenkins & Leitch (1986) did not consider the number of pods and competition between them to be a major determinant of seed number per pod. This conclusion is supported in the present study by the high seed retention in 1993 compared with 1991 despite similar pod numbers. Mendham *et al.* (1984) suggested that inadequate crop growth at flowering was a major cause of seed abortion, and poor seed yields were associated with an inability of small crops to support their seeds when excessive pod production occurred (Mendham *et al.*, 1990). The crop size at flowering was considered to be a measure of the size of the assimilate source available to support the developing pods (Mendham *et al.*, 1981). Shipway (1981) found a relationship between intercepted solar radiation per pod and seed number per pod but still considered crop size at

flowering to be important. Jenkins & Leitch (1986) found no relationship between the size of the assimilate source (crop DM per pod at full-flower) and the number of seeds per pod at maturity, and concluded that seed number per pod is not determined in this way. These workers considered the most important determinant of high seed retention to be high incident solar radiation at the time when seed numbers per pod were determined. This supports the findings from the present study that:

1. Crop size at flowering does not determine the size of the yield components.
2. Remobilisation of DM is not an important source of assimilate for seed-filling.
3. The magnitude of photosynthesis in Stage IV is the major determinant of final yield.

Further conclusions from this section are listed below:

4. Radiation interception by leaf declined in Stage III, the extent depending on season.
5. The amount of radiation intercepted by leaf was determined by leaf retention and the size of the pod canopy, which removed an increasing proportion of the incident radiation.
6. Pod retention was influenced by position in the canopy and was greatest in the middle region.
7. Pod number determination was largely supported by leaf assimilation.
8. Assimilation in stem and branches was important in the transition between Stages III and IV when leaf was declining and pods were still small.
9. Stage III was important in the determination of seed number per pod.
10. Seed retention was determined primarily by the number of pods and the availability of assimilate.
11. Prior to Stage IV, determination of seed number per pod was supported largely by leaf assimilation.
12. Initial large seed losses at the top of the crop were caused by inter-pod competition for assimilates produced by leaves, with lower pods initially taking priority with respect to these.
13. The decline in seeds per pod down the canopy was determined partly genetically (more seeds in upper pods) and partly by the assimilate supply, and was probably influenced by hormonal factors.

14. Radiation interception by the pod itself was not important in the determination of seed number per pod prior to Stage IV.

3.8.7. **Yield component determination in Stage IV**

By the end of Stage III (late May/early June), the thick canopy in 1992 contained 9500 pods m^{-2} while the thinner 1991 and 1993 canopies contained 7000 and 6400 pods m^{-2} respectively (Fig. 3.6). During early seed development, the top two layers (100-140+ cm) in the thick 1992 canopy intercepted more than 75% of the available solar radiation and substantially reduced the amount available to the lower layers (Fig. 3.12). From 12-25 June, 212 MJ m^{-2} were intercepted in the top two layers (from R_T 277 MJ m^{-2}), leaving only 65 MJ m^{-2} available to the lowest pod layer. This layer and the two layers below contained nearly all the leaf and therefore, the amount of radiation intercepted by leaf was very small. By contrast, the thinner pod canopies of the 1991 and 1993 crops allowed 45% and 47% respectively of the total incident radiation to pass through to the leaf layer at the base of the pod canopy. Therefore, over similar developmental periods in 1991 (20 June - 3 July) and 1993 (15-29 June) the radiation available to the leaf layers was 76 MJ m^{-2} (incident radiation was lower than normal in 1991) and 136 MJ m-2 in 1991 and 1993 respectively. The three main leaf layers at this time intercepted 46 MJ m^{-2} (27%), 30 MJ m^{-2} (11%) and 115 MJ m^{-2} (40%) in 1991, 1992 and 1993 respectively. When the heavy 1992 crop lodged in late June, further restriction of radiation penetration down the pod canopy probably occurred but, because of the method used to determine radiation interception within the canopy (Appendix IV), this could not be detected (Fig. 3.12.b). The thin 1993 crop remained erect throughout.

In 1991 and 1993, fertile pod numbers remained fairly constant until late in seed development, when other factors became important. However, in 1992 fertile pod number declined markedly in early June which was due to abscission in all layers of the pod canopy, particularly in the lowest layer (5) (Fig. 3.7). This was probably a consequence of the unusually low incident radiation levels in early June (Fig. 3.12).

Leaf retention and therefore LAI were greater in 1993 during the seed development

stage (Fig. 3.12). This may have been due to the improved radiation environment, which was reflected in the lower k values for the pod canopy in this season (average $k = 0.35$ during seed development in 1993 compared with 0.45-0.50 in 1991 and 1992; Appendix IV). The role of leaves in seed-filling is thought to be minor in winter oilseed rape (Bilsborrow & Norton, 1984) but they can make a significant contribution to seed growth in spring rape (Major & Charnetski, 1976; Brar & Thies, 1977). Although largely self-sufficient at this time, the pods of spring rape plants import assimilates from other organs (Rood & Major, 1984). The level of autonomy probably depends on solar radiation availability and therefore on the degree of radiation penetration through the canopy and/or pod position in the canopy. In the present study, leaf remaining in Stage IV was located largely at the base of the pod canopy in all seasons. The ability of this leaf to contribute to seed-filling was dependent on the amount of solar radiation it received, which in turn depended on the transmission through the canopy. Major & Charnetski (1976) showed that in spring rape, most assimilate movement is acropetal. Similar movement of assimilates from retained leaf in winter rape could promote pod and seed retention and/or seed growth. Radiation interception by the mainstem, which constituted the entire lower layers in Stage IV, was negligible, with the implication that assimilation in the mainstem made little contribution to seed-filling.

The improved radiation penetration in the 1993 crop resulted in a change in the relative proportions of leaf and pod/stem photosynthesis. This occurred because increased availability of radiation lower in the crop profile resulted in increased leaf retention. Therefore most of the radiation that was not intercepted by the pod canopy was intercepted by the leaf below. Total radiation interception was also high in Stage IV in 1993 because incident levels were high (Fig. 3.12). In 1993, 190 MJ m^{-2} were intercepted by leaf in Stage IV, which amounted to 30% of the total intercepted in this stage compared with 17% (60 MJ m^{-2}) and 10% (58 MJ m^{-2}) in 1991 and 1992 respectively (Table 3.17). The increased assimilation in 1993 enabled the crop to support a higher number of seeds per pod throughout the canopy in 1993 (Section 3.7). In the thick canopy in 1992, few seeds per pod were lost in the well-illuminated pods at the top, but losses were progressively greater lower down where the pods were

more shaded. In 1993, seed number per pod still declined with depth in the canopy at maturity, but seed losses did not increase with depth. This contradicts the suggestion of Jenkins & Leitch (1986) that better radiation penetration in an upright canopy would increase photosynthesis and seed growth, but that it would be unlikely to affect any other yield components. However, the present findings support Australian work with an apetalous variety where leaf persistence was promoted by a combination of irrigation and better radiation penetration into the canopy (Rao *et al.*, 1991). The resulting increase in photosynthesis at the base of the pod canopy improved seed retention in pods lower in the canopy (Rao *et al.*, 1991). The decline in seed number per pod down the canopy in the present study was also partly attributable to genetic factors since findings in Section 3.5.2. indicated that ovule number per ovary declined with depth. Such an adaptation would be beneficial for resource management because pods with the lowest potential (at the base of the canopy in shade) would have fewer seeds than the potentially higher-yielding pods in the high radiation environment at the top of the canopy.

Table 3.17. Radiation interception in each of the upper four layers of the crop profile divided into components according to green area (lower layers not included in totals)

		MJ m^{-2}			Proportion of total	
		Pod/stem	Leaf	Total	Pod/stem	Leaf
1991	Layer 7	90.6	0	90.6	100	0
	6	154.8	5.6	160.4	97	3
	5	41.2	35.3	76.5	54	46
	4	13.0	18.8	31.8	41	59
	Total	299.6	59.7	359.3	83	17
1992	Layer 7	240.4	0.8	241.2	100	0
	6	234.8	12.6	247.4	95	5
	5	37.7	34.4	72.1	52	48
	4	12.2	10.5	22.7	54	46
	Total	525.1	58.3	583.4	90	10
1993	Layer 6	94.7	0	94.7	100	0
	5	233.5	18.9	252.4	93	7
	4	62.5	93.3	155.8	40	60
	3	51.8	77.9	129.7	40	60
	Total	442.5	190.1	632.6	70	30

The effect of position in the pod canopy on 1000-seed weight was the same in 1991 and 1993. At the onset of seed-filling, 1000-seed weights were greatest in the lowest pods. Since flowering and pod development proceed acropetally, pods at the base of the terminal raceme were developmentally superior (Addo-Quaye *et al.*, 1986), and initially had a higher sink strength. Seed growth rates decreased with depth in the canopy so that the heaviest seeds were in the top layer at maturity. Diepenbrock & Geisler (1979) showed that rates of DM accumulation depended on pod position, and that seeds on axillary branches initially developed more rapidly but then declined after reaching a maximum, while the rate in terminal raceme seeds did not decline. In the present study, the usual stratification effect was lost by maturity in 1992 because of lodging. Higher growth rates at the top of the pod canopy were partly the result of greater radiation interception by pods and branches. In addition it is possible that upper pods possessed greater sink strength and were more able to attract assimilates from lower parts of the crop, particularly from leaf, as in 1993. In spring rape in Canada, Clarke & Simpson (1978a) suggested that the

> *"rapid increase in seed weight late in the ripening phase.....could have provided the high sink demand which in turn increased photosynthetic activity"*.

This occurred because the seeds were the dominant sink and exerted a controlling influence on the assimilate management of the source. The sink demand may have become higher in upper pods because seed growth was more rapid in these, and growing seeds probably released hormones that attracted assimilates from other sources (Scarisbrick *et al.* 1986). This would account for the predominantly acropetal movement of assimilates in the present study and will be investigated further in Section 3.8.8.

Conclusions

1. Leaf retention in Stage IV was improved in a more open canopy where radiation transmission was more favourable (1993).
2. Increased leaf retention in Stage IV increased total radiation interception and the amount of assimilate available. The contribution of leaf to total assimilation was also increased.

3. Increased assimilate production (in leaf) improved seed retention.
4. Below the pod canopy, assimilation in the mainstem contributes little to seed-filling.
5. Lodging in some seasons may reduce radiation penetration and could cause seed losses.

3.8.8. The efficiency of seed dry matter production in the pod canopy

In Section 3.7.4, it was shown that the overall efficiency of seed production in Stage IV was considerably greater in 1991 than in 1992 and 1993. The quantitative aspects of radiation interception and use by the crop were discussed in Sections 3.8.4 - 3.8.7 and in this section, the functioning of the pod canopy will be investigated in more detail. By relating DM changes to radiation interception, the efficiency of seed DM production during Stage IV was calculated for each layer of the pod canopy and for the pod canopy as a whole (Table 3.18). The efficiency of the pod canopy was also highest in 1991. Calculations of efficiencies for the first two and four weeks of Stage IV indicate slight variations in efficiencies during Stage IV in each season (Table 3.18). As for the whole crop, the efficiency declined in Stage IV irrespective of radiation interception, although the decline was only slight in 1993.

The greater overall efficiency in 1991 was associated with greater efficiency in all layers of the pod canopy. In all seasons, the middle layer of the pod canopy (6) was generally the most efficient, while the efficiency of the bottom layer was lowest. These efficiencies do not reflect actual radiation use per layer because they represent the sum of the DM produced in that layer and that imported from other sources. During Stage IV, the bottom layer of the pod canopy contained much of the remaining leaf, which intercepted 35 MJ m^{-2}, 34 MJ m^{-2} and 93 MJ m^{-2} in 1991, 1992 and 1993 respectively (Table 3.17). In 1993, interception by leaf in this layer accounted for 13% of all the radiation intercepted in Stage IV. Working at an average efficiency of 1.4 g seed MJ^{-1} (Table 3.17) in 1991 and 1992, leaf interception in the bottom layer of the pod canopy could have provided 49 g and 48 g DM in 1991 and 1992 respectively, which is equivalent to 12% and 11% of final seed yield in 1991 and 1992 respectively. In 1993, despite a lower efficiency in Stage IV (1.1 g MJ^{-1}), leaf interception in this layer (86 MJ m^{-2}) would have produced 95 g DM, which is

equivalent to 19% of final seed yield (491g m^{-2}).

In all seasons, most of the assimilates produced in the bottom layer of the pod canopy were probably translocated to the upper layers, thereby accounting for its low efficiency and for the unusually high efficiencies in the upper layers. The high efficiency in layer 6 suggests that this layer was the major sink for DM because of its large number of pods, and indicates that DM accumulation may be driven by sink size. In 1993, the calculated efficiency of the middle layer was little greater than the top layer, which may be due to the greater contribution of leaf photosynthesis in this season. The extent to which assimilation in pod walls can supply seed growth must depend on the amount of radiation intercepted by the pod, which will not be even throughout the layer, since upper pods will intercept more and lower ones less. Table 3.19 indicates the average radiation intercepted per pod in each layer during Stage IV for interception by all GAI and for pod and stem. Interception per pod for the whole canopy was much higher in 1993 due to both increased leaf interception and greater incident radiation. In all seasons, the omission of leaf interception greatly reduced energy availability per pod in the bottom layer but not in the upper layers. With the exception of 1993, the productivity of pods in the bottom layer was low, which supports the conclusion that the products of assimilation in this layer must have been important in supporting pods higher in the canopy. This would have been particularly important for those pods in the dense middle layer whose photosynthetic capacity would have been severely limited by shading.

The association of the low efficiency of radiation use in 1993 with an increased contribution of leaf photosynthesis suggests that leaves may be less efficient than pods and stems. This is supported by the observation that, despite the rapid decline in GAI in Stages III and IV due to leaf senescence, DM continued to be produced at an almost constant rate (Figs. 3.1 and 3.3). In addition, calculated efficiencies of DM production in Stage IV were of a similar magnitude to those in Stage II (Table 3.8) (when the sources of assimilate were mostly leaf and stem), despite the greater energy expenditure required in Stage IV because of the high lipid content of seed. However, although leaf retention did not improve crop efficiency, it increased total interception.

Table 3.18. Efficiency of seed DM production in layers of the pod canopy in each season

	Interval	Layer 5	Layer 6	Layer 7	Whole pod canopy
1991	13 June-28 June	0.95	1.69	0.91	1.30
	13 June-4 July	0.88	1.71	1.34	1.41
	13 June-17 July	0.56	1.88	1.62	1.50
	13 June-29 July	0.81	1.61	1.02	1.27
1992	29 May-12 June	0.36	1.90	1.25	1.38
	29 May-26 June	0.70	1.54	0.84	1.12
	29 May-9 July	2.55*	0.98	0.58	1.01
1993		Layer 4	Layer 5	Layer 6	
	1 June-15 June	0.51	1.59	1.40	1.19
	1 June-30 June	0.50	1.36	1.32	1.09
	1 June-13 July	0.24	1.29	1.58	1.08

** Not a real effect. The large DM increase in this layer late in the season was due to lodging.*

Table 3.19. Radiation interception per pod in each layer of the pod canopy in Stage IV for interception by (a) all organs and (b) pod+stem

		Pod number m^{-2}	MJ m^{-2}		MJ m^{-2} pod^{-1}	
			Pod/stem+ leaf	Pod/stem	Pod/stem+ leaf	Pod/stem
1991	Layer 7	2000	90.6	90.6	0.045	0.045
	6	4000	160.4	154.8	0.040	0.039
	5	1000	76.5	41.2	0.077	0.041
	Total	7000	327.5	286.6	0.047	0.041
1992	Layer 7	3000	241.2	240.4	0.080	0.080
	6	5000	247.4	234.8	0.049	0.047
	5	1000	72.1	37.7	0.072	0.038
	Total	9000	560.7	512.9	0.062	0.057
1993	Layer 6	1500	99.5	99.5	0.066	0.066
	5	4000	263.4	243.6	0.066	0.061
	4	1000	155.3	62.4	0.155	0.062
	Total	6500	518.2	405.5	0.080	0.062

In conclusion, assimilates produced by leaf in all seasons moved acropetally and supported pods higher in the canopy, which may have occurred because of higher sink strength in upper pods. This effect was particularly important in 1993, when increased leaf retention resulted from a combination of a more open canopy, higher incident radiation and, probably, adequate rainfall. Total assimilate production was increased and seed retention improved. These effects were manifested through increased seed number per pod and 1000-seed weight. Movement of assimilates from source in the bottom layer to sink in the upper layers explains why 1000-seed weight declined with depth in the canopy in all seasons even though radiation interception per pod only declined down the profile in 1992. Assimilate distribution and utilisation seem to be determined not by supply but by some overall control mechanism, possibly hormonal.

3.9. OTHER FACTORS AFFECTING YIELD DETERMINATION

The decline in pod numbers in each season during late Stage IV was not due directly to the radiation environment, which changed little, but to other factors causing premature pod-ripening, namely disease and drought. Disease caused pods to be lost directly through loss of green pod area, and also indirectly since premature ripening and pod-shatter often resulted (Section 3.7.2). The main disease pressures were sclerotinia in 1991 and 1992, and stem canker in 1993 (Section 4). Particularly in 1992, sclerotinia may have reduced the average 1000-seed weight at final harvest, largely because of premature senescence of whole plants, which reduced the time available for radiation interception. In addition, temperatures were high in Stage IV (mainly June) in 1992 (Table 3.2). Shipway (1981) observed that total intercepted radiation in rapid growth periods was often low because high temperatures curtailed the duration of growth. Determination of the extent of the contribution of each of these factors to the reduction in seed growth in 1992 is not possible. The partial lodging which occurred in late June in 1992 condensed the pod canopy further but the effect on radiation interception is not clear. This coincided with a large reduction in seed number per pod, however, which was most extreme in the lowest pod layer (Fig. 3.8). Although lodging may have been a contributory factor, the most likely reason for this was probably the high soil moisture deficit (SMD) that developed during the summer (Fig. 3.13). Almond (1985) observed no adverse effects on growth and

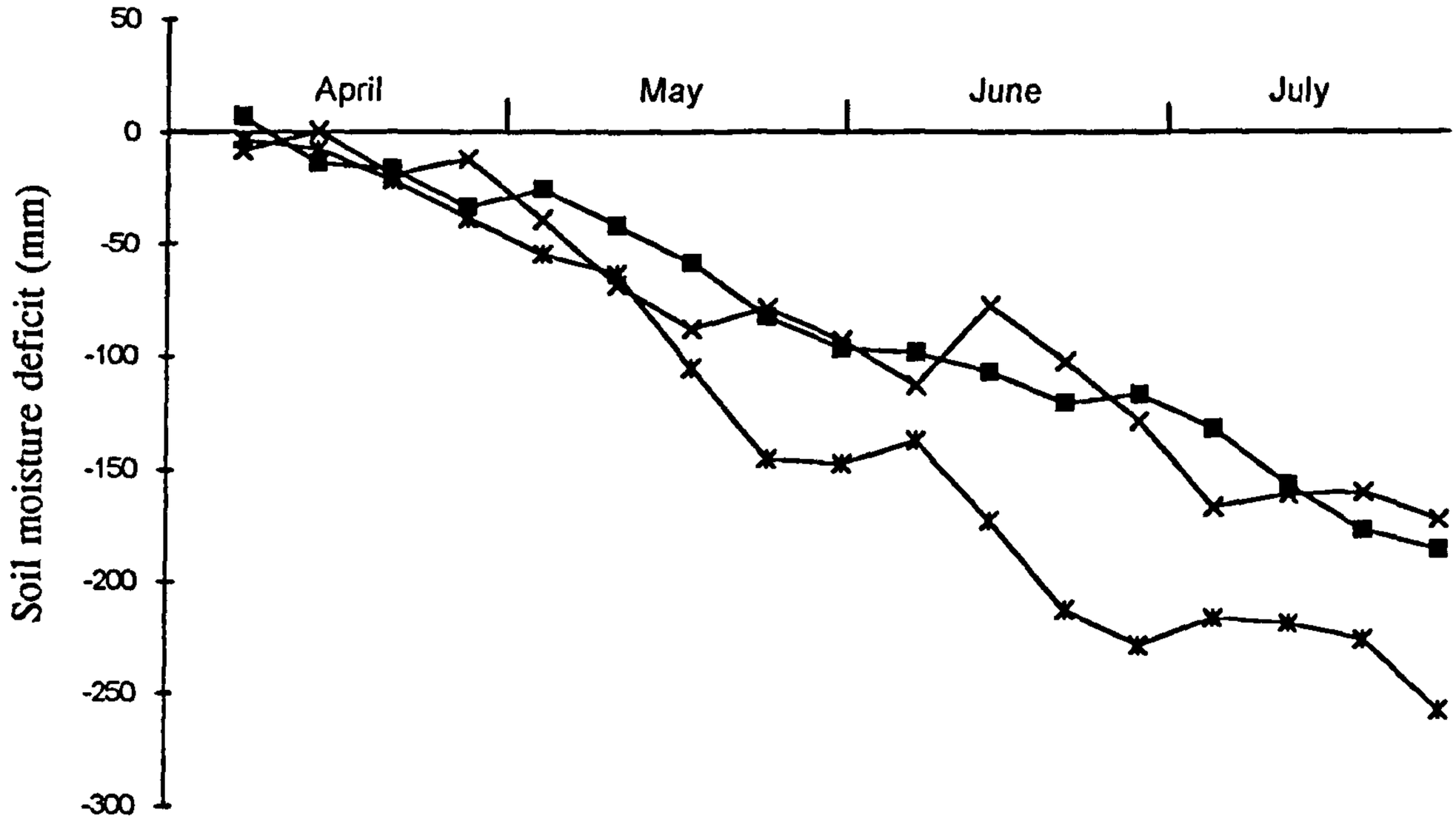


Fig. 3.13. The development of the soil moisture deficit with time from 1 April in each season

■ 1991

✱ 1992

x 1993

development at SMDs of up to 140 mm, but in the present study, the SMD in late June in 1992 exceeded 220 mm. The effects of moisture stress are accentuated in hot weather and maturity is hastened (Whitfield, 1992), and dry conditions from late flowering onwards caused substantial seed losses in Australia (Mendham *et al.*, 1990). In soybean, when good growing conditions were followed by drought stress during seed development, many pods were retained to maturity but both seed numbers and seed size were reduced (Vasilas, Fuhrman & Gray, 1989). In conclusion, the substantial seed losses at the end of June and the low final 1000-seed weight in 1992 were due to limitations to the assimilate supply late in development caused by the effects of sclerotinia and the high SMD, which were accentuated by high temperature.

3.10. MAIN CONCLUSIONS

This section has shown that under normal growing conditions in the UK, final seed yield is dependent on the magnitude of photosynthesis in Stage IV, which is determined by total radiation interception during this stage. Therefore it is largely independent of preceding events and is unlikely to be limited by the size of the potential yield. This explains why crops that are small at flowering, as in 1993, are able to yield equally as well or sometimes better than large crops. The relationship between total radiation interception and seed yield was dependent upon the absence of other limiting factors such as a high SMD, high temperatures and disease pressure which severely limited seed yield in 1992. Also, this was not a direct relationship because the efficiency of utilisation of intercepted radiation was variable between seasons.

The main phase of yield component determination occurred in Stage III (pod development) when heavy pod and seed losses occurred coinciding with expansion of pod walls. At this time the main assimilate source (leaf) was in rapid decline and its role was taken over by stem and pod. However, ultimate seed yield was determined in Stage IV (seed development) by the photosynthetic capacity of the crop and its ability to supply assimilates to its seeds, since seed losses continued during this stage and individual seed weight was determined. Although radiation interception by the pod canopy depended on pod number (and area), interception per pod was variable

within the canopy. Seed retention and growth were enhanced by assimilate export from lower in the profile, since more assimilates were produced in the bottom layer of the canopy than were utilised in seed-filling. The net result was greater DM production in upper pods than would be expected from the amount of radiation intercepted. Leaf played a significant role in this in all seasons, but particularly in 1993, when leaf retention was increased due largely to a more open canopy and high incident radiation. Leaf photosynthesis was probably less efficient than that of pod and stem, but its contribution allowed the utilisation of radiation which would otherwise have been lost to the ground.

Section 4: THE EFFECT OF PROCHLORAZ ON DISEASE INCIDENCE AND SEVERITY

4.1. INTRODUCTION

The effect of prochloraz on diseases of oilseed rape has previously been investigated in field trials aimed at finding both optimum rates and times of application, in order to maximise yield. Trials have involved comparisons with other fungicides or applications in combination with these. Results have often varied between seasons and depended on the time of application. The most important factor determining the effectiveness of prochloraz is the timing of application in relation to both disease development and climatic conditions, rather than the rate of application (Rawlinson, 1979). Prochloraz is particularly effective against light leaf spot (*Pyrenopeziza brassicae*), and has produced significant yield increases in seasons when this has been the most prevalent pathogen (Wakerley & Russell, 1987). It is equally active against another damaging pathogen of oilseed rape, stem canker (*Leptosphaeria maculans*), but less active against alternaria dark leaf and pod spot (*Alternaria spp.*), stem rot (*Sclerotinia sclerotiorum*) and grey mould (*Botrytis cinerea*), and inactive against downy mildew (*Peronospora parasitica*).

The major objective of this research programme was to quantify specifically the phytotonic effects of prochloraz on oilseed rape. The relative contribution of the fungicidal properties of prochloraz to yield was estimated by means of disease assessments made at intervals through each season as described in Section 2. Tabulated results from data analysis using Genstat5 are presented in Appendix II. Abbreviations for prochloraz treatments are given in Appendix I, Table 2.

4.2. RESULTS

4.2.1. **Disease and pest incidence in each season**

Data are presented from each season for the incidence and severity of diseases and pest damage based on mean values for control plots. Sclerotinia stem rot was a problem in all three seasons, particularly in Season 2 (S2), but was controlled in Season 3 (S3) by applying iprodione. Botrytis also developed to damaging levels in

S2. Light leaf, stem and pod spot was widespread in Season 1 (S1), and a severe stem canker epidemic developed in S3.

4.2.1.1. *Season 1 (1990/91)*

(a) Diseases

In mid-December, downy mildew was the most prevalent disease, affecting 28.6% of plants (Table II.1). There were very low incidences of both phoma leaf spot and alternaria on leaves (1.6% and 0.5% of plants respectively). Leaves infected by phoma had, on average, 0.5 leaf spots per leaf.

By mid-April, shortly before the onset of flowering, downy mildew remained the most prevalent disease, affecting all plants examined, and 30.3% of leaves (Table II.2). The incidence of phoma leaf spot had also increased, affecting 60% of plants, but its severity was low: only 5.3% of leaves were infected, and there were 1.4 lesions per infected leaf, and only 1.6 lesions per infected plant. Alternaria remained at very low incidence and severity. Light leaf spot (LLS) appeared in early spring, and by mid-April, affected 50% of plants, but few leaves were infected (8.0%), and the mean leaf lesion score was 0.245 per plant.

At the end of May (late-flowering), downy mildew remained the most prevalent disease, with most plants (95%) having at least one leaf infected (Table II.5), but severity had changed little since April (26% of leaves affected). The incidence of LLS (45% of plants), had also changed little during flowering, but more leaves showed symptoms (44%, Table II.3), although disease severity (lesion scores) remained low. LLS also affected the stems of 50% of plants, but again severity was low (lesion score per infected plant: 0.10). Symptoms of phoma leaf spot had virtually disappeared by the end of May (Table II.5). The incidence of alternaria had increased to 10% of plants (Table II.4), but severity remained very low with only 1 lesion per infected leaf. Botrytis occurred at low levels at the end of May (Table II.4) but none of the untreated (control) plants assessed was infected.

In early July, the amount of leaf area remaining was small, so leaf diseases were not

assessed. Light leaf and pod spot (LLPS) affected all pods and 80% of stems (Table II.8), although infected plants had lesions affecting only 0.46% of the total pod area, and an average stem lesion score of only 0.10. The incidence and severity of stem canker were relatively low (23% of plants infected; mean severity score 0.1; Table II.10). Alternaria affected the pods of 30% of plants, which was disproportionate to the earlier leaf infection (Table II.12), although less than 0.1% of the total pod area of all plants was affected (0.28% on infected plants). Powdery mildew was very common on stems, but affected pods on only 3.3% of plants (Table II.12). Sclerotinia stem rot affected 6.7% of plants (lesion score 1.0 per infected plant, Table II.10), although one month later, at final harvest, its incidence and severity were considerably greater (25% plants infected; mean lesion score 3.5 per infected plant).

(b) Pests

Damage by larvae of the cabbage stem flea beetle (CSFB) affected 7% of plants in December and, on average, caused 1.0 petiole scars per affected plant (Table II.1), but by mid-April, it was negligible. In late May, however, the incidence of damage by adult beetles had increased to 30% of plants, with 3.4% of leaves damaged, and an average of 0.35 feeding holes in leaves per plant, and 1.0 per affected plant (Table II.6). Stem damage by CSFB in early July affected 3.3% of plants (Table II.14). Pigeon damage affected less than 1% of leaves in mid-December (Table II.1), and ceased to be much of a problem by mid-April.

4.2.1.2. *Season 2 (1991/92)*

(a) Diseases

The S2 crop was not assessed for disease until 20 March when LLS and downy mildew were the most prevalent diseases (Table II.15), affecting 50.0% and 43.8% of plants respectively. LLS lesion scores were low (0.01 per leaf; 0.10 per infected leaf). Phoma leaf spot and alternaria were present at very low incidence and severity.

In late May, the incidence of downy mildew had increased to 87.5% of plants and 36.5% of leaves (Table II.19). At this time, botrytis infected almost all plants (94%) and nearly half of all leaves (48.3%) (Table II.18), but very few stems (2.5%). The

overall incidence of LLPS had increased to 50% (stem infection) and 26.2% (pod infection) of plants, but only 8.7% of plants had leaf infections (Table II.16): severity was low on all parts. The incidence of phoma leaf spot was 7.6% of plants, but only 1.5% of leaves, with fewer than 0.1 leaf lesions per plant (Table II.17). The incidence and severity of alternaria remained very low (Table II.18).

In mid-July, LLPS affected the stems and pods of 33% and 69.5% of plants respectively (Table II.20). Severity remained low for both (stem lesion score 0.1; 1.39% of pod area lesioned on infected plants). The incidence of stem canker had increased to 60% but severity was still relatively low (0.10 lesions per infected leaf; Table II.21). Phoma infection of pods was low (5% plants and 1.5 lesions per infected plant). The incidence of botrytis on stems (37.5%) and pods (14.1%) was considerably lower than for leaf infection at the end of May (Table II.22). Disease severity on stems was relatively high (lesion score 3.0 per infected plant), but the severity of pod disease was very low (0.17 pods per plant; 1.0 pods per infected plant). The incidence of alternaria on pods was relatively high (58.8% of plants, Table II.23), but only 0.2% of the total pod area was lesioned (0.10% on infected plants). Sclerotinia occurred at a relatively high incidence in early July (32.5% of plants infected; lesion score 1.00 per infected plant, Table II.23). Other diseases occurred at varying incidences: downy mildew affected pods on 5% of plants; *Rhizoctonia* affected the stems of 20% of plants. *Cladosporium* affected the pods of 56% of plants, but this was saprophytic colonisation, usually associated with previous infection by sclerotinia or botrytis. At final harvest, 39% of plants were infected with sclerotinia and 20% with botrytis. Most plants infected by these pathogens were dead at, or before, final harvest.

(b) Pests

In March, CSFB damage was common (60% of plants) but of a low severity (Table II.15). At the end of May, incidence was 18% (Table II.19) and, in July, 35% (Table II.23). Pigeon damage was widespread in 1991/92 and this was the reason for the relocation of the experiment during the spring of this season. Grazing was so severe at the original site that virtually all plants had lost most of their leaf area by early

spring, reducing their competitiveness against weeds and making their recovery unlikely. There was also widespread (84% of plants), but less severe, pigeon damage at the new site: on average, 3.24 leaves were damaged on each grazed plant (Table II.15), but leaves were generally torn only at the edges, so leaf area was not greatly reduced.

4.2.1.3. *Season 3 (1992/93)*

(a) Diseases

At the end of November, downy mildew affected 52.5% of plants but only 16% of leaves (Table II.24). Phoma leaf spot was present at a very low incidence (2.5% of plants and 0.64% of leaves infected) and severity (0.5 lesions per infected leaf).

At the end of March, the incidence of downy mildew was unchanged, but the proportion of infected leaves had fallen to 10.9% (Table II.25). The incidence of phoma leaf spot had increased considerably to 83.7% of plants infected, but only 17.5% of leaves were infected (1.80 infected leaves per infected plant). The incidence of LLS was also high (63% of plants infected; 15.5% of leaves), but there were only 0.18 infected leaves per infected plant. Botrytis infected 27.5% of plants and 4.4% of leaves (1.27 leaves per infected plant).

At the end of April, most plants (98%), and 39.5% of leaves were infected with downy mildew (Table II.30). The incidence of phoma leaf spot had fallen to 52% of plants and 8.7% of leaves (0.76 leaf lesions per plant; 1 lesion per infected leaf; 1.25 lesions per infected plant, Table II.28). Upper stem infection was very slight and only 2.5% of plants had stem cankers. LLS incidence remained high (57% of plants and 12% of leaves) but at a low severity (Table II.27). It infected 26% of stems but severity remained very low (lesion score 0.1 per infected plant). Botrytis affected leaves on only 10% of plants (1.2% of leaves; 1.1 leaves affected per infected plant, Table II.29). The incidence of botrytis on stems (9%) reflected that on leaves and the lesion score per infected plant was 0.75. The incidence of alternaria was very high (90% of plants) but severity remained very low (0.64 lesions per plant; Table II.29).

In early July, phoma had become the predominant disease, and 91.2% of plants had basal stem cankers (Table II.35): severity was moderate (overall lesion score 3.30 in iprodione-treated plots; 3.42 in untreated plots; not tabulated). The few remaining leaves had little LLPS, but 79% of plants had infected pods and 40% had infected stems (Table II.33). The lesion score for pods was 6.63 per infected plant, and there was only slight infection of stems (lesion score 0.158 per infected plant). Alternaria remained scarce on leaves, and 9% of plants had pods with slight infections (Table II.39). Botrytis affected pods on 15.5% of plants, but leaf and stem infection was slight (Table II.37). In plots sprayed with iprodione, sclerotinia showed low incidence (20%; mean lesion score 2.50, Table II.39), but this was higher in untreated plots (40%; not tabulated). Downy mildew affected all the leaves of all plants, and pods on 46% of plants (Table II.41). Powdery mildew affected 19% of stems and the pods on 34% of plants (Table II.41). At final harvest (mid-July), the incidence of basal stem canker was 95% of plants in plots sprayed with iprodione and the severity score was 3.89 (Table II.49).

(b) Pests

The incidence of CSFB was low at the end of November (16% of plants; 3.8% of leaves; 1.2 damaged leaves per affected plant). At the end of March, damage by larvae and adults occurred on 15% and 25% of plants respectively, and 2.75% and 2.9% of all leaves respectively. At the end of April, CSFB remained at a relatively high incidence (62% of plants affected; 10% with damaged stems, Table II.31). Larvae and adults affected 1.3 and 3.4 leaves per affected plant respectively. By early July, CSFB had damaged 41% of stems (Table II.41).

Pigeon damage was slight at the end of November (15% of plants; 5.3% of leaves affected; 1.5 damaged leaves per affected plant; Table II.24). At the end of March, the incidence had increased to 56.2% of plants, although only 17% of all leaves were affected (2.3 damaged leaves per damaged plant; Table II.26). At the end of April, pigeons had damaged 45% of plants (11% of leaves affected; 2.7 damaged leaves on each affected plant; Table II.30).

4.2.2. The effects of prochloraz on diseases and pests in each season

4.2.2.1. *Season 1 (1990/91)*

(a) Diseases

(i) Autumn application

Disease was slight in mid-December, approximately one month after the autumn application of prochloraz, and there were no significant differences between treatments (Table II.1). In mid-April, the incidence of LLS was reduced from 50-12.5% in AU-plots ($P < 0.05$; Table II.2).

(ii) Autumn and Spring applications

The incidence and severity of LLS were moderate in late May and were unaffected by applications of prochloraz in autumn or spring (Table II.3). While the incidence and severity of phoma were low (Table II.5), leaf lesions were more common in AU+SP plots ($P < 0.10$). Alternaria, botrytis (Table II.4) and downy mildew (Table II.5) were unaffected by either autumn or spring prochloraz.

(iii) Autumn, Spring and Summer applications

In early July, the incidence and severity of LLPS on stems were reduced by both autumn and spring prochloraz. The autumn application also reduced the incidence, but not the severity, of subsequent pod disease (92.0% vs. 99.2%; $P < 0.01$; Tables II.7 and II.8). Autumn prochloraz (in any combination) was more effective in reducing the incidence of stem infection (from 88 to 26%; $P < 0.001$) than the spring application (from 64 to 50%; $P < 0.01$). For LLPS on stems, there was a significant interaction between autumn and spring prochloraz applications: the AU and AU+SP treatments reduced disease incidence but the SP treatment did not ($P< 0.05$). Disease severity (lesion score per infected plant) was not affected (Table II.8). Prochloraz had no significant effect on stem canker, sclerotinia, alternaria or botrytis assessed in early July (Tables II.9, II.11 and II.13). The incidence and severity of powdery mildew on stems was high, but generally unaffected by prochloraz (Tables II.11 & II.12), with the exception of the SP+SU treatment, which reduced incidence (from 93% to 23%; $P < 0.05$; Table II.12).

(b) Pests

CSFB was unaffected by prochloraz for most of the season (Tables II.1 and II.6), but in early July, the incidence of stem damage in AUTUMN-treated plots was higher (25% vs. 11.7% untreated; $P < 0.05$, Table II.13). Prochloraz had no effect on the extent of pigeon damage in December (Table II.1).

4.2.2.2. Season 2 (1991/92)

(a) Diseases

(i) Spring application

There was no autumn application in S2, and the first disease assessment in which prochloraz treatments could be compared was made at the end of May, one month after the spring application. By then, the incidence and severity of LLPS had been significantly reduced by spring prochloraz (Table II.16). Disease incidence was reduced from 50% to 8.7% on pods ($P < 0.01$) and from 26.2% to 13.7% of stems ($P < 0.05$). The incidences of phoma leaf spot and stem canker, alternaria and downy mildew were very low and did not depend on prochloraz treatment (Tables II.17, II.18 and II.19). Botrytis showed a higher incidence but was also unaffected by prochloraz (Table II.18).

(ii) Spring and Summer applications

Assessments in early July, one month after the summer prochloraz application, showed that neither the spring nor the summer prochloraz applications had affected the incidence and severity of LLPS (stems and pods), phoma on pods and stem canker, botrytis (stems and pods), alternaria (pods), or sclerotinia (stems) (Tables II.20-II.23). At final harvest (mid-July), the incidence of sclerotinia was significantly lower in plots treated with prochloraz in spring (29.8% vs. 37.5%; $P < 0.05$; not tabulated). The incidence of plants killed by either botrytis or sclerotinia or both was reduced by spring prochloraz (from 59% to 48%; $P < 0.05$; not tabulated).

(b) Pests

Prochloraz applied in spring did not affect the incidence of CSFB at the end of May (Table II.19). In early July, however, the incidence of damaged stems was

significantly lower in plots sprayed in spring (13.7% vs. 35% untreated; $P < 0.05$, Table II.23).

4.2.2.3. *Season 3 (1992/93)*

(a) Diseases

(i) Autumn application

In late November, both the incidence and severity of phoma leaf spot were extremely low and unaffected by prochloraz (Table II.24). The incidence of downy mildew was significantly greater in sprayed plots (70% vs. 52.5% untreated; $P < 0.05$). At the end of March, downy mildew and LLS were both widespread, but unaffected by the autumn prochloraz application (Table II.25). The incidence of the predominant disease, phoma leaf spot, was unaffected by prochloraz, but treated plants had fewer affected leaves (1.61 vs. 1.80 untreated; $P < 0.05$).

(ii) Autumn and Spring applications

At the end of April, the incidence of phoma leaf spot was reduced by autumn (from 36.5% to 22.5%; $P < 0.05$) and spring (from 38.3% to 20.6%; $P < 0.01$) prochloraz applications (Table II.28). Autumn prochloraz did not affect disease severity (which was relatively low), but spring prochloraz reduced the number of lesions per plant from 0.594 untreated to 0.256 ($P < 0.01$). However, severity on infected plants was not affected (Table II.28). Spring prochloraz reduced the proportion of leaves infected with phoma leaf spot from 6.1% (untreated) to 2.3% ($P < 0.01$) (Table II.28). There was a significant interaction between autumn and spring prochloraz for the incidence of phoma leaf infection ($P < 0.05$). All treatment combinations, ie. single prochloraz applications or combined autumn and spring prochloraz, approximately halved disease incidence, but the effect of the autumn application was improved upon slightly by the spring application. There were no effects of either autumn or spring prochloraz on the incidence and severity of stem canker (which was very low) at the end of April (Table II.28). The incidence and severity of LLPS were not affected by either autumn or spring prochloraz applications (Table II.27), but spring prochloraz reduced the incidence of stem disease (from 22.3% to 3.1%; $P < 0.05$; Table II.27). The incidence and severity of botrytis and alternaria were not affected by prochloraz (Table II.29).

(iii) Autumn, Spring and Summer applications

Disease was assessed in early July 1993, one month after the summer prochloraz application and 62 days after the application of iprodione to half of the plots just before full-flower. Results are presented for the effects of both chemicals.

Phoma/stem canker

Stem canker was the most prevalent disease in early July, affecting approximately 90% of all plants. Iprodione did not affect either stem canker or phoma on leaves and pods (Table II.34). The incidence of leaf disease (which was very low at this time) was reduced by prochloraz applied in spring (from 1.6% of plants to 0%; $P < 0.05$; Table II.34). The incidence of stem canker was unaffected by prochloraz, but its severity was reduced by the autumn application (lesion score from 3.43 to 3.08; $P < 0.05$; Table II.34). There was an interaction ($P < 0.05$) between autumn and spring prochloraz for the severity of stem canker: while autumn prochloraz decreased the severity, its effect was negated by a spring prochloraz application (Table II.35).

Light leaf and pod spot

The incidence of LLPS on pods in July was reduced by iprodione (Table II.32) but severity (lesion score per infected plant) was not affected. Summer prochloraz reduced the incidence (41.5% vs. 59% untreated; $P < 0.05$) and severity (0.55 vs 5.29 untreated; $P < 0.01$) of LLPS on pods (Table II.32). Spring prochloraz also reduced disease severity (1.47 vs. 4.38 per infected plant; $P < 0.05$). The incidence of LLPS on stems was reduced by summer prochloraz (from 30% untreated to 16.6%; $P < 0.05$), but autumn and spring applications were ineffective (Table II.32). Spring prochloraz decreased the stem lesion score per plant (from 0.114 untreated to 0.059; $P < 0.05$). The lesion score per infected plant was reduced by both spring (from 0.243 to 0.102; $P < 0.001$) and summer (0.239 to 0.105; $P < 0.01$) prochloraz applications.

Alternaria

The incidence and severity of alternaria on pods were very low throughout the experiments and were not affected by prochloraz (Table II.39).

Botrytis

The incidence of botrytis on leaves and stems was very low, but stem disease incidence and severity were reduced by summer prochloraz and combinations thereof, and by iprodione (Table II.36). The summer prochloraz application also reduced the incidence of botrytis on pods (from 14.8% untreated to 8.4% of plants; $P < 0.05$).

Sclerotinia

Disease incidence was not affected by prochloraz but its severity was increased by autumn prochloraz application (from 2.36 untreated to 2.75; $P < 0.01$; Table II.38). The incidence of sclerotinia was reduced by iprodione (from 17% untreated to 1%; $P < 0.001$) but its severity was unaffected (Table II.38).

Downy mildew

Downy mildew, which infected all plants, most leaves, and pods on 45% of plants, was unaffected by both prochloraz and iprodione (Table II.40).

Powdery Mildew

Summer prochloraz reduced the incidence of powdery mildew on pods (from 19.7% untreated to 6.6%; $P < 0.001$) and stems (from 14.4% to 4.7%; $P < 0.05$; Table II.40). Iprodione reduced the incidence of stem disease (from 14% untreated to 5%; $P < 0.05$) but not pod disease.

(b) Pests

Cabbage stem flea beetle

By the end of November, autumn prochloraz had not affected the incidence of CSFB damage or the (low) proportion of leaves affected (Table II.24), but at the end of March, the incidence of larval damage was greater in sprayed plots (28.7% of plants vs 15% untreated; $P < 0.05$; Table II.26). By the end of April, fungicides had not affected adult feeding on leaves, but there was more damage to stems by larvae in prochloraz-treated plots, and the AU-treatment increased this significantly (from 10.1% untreated to 27.5% of plants; $P < 0.05$; Table II.31).

Pigeons

The incidence and severity of pigeon damage were not significantly affected by prochloraz throughout the season (Tables II.24, II.26 and II.30).

4.2.3. Detailed analysis of the effects of severe stem canker and sclerotinia on plant growth and yield, and control by prochloraz in 1993 (Season 3)

4.2.3.1. *The effect of prochloraz on the incidence and severity of stem canker*

Because of the unusually high levels of stem canker in 1993, its development was studied in detail. The incidence and severity of stem canker did not differ significantly between the control and AU+SP+SU prochloraz treatments throughout June. On 13 July, the incidence of plant-kill by stem canker was reduced by the AU+SP+SU treatment (from 13.8% untreated to 9.7% of plants; $P < 0.05$). When all treatments were compared at final harvest (in iprodione-sprayed plots), stem canker incidence and severity were lower in AUTUMN-treated plots (93.13% vs. 96.63%; $P < 0.01$; Table II.48). Autumn prochloraz application increased the incidence of low canker scores (2 or lower) from 29.5% to 39.3% ($P < 0.05$), and reduced the incidence of high disease scores (4 or higher) from 67.5% to 53.2% ($P < 0.01$) and the incidence of plant-kill from 21.6% to 14.4% ($P < 0.05$). The AU+SP treatment reduced stem canker severity at harvest (2.776 vs. 3.892; $P < 0.01$) whereas the AU and AU+SP+SU treatments did not (Table II.49). Canker severity at final harvest was lower in plots that had received autumn prochloraz (3.445 vs. 3.994 untreated; $P < 0.01$; Table II.48), although autumn prochloraz alone was not enough to reduce disease severity (Table II.49).

4.2.3.2. *The effects of stem canker and sclerotinia on growth and yield in prochloraz-treated and untreated plots*

Regression analysis was used to investigate the possibility that the high incidence and severity of stem canker and sclerotinia might have affected crop productivity. Total crop dry matter per m^2 for each sample from 15 June until maturity was regressed against the incidence of stem canker and the mean severity score for control (untreated) and AU+SP+SU plots, but no relationships were found. There were also no significant relationships between final seed yield (hand-harvested and combine) and

the incidence and severity of stem canker. In contrast, combine yield for all plots, including those not sprayed with iprodione in May, was very significantly correlated with both the incidence (r^2 = -0.66; P < 0.001) and severity (r^2 = -0.62; P < 0.001) of sclerotinia in July. The average reduction in combine yield in plots not sprayed with iprodione was 0.525t ha-1, suggesting that sclerotinia may have reduced combine yield by up to 20% (average 13%) because disease levels were otherwise very low in iprodione-sprayed plots (Table II.38).

4.2.4. **Summary**

The main fungicidal effects of prochloraz in the three seasons are summarised in Table 4.1. The most important effects were on LLPS and stem canker, and disease severity was affected only in the third season.

4.3. DISCUSSION

4.3.1. **Downy mildew**

Prochloraz, which is ineffective against Oomycete fungi (Birchmore *et al.*, 1977), did not reduce the incidence of downy mildew in any season, and in S3, incidence was actually higher in AUTUMN-treated plots in December. Other workers have also shown that downy mildew is unaffected by either prochloraz or iprodione (Rawlinson & Williams, 1990). The apparent increase in treated plots may be related to prochloraz delaying leaf senescence (Section 5): older leaves, which are usually more infected, are retained in treated plots. Alternatively, prochloraz might have enhanced infection by downy mildew by reducing competition from prochloraz-sensitive pathogens and micro-organisms on the leaf surface (Daniels & Lucas, 1990). Despite its widespread occurrence, however, downy mildew is unlikely to affect yield because the disease is usually severe only on lower senescing leaves (Rawlinson & Muthyalu, 1979).

4.3.2. **Light leaf and pod spot (LLPS)**

LLPS was common in all seasons, but particularly S1. Many factors, such as climate and proximity of a source of infection, may interact to affect the rate of development of LLPS in a crop (Rawlinson, 1979). Therefore, the high incidence in S1 is

Table 4.1. Summary table of the main effects of prochloraz over three seasons (control incidences or scores are given first and treated second)

Year	Date of assessment	Pathogen	Spray causing effect	Plant organ assessed	Incidence (% plants affected	Severity (lesion score per infected plant
1991	16 April	Light leaf, stem and pod spot	AUTUMN	leaf	50.0, 12.5*	
	26 July			stem	88.3, 25.8***	
				pod	99.2, 92.0**	
			SPRING	stem	64.2, 50.0**	
1992	26 May	Light leaf, stem and pod spot	SPRING	stem	50.0, 8.7**	
				pod	26.2, 13.7*	
1993	29 April	Phoma leaf spot	SPRING	leaf	38.3, 20.6**	
		Light leaf, stem and pod spot	AUTUMN	pod		4.38, 1.47*
	7 July		SUMMER	stem	30.0, 16.6*	
				pod	59.0, 41.5*	5.29, 0.55**
		Stem canker	AUTUMN	stem		3.246, 2.890*
	16 July	Stem canker	AUTUMN	stem	96.63, 93.13**	3.994, 3.445**

(*, **, *** significant at $P < 0.05$, 0.01 and 0.001 respectively)

surprising because rainfall is the main determinant of disease severity in the autumn (Rawlinson, 1979), but this did not differ markedly in S1 from the other seasons. Similarly, while disease development is favoured by mild temperatures in the autumn and winter, S1 was no warmer than S2 and S3. The high overall incidence is also surprising given that none of the experiments was situated near a previous infected crop from which inoculum could have been derived (Rawlinson, 1979).

The incidence and severity of LLPS were reduced by prochloraz in all seasons but the effectiveness of the applications, and the growth stages at which their effects were manifested, differed between seasons. Different times of application may have accounted for some of the differences between years because Rawlinson & Cayley (1984) suggested that the timing of applications was more important than the rates used. Autumn prochloraz decreased the incidence and severity of LLPS in mid-April in S1, but in S3, prochloraz had no effect in either late March or late April. The negative effects in S3 were surprising because Rawlinson *et al.* (1988b) showed that autumn prochloraz reduced the incidence of LLPS in February, while application in both autumn and spring reduced the incidence in April. In S2, spring prochloraz had reduced the incidence and severity of LLPS by the end of May, but in S1 and S3, neither autumn nor spring prochloraz had any effects at this time. The reason for the apparent ineffectiveness of autumn and spring prochloraz in S1 and S3 is unknown. It is not related to the incidence of the pathogen as this was similar in all three seasons. The negative response to prochloraz at this time is important because during stem extension (April), infection spreads to inflorescences, killing buds and preventing flowers from opening (Rawlinson *et al.*, 1988b). Since all plots, irrespective of treatment, had the same level of infection in S1 and S3, any effects on potential yield development (Section 3.4) should have been similar. Despite the transient differences between treatments by the end of May in S2, no lasting protection was conferred on treated plots.

The lack of response to spring prochloraz in July in S2 could be due to the missing autumn application, because in S1, there was an interaction between autumn and spring prochloraz so that the effect of the spring application in July was enhanced by

the autumn application. Rawlinson *et al.* (1988b) noted that the autumn application of prochloraz contributed most to the control of LLPS. The summer prochloraz application was effective against this pathogen only in S3. The smaller size and more open canopy of the S3 crop (Section 3) probably enabled more efficient penetration of the prochloraz through the canopy than in S1 and S2. Also, in S1, effects on LLPS may have been negated by the very late application of summer prochloraz.

Symptoms of LLPS only became visible in March in each season, but plants would already have had symptomless infections, and may have been infected prior to the autumn prochloraz application. Rawlinson & Muthyalu (1985) suggested that, even when symptoms were not obvious in winter, the pathogen may have been damaging primordial tissues. This would account for the beneficial effect of autumn prochloraz later in the season. The reason why autumn prochloraz had no effect on LLPS symptoms in spring in S3 may be that its application was so early compared with S1 (by almost a month), which might have preceded much of the infection. Prochloraz is primarily a contact fungicide with negligible systemicity (Copping *et al.*, 1984), and much of its potency could have been lost prior to infection. Cooke *et al.* (1993) determined that the half-life of prochloraz on unweathered wheat foliage was only six days, and Gisi *et al.* (1986) found that no activity remained after 13 days. The long-term effect of autumn and spring prochloraz was reported by Rawlinson *et al.* (1986a; 1988b) to be due to a reduction in inoculum and a slowing-down of the epidemic.

Wakerley & Russell (1987) showed that prochloraz can effect good yield increases when LLPS is the most important disease. In the present experiments, it seems unlikely that LLPS would have had more than a negligible effect on yield because disease severity was low and only a relatively small proportion of the total photosynthetic area was lost. However, the incidence and severity levels required to have deleterious effects on yield are unknown, although these depend on the susceptibility of the oilseed rape cultivar (Doughty *et al.*, 1995). Yield is only markedly affected when very susceptible cultivars become severely infected (Davies, 1986). Hence, in cases where prochloraz did affect disease incidence and severity, it is unlikely that these effects would have influenced yield, especially as compensation

by unaffected plants could have occurred. This view is supported by the findings of experiments in which effects on disease levels have not necessarily been associated with yield increases (eg. Mercer *et al.*, 1989).

4.3.3. **Phoma/stem canker**

The high levels of phoma leaf spot, and the eventual development of a severe stem canker epidemic in S3, may have been due to a combination of favourable weather and the proximity of a source of inoculum. Late autumn in S3 was very wet. Mild, wet autumn conditions are thought to favour the development of leaf infections, which are essential for later stem cankers (Gladders & Musa, 1979), although once established, disease incidence is less influenced by weather conditions (Rawlinson & Muthyalu, 1979).

The incidence of phoma symptoms was low at the end of November. Infection may already have occurred during the conducive wet conditions in October. Nathaniels & Taylor (1983) suggested that symptomless infections could be continuously active in the autumn and winter, often resulting in hyphal proliferation deep into non-necrotic tissue. As was the case for LLPS, autumn prochloraz had no effect at the end of November, whereas both autumn and spring prochloraz had reduced the incidence and severity of phoma by the end of April (Table II.28). Humpherson-Jones (1984) concluded that uniform infection of leaves by December indicated that the inoculum was air-borne. By the end of March in S3, the majority of plants were infected. Since it is possible for production of air-borne ascospores to continue for much of the season, it is possible that new infections could have been continuous through the winter. Therefore, the source of the inoculum and the timing of infection may have influenced the effects of the autumn prochloraz application.

Gladders and Musa (1979) showed that there was a strong correlation between the maximum incidence of leaf spot infection in the autumn and the incidence of severe canker at harvest. The incidence of phoma was low in the autumn of S3, so a high incidence of severe stem cankers in July was not expected. However, spring infections are capable of producing cankers (Gladders & Musa, 1980), although of less

severity (Gladders & Musa, 1979). Hammond & Lewis (1986a) reported that delayed ascospore release as the result of dry weather delayed the onset of a stem canker epidemic. The very dry weather in February and March 1993 probably inhibited infection, so the high disease incidence at the end of March was a consequence of infection that had occurred prior to the dry period.

At the end of April in S3, only about half of the plants had phoma leaf infections, compared with most plants at the end of March. This was because many infected leaves would have been lost in the interim period, but infection could have reached the stem. Latent stem infections are probably insensitive to prochloraz applied in the spring (Hammond & Lewis, 1986a), which would account for the ineffectiveness of the spring prochloraz application. The rate of leaf senescence relative to the rate of advancement of fungal hyphae from a leaf lesion into the stem is important in determining the likelihood of a severe epidemic of stem canker (Hammond & Lewis, 1986a). Because prochloraz promotes leaf retention (Section 3), it could favour canker development by allowing the pathogen more time to reach the stem. Temperature is also important because the rates of leaf senescence and fungal development may be affected differently. The development of the pathogen is sensitive to temperature (Rawlinson & Muthyalu, 1979; Hammond & Lewis, 1986a), whereas growth analysis studies (Section 3) indicated that the rate of leaf senescence was not greatly affected by temperature during the relatively mild winter in S3. Therefore the severe stem canker in S3 may have been due to greater mycelial ingress into stems at the higher temperatures.

Since seed yield was not related to the level of stem canker in S3, reductions in stem canker incidence and severity elicited by prochloraz did not lead to a significant improvement in seed yield. Indeed, the present findings indicate that, even at relatively high incidence and severity, stem canker need not affect yield. In this particular season, however, the high levels of stem canker may have negated the phytotonic effects of prochloraz. Despite the very high incidence of moderately severe stem canker, seed yields at final harvest (combine yield 4.0 t ha^{-1}) were still higher than in S1 (2.90 t ha^{-1}) and S2 (3.22 t ha^{-1}). Rawlinson & Muthyalu (1979) suggested

that even slight disease could be associated with a loss in yield of 13.6% per unit increase on a 0-3 severity scale. As with LLPS, however, prediction of yield losses is difficult because of the ability of the crop to compensate and the lack of competition from diseased plants (McGee & Emmett, 1977). In S3, nearly all plants were infected with stem canker, so compensation was unlikely to have been important, and the majority of the final yield would have been produced by diseased plants. There were no reductions in yield components compared with S1 and S2 : pod numbers m^{-2} were similar, but seed numbers per pod and harvest index were higher than in S1 and S2, and plants did not senesce prematurely. When the present series of experiments was initiated, the cultivar Capricorn, which was used in each experiment, had the highest rating for stem canker resistance of all those available (PBI, 1990). Although prochloraz reduced the incidence and severity of leaf disease at the end of April, these reductions were not related to final seed yield. Together with the lack of a relationship between stem canker and final yield, these findings suggest that the significant reduction in disease levels elicited by autumn prochloraz in July was unlikely to have influenced seed yield.

4.3.4. **Botrytis**

Botrytis was relatively common in the summer of S2, but as in S1, it was not controlled by prochloraz. Rawlinson *et al.* (1988b) also found that botrytis was unaffected by autumn and spring prochloraz applications (and summer iprodione). The high incidence in S2 was probably related to rainfall in the spring because most plants were already affected by late May, and Rawlinson *et al.* (1988a) showed that botrytis colonised maturing pods during prolonged wet weather before harvest. Seed yields in S2 are not likely to have been affected because uninfected plants would have compensated for the loss of those infected. Compensation is unlikely to have been important in S3 because of the overriding effects of stem canker. Also, the incidence and severity of botrytis were very low in S3 and, although disease incidence was reduced by summer prochloraz, this was probably of minor importance with respect to yield response in the prevailing conditions.

4.3.5. Sclerotinia

Although the incidence of sclerotinia in early July was not affected by prochloraz in any season, it was reduced to negligible levels by iprodione in S3. In S2, however, spring prochloraz reduced disease incidence at final harvest, possibly as a result of the coincidence of the application with the release of spores from the apothecia. Conversely, the failure of spring prochloraz to affect the incidence of sclerotinia in S1 suggests that its application did not coincide with ascospore release. The apparent increase in the severity of sclerotinia in July in S3 in AUTUMN-treated plots cannot be satisfactorily explained. In S2, the incidence of sclerotinia in control plots at final harvest was 37.5%. Yield losses of up to 10% have been recorded when more than 10% of plants were affected (Davies, 1986), and sclerotinia undoubtedly contributed to losses in S2. In S3, disease incidences of up to 40% were associated with yield losses of up to 20%. However, because the spring application of prochloraz (which had the greatest effect on yield in this season) reduced disease incidence by only 3.7% (from 15.6% to 11.9%), this effect was unlikely to have affected yield.

4.3.6. Pests

The increased incidence of pigeon damage in late November and CSFB damage severity in both November and April of S3 suggests that plants in prochloraz-treated plots were made more attractive to them, perhaps because of the increased leaf retention promoted by prochloraz. The reason why the incidence of CSFB in July of S1 was higher in autumn-sprayed plots is unknown. Similarly, the reductions in the incidence of CSFB due to summer prochloraz in S1 and spring prochloraz in S2 cannot be readily explained.

4.4. CONCLUSIONS

The aim of this section was to establish the background to the phytotonic effect of prochloraz in order to ensure that fungicidal effects were not wrongly attributed to effects on crop physiology. Differences between seasons in the effects of prochloraz on disease incidence and severity were the result of several interacting factors: climatic conditions, the amounts of inoculum, which may themselves be influenced by climate, and the different times of prochloraz application between seasons. High

levels of stem canker in S3 may have overridden the phytotonic effects of prochloraz. Despite such high levels, however, it was not possible to establish a relationship between either disease incidence or severity and yield and it is concluded that, in this particular season, yield differences between treatments could not be attributed to stem canker, or to fungicidal effects of prochloraz on this disease. High levels of sclerotinia in S2 almost certainly contributed to late seed losses and curtailed seed growth in this season (Section 3), which led to difficulties in the interpretation of the phytotonic effect. However, although sclerotinia was also a problem in S1, its incidence was lower, and was not affected by prochloraz.

Throughout the experiments, the severity of most pathogens was very low even when disease incidence was high. Determining the effects of recorded disease incidence and severity on final yield is very difficult because of the many interacting factors that are involved. In many cases, however, even when disease levels were relatively high, they were unaffected by prochloraz. In those cases where prochloraz did have significant effects on disease incidence and severity, these fungicidal effects were unlikely to have significantly affected seed yield. Many plants were infected with LLPS on pods in the summer, particularly in S1, but only a very small proportion of the total pod area was diseased. Therefore, the reduction in the incidence and severity elicited by autumn prochloraz in S1 probably had no effect on seed yield. With this established, any differences in growth and development in treated plots may be attributed to the phytotonic effect, which will therefore be studied in detail for this season in Section 5.

Section 5: THE EFFECTS OF PROCHLORAZ ON THE PHYSIOLOGY OF OILSEED RAPE

5.1. INTRODUCTION

Evidence for host physiological responses to fungicides in oilseed rape is mostly associated with triazoles. By virtue of their existence in different isomeric forms, many of these are able to act both as fungicides and as plant growth regulators (Büchel, 1986; Lürssen, 1988). Prochloraz is an imidazole, and differs from triazoles in substitution into the azole ring structure. However, the mode of action of prochloraz in the fungus is the same as that of triazoles in that it inhibits sterol biosynthesis. Another imidazole fungicide, imazalil, has shown growth retarding effects in cereals (Kuck & Scheinpflug, 1986). Unlike imazalil and most triazoles, however, prochloraz exhibits negligible movement within the host plant.

Prochloraz applications to oilseed rape have been shown to increase crop vigour (ADAS, 1983), crop height (Bock *et al.*, 1991), dry matter, main-stem leaf area, branch number, fertile pod number, pod dry weight, harvest index (Leach *et al.*, 1988), 1000-seed weight (Rawlinson, Leach, Darby, Evans, Digby & Williams, 1986c), and seed oil content and yield (Rawlinson, Evans & Williams, 1988c) through its fungicidal properties. However, applications of autumn and spring prochloraz with summer iprodione have produced substantial yield increases in double-low cultivars that were not associated with reductions in disease incidence or severity (Rawlinson, Church, Inman & Wilson, 1988b; Rawlinson, Doughty, Bock, Church, Milford & Fieldsend, 1989; Rawlinson & Williams, 1990). A host physiological effect of the fungicide was suspected, which was considered to be due to the structural similarity of prochloraz to growth regulatory chemicals, such as the triazole triapenthenol, which also possesses fungicidal activity (Bock *et al.*, 1991).

Physiological effects of prochloraz may occur widely but are not always recognised. The nature of this phytotonic effect remains unresolved and warrants further investigation. The physiological processes determining the development of yield in oilseed rape were described in Section 3. From the findings in Section 4, it was

concluded that the fungicidal effects of prochloraz in the present study were insufficient to significantly affect seed yield. On this basis, the aim of this section is to investigate the effects of prochloraz on crop physiology and yield development.

5.2. THE EFFECTS OF PROCHLORAZ : THE OVERALL RESPONSE

5.2.1. **Introduction**

Effects will be presented in detail for 1991 because it was only in this season that a clear positive response was obtained following three applications of prochloraz. No response was obtained when the experiment was repeated in 1992 when only two prochloraz applications were made. The autumn application was omitted because the experiment had to be resited in the early spring following pigeon damage to the original plots. A full experiment with all three prochloraz applications in 1993 was inconclusive because responses obtained in Stage I were negated during Stage II. The reasons for this have not been identified but the widespread and severe stem canker epidemic in this season may have been responsible (Section 4).

5.2.2. **Final yield components**

In 1991, the AU+SP+SU prochloraz treatment increased seed yield, the number of yield-forming pods and the number of seeds m^{-2} at final harvest (Table 5.1). This response at final harvest will be examined in more detail in the next subsection (5.2.3), with a consideration of all treatments. Data for 1992 and 1993 are presented in Appendix III.

Table 5.1. The effects of prochloraz (AU+SP+SU) on seed yield and components in 1991

	Seed yield ($g\ m^{-2}$)	Pod no. m^{-2} #	Seeds/pod	1000-seed weight (g)	Harvest index
Control	414.1	4001	16.13	6.627	0.35
Prochloraz	480.1***	4668+	17.82	6.683	0.36
S.E.D. (23 df)	13.85	378.2	1.091	0.078	0.01

 # yield-forming pods
+, *** significant at $P < 0.1$, $P < 0.001$

5.2.3. Effects on growth and yield production in 1991 (final harvest)

(a) Dry matter (DM)

The number of plants m^{-2} was not significantly affected by prochloraz (Table 5.3). Stem DM in the pod-bearing layers (above 80 cm) was increased by autumn prochloraz ($P < 0.10$; Table 5.2), but only AU and AU+SP treatments gave a significant increase ($P < 0.05$; Table 5.3). Total crop DM m^{-2} was increased significantly only by autumn prochloraz application (Table 5.2), and by all treatments that included this (Table 5.3). Total pod DM production (fertile + shattered pod DM) and hull DM were increased by the autumn prochloraz application only (6.6%) (Table 5.4). All treatments increased total pod DM production except the SP+SU treatment (Table 5.5).

(b) Seed yield and components

Seed yield m^{-2} was increased by 6.0% by autumn prochloraz application ($P < 0.01$) (Table 5.8). Spring and summer applications also increased seed yield, but to a lesser extent (summer not significant). The largest yield increase (of 15.9%) was given by the AU+SP+SU treatment ($P < 0.001$) (Table 5.9). Autumn prochloraz significantly increased the number of yield-forming pods m^{-2} at final harvest by 11% ($P < 0.05$) (Table 5.6). Total pod number m^{-2} was increased by 9.6% by autumn prochloraz application ($P < 0.05$). The single largest increase was prompted by the AU treatment, which increased total pod number m^{-2} by 18.9% ($P < 0.05$) (Table 5.7).

Seed number per pod at final harvest was not significantly affected by any prochloraz application (Table 5.8), but the AU+SP+SU treatment gave a 10% increase ($P < 0.01$; Table 5.9), implying that an interaction occurred. Seed number m^{-2} was increased by 5.7% by autumn prochloraz, but was not affected by spring and summer applications (Table 5.8). 1000-seed weight was increased by the spring prochloraz application only ($P < 0.01$) (Table 5.8).

Table 5.2. The effects of prochloraz on plant number m^{-2} and leaf, stem and total dry matter at final harvest, 1991

		PLANT NUMBER m^{-2}	DRY MATTER ($g\ m^{-2}$)				
			Leaf		Stem		Total
			> 80cm	< 80cm	> 80cm	< 80cm	
AUTUMN	0	86.0	2.83	0.41	114.1	383.2	1231.7
	1	88.7	4.56***	1.10*	122.0+	394.2	1301.3**
SPRING	0	87.8	3.19	0.52	117.1	383.9	1253.1
	1	86.8	4.20*	0.98	119.0	393.5	1279.9
SUMMER	0	85.7	3.12	0.46	115.7	383.2	1251.4
	1	88.9	4.27**	1.04	120.4	394.2	1281.5
S.E.D.		4.71	0.42	0.30	3.86	10.53	18.38

(+ , *, **, *** significant at $P < 0.10, 0.05, 0.01, 0.001$, 23 total & 14 residual degrees of freedom (df))

Table 5.3. Treatment means for the effects of prochloraz on plant number m^{-2} and leaf, stem and total dry matter at final harvest, 1991

	PLANT NUMBER m^{-2}	DRY MATTER m^{-2}				
		Leaf		Stem		Total
		> 80cm	< 80cm	> 80cm	< 80cm	
CONTROL	89.3	3.78	0.53	105.4	390.3	1190.6
AUTUMN	83.7	3.15	0.35	123.6*	377.2	1281.7*
SPRING	80.3	2.34	0.29	111.6	378.0	1248.1
SUMMER	89.3	1.76*	0.57	118.2	382.9	1250.6
AU + SP	89.7	3.22	0.69	122.4*	387.4	1285.3*
AU + SU	89.0	4.07	0.64	121.4+	385.4	1289.4*
SP + SU	85.0	3.44	0.24	121.2+	381.7	1237.3
AU + SP + SU	92.3	7.80***	2.73**	120.7+	426.8	1348.7***
S.E.D.	9.41	0.849	0.609	7.72	21.06	36.76

(+, *, *** significantly different from control at $P < 0.10, 0.05$ and 0.001; 23 total and 14 residual df)

Table 5.4. The effects of prochloraz on pod and hull dry matter at final harvest, 1991

		POD DM ($g\ m^{-2}$)			HULL DM ($g\ m^{-2}$)
		Fertile	Shattered	Total	
AUTUMN	0	471	247.7	718.4	277.6
	1	540*	226.0	766.0**	301.8*
SPRING	0	478	257.7	735.8	288.3
	1	532*	216.0*	748.6	291.1
SUMMER	0	481	254.9	735.7	287.0
	1	530+	218.8*	748.6	292.3
S.E.D.		4.71	23.9	14.8	9.31

(+, *, ** significant at $P < 0.10$, 0.05 and 0.01; 23 total and 14 residual df)

Table 5.5. Treatment means for the effects of prochloraz on pod and hull dry matter at final harvest, 1991

	POD DM ($g\ m^{-2}$)			HULL DM ($g\ m^{-2}$)
	Fertile	Shattered	Total	
CONTROL	466	208.5	674.1	260.0
AUTUMN	483	282.2	765.5**	306.4*
SPRING	465	278.0	743.0*	287.5
SUMMER	462	273.8	735.7+	282.5
AU + SP	509	251.0	760.3**	294.3+
AU + SU	501	266.4	767.7**	304.3*
SP + SU	490	230.4	720.8	280.6
AU + SP + SU	665***	104.4**	770.3**	302.0*
S.E.D.	47.7	31.82	29.57	18.61

(+, *, **, *** significant at $P < 0.10$, 0.05, 0.01, 0.001; 23 total and 14 residual df)

Table 5.6. The effects of prochloraz on pod numbers m^{-2} at final harvest, 1991

		Fertile	Shattered	Yield-forming	Total
AUTUMN	0	3053	1754	4458	4807
	1	3618*	1640	4968*	5268*
SPRING	0	3203	1845	4725	5049
	1	3467	1549*	4700	5026
SUMMER	0	3195	1812	4695	5008
	1	3475	1582*	4730	5066
S.E.D.		219.8	105.2	189.1	169.9

(* significant at $P < 0.05$; 23 total and 14 residual df)

Table 5.7. Treatment means for the effects of prochloraz on pod numbers m^{-2} at final harvest, 1991

	Fertile	Shattered	Yield-forming	Total
CONTROL	2821	1706	4001	4527
AUTUMN	3454	1928	5217**	5382*
SPRING	3042	1834	4612	4876
SUMMER	3096	1909	4648	5005
AU + SP	3465	1781	4951*	5247+
AU + SU	3443	1838	5035*	5281*
SP + SU	3251	1568	4570	4819
AU + SP + SU	4108*	1012**	4668+	5161+
S.E.D.	439.5	210.5	378.2	339.8

(+, *, ** significant at $P < 0.10$, 0.05 and 0.01; 23 total and 14 residual df)

Table 5.8. The effects of prochloraz on seed yield and components at final harvest, 1991

		Seed DM ($g\ m^{-2}$)	1000-seed weight (g)	Seed no. per pod	Seed no. m^{-2}	Harvest index
AUTUMN	0	440.8	6.619	16.31	66456	0.357
	1	467.2**	6.642	15.88	70253**	0.360
SPRING	0	447.5	6.562	15.83	68029	0.358
	1	460.5+	6.699**	16.36	68680	0.360
SUMMER	0	448.7	6.606	15.78	67734	0.359
	1	459.2	6.655	16.42	68975	0.358
S.E.D.		6.92	0.0389	0.546	1092.7	0.00385

(+, ** significantly different at $P < 0.10, 0.01$; 23 total and 14 residual df)

Table 5.9. Treatment means for the effects of prochloraz on seed yield ($g\ m^{-2}$) and components at final harvest, 1991

	Seed DM ($g\ m^{-2}$)	1000-seed weight (g)	Seed no. per pod	Seed no. per m^{-2}	Harvest index
CONTROL	414.1	6.627	16.13	61636	0.348
AUTUMN	459.2**	6.503	15.03	70608**	0.363
SPRING	455.5**	6.707	16.23	67940*	0.363
SUMMER	453.2**	6.323**	17.22	71669***	0.362
AU + SP	466.0**	6.587	15.72	70753**	0.362
AU + SU	463.4**	6.793*	14.95	68203**	0.359
SP + SU	440.2+	6.820*	15.67	64579	0.357
AU + SP + SU	480.1***	6.683	17.82**	71449***	0.356
S.E.D.	13.85	0.0778	1.091	2185.4	0.0077

(+, *, **, *** significant at $P < 0.10, 0.05, 0.01$ and 0.001; 23 total and 14 residual df)

(c) Combine yield

Combine yield was significantly increased only by the autumn prochloraz application (by nine per cent) (Table 5.10). All treatments involving autumn prochloraz application increased combine yield, but the AU+SP treatment elicited the largest

response, increasing combine yield by 21.3% ($P < 0.01$; Table 5.11). The 1000-seed weight of combine seed was unaffected by prochloraz (Table 5.10). Seed moisture content was increased by all prochloraz applications, particularly autumn prochloraz ($P < 0.001$; Table 5.10), and the AU+SP+SU treatment produced a 13% increase ($P < 0.001$; Table 5.11).

Table 5.10. The effects of prochloraz on combine yield at 9% moisture, combine 1000-seed weight and seed moisture content in 1991

		Combine yield (t ha^{-1})	1000-seed weight (g)	Seed moisture content (%)
AUTUMN	0	3.088	6.384	7.267
	1	3.366**	6.364	7.683***
SPRING	0	3.148	6.367	7.363
	1	3.306	6.382	7.587*
SUMMER	0	3.211	6.316	7.350
	1	3.243	6.432	7.600*
S.E.D.		0.0914	0.0701	0.0899

(*, **, *** significant at $P < 0.05$, 0.01 and 0.001; 23 total and 14 residual df)

Table 5.11. Treatment means for the effects of prochloraz on combine yield at 9% moisture, combine 1000-seed weight and seed moisture content in 1991

	Combine yield (t ha^{-1})	1000-seed weight (g)	Seed moisture content (%)
CONTROL	2.903	6.303	7.057
AUTUMN	3.207	6.273	7.437*
SPRING	3.387*	6.347	7.287
SUMMER	2.963	6.410	7.257
AU + SP	3.347*	6.340	7.620**
AU + SU	3.520**	6.480	7.703**
SP + SU	3.100	6.477	7.467*
AU + SP + SU	3.390*	6.363	7.973***
S.E.D.	0.1828	0.1402	0.1799

(*, **, *** significant at $P < 0.05$, 0.01 and 0.001; 23 total and 14 residual df)

5.2.4. **Analysis of the response to prochloraz over three seasons**

There was a very significant seasonal effect of prochloraz on seed yield, pod and seed number m^{-2}, and pod, stem and total DM m^{-2} (Table 5.12). Autumn prochloraz significantly increased total pod number m^{-2}, stem DM m^{-2} and total DM m^{-2}. Spring prochloraz also significantly increased total DM m^{-2}, seed yield, pod DM m^{-2} and seed number m^{-2}. Prochloraz applied in summer had no effects.

Table 5.12. The effects of autumn and spring prochloraz applications over all three seasons: percentage increase in each component and significance level

	AUTUMN#	SPRING##
Combine yield (t ha^{-1})	4.13^{+}	2.04
Seed yield (g m^{-2})	4.67^{+}	7.57^{***}
Pod number m^{-2}	8.91^{*}	3.65
Seed number m^{-2}	4.00	6.27^{**}
Pod dry matter (g m^{-2})	4.62^{+}	7.38^{***}
Total dry matter (g m^{-2})	4.75^{**}	4.47^{***}
Stem dry matter (g m^{-2})	4.20^{**}	-

(# 1991 and 1993; ## all seasons; +, *, **, *** increase significant at $P < 0.10, 0.05, 0.01, 0.001$)

5.3. THE EFFECTS OF PROCHLORAZ ON GROWTH AND DEVELOPMENT

5.3.1. **The overall response in 1991**

The effect of prochloraz on growth and development was examined in detail only for the three-application treatment (AU+SP+SU), which elicited the largest response at final harvest. Comparison of growth curves between treatments indicated that the pattern of development was the same in both (Fig. 5.1). Prochloraz promoted growth throughout development. Total dry matter (DM), green area index (GAI), leaf area index (LAI) and stem area index (SAI) were all increased beginning shortly after the first application and throughout until maturity (Figs. 5.1-5.4).

5.3.2. **Effects of prochloraz during individual developmental stages**

I. The vegetative stage

Growth until late January was unaffected by application of prochloraz in late

November, but by 19 March, LAI, leaf DM and total DM had been promoted (15%, $P < 0.01$; 13%, $P < 0.001$ and 13%, $P < 0.001$ greater respectively) (Figs. 5.3, 5.5 & 5.1). Stem DM and SAI were 13% and 20% greater respectively in sprayed plots (both $P < 0.05$) (Figs. 5.6 & 5.4).

Prochloraz increased LAI by delaying leaf senescence. A similar effect was also observed in more detailed studies of Stage I in 1993 (Appendix III, Figs. III.1 & III.2). In this season, the large increase in LAI (Fig. 1.a) was due partly to an increase in leaf area per plant (Fig. 1.b) and, initially, to an increase in plant number m^{-2} (Fig. 1.d). The greater leaf area per plant in treated plots was due partly to an increased individual leaf area (Fig. 1.c) and partly to an increased green leaf number per plant (Fig. 2.b). Prochloraz did not affect total or senesced leaf numbers per plant (Fig. 2.b). Therefore the slightly increased green leaf numbers were a consequence of increased retention.

II. Stem extension, development of the reproductive framework and flowering

Growth responses observed in Stage I were essentially maintained in Stage II. LAI and GAI, total DM, stem DM and area were greater in treated plots throughout Stage II (Figs. 5.1-5.4), and differences increased towards the end of the stage as flowering progressed due to prolonged leaf and stem growth. Stem DM and area were approximately 10% greater in treated plots (Figs. 5.6 & 5.4). Maximum LAI was attained one week later in treated plots (Fig. 5.3), and by mid-May, LAI and leaf DM were 22% and 15% respectively greater in these (Fig. 5.3. & 5.5). Maximum stem DM and SAI coincided in control and treated plots at the end of Stage II and remained constant thereafter (Figs. 5.4 & 5.6). The late development of maximum GAI in treated plots was followed by a decline in GAI that was similar in pattern in both treatments (Fig. 5.2).

III. Pod development

At the beginning of pod development, total DM was 10% greater in treated plots (Fig. 5.1), and this difference was maintained throughout this stage. Total GAI also remained higher in treated plots (Fig. 5.2). The decline in GAI was similar in both

Fig. 5.1. The effect of prochloraz on the development of total crop dry matter m^{-2} in 1991

Solid line/closed symbols = control
Broken line/open symbols = prochloraz-treated

I = S.E.D.

Arrow indicates onset of flowering

Stages are indicated by Roman numerals

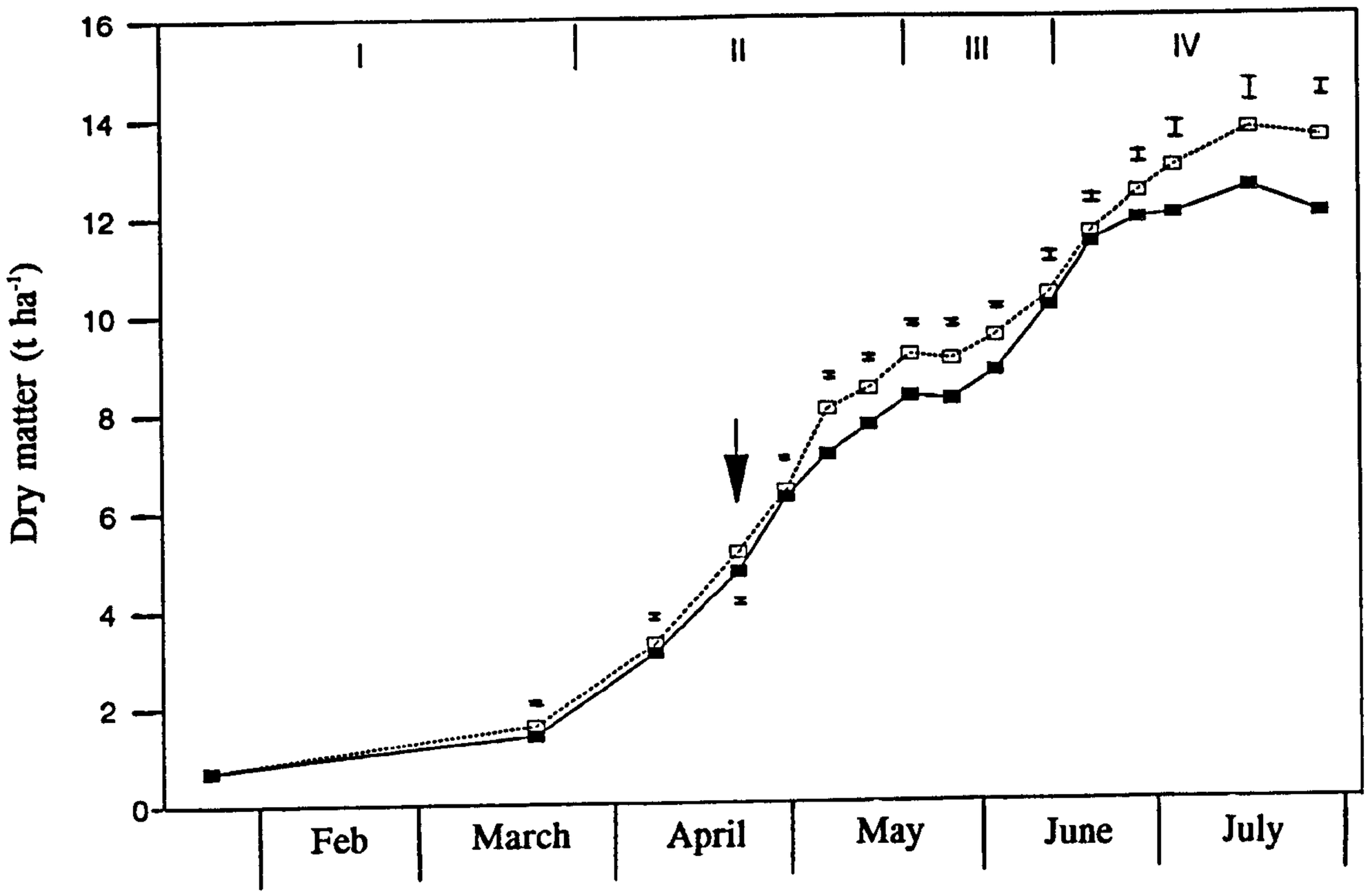
Fig. 5.2. The effect of prochloraz on the development of green area index in 1991

Solid line/closed symbols = control
Broken line/open symbols = prochloraz-treated

I = S.E.D.

Arrow indicates onset of flowering

Stages are indicated by Roman numerals


Dry matter (t ha-1)
16
14
12
10
8
6
4
2
0
I
II
III
IV
Feb
March
April
May
June
July

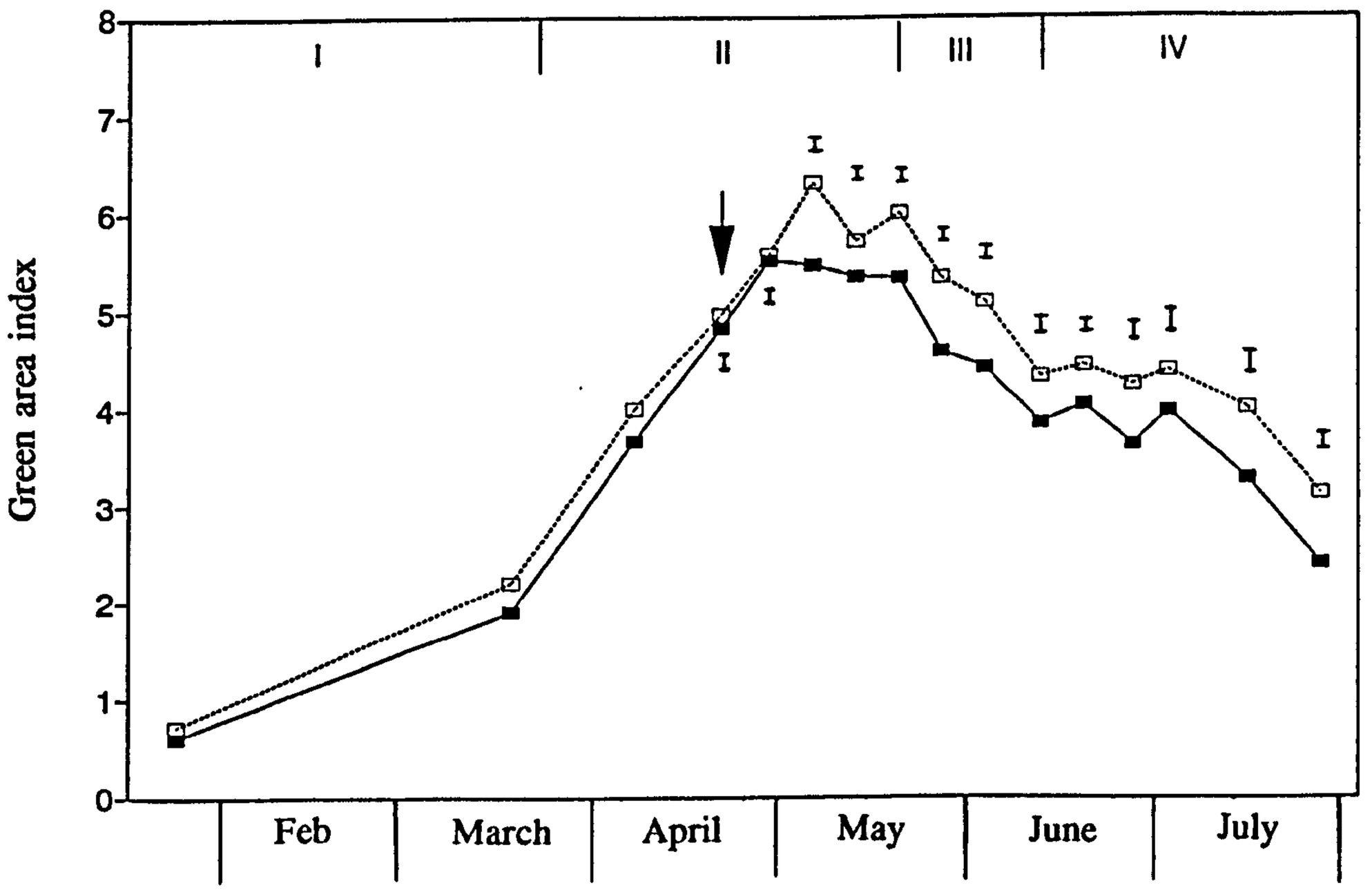

Green area index
8
7
6
5
4
3
2
1
0
I
II
III
IV
Feb
March
April
May
June
July

Fig. 5.3. The effect of prochloraz on the development of leaf area index during development in 1991:

Solid line/closed symbols = control;
Broken line/open symbols = prochloraz-treated

I = S.E.D.

Arrow indicates onset of flowering

Stages are indicated by Roman numerals

Fig. 5.4. The effect of prochloraz on the development of stem area index in 1991:

Solid line/closed symbols = control;
Broken line/open symbols = prochloraz-treated

I = S.E.D.

Arrow indicates onset of flowering

Stages are indicated by Roman numerals

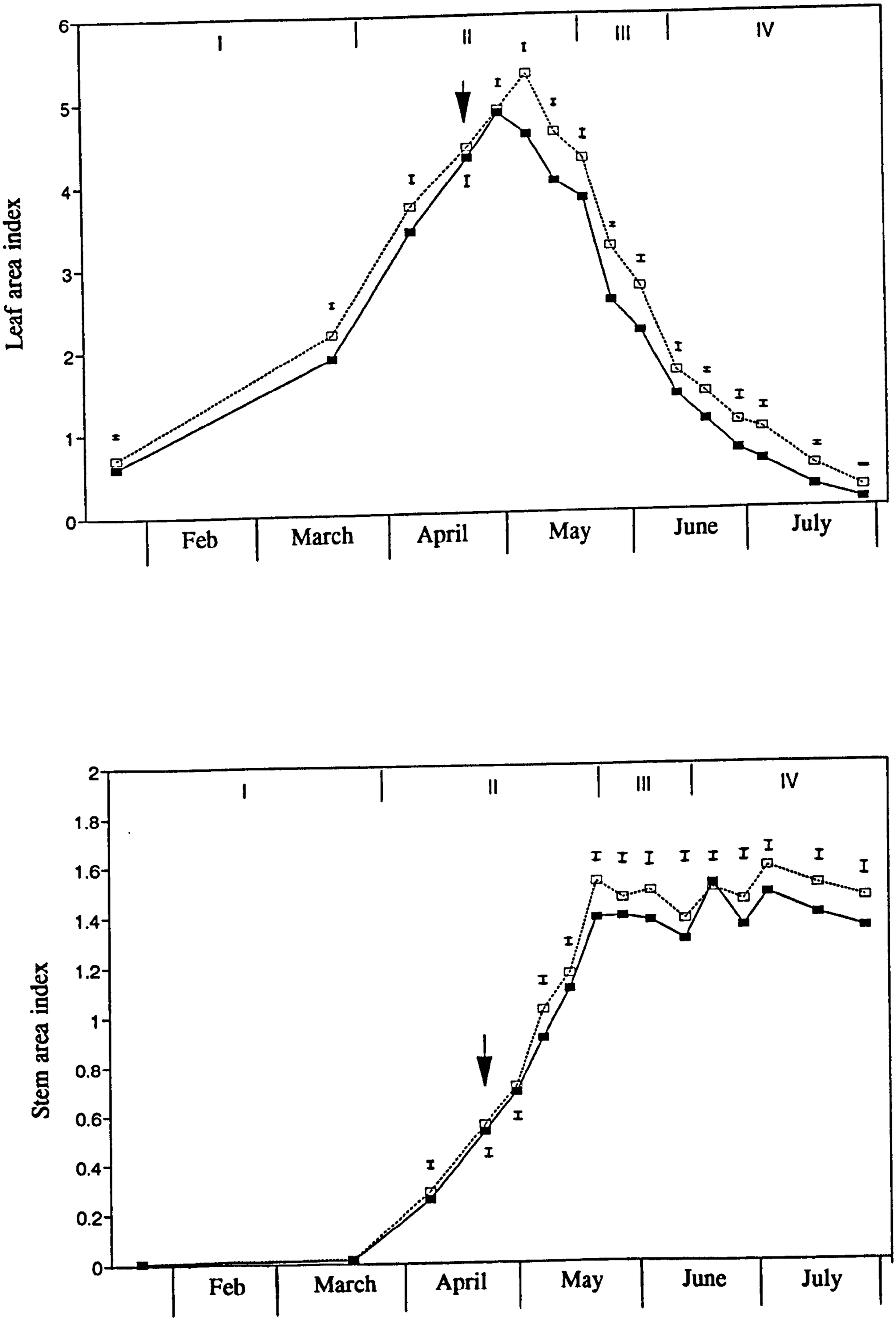

Leaf area index
6
5
4
3
2
1
0
I
II
III
IV
Feb
March
April
May
June
July
Stem area index
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0

Fig. 5.5. The effect of prochloraz on the development of leaf dry matter in 1991:

solid line/closed symbols = control;
broken line/open symbols = prochloraz-treated

I = S.E.D.

Arrow indicates onset of flowering

Stages are indicated by Roman numerals

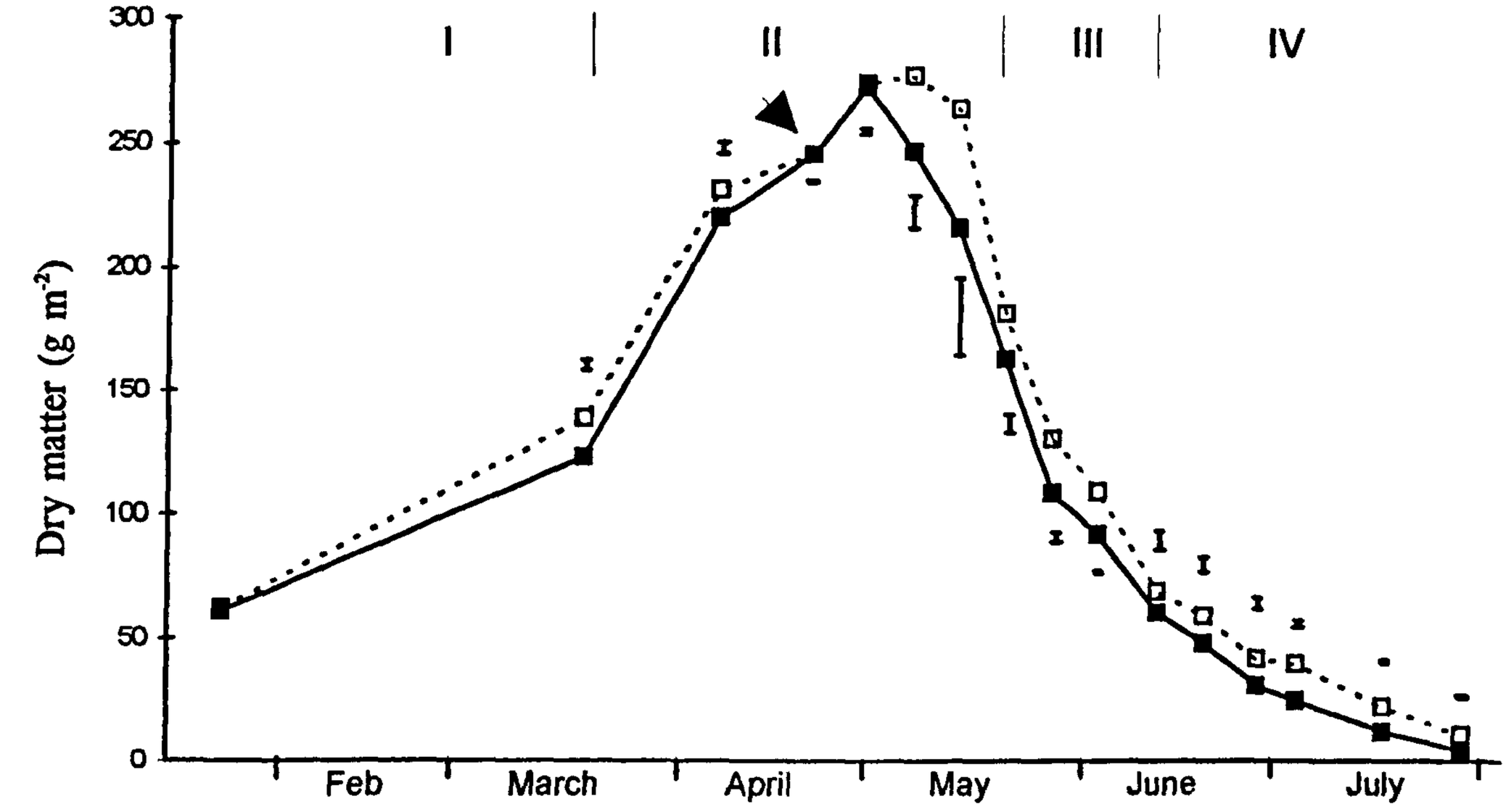
Fig. 5.6. The effect of prochloraz on the development of stem dry matter in 1991:

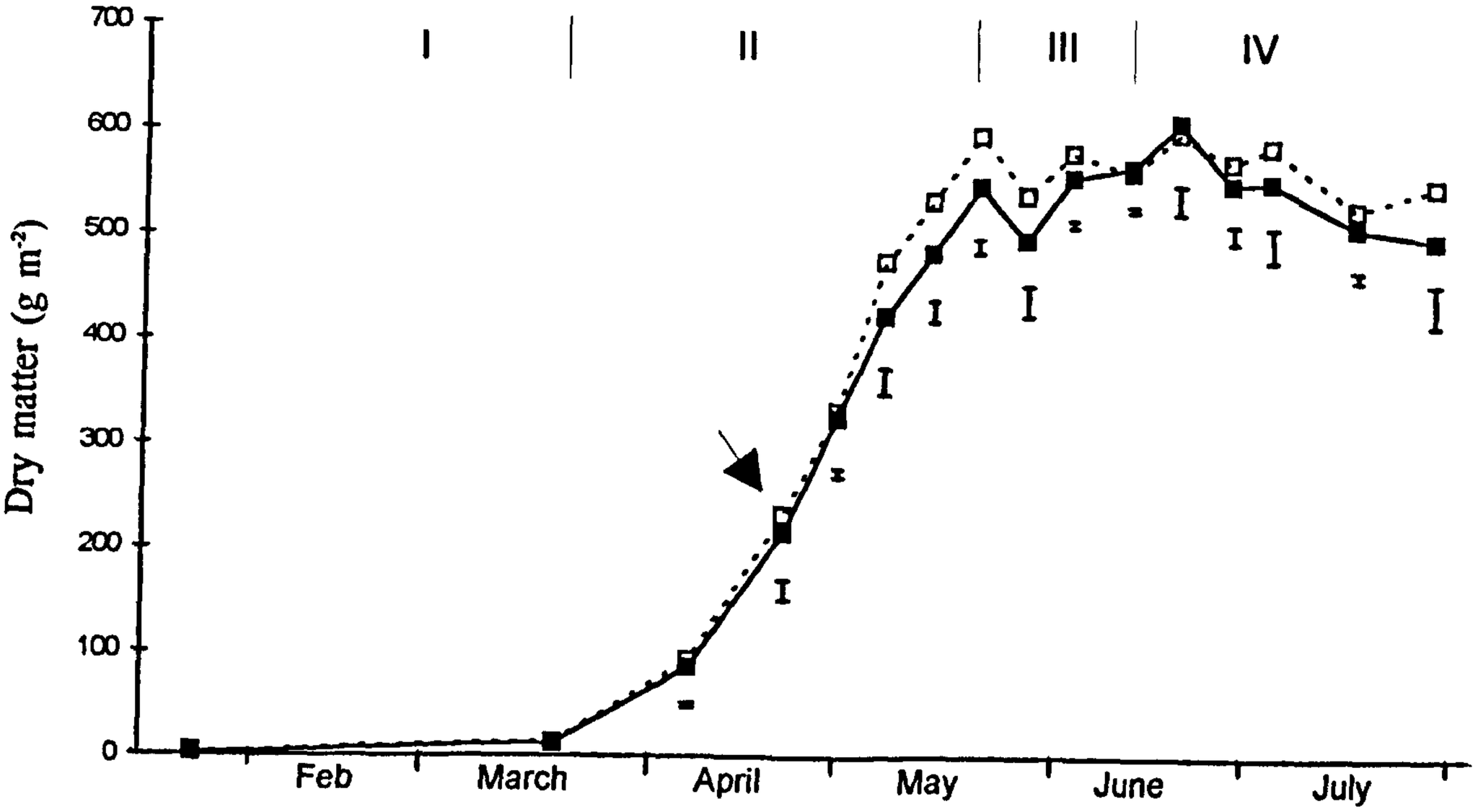
Solid line/closed symbols = control;
Broken line/open symbols = prochloraz-treated

I = S.E.D.

Arrow indicates onset of flowering

Stages are indicated by Roman numerals


I
II
III
IV
Dry matter (g m-2)
300
250
200
150
100
50
0
Feb
March
April
May
June
July


I
II
III
IV
Dry matter (g m-2)
700
600
500
400
300
200
100
0
Feb
March
April
May
June
July

treatments and was due mainly to the declining LAI. Prochloraz delayed the onset of this process but not its extent, and the decline in LAI was approximately 60% to 1.3 and 1.5 in control and treated plots respectively (Fig. 5.3). Stem DM and area remained constant in both treatments but greater in treated plots (Figs. 5.6 & 5.4). Pod area index (PAI) and pod DM were increased by prochloraz, the difference between treatments increasing as pod development progressed (Fig. 5.7).

IV. Seed development

During seed development, differences in DM, GAI, LAI, SAI and PAI (Figs. 5.1-5.7) between treated plants and controls were maintained. GAI declined at a constant rate in both treatments due to the declining LAI, but the prochloraz treatment lagged behind the control (Fig. 5.3). Throughout Stages II and III, the proportion of the GAI that was leaf was the same in both treatments, but by mid-Stage IV (1 July), leaf accounted for 17% of the total GAI in controls compared with 23% in treated plots. PAI development was completed by early July and coincided in both treatments. Pod and hull DM were greater in treated plots throughout, but seed DM only became greater in treated plots as development proceeded (Fig. 5.8).

5.4. THE EFFECTS OF PROCHLORAZ ON CROP STRUCTURE (1991)

At the onset of flowering total DM was greater in every layer of the crop profile in treated plots, but the differences were marked from layer 4 upwards (Fig. 5.9). During Stages III and IV, total DM in layers 5-7, which comprised the pod canopy, was greater in treated plots because pod and stem DM were greater. Because treated plots were slightly taller than controls, layer 7 made a slightly greater contribution to the total pod DM and numbers in treated plots while the reverse was true in layer 5. Seed yield production also followed this pattern, and at final harvest, the 16% increase in seed yield in sprayed plots was mainly due to layer 6.

At the onset of flowering (first week), the greatest difference between treatments in LAI was in layer 2, which was the main leaf layer at this time (Fig. 5.10). The progression of senescence of leaf material up the crop profile was slower in treated plots while the production of new leaf area in the pod canopy was slightly greater

Fig. 5.7. The effect of prochloraz on the development of pod area index in 1991

solid line/closed symbols = control;
broken line/open symbols = prochloraz-treated

I = S.E.D.

Arrow indicates onset of flowering

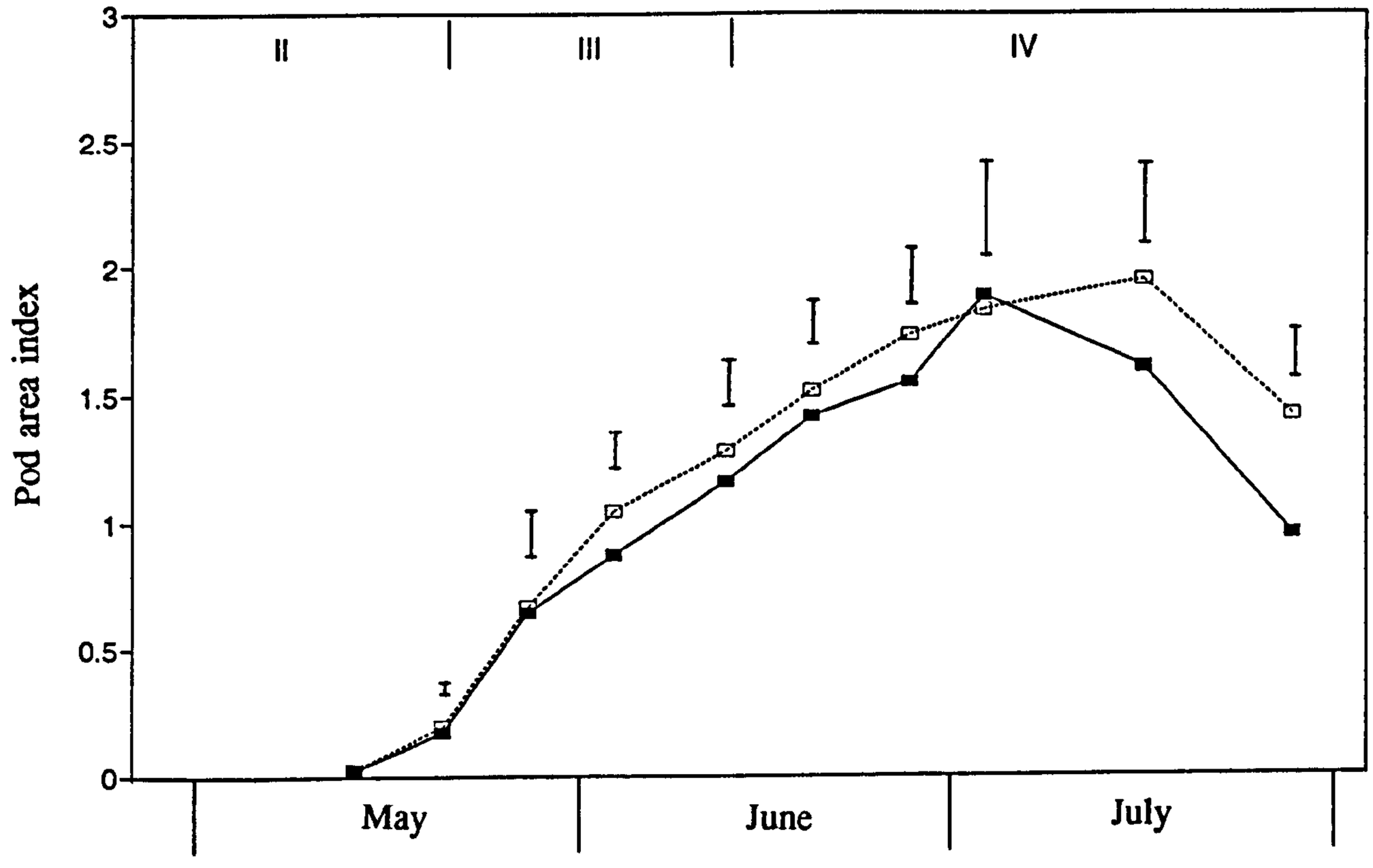
Stages are indicated by Roman numerals

Fig. 5.8. The effect of prochloraz on the development of seed dry matter during Stage IV in 1991

Solid line/closed symbols = control;
Broken line/open symbols = prochloraz-treated

I = S.E.D.

Arrow indicates onset of flowering


Pod area index
3
2.5
2
1.5
1
0.5
0
II
III
IV
May
June
July

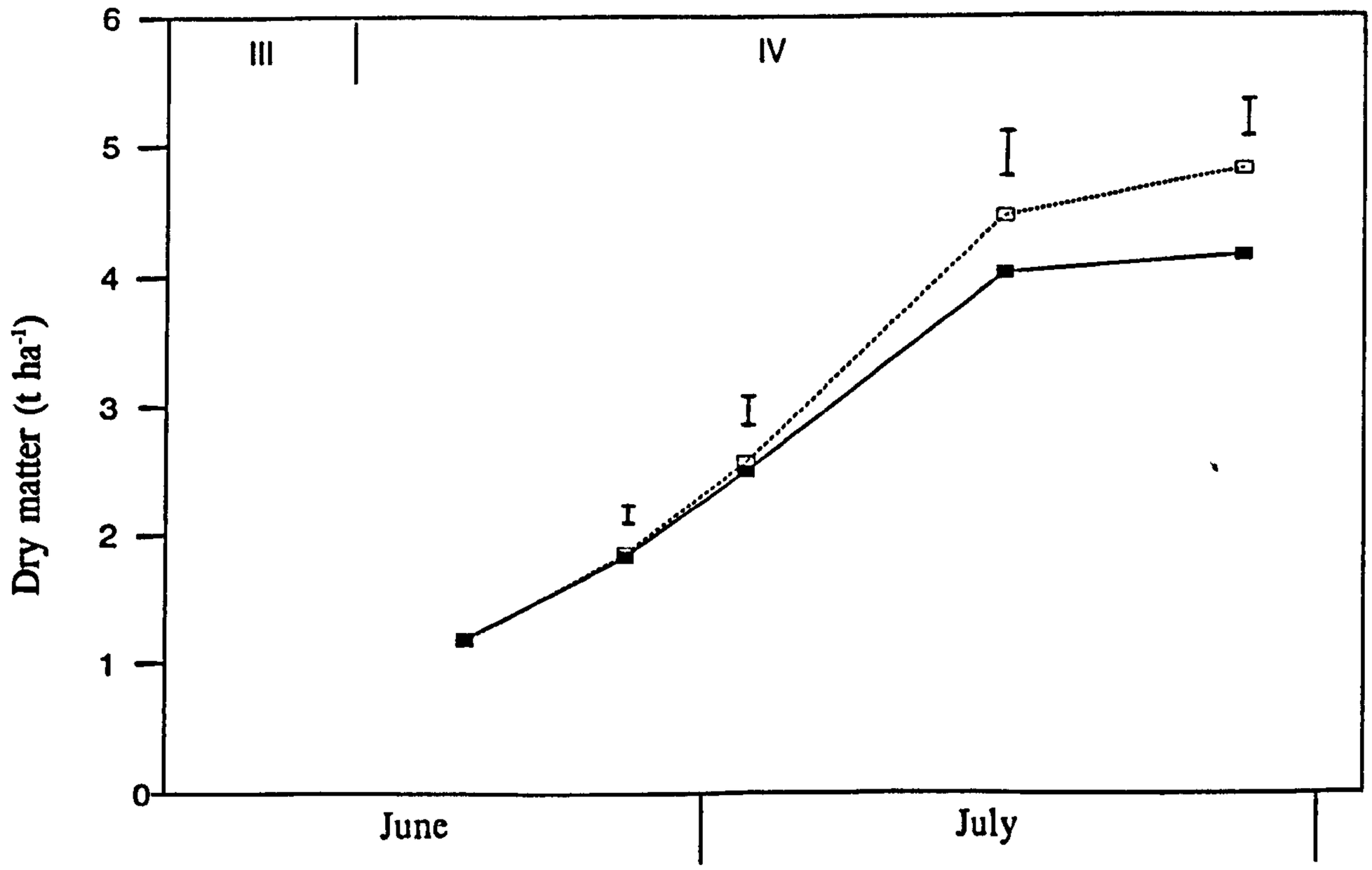

Dry matter (t ha-1)
6
5
4
3
2
1
0
III
IV
June
July

Fig. 5.9. The effect of prochloraz on the development of the dry matter of each component in each 20 cm layer of the crop profile in 1991:

♦ leaf

▲ stem

● pod

■ total

Solid line = control
Broken line = prochloraz-treated

Arrow indicates onset of flowering

Stages are indicated by Roman numerals

II
III
IV
Layer 7
Layer 6
Layer 5
Layer 4
Layer 3
Layer 2
Layer 1
Dry matter (g m-2)
May
June
July

(Fig. 5.10). With time, differences between treatments in LAI in the lower layers disappeared due to senescence. At the end of Stage II, the development of the reproductive framework was completed and maximum LAI was attained in layer 4, but leaf production continued in layer 5 during Stage III. Total GAI was higher in the upper layers of treated plots due to larger contributions of PAI and SAI (mainly layers 6 and 7). At the onset of Stage III, layers 3 and 4 still contained most of the leaf in both treatments but the prochloraz-treated in particular. LAI increased in the upper layers during Stages III and IV because of slower leaf senescence in treated plots. In Stage IV, most of the remaining leaf was in layers 4 and 5, but the decline continued more rapidly in controls. During late seed development, most of the leaf was at the base of the pod canopy (layer 5). Although almost negligible, the LAI in treated plots (0.4) on 17 July was twice that in controls (0.2).

5.5. THE EFFECTS OF PROCHLORAZ ON SOLAR RADIATION INTERCEPTION (1991)

5.5.1. Green area index and solar radiation interception

Prochloraz had little effect on total solar radiation interception prior to Stage III despite the differences in GAI distribution described in Section 5.4 (Fig. 5.10). It must be pointed out that the very small differences between treatments to be described in Stages III and IV are not statistically valid because the techniques used to obtain these data would not have been sensitive to less than 10%.

In the first week of Stage III (21 May), the GAI of the developing pod canopy was greater in treated plots, and the top two layers (6+7), consisting mainly of pod and stem, intercepted slightly more radiation (19.3 MJ m^{-2} (19% total incident radiation, R_T) compared with 17.2 MJ m^{-2} (17%) in controls) (Fig. 5.10). The decline in LAI began earlier in control plots, resulting in treated plots having a higher proportion of leaf in the lowest layer of the pod canopy. More radiation was intercepted by the top two pod layers in treated plots, and consequently, less was available for interception by leaf in this layer and below. During this stage, treated plots intercepted 6% more radiation than controls, which was due almost entirely to increased interception by pod and stem in the top two layers (Table 5.13). The proportions of interception attributed

to leaf and pod/stem in Stage III were approximately equal in both treatments.

During Stage IV, prochloraz increased total radiation interception again by 6%. This increase was due equally to increased interception by pod and stem (10.6 MJ m^{-2} extra), mainly in the top two layers, and leaf (also 10.6 MJ m^{-2}) (Table 5.13). Prochloraz only marginally increased the contribution of leaf to total assimilation on the basis of intercepting area. Bearing in mind the techniques used, the validity of these findings is uncertain. It will be shown, however, that even very small differences could be potentially important. Assuming an average efficiency of radiation use of 1.5 g MJ^{-1}, the interception of an extra 21.2 MJ m^{-2} in treated plots during Stage IV could have produced 32 g DM. This is insufficient to account for the yield increment of 66 g m^{-2} (4.80 vs. 4.14 t ha^{-1}), and indicates that the intercepted radiation was probably used more efficiently in treated plots. This will be investigated in the next section.

Table 5.13. The effects of prochloraz on total radiation interception (divided into pod/stem and leaf) in Stages III and IV

		MJ m^{-2}			Proportion of total	
		Pod/stem	Leaf	Total	Pod/stem	Leaf
Stage III	Control	130.2	120.5	250.7	52	48
	Treated	144.5	121.4	265.9	54	46
Stage IV	Control	299.6	59.7	359.3	83	17
	Treated	310.2	70.3	380.5	81	19

In conclusion, prochloraz slightly increased total radiation interception in Stages III and IV. This effect was of little consequence in Stage III since this was prior to the important yield-determining phase. In Stage IV, however, the increased radiation interception, which was due to increases in interception by all organs, could have accounted for approximately half of the yield increase promoted by prochloraz. This was achieved by greater pod and stem areas in the upper layers of the pod canopy, and by improved leaf retention in treated plots which slightly increased the contribution of leaf interception and, therefore, probably assimilation to seed-filling.

(a) Control

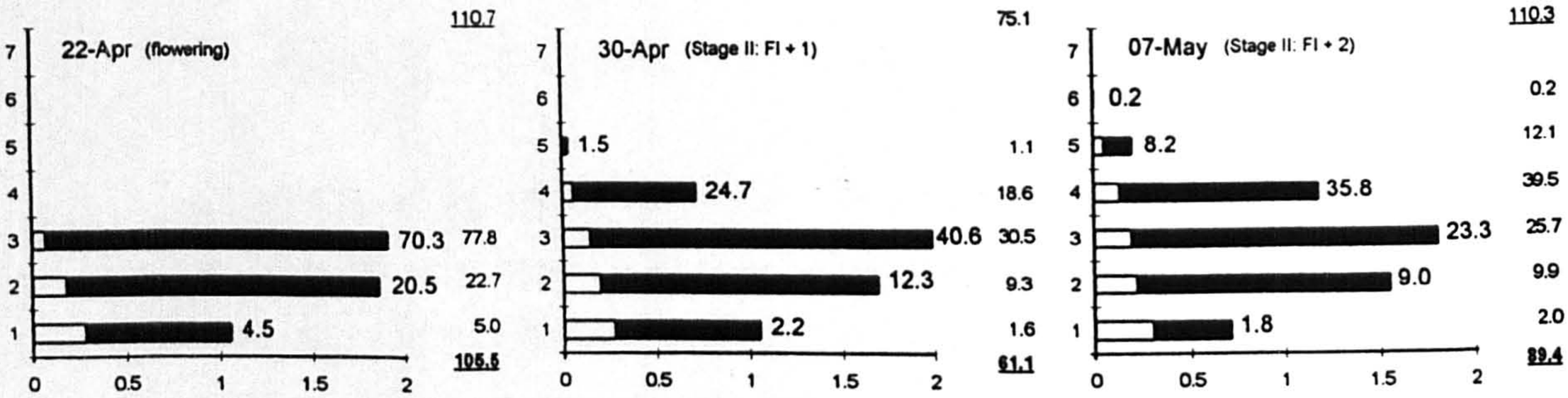
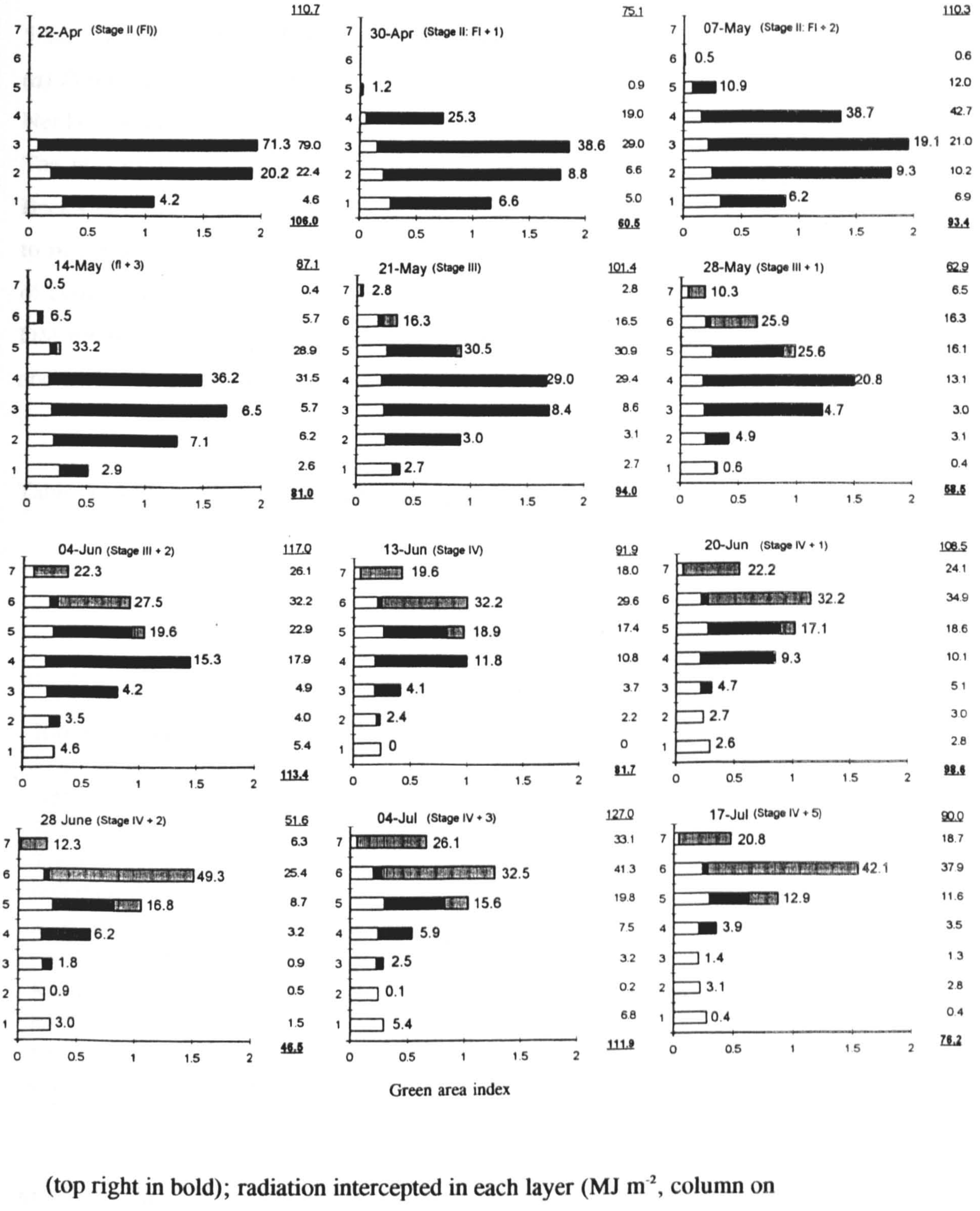


Fig. 5.10. The effect of prochloraz on radiation interception in the crop profile in relation to green area index.

Contents: GAI in each layer of the profile (bars: □ stem, ■ leaf, ▒ pod); % of total incident radiation intercepted in each layer (figures next to bars); total incident radiation (MJ m^{-2}) in intervals between sampling dates

(b) Prochloraz-treated



(top right in bold); radiation intercepted in each layer (MJ m^{-2}, column on right); and the total radiation intercepted in each interval (bottom right in box) for reproductive development: (a) control, (b) prochloraz-treated. Developmental stages (in weeks) in parentheses.

5.5.2. The effect of prochloraz on crop productivity

(a) Potential yield determination

Net DM production at the end of Stage I was 8% greater in treated plots (Table 5.14). The proportion of solar radiation intercepted (estimated from total GAI values and Beer's Law, using a *k* value of 0.6 (Mendham & Salisbury, 1995)) from late January to mid-March was also slightly greater in treated plots and the calculated efficiency of conversion of solar radiation (*E*) was increased by prochloraz. Similarly, greater DM production in treated plots in Stage II was due to greater radiation interception and an increased efficiency, indicated by *E* (Table 5.14).

Table 5.14. The effects of prochloraz on crop productivity during Stages I, II and III (C - control; Pr - treated)

	Stage I		Stage II				Stage III	
			Total		Flowering-full flower			
	C	Pr	C	Pr	C	Pr	C	Pr
Biomass at end of Stage (g m^{-2})	138	156	875	944	875	944	875	944
Net biomass produced (g m^{-2})	69.8	86.9	684	751	350	397	185	124
Total incident solar radiation (MJ m^{-2})	301	301	844	844	397	397	397	397
Average fraction of radiation intercepted	0.37	0.40	0.63	0.65	0.63	0.64	0.63	0.64
Radiation intercepted (MJ m^{-2})	111	121	532	549	250	255	250	255
Efficiency (*E*) of conversion (g MJ^{-1})	0.63	0.72	1.29	1.37	1.40	1.56	0.74	0.49

(b) Final yield development

Biomass production during Stage III (pod development) was lower in treated plots. This must have been due to a lower efficiency as indicated by the lower *E* (Table 5.14). The reason could have been the slightly lower radiation interception by leaf in this stage (Section 5.5.1) at a time when the crop was still relying heavily on leaf

assimilation to support early pod development. Otherwise the low E and DM production in treated plots may have been an artefact of plot variation and the short time-scale involved.

In Section 3, it was shown that seed yield was determined by the amount of radiation intercepted in Stage IV. Seed yield production in Stage IV was greater overall in treated plots due mainly to greater radiation interception. The efficiency, indicated by the E value, was increased only slightly. In the previous section, it was shown that the increased radiation interception in treated plots could have accounted for half of the yield increase, but this assumed a higher E than in reality. Over the whole of Stage IV, E was increased by 0.07 g MJ^{-1} (Table 5.15). Since 381 MJ m^{-2} were intercepted by the top four layers in Stage IV in treated plots (Table 5.13), a marginally increased efficiency, indicated by E, could have produced an extra 27 g DM. There was little difference in E between treatments, however, until late July, when DM production was very low in control plots. DM production was reduced in both treatments partly due to large pod (and seed) losses because the 1000-seed weight continued to increase. Prochloraz could have increased crop efficiency by prolonging the life of the green organs. The combined effect of greater radiation interception and slightly increased efficiency was increased assimilate production throughout Stage IV, which enabled more pods to be supported throughout the canopy. The proportionate increase in total DM at final harvest in treated plots was commensurate with the increase in seed yield, with harvest index being unaffected. This indicates that prochloraz did not affect the partitioning of DM between components.

In conclusion, DM production may have been lower in treated plots in Stage III due to a reduction in the efficiency of radiation use due to less leaf interception. In Stage III, leaf was still young and active, and its photosynthetic efficiency should have been high. DM production in Stage IV was similar in both treatments until the end of this stage. It was shown in Section 5.2.2. that pre-harvest pod (and seed) losses due to shattering were largely unaffected by prochloraz. Therefore the greater DM production in treated plots in late Stage IV must be attributed to a continued maintenance of efficiency due to a delay of crop senescence.

Table 5.15. The effects of prochloraz on crop productivity during Stage IV. Efficiency, E (g MJ^{-1}) calculated for cumulative weeks for cumulative seed DM (g m^{-2}) and intercepted radiation (R, MJ m^{-2})

	Control			Treated		
Interval	Seed DM	R	E	Seed DM	R	E
13 June - 20 June	119.1	76.4	1.56	118.8	81.7	1.45
13 June - 28 June	183.4	165.2	1.11	185.4	180.3	1.03
13 June - 4 July	250.1	208.1	1.20	257.0	226.8	1.13
13 June - 17 July	401.0	311.4	1.29	445.0	338.7	1.31
13 June - 29 July	414.1	381.5	1.09	480.1	414.9	1.16

(c) *Productivity within the pod canopy*

Prochloraz did not affect the *E* of the whole pod canopy until mid-July, when this was increased relative to the control (Table 5.16). Prochloraz did not change the variation in *E* down the canopy, and the middle layer still had the highest *E* and the bottom layer the lowest. However, *E* in the middle layer was increased by prochloraz after the first week of Stage IV. This effect was small but was sufficient to account for the slightly increased *E* for the whole pod canopy. In Section 3, a higher *E* in the middle layer was attributed to the accumulation of assimilate produced in lower horizons by branches and leaves. Prochloraz, therefore, could have slightly changed the pattern of DM movement between layers of the pod canopy. This was probably due to the different distributions of pods within the canopy. This will be considered with respect to yield determination in Section 5.6. Alternatively, prochloraz may have increased the supply of assimilate to the middle layer by prolonging the activity of the assimilatory organs (leaf and stem) at the base of the canopy.

5.6. THE EFFECTS OF PROCHLORAZ ON YIELD DEVELOPMENT WITHIN THE CANOPY

5.6.1. **Introduction**

In this section, yield component development as affected by prochloraz will be considered with respect to the extent and location of pod and seed losses in layers of

the canopy. The distribution of pods in the canopy was similar between treatments (Table 5.17). More than half of the total pods were located in the middle layer of the canopy. The top layer contained more in treated plots while, in the bottom layer, the reverse was true due to treated plots being slightly taller.

Table 5.16. The effect of prochloraz on the efficiency of DM production in layers (5-7) of the pod canopy and the whole canopy (total), calculated for cumulative intervals from the onset of Stage IV (13 June)

	Control				Treated			
Interval	5	6	7	Total	5	6	7	Total
- 20 June	0.80	2.62	1.86	1.91	0.60	2.41	2.07	1.83
- 28 June	0.95	1.69	0.91	1.30	0.78	2.05	0.60	1.30
- 4 July	0.88	1.71	1.34	1.41	0.68	1.76	1.41	1.40
- 17 July	0.56	1.88	1.62	1.50	0.84	2.23	1.21	1.61
- 29 July	0.81	1.61	1.02	1.27	0.74	1.83	1.14	1.39

5.6.2. The effect of prochloraz on yield components

Pod number

Prochloraz increased the number of potential pods m^{-2} by 11% ($P < 0.05$) (Fig. 5.11). However, the proportion of the potential pods developing into fertile pods was not affected by prochloraz, and at the onset of seed development, fertile pods amounted to 50% of the maximum potential pods. Fertile pod numbers were 10% greater (7500 vs. 6800 m^{-2}) in treated plots during early pod development (21 May) (Fig. 5.11). This difference was increased during Stages III and IV to give the 17% and 14% more yield-forming pods and total pods respectively at final harvest. Therefore the higher pod numbers at final harvest in the prochloraz treatments were due to increased pod-set in Stage II and the maintenance of more of these pods to maturity. These higher pod numbers m^{-2} were due to more pods in the top and middle layers in treated plots (Fig. 5.12). Better pod-set overall was due to higher retention mainly in the top layer (7). Pod losses (= abscised pods) were greater in this layer in late June (early Stage IV) in treated plots, and at maturity, improved pod retention in the middle layer

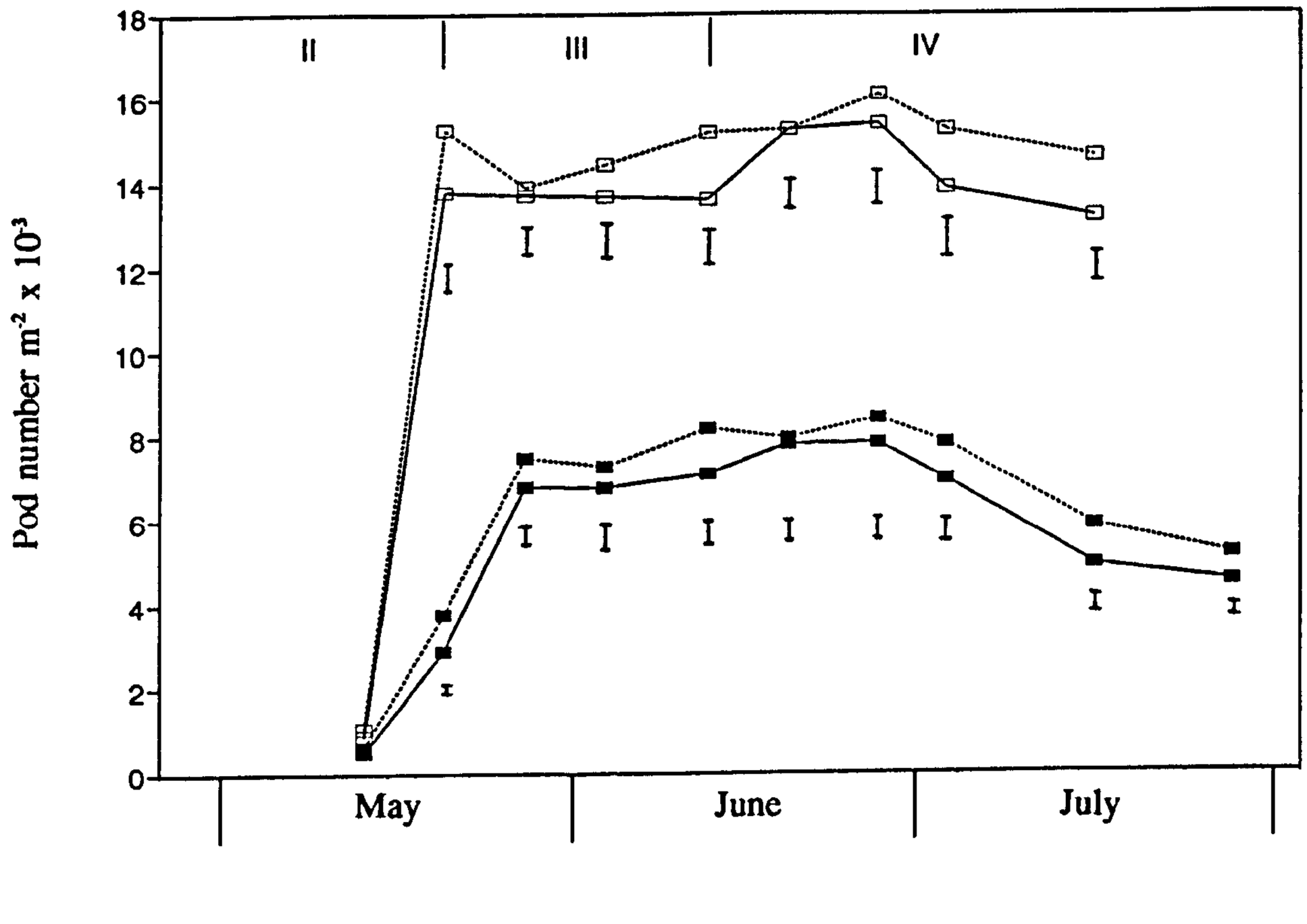


Fig. 5.11. The effect of prochloraz on the development of pod numbers in 1991:

■ fertile

□ potential

Solid lines = control
Broken lines = prochloraz-treated

Stages are indicated by Roman numerals

Fig. 5.12. The effect of prochloraz on the development of pod numbers in each layer of the pod canopy in 1991

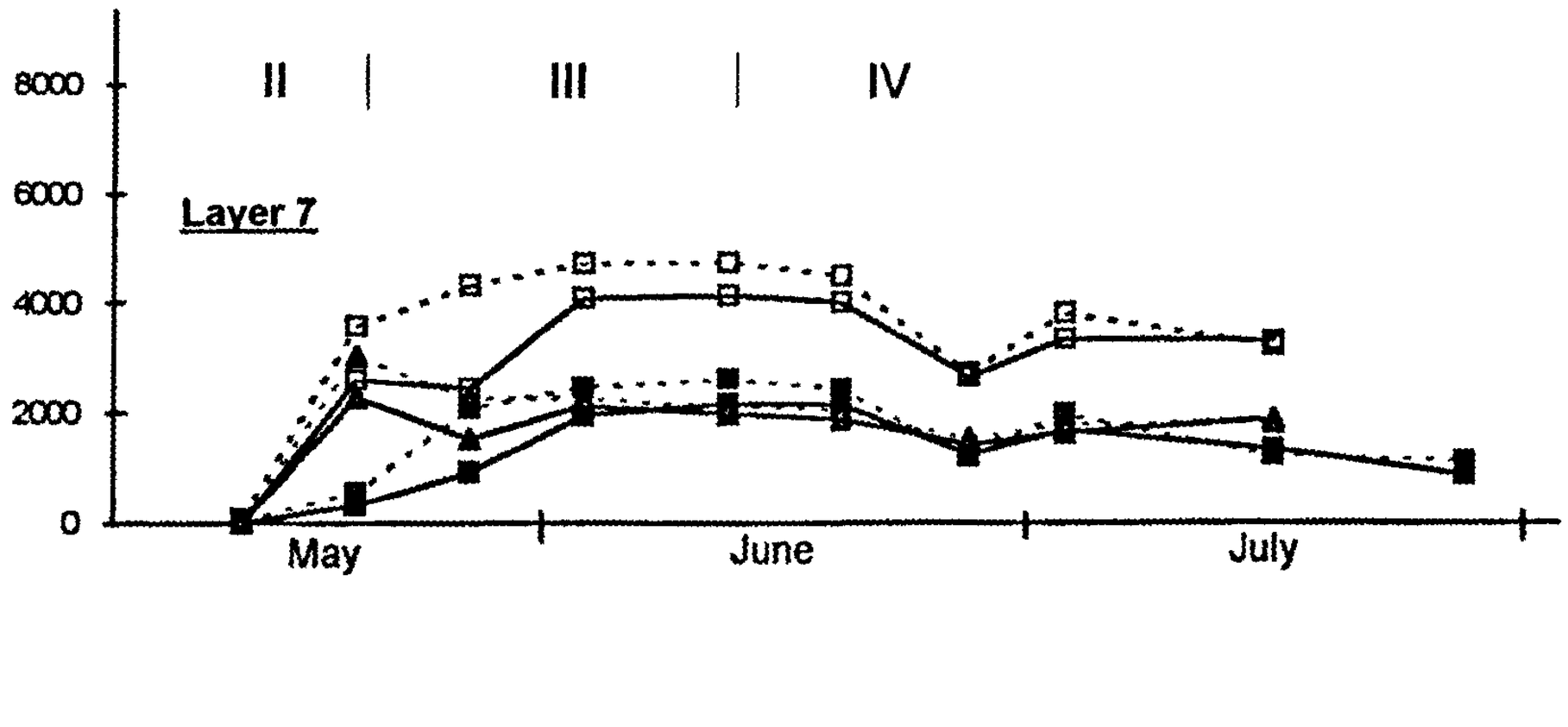
■ fertile

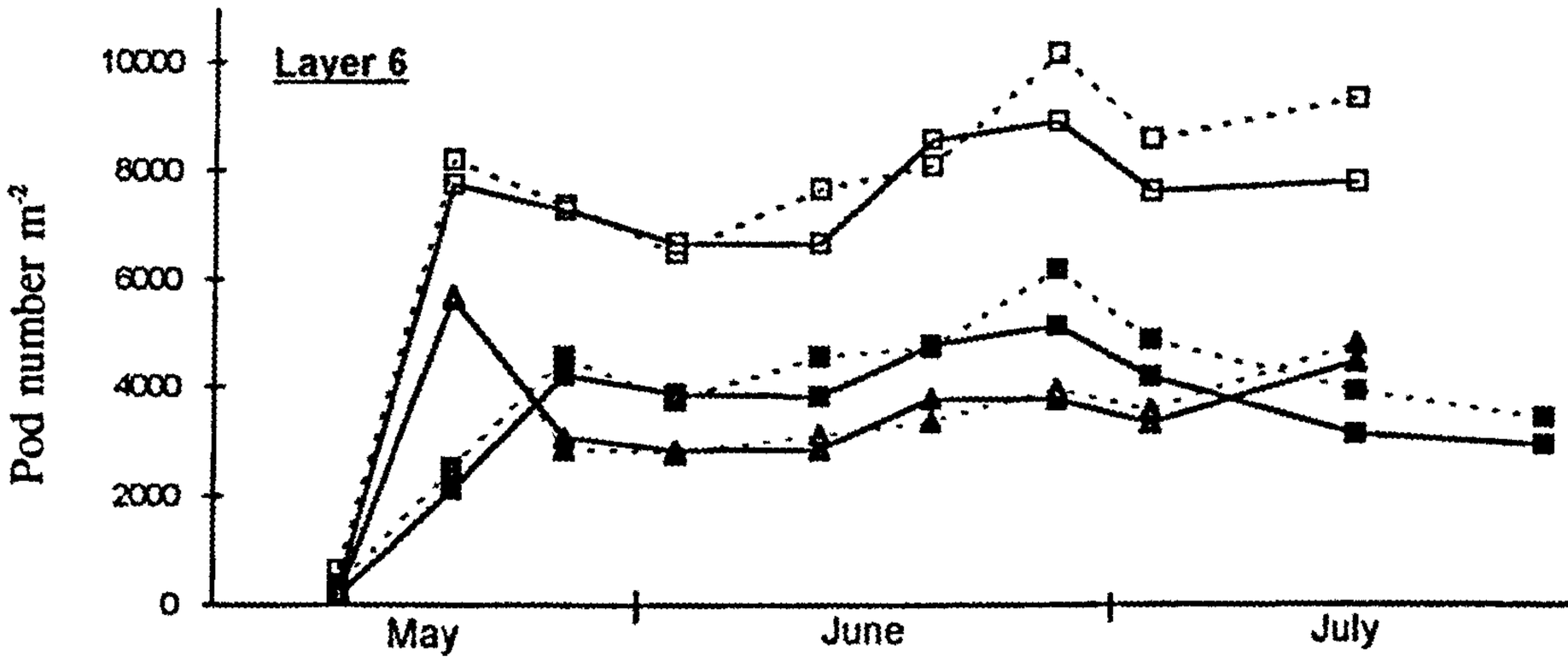
▲ abscised

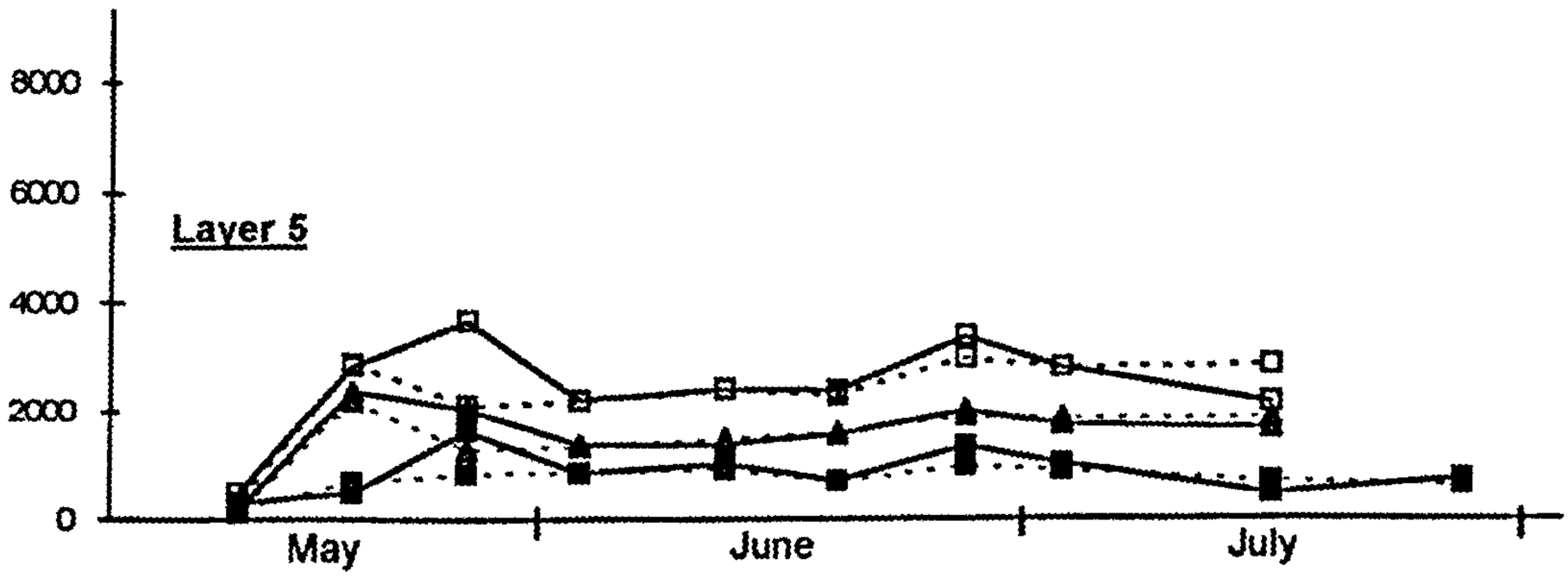
□ potential

Solid lines = control
Broken lines = prochloraz-treated

Stages are indicated by Roman numerals


8000
6000
4000
2000
0
II
III
IV
Layer 7
May
June
July


Pod number m-2
10000
8000
6000
4000
2000
0
Layer 6
May
June
July


8000
6000
4000
2000
0
Layer 5
May
June
July

accounted for much of the difference between treatments.

Prochloraz did not affect the proportion of the total remaining pods that contributed to final yield (90% in treated compared with 88% in controls). This indicated that the extent of pre-harvest pod shattering was similar in both treatments and the contribution of pods in the respective layers to final yield was the same. Prochloraz did reduce total shattering, however, implying that post-harvest losses were reduced (Section 5.2).

Seed number per pod

Although slightly higher in treated plots throughout, seed numbers per pod were not significantly different between treatments until final harvest when the difference was 10% ($P < 0.01$) (Fig. 5.13). At final harvest, seed number per pod decreased with depth down the canopy in control plots but not in treated plots (Table 5.17).

Table 5.17. The effects of prochloraz on seed yield and components in 20 cm layers of the pod canopy in 1991

	Layer	Seed DM (t ha^{-1})	Pod no. m^{-2}		Seed no. per pod	1000-seed weight (g)
			Total	Yield-forming		
Control	7	0.89	862	822	18.3	6.77
	6	2.66	2893	2578	15.9	6.71
	5	0.59	748	644	14.2	6.40
	Total*	4.14	4527	4004	16.1	6.63
Treated	7	1.14	1113	1043	18.2	6.79
	6	3.09	3405	3085	16.5	6.72
	5	0.56	625	523	18.8	6.55
	Total*	4.80	5161	4668	17.8	6.68

* Weighted average of layers for seed number per pod and 1000-seed weight

1000-seed weight

Prochloraz had no significant effects on mean 1000-seed weight throughout seed development or at final harvest (Fig. 5.13). 1000-seed weight decreased with depth in the canopy in both treatments at final harvest (Table 5.17). Seed number m^{-2} was

Fig. 5.13. The effect of prochloraz on the development of seed number per pod and 1000-seed weight in 1991:

● seed number per pod

▲ 1000-seed weight

solid lines = control
broken lines = prochloraz-treated

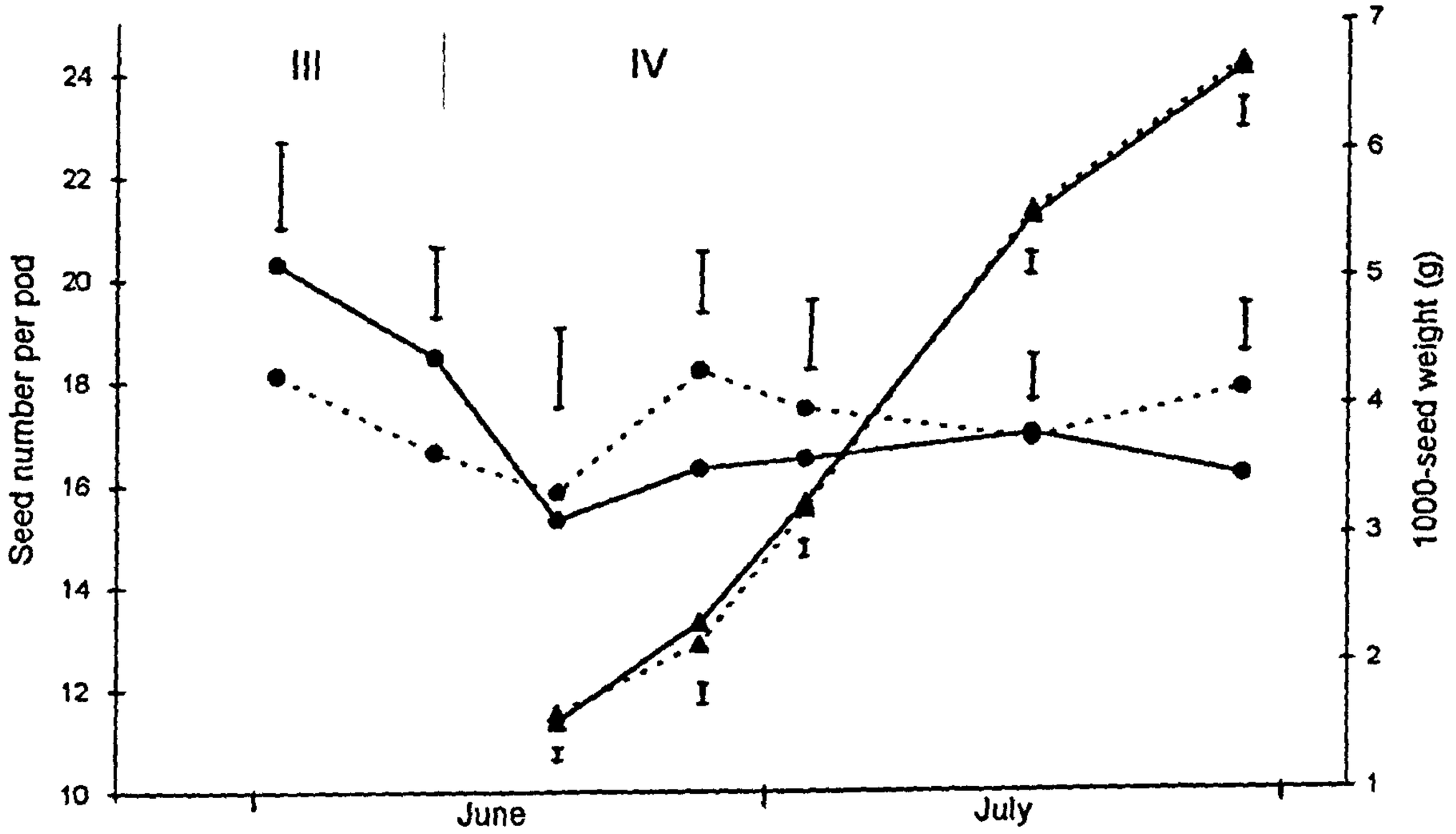
I = S.E.D.

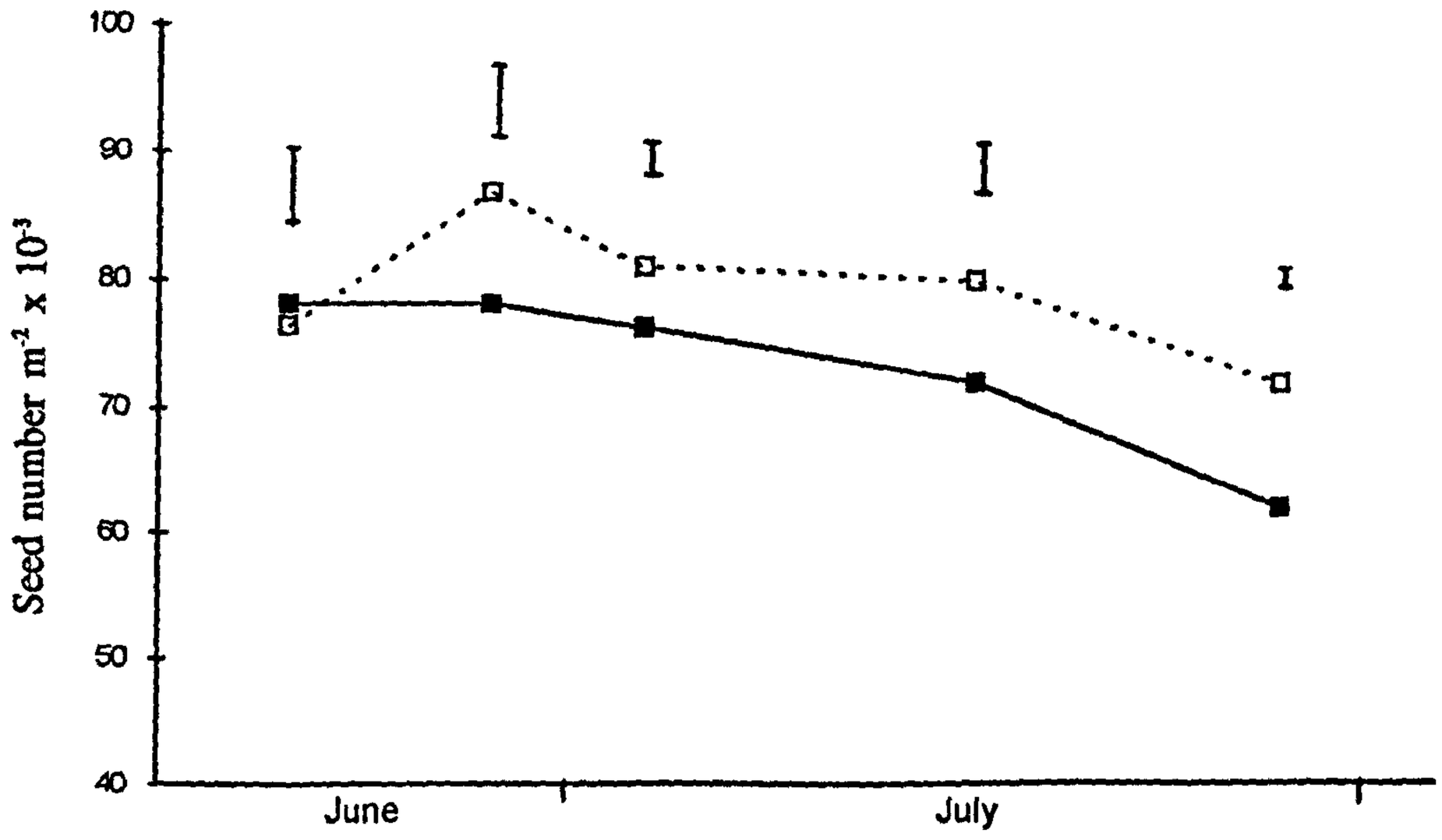
Stages are indicated by Roman numerals

Fig. 5.14. The effect of prochloraz on the development of seed number m^{-2} in 1991

solid line/closed symbols = control
broken line/open symbols = prochloraz-treated

I = S.E.D.


III
IV
Seed number per pod
1000-seed weight (g)
24
22
20
18
16
14
12
10
7
6
5
4
3
2
1
June
July


Seed number m^{-2} x 10^{-3}
100
90
80
70
60
50
40
June
July

greater in treated plots (Fig. 5.14). In June, seed DM production was equal in control and treated plots (Section 5.2), but prochloraz treatment delayed senescence and prolonged growth in late Stage IV, thereby promoting seed yield.

5.7. DISCUSSION

5.7.1. **Introduction**

It was shown in Sections 5.5 and 5.6 that prochloraz increased seed yield by increasing total assimilation by the whole crop. This was achieved largely by increasing radiation interception through a higher GAI. Treated plots were able to support greater pod (and seed) numbers during Stage IV by prolonged assimilate production. The mechanisms involved in the promotion of seed yield by prochloraz will be discussed in this section by considering firstly the direct effects on crop physiology and secondly the effects on radiation interception and yield production. The reasons for negative effects of prochloraz in 1992 and inconclusive findings in 1993 will then be considered, and the section will end with a discussion of the mediation of the phytotonic effect.

5.7.2. **The effects of prochloraz on growth and development**

The additional assimilation promoted by prochloraz that was responsible for the improved pod and seed retention was a consequence of a larger photosynthetic area. This section will discuss the effects of prochloraz on growth and development and their significance in yield production.

The effect of prochloraz on crop growth during the autumn and winter was examined in detail only in 1993, and it was assumed that the same mechanism applied in 1991. From November until stem extension in 1993, LAI and leaf DM were always greater in treated plots due to increased individual leaf size and leaf numbers. The higher numbers of green leaves were due to slower senescence. Delays in leaf senescence resulting from fungicide applications are well documented (Kettlewell & Davies, 1983). Growth regulators induce a similar effect by inhibiting ethylene formation and enhancing cytokinin levels (Akers *et al.*, 1990). In the present study, numbers of senesced and senescing leaves were identical in both treatments from early February

onwards, but more green leaves were retained in the treated plots. Generally, treated plants had higher leaf numbers than controls. Rawlinson & Williams (1990) reported that prochloraz increased leaf numbers, while Leach *et al.* (1988) noted an increase in the area of leaves on the mainstem elicited by November and April prochloraz applications. The effects of the triazole, triapenthenol, on leaf number were species-dependent (Lürssen, 1988).

The increase in individual leaf area promoted by prochloraz was far more pronounced than the effect on leaf numbers. Triazole growth regulators generally reduce leaf area but produce thicker leaves (Butler *et al.*, 1989). In 1993, leaf size decreased similarly in both treatments with lower autumn temperatures to form the rosette growth habit. As well as causing leaves to be smaller and thicker, triazoles enhance leaf greenness (Scarisbrick *et al.*, 1985; Lembrich, 1988; Butler *et al.*, 1989). Observations in the present study suggested that prochloraz may have promoted darker green leaf production, which could have increased absorption of incident radiation (Butler *et al.*, 1989). This effect could be important in reducing the decline in efficiency in late Stage IV since plants remained greener for longer in treated plots.

CO_2 assimilation has been increased following application of triazoles to oilseed rape (Lürssen & Reiser, 1985; Lürssen, 1988; Lembrich, 1988). Higher rates of photosynthesis per unit area were due to higher chlorophyll contents per unit area (Butler *et al.*, 1989). When paclobutrazol was applied to soybean, smaller but thicker leaves were produced and the rate of CO_2 fixation was increased on a unit area basis (Hawkins *et al.*, 1985). In the present study, prochloraz slightly altered leaf morphology in the vegetative stage and photosynthesis may have been affected as in soya bean. However, overall DM production differed little between treatments, and it must be concluded that there were no long-term effects on crop DM production. Prochloraz may also have enhanced leaf, stem and pod photosynthesis post-flowering through higher chlorophyll contents per unit area. This is supported by observations of greener pods in treated plots, particularly during the latter part of the seed development stage. Treated plots would have been able to maintain more assimilates to seeds for a longer period. Luib *et al.* (1987) reported that the translocation of

assimilates into the growing seeds was promoted following triazole applications. A similar effect could have been responsible for the increased 1000-seed weight elicited by the spring prochloraz application in 1991. Leaf retention in the lower layers in crops sprayed with the triazole, triapenthenol, enabled plants to photosynthesise for longer (Lembrich, 1988). Similarly, Luib *et al.* (1987) found that triazole application delayed pod senescence, while Child *et al.* (1987) noted that treated plots were greener at harvest due to a greater proportion of younger and unripe pods. In the present study, the increased seed moisture content at final harvest supports the conclusion that prochloraz delayed maturity. However, the extent of pre-harvest pod shattering was not affected. Conversely, pod shattering was reduced in the cultivar Bienvenu following autumn and spring prochloraz applications and summer iprodione (Rawlinson *et al.*, 1988b).

In the present study, flowering and its duration were unaffected by prochloraz. In contrast, cauliflower plants treated with prochloraz flowered two weeks earlier than plants sprayed with other fungicides (Cheah *et al.*, 1981). Triazole growth regulators, however, delayed the onset of flowering (Baylis & Wright, 1990), and either extended (Child *et al.*, 1987) or shortened (Armstrong & Nichol, 1991) its duration.

The larger pod area index of treated plots in 1991 in turn contributed to the higher GAI of these plots. Such differences were due to more pods in treated plots, and not individual pod area. Although Pechan & Morgan (1985) suggested that the expansion of the pod walls was dependent upon the presence of developing seeds, prochloraz slightly increased seed number per pod in 1991 but did not affect individual pod areas.

The greater area of stem in the upper layers of treated plots would have contributed a proportional amount to the total crop photosynthesis during the seed-filling stage. Bock *et al.* (1991) also noted increased stem production following prochloraz application, and this could have improved standing ability. Baylis & Hutley-Bull (1992) suggested that greater branching in plants treated with a triazole plant growth regulator may have stabilised the canopy by increasing the interlocking between plants. Prochloraz, however, promoted longer rather than more numerous branches.

Prochloraz had no consistent effects on harvest index, which indicated that the chemical does not change the proportions of DM allocated to the reproductive framework and the seed. In contrast, the triazole paclobutrazol and related compounds increased yield by altering the distribution of assimilates to the reproductive parts (Addo-Quaye *et al.*, 1985; Baylis & Hutley-Bull, 1991).

5.7.3. The effect of prochloraz on the determination of pod number

Mendham *et al.* (1981) considered that potential yield depended on the size of the crop at flowering. Prochloraz increased the number of potential pods m^{-2} but this could not be attributed to the larger size (DM) of treated plants (Section 3.4). Potential pod numbers were also increased by prochloraz in 1992 and this was not associated with increased crop size (and there was no effect in 1993). Prochloraz, therefore, may have had a direct effect on flower formation by an unknown mechanism. Triazoles such as triapenthenol have been shown to encourage flowering through increased branching (Lürssen, 1988). Prochloraz increased stem production in the pod canopy in the form of longer rather than increased branches (Section 5.4) which may have increased flower production.

The higher pod numbers in treated plots at maturity were mainly responsible for the greater seed yield in 1991. Lürssen (1988) regarded increased branch and pod production to be an essential precondition for increased yields following application of the triazole triapenthenol. While prochloraz increased fertile pod numbers, it did not alter the proportion of potential pods that set. The triazole, paclobutrazol, increased numbers of flowers and pods in oilseed rape but the fertile pods did not increase in proportion and this led to more unproductive pods (Child *et al.*, 1987; Rao *et al.*, 1991). Rao *et al.* (1991) attributed such losses to plants being too small to support all the additional potential pods produced. Likewise, Mendham *et al.*, (1984) considered that plant size at flowering was a major constraint on the ability to support pods. It has been shown conclusively in this study (Section 3) that pod-set was independent of crop size but instead depended upon the rate of DM production in Stages IIb and III, which was dependent upon radiation interception and the efficiency of radiation use. Total DM production in Stage III was lower in treated plots than

controls due to a lower efficiency. This implies that the higher pod-set in treated plots was dependent upon the greater assimilate production in Stage IIb. The larger GAI (leaf and stem areas) in treated plots should have supported a proportionately larger assimilate production (Clarke & Simpson, 1978a). However, total radiation interception in each 20 cm layer of the pod canopy at this time was similar in both treatments. It must be concluded that increased DM production in treated plots in Stage II was the result of more efficient radiation use (Section 5.5). This could have been due to the maintenance of functional leaf tissue in these plots since senescing leaves lose their capacity for assimilation while still appearing green. Such leaves would intercept radiation but this would have been used less efficiently, particularly in control plots where incipient senescence was more advanced.

The greater pod losses at the top of the canopy in treated plots were probably due to competition between pods, resulting from a continued dependence on assimilate from other sources (leaf). By changing the distribution of pods within the canopy, prochloraz may have modified the pattern of assimilate distribution. In Section 3, it was shown that assimilates probably moved from the leaf layers to the upper pod layers. Efficiency values calculated in Section 5.5 indicated that assimilate movement to the upper layers was slightly greater in treated plots as a consequence of the higher sink strength created by greater pod numbers. Developing seeds are known to be rich sources of hormones (auxins) which move through the pod into the stem and may direct assimilate movement to the seeds (Street & Opik, 1981). More assimilates, therefore, would be diverted to regions with more numerous and better-developed seeds because of increased hormone concentrations. Conversely, more DM was probably retained in the lowest pod layer in controls because this contained a greater proportion of the pods than in treated plots.

Bouttier & Morgan (1992b) considered it likely that the process of pod abscission was regulated by a hormonal mechanism, but was ultimately determined by the availability of assimilates. The abscission process may involve an increase in ethylene production, and since most ethylene production by the reproductive structures is in the seeds (Meakin & Roberts, 1992), the process may be determined by the seeds themselves.

It is possible that increased ethylene production could be associated with seeds that fail to attract assimilates. Thus the survival of a pod may be dependent on its ability to supply assimilates to the developing seeds and, in addition, on the contribution of leaf and stem photosynthesis.

5.7.4. **The effect of prochloraz on the determination of seed number per pod**

The effect of prochloraz on seed number per pod at maturity was small and accounted for only a small proportion of the yield increase. Scarisbrick *et al.* (1985) showed that the time of application of the triazole, paclobutrazol, to spring rape affected the number of seeds per pod due to compensation between the yield components. Early application led to fewer pods but the number of seeds per pod and seed size were increased, whereas late application reduced the number of seeds per pod and increased seed size. Mendham *et al.* (1981) considered pod number to be an important determinant of seed number per pod because of competition between the pods for assimilates. In the present study, despite higher pod numbers in treated plots (10%), seed numbers per pod were similar throughout development until late Stage IV, and the greater pod numbers were not offset by either a lower seed number per pod or a lower 1000-seed weight at maturity. Eberhardt (1988) observed a similar effect with the triazole triapenthenol, in which both pod numbers and seed numbers per pod were increased. In Section 3, it was shown that seed number per pod was dependent upon the assimilate supply during Stage III, which was indicated by DM production in this stage. In 1991, however, DM production during Stage III was lower in treated plots, which implies that the assimilate supply was also lower in treated plots. Therefore, some other factor must have been involved such as redistribution of DM within the crop. In summary, prochloraz increased pod number and productivity through improved assimilate supply from the increased green area including leaves, the retention of which was promoted by prochloraz.

The reduction in seed losses down the pod canopy cannot be accounted for by the pattern of assimilate distribution outlined in Section 5.5, with preferential supplies to the upper and middle layers at the expense of the lowest layer in treated plots. Substantial losses occurred late in Stage IV in the lower layers of control plots

because assimilates supplies were inadequate to sustain seed growth. Those pods starved of assimilates, due to shading of the pod itself and a low priority for assimilates from other sources, were most likely to be lost. This process was probably mediated through changes in hormone levels (de Bouille *et al.*, 1989). Seeds that were filling normally probably produced greater quantities of hormones that moved into the plant and attracted more of the available assimilates produced by leaf and stem.

In Section 5.5, it was shown that radiation interception by the two upper layers of the pod canopy was greater in treated plots due to the larger pod numbers and pod area. This would have resulted in greater assimilation in pods and branches in treated plots. Despite the lower radiation availability in treated plots, interception by the leaf layers was similar in both treatments due to increased leaf retention and LAI in treated plots, and assimilate production by leaf would have been similar in both treatments. However, leaf senescence was slower in the treated plots, resulting in a slower decline in the efficiency of radiation use, which enabled treated plots to maintain a higher rate of DM production to maturity. This is supported by the findings in Section 5.4 which indicated that DM production continued for a longer time period in treated plots. Therefore continued assimilation by leaf in treated plots could have maintained seed number per pod in lower pods, which were favoured by their proximity to the extra assimilate supply. Assimilation by individual pods was probably similar between treatments because radiation interception by the pod canopy was related to pod number. However, the efficiency of pod photosynthesis could have declined in controls in late Stage IV because of the earlier senescence of the whole crop. This could have contributed to increased seed losses late in development in control plots.

5.7.5. The effect of prochloraz on the determination of final yield

Leaf retention by treated plants was most pronounced during pod and seed development, particularly in the lowest pod layer. The solar radiation available to this layer in treated plots was reduced by greater interception in the upper (pod) layers. However, the greater LAI intercepted some of the radiation that would otherwise have passed to the ground. Greater LAI during Stage IV enhanced the supply of assimilates

to the seeds, especially towards the end of development. Most of the assimilates for seed-filling are supplied by the pods themselves and the branches on which they are carried (Bilsborrow & Norton, 1988), but a proportion may also be supplied by the leaves (Chapman *et al.*, 1984; Addo-Quaye *et al.*, 1986). Proximity of the source to the sink is important in assimilate movement (Major & Charnetski, 1976), and since, at least in spring rape, most movement from the upper leaves is acropetal (Major & Charnetski, 1978), the extra leaf in the lower regions of the pod canopy in treated plants was ideally positioned for contributing to seed development.

5.7.6. **Factors causing variation between seasons in the response to prochloraz**

In this section, possible reasons for the different effects of prochloraz in the three seasons will be discussed. The main points to consider are:

1. Why was there a pronounced response in 1991 but not in 1992 and 1993?

2. Why was the autumn application the most effective in 1991?

3. Why did the effect initially seen in 1993 disappear during stem extension?

4. Why was the spring application responsible for most of the effect in 1993?

The effects of prochloraz on final seed yield and its components were strongly dependent on the time of application and on season. The response in 1991 was effected by the autumn prochloraz application while in 1993, both the autumn and spring applications were involved. Although the response was small in 1993, it was largely due to the spring application, but was greatly enhanced when preceded by an autumn application. Therefore the failure to elicit a significant response in 1992 was probably due to the missing autumn application.

The growth regulating effects of triazoles are dependent on the time of application in relation to the stage of development of the plants (Scarisbrick *et al.*, 1985; Child *et al.*, 1987; 1988). Different application times of these growth regulators have markedly different effects on canopy structure, seed yield and its components (Child *et al.*, 1985, 1987, 1988). This is because triazoles inhibit gibberellin synthesis, and, as a consequence, extension growth (Lürssen, 1988). Although prochloraz is an imidazole, and does not inhibit extension growth, the differences between seasons in the effects

of each application may be due to different application times, as well as differences in climate. However, triazoles are applied specifically to inhibit extension growth, whereas the timing of prochloraz applications was determined by the maximal fungicidal response.

In 1991, increased growth promoted by the autumn prochloraz application persisted throughout development, whereas in 1993, the effects had disappeared by flowering. The apparent advantage of treated plants in terms of radiation interception was not manifest in an increased DM production and differences between treatments were maintained at a constant level. This disappearance of the phytotonic effect can only be attributed to either climatic factors or disease. Application of triazole plant growth regulators in the winter may confound the stresses produced by low temperatures (Lembrich, 1988). Similarly, plants treated with prochloraz may have been more adversely affected by the sudden and rapid decline in temperatures which retarded growth in late February 1993. Conversely, many fungicides and plant growth regulators increase winter-hardiness (Musnicki *et al.*, 1988), and some triazoles have the ability to protect plants against other environmental stresses such as drought and heat damage (Fletcher *et al.*, 1986). In the present study, there were no indications of an effect of prochloraz on over-wintering mortality. However, the larger leaf areas of treated plants possibly rendered them more susceptible to temperature stress. Probably more importantly, the 1993 crop showed widespread symptoms of phoma from March onwards which led to a high incidence of stem canker during Stage IV (Section 4). Therefore, the effects of prochloraz in 1993 were probably negated by phoma/stem canker with some possible influence of climatic conditions.

Other factors that may have influenced the effects of prochloraz include the method of application (Section 2) and crop height. Bateman (1987) suggested that the effects of prochloraz in controlling eyespot in wheat were limited by an inability to penetrate the canopy effectively when sprayed conventionally, and this could be similar in dense canopies of oilseed rape. In 1993, the unusually small crop should have allowed better penetration of the chemical into the profile, thereby increasing the likelihood of a response. Effects of the triazole paclobutrazol are dependent on season and may

not occur after a very dry autumn (Scarisbrick *et al.*, 1985). Lürssen (1988) suggested that triapenthenol would only promote yield increases if other factors, mainly the climatic conditions, did not limit the yield. The contrasting weather conditions in the three seasons of the present study would almost certainly have influenced the effects of prochloraz.

In order to prove unequivocally the phytotonic effects of agrochemicals such as prochloraz, crops should ideally be disease-free. This is probably impossible to achieve in the field, but might be aided by careful use of other fungicides that are known not to interact with prochloraz. Difficulties in distinguishing between fungicidal effects and true phytotonic effects could then be avoided. In the ideal experiment, treatments would be applied at the specified growth stages which would enable meaningful comparisons between seasons to be made.

5.7.7. **Mediation of the phytotonic effect of prochloraz**

Unlike triazoles, which have the same fungicidal mode of action (Copping *et al.*, 1984; Buchenauer, 1977), prochloraz did not inhibit extension growth. This could be because prochloraz shows negligible systemicity whereas triazoles are most effective following root uptake and transport via the transpiration stream (Copping *et al.*, 1984). In wheat, the fungicidal activity of prochloraz was optimised if substantial rainfall followed application (Cooke *et al.*, 1992). The half-life of prochloraz on unweathered foliage of wheat was only six days (Cooke *et al.*, 1992), and no activity remained 13 days after leaf application (Gisi *et al.*, 1986), but when deposited at the stem bases, prochloraz remained stable for two weeks (Cooke *et al.*, 1992). Since prochloraz is immobile within the plant and shows little uptake into the leaf (Stevens *et al.*, 1988), its action must be strictly local. Because the half-life is so short, fungicidal activity must involve direct contact, but long-term effects of prochloraz on fungal pathogens have been observed in July in the present study and other studies (eg. Rawlinson *et al.*, 1984). Since prochloraz is lipophilic, some of the long-term fungicidal effects may be due to the fungicide being retained in the wax layer on the leaf surface and slowly released. This effect would depend on the rate of leaf senescence which, this study has shown, is reduced by prochloraz. The long-term fungicidal effect may be

due to the effect on initial infections if applied at the correct time. Similarly, the phytotonic effect of autumn application must result from influencing some mechanism that has implications for the remainder of development. This is likely to be at the hormonal level, which would account for the continued effects on leaf senescence.

Following application of prochloraz, a high concentration gradient exists across the cuticle since prochloraz is rapidly metabolised on entering the leaf (Stevens *et al.*, 1988). Metabolism may result in the loss of biological activity or the production of active metabolites. The fungicide triadimefon is only biologically active following metabolism in the fungus, and similar metabolism can occur in the plant at a slower rate (Gasztonyi & Josepovits, 1979). Although prochloraz remains largely in the leaf surface wax (Stevens *et al.*, 1988), its metabolites could pass into the leaf (or pod) and influence hormonal or cellular function. Many triazole fungicides and/or growth regulators influence the synthesis of plant hormones. Since the mode of action of prochloraz and triazole fungicides in fungi is similar, prochloraz probably has similar effects on plant metabolism (hormone synthesis and action). Buchenauer (1977) suggested that compounds affecting gibberellin and sterol biosynthesis were acting at the membrane level, and inferred that membrane-formation and permeability may be affected. In addition, water relations could be affected through abscisic acid metabolism, and leaf and pod abscission influenced through an interaction with ethylene and abscisic acid. Delayed senescence and increased greening of pods and leaves could also be due to a direct influence on chloroplasts. The ultimate fate of applied prochloraz and/or its metabolites is unknown. Possibly most are lost when leaves senesce but retention in the plant could allow continuous effects on growth and development.

5.8. CONCLUSIONS

Prochloraz increased seed yield in one season (1991) by increasing the number of pods supported to final harvest. This was achieved by increasing the assimilate production of the whole crop. At flowering, pod-set was improved by greater assimilate production resulting from increased leaf retention. Prochloraz treatment enabled the productivity of individual pods to be at least as high as in untreated plots despite the

greater pod numbers because of increased assimilate production. Assimilation was increased mainly by the interception of more radiation but partly by a slightly increased efficiency of radiation use, and maintaining DM production over a longer time period in Stage IV. This improved both pod and seed survival. Seed survival in pods at the base of the pod canopy was slightly improved by prochloraz. Most of the increase in yield, however, was due to the retention of more pods in the upper and middle regions of the pod canopy. The better assimilate supply enabled more surviving pods to retain at least as many seeds per pod as in control plots. Furthermore, despite their greater numbers, seeds in treated plots were grown to the same size as in control plots.

Section 6: GENERAL DISCUSSION AND CONCLUSIONS

Based on the findings of Sections 3 and 5, the aim of this section is to identify the important factors responsible for high yield production. In Section 3, mechanisms involved in increasing seed yields in certain crops were elucidated, and these findings were extended in Section 5 by the use of the phytotonic fungicide prochloraz which increased seed yield. This section will investigate how seasonal, morphological and physiological factors interact to determine crop yields and how these might be exploited to produce an ideotype oilseed rape crop which would maximise yield production from the available resources.

The factor identified as the most important determinant of seed yield was the total solar radiation intercepted in Stage IV (seed development). Seed yield was determined by the extent of photosynthesis in this stage, which was dependent upon cumulative radiation interception. There was no direct relationship, however, between yield and intercepted radiation because the efficiency of radiation use (E) differed between seasons, possibly related to environmental conditions. Leach, Pearman & Rainbow (1988) were similarly unable to explain marked differences between seasons in the efficiency of radiation use during the post-flowering period. Since, in the present study, E was much higher when incident radiation was low (1991), it is proposed that there is a critical level of interception below which yield is directly related to interception, and above which other factors become limiting. The possibility cannot be ruled out that the low E values may have been due to light saturation.

No remobilisation of reserve materials occurred during Stages III and IV, which implies that seed-filling depended entirely on current photosynthesis. The stem, therefore, did not serve as a store for assimilates produced earlier in development, and its primary function was to support the developing yield components both structurally and through the provision of assimilates from current photosynthesis. This forms an interesting comparison with cereals such as winter wheat, in which, depending on season, stem reserves contribute 20 - 40% of the dry matter utilised in grain-filling (M.J. Foulkes, personal communication).

Seed yield was independent of pre-flowering events and was not related to plant size at flowering. The function of events prior to Stage III was the development of the potential yield which, again, was not dependent upon plant size at flowering. In normal seasons, potential yield was always in considerable excess of that required and, even in poor seasons, potential yield was unlikely to be limiting. Pod losses were continuous from the onset of flowering, but potential pod and seed numbers were in excess at the end of flowering. Further and much more substantial pod and seed losses occurred in Stage III, the main phase of yield component determination. Losses late in Stage IV were associated with adverse environmental conditions.

Factors that moderated the yield and disrupted the relationship between seed yield and intercepted radiation were disease and environmental conditions that interacted with radiation interception. Heavy infection with sclerotinia contributed significantly to the inability of the 1992 crop to achieve its potential. Further, the effects of sclerotinia compounded the effects of high temperature which itself contributed to the rapid increase in the soil moisture deficit (SMD) in this season. The net result of these environmental factors was many pods that ripened prematurely and shed seed, while remaining pods had reduced seed numbers and low seed weight. It is not possible to attribute reductions in each component to a particular adverse factor. However, sclerotinia developed throughout June and July in 1992 and was probably the major cause of low 1000-seed weight while the SMD, which became particularly high in late June, may have been largely responsible for the substantial reduction in seed number per pod that occurred at this time. Widespread stem canker infection in 1993 was far less damaging to yield even though most plants were infected and severity was moderate. This has important implications for disease control because it is evident that sclerotinia control should be given priority while stem canker, although potentially damaging, may not warrant prophylactic fungicide application.

Because yield was determined in Stage IV, only those modifications of the yield components that occurred in this stage were important with respect to radiation interception. In the absence of external influences (disease and environmental conditions), pod numbers were largely determined by the end of Stage III following

substantial losses during this stage, which resulted from the competition for assimilate between a large number of pods and seeds. Some pod losses may have occurred early in Stage IV in 1992 due to low radiation levels at a time when exceptionally large numbers of pods were competing for assimilates. Later in Stage IV, however, radiation interception had little influence on pod numbers because other factors became more influential. The distribution of pods within the canopy was similar in all seasons, with the middle 20 cm layer containing approximately half the total. Throughout, pod retention was greatest in the middle of the canopy as a consequence of its large sink size which increased the ability of pods to attract assimilates from the main source in the leaf layers below. DM production was greatest in this layer. At the end of flowering, however, large potential pod losses occurred regardless of the amount of radiation intercepted and at a time when DM production was not limiting. These losses were largely in the form of buds that failed to open, implying that some mechanism, possibly mediated by hormonal or nutritional factors, resulted in the termination of flowering. This would be similar to the "apical switch-off" mechanism postulated for pot-grown spring rape plants by Keiller & Morgan (1988a) in which the onset of pod-filling in older pods caused apical development, and hence flowering, to cease. In the present study, the rapid end of flowering and sudden losses of potential pods occur imply that the system would be controlled not by nutrition, which would be more gradual, but probably by hormones.

Seed number per pod was probably determined by a combination of genetic, hormonal and nutritional factors. The decline in seed number per pod down the canopy is often attributed to the effects of shading which restricts photosynthesis and assimilate supply lower in the canopy (Bilsborrow & Norton, 1988). Evidence from the present study indicates, however, that this distribution may be partly genetically determined since the first-formed ovaries lower in the canopy had fewer ovules than those developing later, higher in the canopy. These numbers were moderated by assimilate supply (radiation interception) and hormones. Shipway (1981) proposed that seed number per pod was related to radiation interception per pod but no such relationship was detected in the present study. Large seed losses occurred prior to the onset of Stage IV which were related to competition for assimilates because seed survival at this time was

dependent upon the availability of assimilate (indicated by DM production) and the number of competing pods. In 1991 and 1992, seed losses were progressively larger down the profile. This was attributed to shading of pods in seasons when seed-filling was mainly dependent on pod and stem photosynthesis. In 1993, however, when more of the assimilate available for filling seeds was supplied by leaf, seed losses did not increase with depth in the canopy. In this season, the crop retained a large number of seeds throughout the canopy because of the availability of assimilate from a number of sources including leaf. When the assimilate supply was limited by low incident radiation and interception, and DM production was low (1991), seed number per pod declined throughout the canopy. These findings indicate that seed number per pod is primarily dependent upon the assimilate supply. This will be affected by the number of competing pods, the radiation available and intercepted, and the availability of assimilate from other sources (leaf).

The determination of 1000-seed weight occurred entirely in Stage IV. It was dependent upon assimilate availability and therefore radiation interception, and was influenced by the sizes of the other yield components (pod number m^{-2} and seed number per pod). The decline in 1000-seed weight down the canopy could be attributed to higher rates of photosynthesis in the better-illuminated upper pods and acropetal transport of assimilates from other sources (leaf and branch) lower in the profile. Assimilates from these sources did not improve seed growth lower down the canopy. Interestingly, average 1000-seed weight was greatest in the season when incident and intercepted radiation were lowest (1991), due probably to the relatively low pod and seed numbers receiving proportionately more assimilate. High radiation interception in Stage IV favoured high seed retention (1993) and 1000-seed weight was lower because of the increased competition between seeds.

Based on radiation interception over the three years, it was concluded that the majority of the assimilate used for seed-filling was provided by photosynthesis in pods and stem material (mainly branches), with little contribution from the mainstem below the pod canopy. This conclusion was consistent with the findings of Bilsborrow & Norton (1988) who showed that more than 95% of the assimilates utilised in seed growth

came from pods and stem, with leaves playing only a minor role in seed-filling. The present study revealed that when leaves were lost rapidly during Stage III, their contribution to seed-filling was relatively small (10% of total interception in 1992). In an open canopy (1993), however, leaf accounted for 30% of the total radiation interception and, by inference, a similar proportion of the total assimilation. Furthermore, it has been calculated that radiation interception by leaf could account for nearly 20% of the final yield in such a season. Some workers have suggested that increased interception by leaf in canopies made more open by application of growth regulators (Child *et al.*, 1987b) or in apetalous varieties (Rao *et al.*, 1991) was beneficial to seed-filling. In the present study, greater leaf interception in 1993 increased total radiation interception but not the efficiency of radiation use. The relatively low efficiency of seed DM production by retained leaf compared with pod and stem may have been due to its age since it was formed during flowering and, in Stage IV, would have been on the verge of senescence. Although leaf photosynthesis is beneficial in increasing total interception in open canopies, where pod and stem interception is reduced, there is no evidence to support the hypothesis that an increase in leaf photosynthesis at the expense of pod and stem would be advantageous. Indeed, in canopies where most of the radiation is intercepted by pod and stem in the top 40 cm of the canopy (1992), the potential for high yield production is available but may be depressed by external influences (disease/high temperature/high SMD).

The main mechanism through which prochloraz increased seed yield in 1991 was an increase in the number of seed-bearing pods at final harvest. The effect on seed number per pod was relatively small and there was no effect on 1000-seed weight. Prochloraz application resulted in the production of more potential pods and the setting and retention of more pods which contained at least as many seeds as controls. This mechanism was similar to that responsible for increasing yields following nitrogen application (Almond *et al.*, 1986). Like the prochloraz effect, nitrogen increased pod numbers at final harvest without causing a downward adjustment in seed number per pod and 1000-seed weight. Nitrogen application increased the assimilate supply to the developing pods and seeds through increased leaf area and duration (Almond *et al.*, 1986). Prochloraz increased leaf area and duration throughout

development, but until Stage IV, when the final yield was determined, this was of little consequence. This is confirmed by events in Stage III in which total radiation interception was slightly increased (by 6%) due entirely to increased interception by pod and stem, while there was little difference between treatments in leaf interception. Radiation interception was increased by prochloraz in Stage IV because the green areas of all components were slightly greater. In addition, prochloraz increased the contribution of leaf to assimilate production because of a slightly greater LAI at the base of the pod canopy and just below. Of the extra radiation intercepted in treated plots, leaf and pod/stem made equal contributions. Therefore the prochloraz effect was due to increased interception and assimilation in all functional organs. It has been assumed throughout that photosynthesis/assimilation is directly related to total radiation interception. In Section 3, it was shown that the efficiency of DM production, as indicated by the *E* value, was relatively low when interception by leaf was high in Stage IV (1993). On this basis, it might be concluded that increased leaf interception due to prochloraz would lower the overall *E*. Prochloraz, however, prolonged leaf life and delayed the decline in *E* that preceded the onset of the physical symptoms of senescence. Therefore, the increased leaf interception may have promoted the efficiency of radiation use in such circumstances. Prochloraz also delayed the senescence of the pods and stem, thereby prolonging assimilate production.

In summary, the ability of plots treated with prochloraz to maintain larger pod numbers was due to greater total assimilate production resulting from greater radiation interception and slightly more efficient radiation use. The effect of prochloraz on efficiency was important towards the end of Stage IV, when maturity was delayed, enabling plants to remain functional for longer, and thereby maintaining *E* values that would otherwise have declined. Increased assimilate production due to prochloraz late in Stage IV did not affect 1000-seed weight because assimilates were partitioned between a greater number of seeds.

The ideal oilseed rape crop

The crops in all three seasons showed that complete ground cover (LAI > 1) over the

winter is not essential. The 1993 crop showed that high yields can be achieved from crops in which complete ground cover is not attained until April. Growth during this period up to flowering forms the potential yield and the structural basis for yield development. Mendham *et al.* (1981) considered that large crop size at flowering was important for yield development in late-sown crops. Together with high seed survival and a long seed development stage, substantial dry matter accumulation before flowering was important in achieving high yields in Tasmania (Mendham *et al.*, 1984). However, the present study indicates no advantage in large size at flowering. Indeed plant size could probably be reduced with advantage. Furthermore, if the same trend continues that has accompanied the move from growing taller to shorter varieties (Section 3.3), harvest index would probably be increased. The reason why this has occurred has not been resolved. An earlier cessation to stem growth probably increases assimilate availability to the earliest pods, but since seed yield is largely determined in Stage IV, the effect on yield and harvest index would be indirect. More importantly, reduced plant size would improve standing characteristics because the bending moments would be reduced and the crop would therefore be less susceptible to lodging. A shorter crop would also facilitate easier access for machinery, while a less dense canopy associated with reduced branching would be less conducive for disease development.

Since potential pods are unlikely to be limiting, these could also be reduced so that fewer assimilates would be wasted in the support of early-formed pods that would eventually be in deep shade and liable to abort. Assimilates would be more usefully utilised in supporting pod development at the top of the canopy where pods are likely to be more productive. Potential pods could be reduced by shortening the duration of flowering. This would also reduce stem growth, branching and crop height. These features could all be incorporated into an ideotype with a determinate growth habit. Canopy structure can be manipulated by changing the plant density which may be possible by varying seeding rates. When oilseed rape plants are grown at high density, branching is reduced and a greater proportion of the yield is borne on the mainstem. This would be an alternative way of reducing stem and potential pod production. The result could be a more even distribution of pods through the canopy.

Leach, Darby, Williams, Fitt & Rawlinson (1994) showed that yield increases following agrochemical treatments were often associated with greater plant numbers per m^2 at final harvest, which implies that, in some circumstances, plant number m^{-2} can be an important yield determinant. Experimental reduction of plant density resulted in sparse crops that used radiation more efficiently than conventional sowings (McWilliam *et al.*, 1995a). However, such crops, with densities as low as 7 plants m^{-2}, were the result of hand-thinning to an even distribution in March. Drilling seed at very low rates would not produce an even distribution and, in addition, very sparse crops would be at increased risk of pigeon damage during the winter, damage from insect pests, and competition from weeds, so that agrochemical inputs would have to be increased.

The pod canopy should be constructed so that radiation interception is maximised in Stage IV. The present study indicates no detriment in having all the yield produced in a 40 cm layer at the top of the crop except that this may reduce standing ability. If leaf were to be retained due to a more open canopy, this could make a contribution to seed growth, but it would not necessarily lead to an increased efficiency of radiation use. The important factor is that the pods and branches should intercept as much radiation as possible. In a dense pod canopy, the photosynthetic capacity of the lower pods would be limited by shading. Evidence from the present study suggests that there may be a minimum radiation requirement per pod to ensure pod and seed survival. It might be possible to alter pod orientation so that the distribution of radiation to pods in the canopy is more even while ensuring that interception by the pod canopy is maximised. This might also reduce light saturation that could occur at the top of the canopy. The contribution of leaf to yield production remains in contention until more is known about the relative efficiencies of the different organs. The present findings indicate that, unless retained leaf can be guaranteed to function optimally, there is no merit in aiming to increase leaf retention. Instead, pod and stem interception in Stage IV should be increased at the expense of leaf. In a closed canopy, there would be negligible radiation available to leaf and this would hasten its senescence while, in an open canopy, leaf retention would be encouraged and would enable the crop to intercept any radiation that had passed through the pod canopy. In

view of this, pod size could be usefully increased because this would increase the assimilatory surface per pod and enhance the assimilate supply to the seeds. In spring rape, however, Chay & Thurling (1989) showed that longer pods did not increase seed yield because the positive correlation of pod length with seed weight was offset by a negative relationship with pod number per plant. In addition, long pods were considered to distribute assimilates less efficiently to seeds because more were required to support pod wall growth (Chay & Thurling, 1989).

Further work

The priority for further work should continue to be increasing yield and enabling crops to achieve a greater proportion of their potential. Long-term aims would be to increase yield by breeding for maximum seed yield and improved efficiency. Alternatively, agronomic methods might involve manipulation of the crop using different plant densities, growth regulators or nitrogen applications in order to optimise radiation use and reduce inputs. The effect of growing the crop at high plant densities would merit further investigation as would growth regulator application aimed at reducing branching and possibly optimising pod angles. High levels of fertiliser nitrogen are normally applied between mid-February and late March to coincide with the rapid uptake associated with the onset of stem extension. It should be possible to restrict this application to ensure that over-production of dry matter does not occur, because nitrogen application increases pod numbers (Almond *et al.*, 1986). In addition to the benefits associated with reduced lodging and disease pressure, a smaller crop would require less nitrogen (Daniels *et al.*, 1986). Growing at high density would reduce weed competition and the impact of disease pressure, and a less dense canopy would be less conducive to disease development. These approaches would therefore reduce input costs in terms of nitrogen and agrochemicals.

Immediate considerations should be more detailed studies aimed at furthering understanding of crop physiology. These should focus on Stage IV which is the phase when final yield is determined. Insufficient is known about the efficiency of photosynthesis of different organs in relation to position in the canopy and with different incident radiation intensities. The contribution of pods, branches and leaves

needs to be determined accurately at different levels in the crop. This would necessitate precise radiation interception measurements, in which detailed growth analysis would be undertaken on the part of the crop where radiation measurements were made. This might be substantiated by making accurate measurements of gross photosynthesis for individual organs throughout the crop profile. The approach could be based on that of Bilsborrow (1985), in which portable apparatus was used to measure $^{14}CO_2$ assimilation *in situ*. Such detailed studies should enable the relationship between radiation interception and yield, and the reasons for the variation in energy use efficiency, to be further elucidated.

Finally, a hypothetical approach to the improvement of seed yield will consider the relative importance of the yield components in Stage IV. Mendham *et al.* (1984) considered seed number per pod to be the most important yield component. High seed retention was also the mechanism allowing sparse canopies in low density crops to yield well (McWilliam *et al.*, 1995). In the present study, the high yield in 1993 was due to high seed number per pod at maturity. Conversely, the mechanism by which prochloraz increased seed yield was mainly by increasing pod number m^{-2}, with only a small effect on seed number per pod. When pod numbers are increased, radiation interception in the pod canopy is increased, but if pod numbers are too great, lower pods will be shaded and their productivity reduced. Therefore a balance is required to allow optimum interception by pods. Judging by events in 1992, this should probably be no more than 7000 pods m^{-2}, since above this number, shading in a low radiation environment (in early June) resulted in large losses down to 7000 m^{-2}. With this number, radiation interception by pods would be maximised. If pods were arranged so that the distribution of radiation through the canopy was even, perhaps by manipulation of pod angles, the productivity of all pods would be equal, and seed retention maximised. Since pods are probably largely autonomous, selection for large pods should increase seed retention by genetic means, since Mendham *et al.* (1984) found that there was a large genetic component involved in the determination of seed number per pod. Because 1000-seed weight is the final component to be determined, there is less opportunity for manipulation, as it is largely dependent on the sizes of the other components. There is probably a large degree of genetic control over 1000-seed

weight so that this tends to be conserved unless adversely influenced by environmental conditions, as in 1992. A regulatory mechanism may operate so that when assimilates are in short supply, as in a low radiation environment (1991), seeds are lost so that remaining ones can grow normally. Mendham *et al.* (1981) showed that most variation in seed weight was seasonal. In conclusion, the ideotype should retain 7000 pods m^{-2} which would be evenly distributed in a canopy of 40 cm depth, with a crop height of no more than 100 cm. High seed retention should be encouraged, but even if, for example, only 15 seeds were retained per pod and grown to an average 1000-seed weight of 6.5 g, this would produce a seed yield of 6.8 t ha^{-1}, which is close to the theoretical maximum of 7.6 t ha^{-1} proposed by Daniels *et al.* (1986).

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APPENDIX I

EXPERIMENTAL DESIGN

Table I.1. Allocation of prochloraz treatments

1991 and 1993	AUTUMN			0				S
	SPRING		00		0S		S0	SS
	SUMMER	000+	00S	0S0	0SS	S00	S0S	SS0	SSS*
					+ Control, * 3-spray			
1992	SPRING			0				S
	SUMMER		00+		0S		S0	SS*
					+ Control, * 2-spray			

Fig. I.1. Experimental design in 1991

1	5	6	17
2	8	8	18
3	6	3	19
4	2	2	20
5	1	4	21
6	3	1	22
7	7	5	23
8	4	7	24
9	2	5	25
10	6	8	26
11	8	7	27
12	7	1	28
13	1	4	29
14	5	3	30
15	4	6	31
16	3	2	32

Each cell represents one plot. Plot numbers are indicated at the edges. Treatment numbers (corresponding to the key in Table I.2) are in the centre.

Table I.2. Key to prochloraz treatments

1	CONTROL
2	AUTUMN (AU)
3	SPRING (SP)
4	SUMMER (SU)
5	AUTUMN + SPRING (AU+SP)
6	AUTUMN + SUMMER (AU+SU)
7	SPRING + SUMMER (SP+SU)
8	AUTUMN + SPRING + SUMMER (AU+SP+SU)

Fig. I.2. Experimental design in 1992

1	3
2	1
3	7
4	4
5	7
6	3
7	1
8	4
9	7
10	3
11	1
12	4
13	1
14	4
15	3
16	7

Treatments correspond to the key in Table I.2.

Fig. I.3. Experimental design in 1993

1	5		5	s	1
2	4		4	s	2
3	8		8	s	3
4	1		1	s	4
5	3	s	3		5
6	7		7	s	6
7	6		6	s	7
8	4		4	s	8
9	8	s	8		9
10	4		4	s	10
11	6		6	s	11
12	2	s	2		12
13	3	s	3		13
14	1	s	1		14
15	7	s	7		15
16	5		5	s	16
17	1		1	s	17
18	5		5		18
19	2	s			19
20	2				20
21	7		7	s	21
22	8		8	s	22
23	2	s	2		23
24	3	s	3		24
25	6	s	6		25
26	1	s	1		26
27	5		5	s	27
28	3	s	3		28
29	4	s	4		29
30	2	s	2		30
31	8		8	s	31
32	7		7	s	32
33	6	s	6		33

Treatment numbers correspond to the key in Table I.2. Main plots are divided into subplots by dashed lines. 's' denotes the subplot receiving iprodione as a precaution against sclerotinia. Plots 19 and 20 on the south side were continuously waterlogged and were discarded immediately. An error was made during AUTUMN prochloraz application in which an extra AUTUMN treatment was made in Block 3 and an extra SUMMER treatment in Block 1 (treatments 2 and 4 respectively). The plots involved (8 and 19/20) were omitted from the data analysis at final harvest. Double lines denote discarded plots.

APPENDIX II

DISEASE ASSESSMENT RESULTS

Tabulated data are given for each disease assessment. Incidence of disease or pest damage is recorded as the percentage of leaves affected and/or the percentage of plants affected. Disease severity is recorded as lesion scores per leaf, per infected leaf, per plant, and per infected plant. Significance levels are denoted by +, *, ** and *** for $p < 0.10, 0.05, 0.01$ and 0.001 respectively. Treatment abbreviations are given in Appendix I.

Table II.1. Season 1 (1990/91): The effects of AUTUMN prochloraz on the incidence of downy mildew, phoma and alternaria (% plants) and the incidence (% plants) and severity of pigeon and CSFB damage on leaves 18 December, 1990)

			% INCIDENCE			
			0	1	MEAN	S.E.D.#
DOWNY MILDEW			28.6	31.6	30.1	7.72
PHOMA			1.59	1.65	1.62	1.451
ALTERNARIA			0.52	0.00	0.26	0.525
PIGEON	lesions per affected plant		1.00	1.00	-	-
	% plants		0.55	1.60	1.07	0.766
CABBAGE STEM FLEA BEETLE	No. of lesions (feeding holes)	per affected leaf/ plant	1.00	1.00	-	-
		per plant	0.350	0.250	0.300	0.1581
	% plants		6.9	5.9	6.4	3.41

7 total and 6 residual degrees of freedom (df).

Table II.2. Season 1. The effects of *AUTUMN* prochloraz on the incidence and severity of downy mildew, phoma, light leaf spot and alternaria on leaves on 16 April, 1991

			0	1	MEAN	S.E.D.#
DOWNY MILDEW		% LEAVES	30.3	32.4	31.4	2.69
		% PLANTS	100	100	100	0
PHOMA	LESION SCORE	per leaf	0.075	0.051	0.063	0.022
		per infected leaf	1.40	1.24	1.32	0.068
		per plant	0.95	0.70	0.82	2.72
		per infected plant	1.56	1.67	1.61	0.24
		% LEAVES	5.33	4.36	4.85	1.449
		% PLANTS	60.0	42.5	51.2	13.77
LIGHT LEAF SPOT	LESION SCORE	per leaf	0.018	0.002	0.0097	0.009
		per infected leaf	0.10	0.10	-	-
		per plant	0.245	0.020	0.132	1.217
		per infected plant	0.250	0.167	0.208	0.041
		% LEAVES	8.0	1.5+	4.8	3.05
		% PLANTS	50.0	12.5*	31.2	13.77
ALTERNARIA	LESION SCORE	per leaf	0.0021	0.016+	0.009	0.006
		per infected leaf	1.0	1.0	-	-
		per plant	0.025	0.200+	0.112	0.75
		per infected plant	1.0	1.0	-	-
		% LEAVES	0.21	1.60+	0.90	0.633
		% PLANTS	2.50	20.0+	11.2	7.50

7 total and 6 residual df; + $P < 0.10$; * $P < 0.05$.

Table II.3. Season 1. The effects of AUTUMN and SPRING prochloraz on the incidence and severity of LLPS on leaves and stems on 25 May, 1991: effects of each prochloraz application and treatment means

		LEAF						STEM		
		Lesion score per:				% leaves	% plants	Lesion score per:		% plants
		Plant	Inf. plant	Leaf	Inf. leaf			Plant	Inf. plant	
AUTUMN	0	0.98	0.31	0.095	0.17	30	50	0.195	0.10	38
	1	0.11	0.31	0.011	0.17	9	48	0.048	0.10	48
SPRING	0	0.91	0.31	0.088	0.17	28	50	0.222	0.10	65
	1	0.18	0.31	0.019	0.17	12	48	0.020	0.10	20
S.E.D.#		0.869	-	0.0838	-	23.5	32.3	0.1827	-	26.7
CONTROL		1.72	0.31	0.0165	0.17	44	45	0.365	0.10	50
AU		0.11	0.31	0.011	0.17	11	55	0.080	0.10	80
SP		0.25	0.31	0.025	0.17	16	55	0.025	0.10	25
AU + SP		0.11	0.31	0.012	0.17	7	40	0.015	0.10	15
S.E.D.#		1.229	-	0.1185	-	33.3	45.7	0.258	-	37.7

# 7 total and 4 residual df.
inf. = infected.

Table II.4. Season 1. The effects of AUTUMN and SPRING prochloraz on the incidence and severity of BOTRYTIS (on stem) and ALTERNARIA (on leaves) on 25 May 1991: effects of each prochloraz application and treatment means

		BOTRYTIS (stem)			ALTERNARIA (leaf)					
		LESION SCORE		% plants	LESION SCORE				% leaves	% plants
		per plant	per inf. plant		per leaf	per inf. leaf	per plant	per inf. plant		
AUTUMN	0	0.00	1.0	0.0	0.0150	1.0	0.150	1.0	0.99	10.0
	1	0.05	1.0	5.0	0.0072	1.0	0.025	1.0	0.25	2.50
SPRING	0	0.00	1.0	0.0	0.0095	1.0	0.050	1.0	0.48	5.00
	1	0.05	1.0	5.0	0.0127	1.0	0.125	1.0	0.76	7.50
S.E.D.#		0.025	-	2.5	0.01251	-	0.1146	-	0.744	7.50
CONTROL		0.0	1.0	0.0	0.0095	1.0	0.100	1.0	0.96	10.0
AU		0.0	1.0	0.0	0.0095	1.0	0.000	1.0	0.00	0.0
SP		0.0	1.0	0.0	0.0205	1.0	0.200	1.0	1.02	10.0
AU + SP		1.0	1.0	10.0	0.0050	1.0	0.050	1.0	0.50	5.0
S.E.D.#		0.707	-	7.07	0.0177	-	0.162	-	1.053	10.61

# 7 total and 4 residual df.
inf. = infected.

Table II.5. Season 1. Effects of AUTUMN and SPRING prochloraz on the incidence and severity of PHOMA and the incidence of DOWNY MILDEW on leaves on 25 May, 1991: effects of each prochloraz application and treatment means

		PHOMA (on leaves)					DOWNY MILDEW	
		LESION SCORE			% LEAVES	% PLANTS	% LEAVES	% PLANTS
		per leaf	per inf. leaf and plant	per plant				
AUTUMN	0	0.0102	1.0	0.10	0.76	7.5	25.9	98
	1	0.0155	1.0	0.15	1.29	12.5	19.4	78
SPRING	0	0.0000	1.0	0.00	0.00	0.0	23.6	98
	1	0.026+	1.0	0.25	2.06	20.0	21.7	78
S.E.D.#		0.0103	-	0.10	0.796	7.91	10.11	22.6
CONTROL		0.00	1.0	0.0	0.0	0.0	26.0	95
AU		0.00	1.0	0.0	0.0	0.0	21.2	100
SP		0.0205	1.0	2.0	1.53	15.0	25.9	100
AU + SP		0.0310	1.0	3.0	2.59	25.0+	17.5	55
S.E.D.#		0.0145	-	1.414	1.126	11.18	14.29	32.0

# 7 total and 4 residual df; + $P < 0.10$.
inf. = infected.

Table II.6. Season 1. The effects of AUTUMN and SPRING prochloraz on the incidence and severity of CABBAGE STEM FLEA BEETLE on leaves on 25 May, 1991: effects of each prochloraz application and treatment means

		LESION SCORE (number of feeding holes in leaves)				% LEAVES	% PLANTS
		per leaf	per infested leaf	per plant	per infested plant		
AUTUMN	0	0.0242	1.0	0.25	2.0	2.19	20.0
	1	0.0177	1.0	0.175	2.0	1.78	12.5
SPRING	0	0.0217	1.0	0.225	2.0	2.19	20.0
	1	0.0202	1.0	0.200	2.0	1.79	12.5
S.E.D.#		0.0184	-	0.192	-	1.838	15.21
CONTROL		0.0335	1.0	0.35	2.0	3.36	30.0
AU		0.0100	1.0	0.10	2.0	1.01	10.0
SP		0.0150	1.0	0.15	2.0	1.01	10.0
SUMMER		0.0255	1.0	0.25	2.0	2.56	15.0
S.E.D.#		0.0261	-	0.272	-	2.60	21.51

7 total and 4 residual df.

Table II.7. Season 1. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence and severity of LIGHT LEAF AND POD SPOT on stems and pods on 26 July, 1991: effects of each prochloraz application

		STEM			POD		
		LESION SCORE		% PLANTS	LESION SCORE		% PLANTS
		per plant	per infected plant		per plant	per infected plant	
AUTUMN	0	0.241	0.10	88.3	2.88	0.56	99.2
	1	0.033**	0.10	25.8***	0.38**	0.77	92.0**
SPRING	0	0.202	0.10	64.2	1.89	0.66	96.2
	1	0.072*	0.10	50.0**	1.37	0.66	94.9
SUMMER	0	0.101	0.10	54.2	1.45	0.56	97.4
	1	0.173	0.10	60.0	1.81	0.77	93.7+
S.E.D.#		0.0531	-	4.53	0.733	0.711	2.08

23 total and 14 residual df; + P < 0.10; * P < 0.05; ** P < 0.01; *** P < 0.001.

Table II.8. Season 1. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence and severity of LIGHT LEAF AND POD SPOT on stems and pods on 26 July: treatment means

	STEM			POD		
	LESION SCORE		% PLANTS	LESION SCORE		% PLANTS
	per plant	per infected plant		per plant	per infected plant	
CONTROL	0.207	0.10	80.0	2.36	0.46	100.0
AU	0.037	0.10	36.7***	0.49	0.66	100.0
SP	0.117	0.10	86.7	2.51	0.46	100.0
SU	0.523**	0.10	100.0*	4.37	0.66	100.0
AU + SP	0.013	0.10	13.3***	0.45	0.66	89.7*
AU + SU	0.043	0.10	40.0***	0.35	0.87	85.0**
SP + SU	0.117	0.10	86.7	2.28	0.66	96.7
AU + SP + SU	0.013	0.10	13.3	0.24	0.87	93.3+
S.E.D.#	0.106	-	9.06	1.467	-	4.16

23 total and 14 residual df; + P < 0.10; * P < 0.05; ** P < 0.01; *** P < 0.001.

Table II.9. Season 1. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence and severity of STEM CANKER and SCLEROTINIA on stems on 26 July, 1991: effect of each prochloraz application

		PHOMA STEM CANKER (main stem)			SCLEROTINIA (stem)		
		LESION SCORE		% PLANTS	LESION SCORE		% PLANTS
		per plant	per infected plant		per plant	per infected plant	
AUTUMN	0	0.059	0.10	29.2	0.092	1.75	4.2
	1	0.025	0.10	17.5	0.100	3.25	2.5
SPRING	0	0.059	0.10	21.7	0.083	2.50	3.3
	1	0.025	0.10	25.0	0.108	2.50	3.3
SUMMER	0	0.032	0.10	25.0	0.117	1.75	4.2
	1	0.052	0.10	21.7	0.075	3.25	2.5
S.E.D.#		0.0343	-	7.12	0.068	0.678	2.09

23 total and 14 residual df.

Table II.10. Season 1. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence and severity of STEM CANKER and SCLEROTINIA on stems on 26 July, 1991: treatment means

	PHOMA (main stem)			SCLEROTINIA (stem)		
	LESION SCORE		% PLANTS	LESION SCORE		% PLANTS
	per plant	per infected plant		per plant	per infected plant	
CONTROL	0.023	0.100	23.3	0.067	1.00	6.7
AU	0.053	0.250	23.3	0.000	2.50	0.0
SP	0.043	0.100	43.3	0.133	1.00	3.3
SU	0.147	0.267	26.7	0.133	2.50	3.3
AU + SP	0.010	0.033	10.0	0.267	2.50	6.7
AU + SU	0.013	0.067	13.3	0.133	4.00	3.3
SP + SU	0.023	0.100	23.3	0.033	2.50	3.3
AU + SP + SU	0.023	0.100	23.3	0.000	4.00	0.0
S.E.D.#	0.0069	0.1260	10.07	0.1357	1.36	4.18

23 total and 14 residual df.

Table II.11. Season 1. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence and severity of ALTERNARIA (on pods) and the incidence of POWDERY MILDEW (on pods and stems): effect of each prochloraz application

		ALTERNARIA (pods)			POWDERY MILDEW	
		LESION SCORE		% PLANTS	% PLANTS INFECTED	
		per plant	per infected plant		stems	pods
AUTUMN	0	0.076	0.35	23.5	66.7	0.8
	1	0.097	0.48	38.5	79.9	6.8*
SPRING	0	0.127	0.41	37.7	80.8	5.0
	1	0.047	0.41	24.3	65.7	2.6
SUMMER	0	0.062	0.35	25.2	80.7	6.8
	1	0.111	0.35	36.9	65.8	0.8*
S.E.D.#		0.0448	0.0926	8.56	9.14	0.678

23 total and 14 residual df; * $P < 0.05$.

Table II.12. Season 1. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence and severity of ALTERNARIA (on pods) and the incidence of POWDERY MILDEW (on pods and stems) on 26 July, 1991: treatment means

	ALTERNARIA (pods)			POWDERY MILDEW	
	LESION SCORE		% PLANTS	% PLANTS INFECTED	
	per plant	per infected plant		stems	pods
CONTROL	0.090	0.28	30.0	93.3	3.3
AU	0.133	0.41	43.3	70.0	13.3
SP	0.007	0.28	6.7	80.0	0.0
SU	0.147	0.41	27.5	70.0	0.0
AU + SP	0.020	0.41	20.7	79.7	10.4
AU + SU	0.137	0.55	50.0	90.0	3.3
SP + SU	0.060	0.41	30.0	23.3**	0.0
AU + SP + SU	0.100	0.55	40.0	80.0	0.0
S.E.D.#	0.090	0.1851	17.12	18.28	4.25

23 total and 14 residual df; ** $P < 0.01$.

Table II.13. Season 1. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence and severity of BOTRYTIS (on stems and pods) and the incidence of CABBAGE STEM FLEA BEETLE (stems) on 26 July, 1991: effect of each prochloraz application

		BOTRYTIS						CABBAGE STEM FLEA BEETLE
		STEMS			PODS			
		LESION SCORE		% PLANTS	LESION SCORE		% PLANTS	% plants
		per plant	per infected plant		per plant	per infected plant		
AUTUMN	0	0.067	1.0	4.2	0.142	1.75	10.0	11.7
	1	0.092	1.0	6.7	0.125	1.25	9.8	25.0*
SPRING	0	0.108	1.0	8.3	0.167	1.50	11.2	17.5
	1	0.050	1.0	2.5+	0.100	1.50	8.5	19.2
SUMMER	0	0.058	1.0	3.3	0.125	1.75	9.4	23.3
	1	0.100	1.0	7.5	0.142	1.25	10.4	13.3
S.E.D.#		0.0604	-	3.26	0.0632	0.277	3.51	4.76

23 total and 14 residual df; + $P < 0.10$; * $P < 0.05$.

Table II.14. Season 1. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence and severity of BOTRYTIS (on stems and pods) and the incidence of CABBAGE STEM FLEA BEETLE (stems) on 26 July, 1991: treatment means

	BOTRYTIS						CABBAGE STEM FLEA BEETLE
	STEM			POD			
	LESION SCORE		% PLANTS	LESION SCORE		% PLANTS	% plants
	per plant	per infected plant		per plant	per infected plant		
CONTROL	0.033	0.33	3.3	0.267	2.00	16.7	3.3
AU	0.033	0.33	3.3	0.033	1.50	6.7	30.0*
SP	0.033	0.33	3.3	0.033	2.00	3.3	33.3**
SU	0.200	1.17	10.0	0.200	1.50	13.3	10.0
AU + SP	0.133	1.333	3.3	0.167	1.50	10.7	26.7*
AU + SU	0.167	0.67	16.7*	0.167	1.00	8.3	26.7*
SP + SU	0.000	0.00	0.0	0.067	1.50	6.7	0.0
AU + SP + SU	0.033	0.33	3.3	0.133	1.00	13.3	16.7
S.E.D.	0.1208	0.841	6.52	0.1265	0.554	7.03	9.51

23 total and 14 residual df; * $P < 0.05$; ** $P < 0.01$.

Table II.15. Season 2: The incidence and severity of LIGHT LEAF SPOT, PHOMA, PIGEON and CABBAGE STEM FLEA BEETLE damage on 20 March, 1992 (before prochloraz application)

DOWNY MILDEW	% LEAVES INFECTED		43.84
	% PLANTS INFECTED		100.0
LIGHT LEAF SPOT	LESION SCORE	per leaf	0.007
		per infected leaf	0.10
		per infected plant	0.11
	% LEAVES INFECTED		8.45
	% PLANTS INFECTED		50.0
PHOMA	LESION SCORE	per leaf	0.76
		per infected leaf	1.50
		per infected plant	1.50
	% LEAVES INFECTED		37.0
	% PLANTS INFECTED		6.25
PIGEON	LESIONED LEAVES PER DAMAGED PLANT		3.24
	% PLANTS DAMAGED		83.75
CABBAGE STEM FLEA BEETLE	LESIONS (feeding holes)	per leaf	0.065
		per infested leaf	1.41
		per infested plant	2.00
	% PLANTS INFESTED		60.0

Table II.16. Season 2. The effects of SPRING prochloraz on the incidence and severity of LIGHT LEAF AND POD SPOT on leaves, stems and pods on 26 May, 1992

			0	1	MEAN	S.E.D.#
LEAF	LESION SCORE	per leaf	0.0024	0.0004	0.0014	0.0012
		per plant	0.0137	0.0013+	0.0075	0.0070
	% LEAVES		2.42	0.20+	1.31	1.162
	% PLANTS		8.7	1.2+	5.0	4.06
STEM	LESION SCORE	per plant	0.050	0.009**	0.0294	0.0122
	% PLANTS		50.0	8.7**	29.4	12.22
POD	LESION SCORE	per plant	0.0262	0.0137*	0.0200	0.0051
	% PLANTS		26.2	13.7*	20.0	5.06

15 total and 11 residual df; + $P < 0.10$; * $P < 0.05$; ** $P < 0.01$.

Table II.17. Season 2. The effects of SPRING prochloraz on the incidence and severity of PHOMA/STEM CANKER on leaves and stems on 26 May, 1992

			0	1	MEAN	S.E.D.#
LEAF	LESION SCORE	per plant	0.087	0.037	0.062	0.0477
	% LEAVES		1.49	0.68	1.08	0.895
	% PLANTS		7.6	3.7	5.7	4.59
STEM	LESION SCORE	per plant	0.020	0.0137	0.0169	0.0122
	% PLANTS		8.7	13.7	11.2	3.54

#15 total and 11 residual df.

Table II.18. Season 2. The effects of SPRING prochloraz on the incidence of BOTRYTIS (leaves and stems) and the incidence and severity of ALTERNARIA (leaves) on 26 May, 1992

			0	1	MEAN	S.E.D.
BOTRYTIS						
LEAF	% LEAVES		48.3	38.5+	43.4	4.99
	% PLANTS		93.6	91.2	92.4	3.50
STEM	% PLANTS		2.50	5.0	3.7	2.50
ALTERNARIA						
LEAF	LESION SCORE	per leaf	0.0003	0.0002	0.00022	0.0003
	% LEAVES		0.27	0.19	0.23	0.28
	% PLANTS		1.25	1.25	1.25	1.51

15 total and 11 residual df.

Table II.19. Season 2. The effects of SPRING prochloraz on the incidence of DOWNY MILDEW and CABBAGE STEM FLEA BEETLE on 26 May, 1992

		0	1	MEAN	S.E.D.
DOWNY MILDEW					
LEAF	% LEAVES	36.5	30.2	33.4	5.11
	% PLANTS	87.5	93.7	90.6	4.93
CABBAGE STEM FLEA BEETLE					
STEM	% PLANTS	17.6	25.0	21.3	6.87

#15 total and 11 residual df.

Table II.20. Season 2. The effects of SPRING and SUMMER prochloraz on the incidence and severity of LIGHT LEAF AND POD SPOT on stems and pods on 10 July, 1992: effects of each prochloraz application and treatment means

		STEM			POD		
		LESION SCORE		% PLANTS	LESION SCORE		% PLANTS
		per plant	per inf. plant		per plant	per inf. plant	
SPRING	0	0.043	0.10	31	0.41	0.94	71.9
	1	0.367	0.10	39	1.32	0.54	86.5
SUMMER	0	0.127	0.10	38	1.06	1.05	77.1
	1	0.182	0.10	33	0.66	0.42	81.3
S.E.D.		0.182	-	22.0	0.691	0.721	10.95
CONTROL		0.055	0.10	33	0.53	1.39	69.5
SP		0.200	0.10	43	1.59	0.71	84.7
SU		0.030	0.10	30	0.28	0.49	74.4
SP + SU		0.335	0.10	35	1.04	0.36	88.3
S.E.D.		0.257	-	31.0	0.977	1.019	15.48

# 15 total and 9 residual df;
inf. = infected.

Table II.21. Season 2. The effects of SPRING and SUMMER prochloraz on the incidence and severity of PHOMA/STEM CANKER on stems and pods on 10 July, 1992: effects of each prochloraz application and treatment means

		STEM			POD		
		LESION SCORE		% PLANTS	LESION SCORE		% PLANTS
		per plant	per inf. plant		per plant	per inf. plant	
SPRING	0	0.124	0.16	67.5	0.175	1.25	14.1
	1	0.164	0.43	50.0	0.050+	1.00	5.3
SUMMER	0	0.119	0.25	51.2	0.062	1.25	5.0
	1	0.169	0.34	66.2	0.162	1.00	14.4
S.E.D.		0.054	0.057	10.57	0.061	0.301	4.84
CONTROL		0.127	0.10	60.0	0.075	1.50	5.0
SPRING		0.110	0.40	42.5	0.050	1.00	5.0
SUMMER		0.120	0.21	75.0	0.275*	1.00	23.1*
SP + SU		0.217	0.47	57.5	0.050	1.00	5.6
S.E.D.		0.077	0.081	14.95	0.086	0.426	6.84

# 15 total and 9 residual df; + $P < 0.10$; * $P < 0.05$.
inf. = infected.

Table II.22. Season 2. The effects of SPRING and SUMMER prochloraz on the incidence and severity of BOTRYTIS on stems and pods on 10 July, 1992: Effects of each prochloraz application and treatment means

		STEM			POD		
		LESION SCORE		% PLANTS	LESION SCORE		% PLANTS
		per plant	per inf. plant		per plant	per inf. plant	
SPRING	0	0.69	2.37	27.5	0.12	1.00	11.1
	1	0.79	2.41	33.7	0.69	3.06	29.0
SUMMER	0	0.77	2.25	32.5	0.60	2.44	23.6
	1	0.70	2.54	28.7	0.21	1.63	16.6
S.E.D.		0.248	0.398	10.2	0.326	0.437	7.14
CONTROL		0.97	3.00	37.5	0.17	1.00	14.1
SPRING		0.57	1.50	27.5	1.02	3.88	33.0
SUMMER		0.40	1.75	17.5	0.07	1.00	8.1
SP + SU		1.00	3.33	40.0	0.35	2.25	25.0
S.E.D.		0.351	0.562	14.54	0.461	0.618	10.10

Table II.23. Season 2. The effects of SPRING and SUMMER prochloraz on the incidence and severity of SCLEROTINIA (stems) and ALTERNARIA (pods), and the incidence of DOWNY MILDEW (pods) and CABBAGE STEM FLEA BEETLE (stems) on 10 July, 1992: Effect of each prochloraz application and treatment means

		SCLEROTINIA (Stem)			ALTERNARIA (Pod)			DOWNY MILDEW (Pod)	CABBAGE STEM FLEA BEETLE (Stem)
		LESION SCORE		% PLANTS	LESION SCORE		% PLANTS		
		per plant	per inf. plant		per plant	per inf. plant		% PLANTS	% PLANTS
SPRING	0	0.56	2.25	23.7	0.149	0.10	49.7	6.2	35.0
	1	0.45	3.00	22.5	0.065	0.28	34.6	1.2+	13.7*
SUMMER	0	0.61	1.50	30.0	0.157	0.28	47.6	3.7	28.7
	1	0.40	3.75	16.2	0.056	0.10	36.7	3.7	20.0
S.E.D.		0.22	0.619	7.92	0.076	0.113	12.82	2.50	8.09
CONTROL		0.75	1.00	32.5	0.235	0.10	58.8	5.0	35.0
SPRING		0.47	2.00	27.5	0.080	0.46	36.4	2.5	22.5
SUMMER		0.37	3.50	15.0	0.062	0.10	40.6	7.5	35.0
SP + SU		0.42	4.00	17.5	0.050	0.10	32.8	0.0	5.0+
S.E.D.#		0.30	0.876	11.20	0.108	0.160	18.12	3.54	11.44

# 15 total and 9 residual df; + $P < 0.10$; * $P < 0.05$.
inf. = infected.

Table II.24. Season 3. The effects of AUTUMN prochloraz on the incidence of the main diseases and pests on 27 November, 1992

LEAF INFECTION/ INFESTATION		0	1	MEAN	S.E.D.#
DOWNY MILDEW	% LEAVES	15.9	21.0	18.4	3.41
	% PLANTS	52.5	70.0*	61.2	7.50
PHOMA	No. of lesions per inf. leaf	0.50	0.00	0.25	0.289
	% LEAVES	0.64	0.00	0.32	0.436
	% PLANTS	2.50	0.00	1.25	1.685
PIGEON	No. of affected leaves per damaged plant	1.50	1.50	1.50	-
	% LEAVES	5.31	7.29	6.30	1.765
	% PLANTS	15.0	26.2	20.6	5.47
CABBAGE STEM FLEA BEETLE	No. of lesions (feeding holes) per damaged leaf	1.17	1.45*	1.31	0.052
	No. of lesions (feeding holes) per damaged plant	1.16	1.16	1.16	-
	% LEAVES	3.80	5.13	4.47	1.58
	% PLANTS	16.2	21.2	18.7	6.12

31 total and 27 residual df; + P < 0.10, * P < 0.05.

Table II.25. Season 3. The effects of AUTUMN prochloraz on the incidence and severity of the main diseases on 26 March, 1993

		0	1	MEAN	S.E.D.#
DOWNY MILDEW	% LEAVES	10.9	17.0	14.0	5.44
	% PLANTS	53.7	78.7	66.2	17.32
PHOMA	No. of infected leaves per infected plant	1.803	1.610*	1.707	0.025
	% LEAVES	17.5	16.3	16.9	2.01
	% PLANTS	83.7	83.7	83.7	5.40
LIGHT LEAF SPOT	No. of infected leaves per infected plant	0.181	0.191	0.186	0.037
	% LEAVES	15.5	13.9	14.7	7.405
	% PLANTS	63.0	68.0	65.0	24.6
BOTRYTIS	No. of infected leaves per infected plant	1.265	1.265	1.265	-
	% LEAVES	4.39	6.42	5.41	1.359
	% PLANTS	27.5	42.5	35.0	11.37

31 total and 27 residual df; * P < 0.05.

Table II.26. Season 3. The effects of AUTUMN prochloraz on the incidence and severity of PIGEON and CABBAGE STEM FLEA BEETLE damage on leaves on 26 March, 1993

			0	1	MEAN	S.E.D.#
PIGEON	No. of damaged leaves per damaged plant		2.28	2.22	2.25	0.355
	% LEAVES		16.89	15.86	16.38	1.289
	% PLANTS		56.2	66.2	61.2	6.12
CABBAGE STEM FLEA BEETLE	No. of damaged leaves per damaged plant	Larval	1.89	1.61	1.75	0.20
		Adult	0.86	1.42	1.14	0.202
	% LEAVES	Larval	2.75	4.93	3.84	1.701
		Adult	2.89	2.20	2.55	0.905
	% PLANTS	Larval	15.0	28.7*	21.9	3.15
		Adult	25.0	13.7	19.4	6.88

31 total and 27 residual df; * $P < 0.05$.

Table II.27. Season 3. The effects of AUTUMN and SPRING prochloraz on the incidence and severity of LIGHT LEAF AND POD SPOT on leaves and stems on 29 April, 1993: Effect of each prochloraz application and treatment means

		LEAF					STEM		
		LESION SCORE			% LEAVES	% PLANTS	LESION SCORE		% PLANTS
		per inf. leaf	per plant	per inf. plant			per plant	per inf. plant	
AUTUMN	0	0.10	0.156	0.23	9.3	47.4	0.0137	0.10	13.5
	1	0.10	0.069	0.21	6.1	35.6	0.0119	0.10	11.9
SPRING	0	0.10	0.153	0.22	8.8	44.2	0.0225	0.10	22.3
	1	0.10	0.072	0.22	6.6	38.7	0.0031	0.10	3.1
S.E.D.#		0.10	0.0783	0.0956	3.11	13.65	0.0087	-	8.60
CONTROL		0.10	0.244	0.23	12.0	57.2	0.0262	0.10	25.8
AUTUMN		0.10	0.062	0.21	5.6	31.2	0.0187	0.10	18.7
SPRING		0.10	0.069	0.23	6.6	37.5	0.0012*	0.10	1.3+
AU + SP		0.10	0.076	0.21	6.7	40.0	0.0050+	0.10	5.0+
S.E.D.#		-	0.1107	0.1352	4.40	19.31	0.0087	-	12.17

# 31 total and 25 residual df; + $P < 0.10$; $P < 0.05$.
inf. = infected.

Table II.28. Season 3. The effects of AUTUMN and SPRING prochloraz on the incidence and severity of PHOMA/STEM CANKER on leaves and stems on 29 April, 1993: Effects of each prochloraz application and treatment means

		LEAF					STEM		
		LESION SCORE			% LEAVES	% PLANTS	LESION SCORE		% PLANTS
		per inf. leaf	per plant	per inf. plant			per plant	per inf. plant	
AUTUMN	0	1.00	0.512	1.25	5.54	36.5	0.0019	0.10	1.87
	1	1.00	0.338	1.08	2.88	22.5*	0.0019	0.10	1.87
SPRING	0	1.00	0.594	1.16	6.10	38.3	0.0025	0.10	2.50
	1	1.00	0.256**	1.16	2.31**	20.6**	0.00125	0.10	1.25
S.E.D.#		-	0.1074	0.234	1.303	5.50	0.00144	-	1.436
CONTROL		1.00	0.762	1.25	8.71	51.7	0.0025	0.10	2.50
AUTUMN		1.00	0.425*	1.08	3.50**	25.0**	0.0025	0.10	2.50
SPRING		1.00	0.262**	1.25	2.36**	21.2**	0.00125	0.10	1.25
AU + SP		1.00	0.250**	1.08	2.25**	20.0**	0.00125	0.10	1.25
S.E.D.#		-	0.1518	0.331	1.842	7.77	0.00203	-	2.031

# 31 total and 25 residual df; * $P < 0.05$; ** $P < 0.01$.
inf. = infected.

Table II.29. Season 3. The effects of AUTUMN and SPRING prochloraz on the incidence and severity of BOTRYTIS (leaves and stems) and ALTERNARIA (leaves) on 29 April, 1993: Effects of each prochloraz application and treatment means

		BOTRYTIS					ALTERNARIA		
		LEAF			STEM		LEAF		
		Inf. leaves per inf. plant	% LEAVES	% PLANTS	LESION SCORE per inf. plant	% PLANTS	LESION SCORE per plant	% LEAVES	% PLANTS
AUTUMN	0	0.70	1.20	10.7	0.94	6.9	0.661	28.6	90.6
	1	0.90	1.55	12.5	0.94	3.1	0.857	31.6	96.2
SPRING	0	0.90	1.59	12.6	0.75	5.1	0.822	30.2	91.9
	1	0.70	1.16	10.6	1.12	5.0	0.696	30.0	95.0
S.E.D.#		0.209	0.481	3.89	0.525	2.83	0.1375	3.18	5.01
CONTROL		1.10	1.16	10.1	0.75	8.9	0.643	27.3	90.0
AUTUMN		1.30	2.02	15.0	0.75	1.2+	1.002+	33.1	93.7
SPRING		1.10	1.24	11.2	1.12	5.0	0.679	30.0	91.2
SUMMER		1.30	1.07	10.0	1.12	5.0	0.712	30.0	98.7
S.E.D.#		0.296	0.681	5.51	0.742	4.01	0.1944	4.50	7.09

# 31 total and 25 residual df; + $P < 0.10$.
inf. = infected.

Table II.30. Season 3. The effects of AUTUMN and SPRING prochloraz on the incidence of DOWNY MILDEW (leaves) and the incidence and severity of PIGEON damage on 29 April, 1993: Effects of each prochloraz application and treatment means

		DOWNY MILDEW		PIGEON		
		% LEAVES	% PLANTS	No. of damaged leaves per damaged plant	% LEAVES	% PLANTS
AUTUMN	0	39.5	98.12	2.69	9.2	40.2
	1	43.5	100.0	1.82	7.1	41.2
SPRING	0	42.3	98.75	2.25	8.7	43.3
	1	40.8	99.37	2.25	7.6	38.1
S.E.D.#		3.47	1.42	0.293	2.21	7.51
CONTROL		38.9	97.5	2.69	11.2	45.4
AUTUMN		45.6	100.0	1.82	6.2	41.2
SPRING		40.1	98.75	2.69	7.2	35.0
AU + SP		41.4	100.0	1.82	8.0	41.2
S.E.D.#		4.91	2.01	0.415	3.12	10.62

31 total and 25 residual df.

Table II.31. Season 3. The effects of AUTUMN and SPRING prochloraz on the incidence and severity of CABBAGE STEM FLEA BEETLE on 29 April, 1993: Effects of each prochloraz application and treatment means

		LARVAL					ADULT		
		LEAF			STEM		LEAF		
		Damaged leaves per damaged plant	% LEAVES	% PLANTS	Feeding holes per plant	% PLANTS	Damaged leaves per damaged plant	% LEAVES	% PLANTS
AUTUMN	0	1.33	2.38	55.5	0.369	16.9	2.03	11.57	55.5
	1	2.00	3.68	56.2	0.475	26.2	2.00	10.85	56.2
SPRING	0	1.66	2.70	58.6	0.351	18.8	2.08	11.87	58.6
	1	1.66	3.36	53.1	0.494	24.4	1.95	10.55	53.1
S.E.D.#		0.306	3.18	6.96	0.137	5.95	0.242	1.858	6.96
CONTROL		1.33	1.20	62.2	0.164	10.1	3.38	12.56	62.2
AUTUMN		2.00	4.20+	55.0	0.537+	27.5*	4.12	11.17	55.0
SPRING		1.33	3.56	48.7	0.575*	23.7	3.38	10.59	48.7
AU + SP		2.00	3.16	57.5	0.413	25.0	4.12	10.52	57.5
S.E.D.#		0.432	1.603	9.84	0.194	8.41	0.342	2.628	9.84

31 total and 25 residual df; + $P < 0.10$; * $P < 0.05$.

Table II.32. Season 3. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence and severity of LIGHT LEAF AND POD SPOT on 7 July, 1993: : Effects of each prochloraz application and iprodione

				STEM			POD		
		% LEAVES	% PLANTS	LESION SCORE per plant	LESION SCORE per inf. plant	% PLANTS	LESION SCORE per plant	LESION SCORE per inf. plant	% PLANTS
AUTUMN	0	0.59	1.25	0.082	0.110	27.2	1.64	2.72	55.5
	1	0.95	1.56	0.091	0.234**	19.5	1.35	3.12	44.9
SPRING	0	0.96	1.56	0.114	0.243	27.2	2.00	4.38	55.6
	1	0.58	1.25	0.059*	0.102***	19.5	0.99	1.47*	44.8
SUMMER	0	1.21	2.19	0.107	0.239	30.0	2.59	5.29	59.0
	1	0.33	0.62	0.065	0.105**	16.6*	0.40**	0.55**	41.5*
IPRODIONE	0	1.40	2.50	0.117	0.172	29.1	2.54	2.92	63.4
	1	0.14*	0.31	0.056*	0.172	17.6	0.45**	2.92	37.0***
S.E.D.#		0.582	1.017	0.0267	0.0403	6.63	0.694	1.749	6.98

# 63 total and 45 residual df; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.
inf. = infected.

Table II.33. Season 3. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence and severity of LIGHT LEAF AND POD SPOT on 7 July, 1993: Treatment means for iprodione-sprayed plots

			STEM			POD		
	% LEAVES	% PLANTS	LESION SCORE per plant	LESION SCORE per inf. plant	% PLANTS	LESION SCORE per plant	LESION SCORE per inf. plant	% PLANTS
CONTROL	0.00	0.00	0.116	0.158	40.0	3.41	6.63	79.3
AUTUMN	2.52	3.75+	0.201	0.585	41.2	3.87	8.53	60.1
SPRING	1.74	3.75+	0.075	0.090	27.5	2.21	4.46	65.1
SUMMER	0.62	1.25	0.062	0.118	11.2*	0.17*	0.61	36.3**
AU + SP	0.56	1.25	0.037	0.125	11.4*	0.88+	1.55	31.2**
AU + SU	0.70	1.25	0.075	0.112	16.2+	0.55*	1.75	46.8*
SP + SU	0.00	0.00	0.072	0.083	30.0	0.78+	0.81	41.4**
AU + SP + SU	0.00	0.00	0.050	0.120	9.0*	0.09*	0.66	41.4**
S.E.D.#	1.165	2.035	0.053	0.057	13.26	1.388	2.473	13.97

# 63 total and 45 residual df; + $P < 0.10$; * $P < 0.05$; ** $P < 0.01$.
inf. = infected.

Table II.34. Season 3. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence and severity of PHOMA/STEM CANKER on 7 July, 1993: Effects of each prochloraz application and iprodione

		LEAF		STEM			POD	
		% LEAVES	% PLANTS	LESION SCORE per plant	LESION SCORE per inf. plant	% PLANTS	INFECTED PODS per plant/inf. plant	% PLANTS
AUTUMN	0	0.83	0.62	3.430	3.246	92.2	0.312	5.4
	1	0.51	0.94	3.076*	2.890*	90.8	0.384	6.5
SPRING	0	1.34	1.56	3.147	3.090	91.8	0.322	6.0
	1	0.00*	0.00*	3.359	3.046	91.1	0.375	5.9
SUMMER	0	1.05	0.94	3.221	3.115	90.5	0.259	4.2
	1	0.29	0.62	3.285	3.021	92.4	0.437	7.8
IPRODIONE	0	0.89	0.94	3.242	3.068	90.6	0.384	6.7
	1	0.45	0.62	3.264	3.068	92.4	0.312	5.2
S.E.D.#		0.683	0.654	0.1650	0.1922	2.60	0.1223	2.54

# 63 total and 45 residual df; * $P < 0.05$.
inf. = infected.

Table II.35. Season 3. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence and severity of PHOMA/STEM CANKER on 7 July, 1993: Treatment means for iprodione plots

	LEAF		STEM			POD	
	% LEAVES	% PLANTS	LESION SCORE per plant	LESION SCORE per inf. plant	% PLANTS	LESION SCORE per plant/ inf. plant	% PLANTS
CONTROL	2.50	1.25	3.300	3.442	91.2	0.125	1.4
AUTUMN	1.70	2.50	2.881	3.015	87.2	0.412	7.5
SPRING	0.00+	0.00	3.510	3.041	92.5	0.250	5.0
SUMMER	0.84	1.25	3.685	3.584	95.0	0.375	9.8
AU + SP	0.00+	0.00	3.191	2.960	91.1	0.250	2.5
AU + SU	0.33	1.25	2.721+	2.318	93.7	0.375	5.4
SP + SU	0.00+	0.00	3.224	2.915	89.9	0.500	5.5
AU + SP + SU	0.00+	0.00	3.510	3.269	91.1	0.500	10.6
S.E.D.#	1.367	1.308	0.3300	0.2718	5.19	0.2446	5.08

# 63 total and 45 residual df; + $P < 0.10$.
inf. = infected.

Table II.36. Season 3. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence and severity of BOTRYTIS on 7 July, 1993: : Effects of each prochloraz application and iprodione

		LEAF		STEM		POD	
		% LEAVES	% PLANTS	LESION SCORE per plant	% PLANTS	NO.OF INFECTED PODS per plant	% PLANTS
AUTUMN	0	0.26	0.31	0.187	0.63	0.828	13.5
	1	0.26	0.31	0.250	0.97	0.729	9.7
SPRING	0	0.26	0.31	0.156	0.63	0.963	12.7
	1	0.26	0.31	0.281	0.97	0.594*	10.5
SUMMER	0	0.52	0.62	0.437	1.60	0.885	14.8
	1	0.00	0.00	0.000*	0.00*	0.672	8.4*
IPRODIONE	0	0.52	0.62	0.437	1.60	0.823	10.8
	1	0.00	0.00	0.000*	0.00*	0.734	12.4
S.E.D.#		0.371	0.447	0.1861	0.678	0.1710	2.86

63 total and 45 residual df; * $P < 0.05$.

Table II.37. Season 3. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence and severity of BOTRYTIS on 7 July, 1993: Treatment means for iprodione plots

	LEAF		STEM		POD	
	% LEAVES	% PLANTS	LESION SCORE per plant	% PLANTS	No. of infected pods per plant	% PLANTS
CONTROL	1.04	1.25	0.375	1.25	1.312	15.5
AUTUMN	0.00	0.00	0.250	1.25	0.979	14.1
SPRING	0.00	0.00	0.375	1.25	0.625+	18.4
SUMMER	0.00	0.00	0.000	0.00	0.875	13.2
AU + SP	1.04	1.25	0.750	2.64	0.625+	11.4
AU + SU	0.00	0.00	0.000	0.00	0.687+	7.9
SP + SU	0.00	0.00	0.000	0.00	0.500*	6.8
AU + SP + SU	0.00	0.00	0.000	0.00	0.625+	5.6
S.E.D.#	0.742	0.895	0.3722	1.356	0.3420	5.71

63 total and 45 residual df; + $P < 0.10$; $P < 0.05$.

Table II.38. Season 3. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence of ALTERNARIA and the incidence and severity of SCLEROTINIA on 7 July, 1993: Effects of each prochloraz application and iprodione

		ALTERNARIA			SCLEROTINIA	
		LEAF		POD	STEM	
		% LEAVES	% PLANTS	% PLANTS	LESION SCORE per infected plant	% PLANTS
AUTUMN	0	0.000	0.00	6.3	2.359	15.6
	1	0.131	0.31	9.7	2.752**	11.9
SPRING	0	0.131	0.31	8.5	2.472	15.6
	1	0.000	0.00	7.6	2.640	11.9
SUMMER	0	0.131	0.31	10.1	2.598	11.6
	1	0.000	0.00	5.9	2.513	15.9
IPRODIONE	0	0.131	0.31	6.2	2.556	16.6
	1	0.000	0.00	9.9	2.556	0.9***
S.E.D.#		0.1312	0.312	2.65	0.151	3.97

63 total and 45 residual df; ** P < 0.01; *** P < 0.001.

Table II.39. Season 3. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence of ALTERNARIA and the incidence and severity of SCLEROTINIA on 7 July, 1993: Treatment means for iprodione plots

	ALTERNARIA			SCLEROTINIA	
	LEAF		POD	STEM	
	% LEAVES	% PLANTS	% PLANTS	LESION SCORE per infected plant	% PLANTS
CONTROL	0.000	0.00	9.1	2.500	20.0
AUTUMN	0.525+	1.25+	15.6	2.627	12.5
SPRING	0.000	0.00	7.0	2.373	8.7
SUMMER	0.000	0.00	5.4	1.832	15.0
AU + SP	0.000	0.00	8.7	2.893	5.0+
AU + SU	0.000	0.00	3.7	2.928	15.0
SP + SU	0.000	0.00	3.8	2.732	18.7
AU + SP + SU	0.000	0.00	10.8	2.560	15.0
S.E.D.#	0.2625	0.625	5.30	0.2133	7.95

63 total and 45 residual df; + P < 0.10.

Table II.40. Season 3. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence of POWDERY MILDEW, DOWNY MILDEW and CABBAGE STEM FLEA BEETLE on 7 July, 1993: Effects of each prochloraz application and iprodione

		POWDERY MILDEW % PLANTS		DOWNY MILDEW		CABBAGE STEM FLEA BEETLE
		POD	STEM	LEAF % Leaves	POD % Plants	% PLANTS
AUTUMN	0	15.6	12.5	99.76	44.7	43.7
	1	10.6	6.6	99.73	43.7	42.5
SPRING	0	13.4	9.7	100.0	43.1	42.2
	1	12.8	9.4	99.49^{+}	45.3	44.1
SUMMER	0	19.7	14.4	99.76	49.4	47.5
	1	6.6***	4.7*	99.73	39.1	38.7
IPRODIONE	0	15.9	14.1	99.73	41.6	41.6
	1	10.3	5.0*	99.76	46.9	44.7
S.E.D.#		3.67	3.79	0.299	8.52	7.74

63 total and 45 residual df; + $P < 0.10$; * $P < 0.05$; *** $P < 0.001$.

Table II.41. Season 3. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence of POWDERY MILDEW, DOWNY MILDEW and CABBAGE STEM FLEA BEETLE on 7 July, 1993: Treatment means for iprodione plots

	POWDERY MILDEW % plants		DOWNY MILDEW		CABBAGE STEM FLEA BEETLE
	POD	STEM	LEAF % leaves	POD % plants	% PLANTS
CONTROL	33.7	18.7	100.0	46.2	41.2
AUTUMN	11.2**	10.0	100.0	47.5	40.0
SPRING	15.0*	15.0	99.04	48.7	52.5
SUMMER	6.2***	8.7	100.0	43.7	43.7
AU + SP	18.7*	13.7	100.0	55.0	56.2
AU + SU	2.5***	1.2*	100.0	35.0	43.7
SP + SU	7.5***	7.5	100.0	40.0	37.5
AU + SP + SU	10.0**	1.2*	98.91^{+}	37.5	30.0
S.E.D.#	7.34	7.57	0.598	17.04	15.49

63 total and 45 residual df; + $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Tables II.42 - II.47. Season 3 (1993): Main interactions between prochloraz applications and with iprodione (7 July, 1993)

Table II.42. PHOMA/STEM CANKER: lesion score per plant

AUTUMN	SPRING	0	1
0		3.492	3.367
1		2.801	3.351
S.E.D. 0.2334			

Table II.43. LIGHT LEAF AND POD SPOT: % leaves infected

	SPRING	0		1	
AUTUMN	IPRODIONE	0	1	0	1
0		0.63	0.00	1.74	0.00
1		3.22	0.00	0.00	0.56
S.E.D. 1.165					

Table II.44. LIGHT LEAF AND POD SPOT: pod lesion score per plant

IPRODIONE	SPRING	0	1	SUMMER	0	1
0		3.87	1.21		4.70	0.39
1		0.12	0.77		0.49	0.40
S.E.D. 0.981						

Table II.45. LIGHT LEAF AND POD SPOT: incidence of pod infection (% plants)

AUTUMN	SUMMER	0	1
0		72.2	38.8
1		45.7	44.1
S.E.D. 9.88			

Table II.46. LIGHT LEAF AND POD SPOT: pod lesion score per infected plant

IPRODIONE	SPRING	0	1	SUMMER	0	1
0		3.87	1.21		4.70	0.39
1		0.12	0.77		0.49	0.40
		F.pr. 0.021			F pr. 0.004	
S.E.D. 0.981						

Table II.47. LIGHT LEAF AND POD SPOT: incidence of stem infection (% plants)

SUMMER	SPRING	0	1	IPRODIONE	0	1
0		40.6	19.4		46.3	13.7
1		13.7	19.5		11.9	21.4
F.pr.		0.048			0.003	
S.E.D.			9.37			

Table II.48. Season 3. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence and severity of PHOMA STEM CANKER at final harvest: The effects of each prochloraz application in iprodione plots

		INCIDENCE	SEVERITY						
		% PLANTS	MEAN SCORE	INCIDENCE OF PLANTS IN EACH SEVERITY CATEGORY (SCORING SYSTEM 0-6)					
				SLIGHT (1+2)	MODERATE (3)	SEVERE (4+5)	DEAD (6)	LOW (1+2+3)	HIGH (4+5+6)
AUTUMN	0	96.63	3.994	12.0	17.46	45.8	21.6	29.5	67.5
	1	93.13**	3.445**	20.4*	18.92	38.8*	14.4*	39.3*	53.2**
SPRING	0	95.55	4.008	14.5	19.02	43.1	18.6	33.6	61.7
	1	94.21	3.980	17.9	17.36	41.6	17.4	35.3	59.0
SUMMER	0	94.46	3.661	18.4	17.91	40.3	17.9	36.4	58.2
	1	95.31	3.778	14.0	18.47	44.3	18.1	32.5	62.5
S.E.D.#		1.045	0.1627	3.01	1.922	2.95	2.95	3.63	4.10

31 total and 21 residual df; * $P < 0.05$; ** $P < 0.01$.

Table II.49. Season 3. The effects of AUTUMN, SPRING and SUMMER prochloraz on the incidence and severity of PHOMA STEM CANKER at final harvest: Treatment means

	INCIDENCE	SEVERITY						
	% PLANTS	MEAN SCORE	INCIDENCE OF PLANTS IN EACH SEVERITY CATEGORY (SCORING SYSTEM 0-6)					
			SLIGHT (1+2)	MODERATE (3)	SEVERE (4+5)	DEAD (6)	LOW (1+2+3)	HIGH (4+5+6)
CONTROL	95.28	3.892	14.7	18.73	41.8	20.8	33.5	62.6
AUTUMN	96.68	3.852	19.1	22.62	37.2	17.5	41.7	54.7
SPRING	97.80	4.125	11.5	16.49	45.9	24.0	28.0	69.8
SUMMER	97.34	3.973	10.9	16.02	48.4	22.4	27.0	70.9
AU + SP	88.07**	2.776**	28.5	13.79	36.5	9.3	42.3	45.8
AU + SU	92.92	3.599	13.4	18.70	44.9	13.8	32.1	58.8
SP + SU	96.11	3.986	10.9	18.58	47.2	19.4	29.5	66.6
AU + SP + SU	94.87	3.553	20.7	20.56	36.8	16.8	41.3	53.6
S.E.D.#	2.090	0.3254	6.02	3.844	5.90	5.89	7.26	8.21

31 total and 21 residual df; ** $P < 0.01$.

APPENDIX III

1. EFFECTS OF PROCHLORAZ ON VEGETATIVE GROWTH IN SEASON 3

Fig. III.1. The effect of prochloraz on leaf area and plant number during the vegetative stage in the 1993 season:

(a) leaf area index

(b) leaf area per plant

(c) individual leaf area

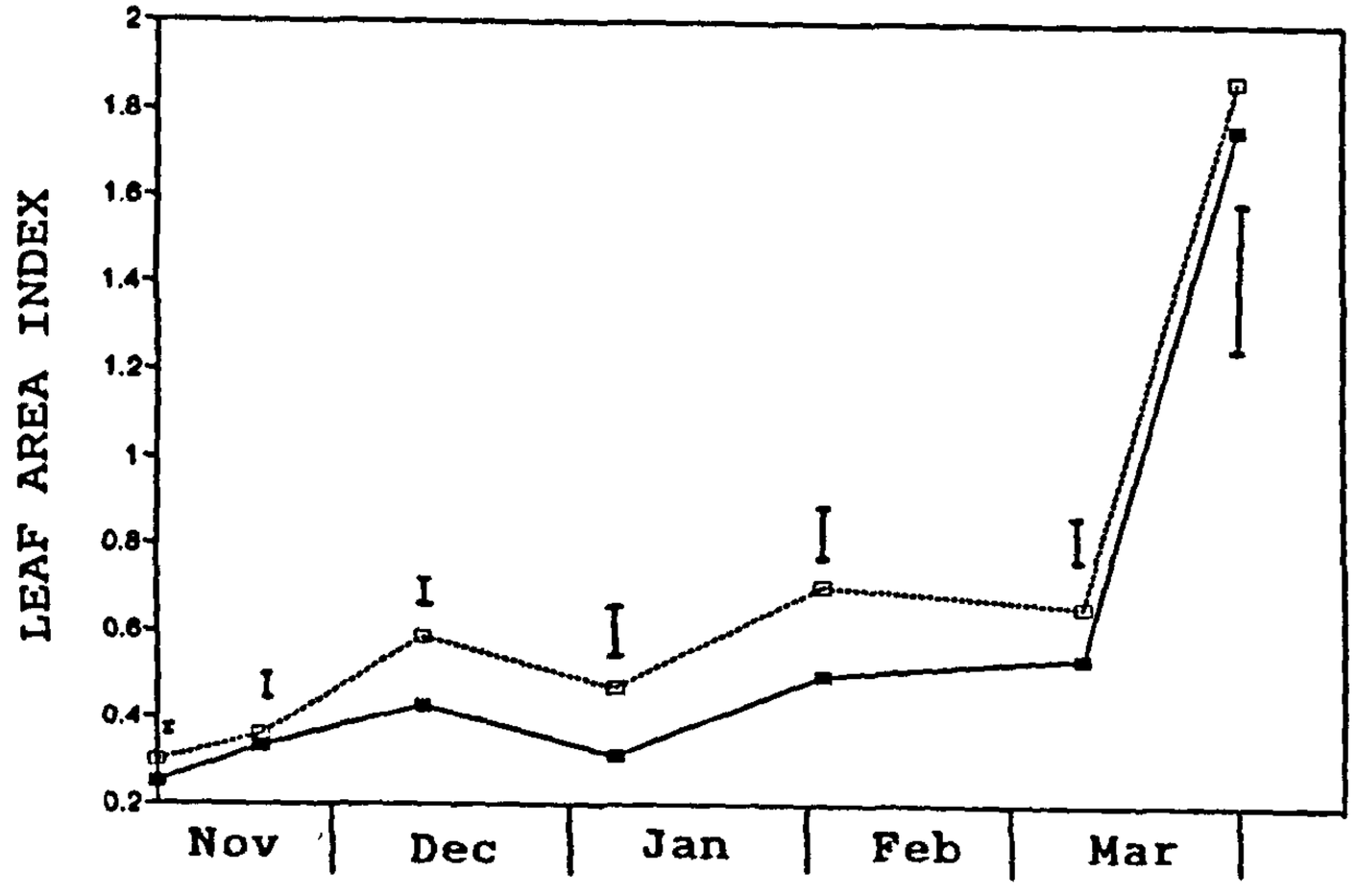
(d) plant number per m^2

Solid lines/closed symbols = control

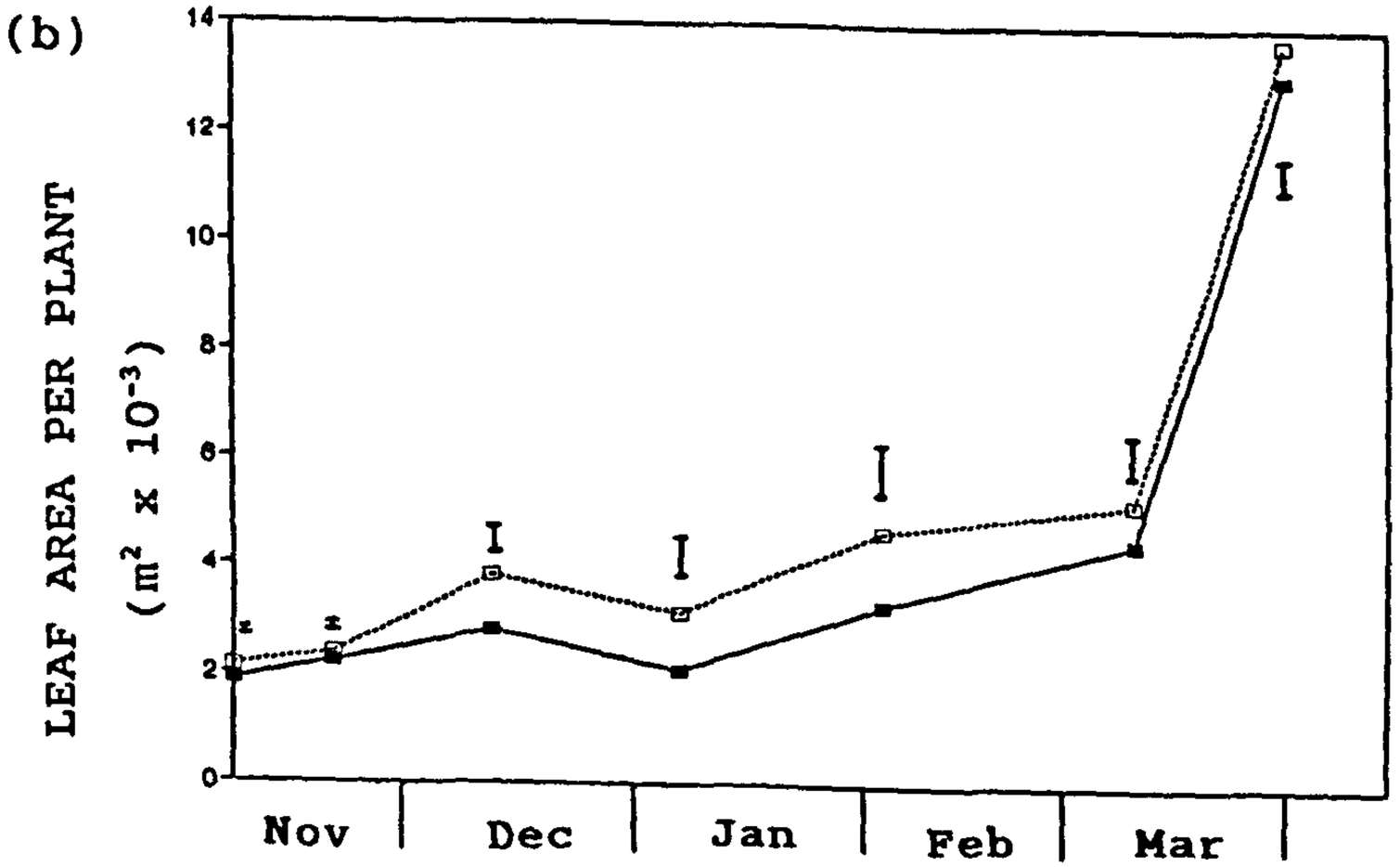
Broken lines/open symbols = prochloraz-treated

I = S.E.D.

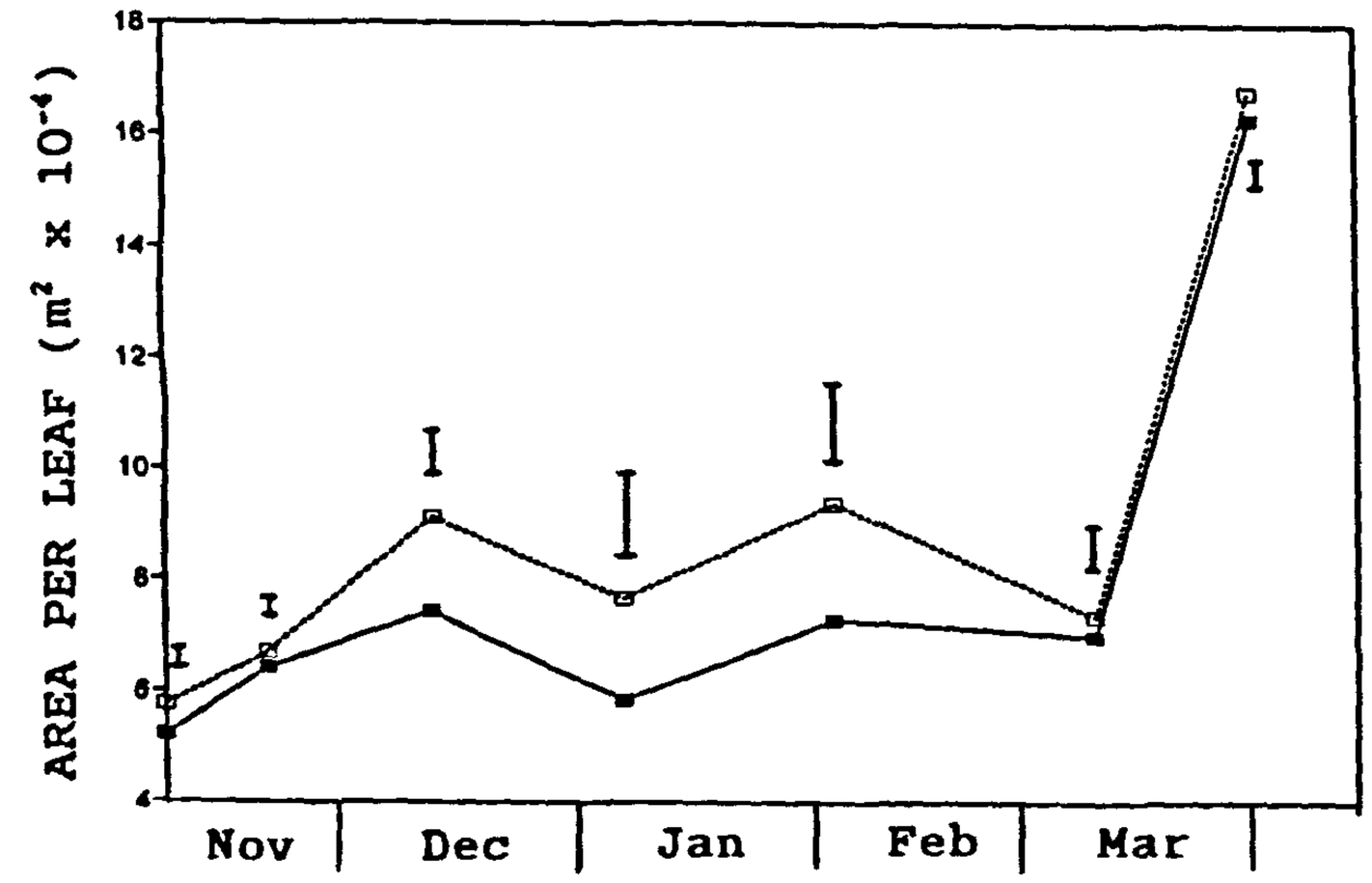
(a)


LEAF AREA INDEX
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
Nov
Dec
Jan
Feb
Mar

(b)


LEAF AREA PER PLANT
(m^2 x 10^{-3})
14
12
10
8
6
4
2
0
Nov
Dec
Jan
Feb
Mar

(c)


AREA PER LEAF (m^2 x 10^{-4})
18
16
14
12
10
8
6
4
Nov
Dec
Jan
Feb
Mar

(d)

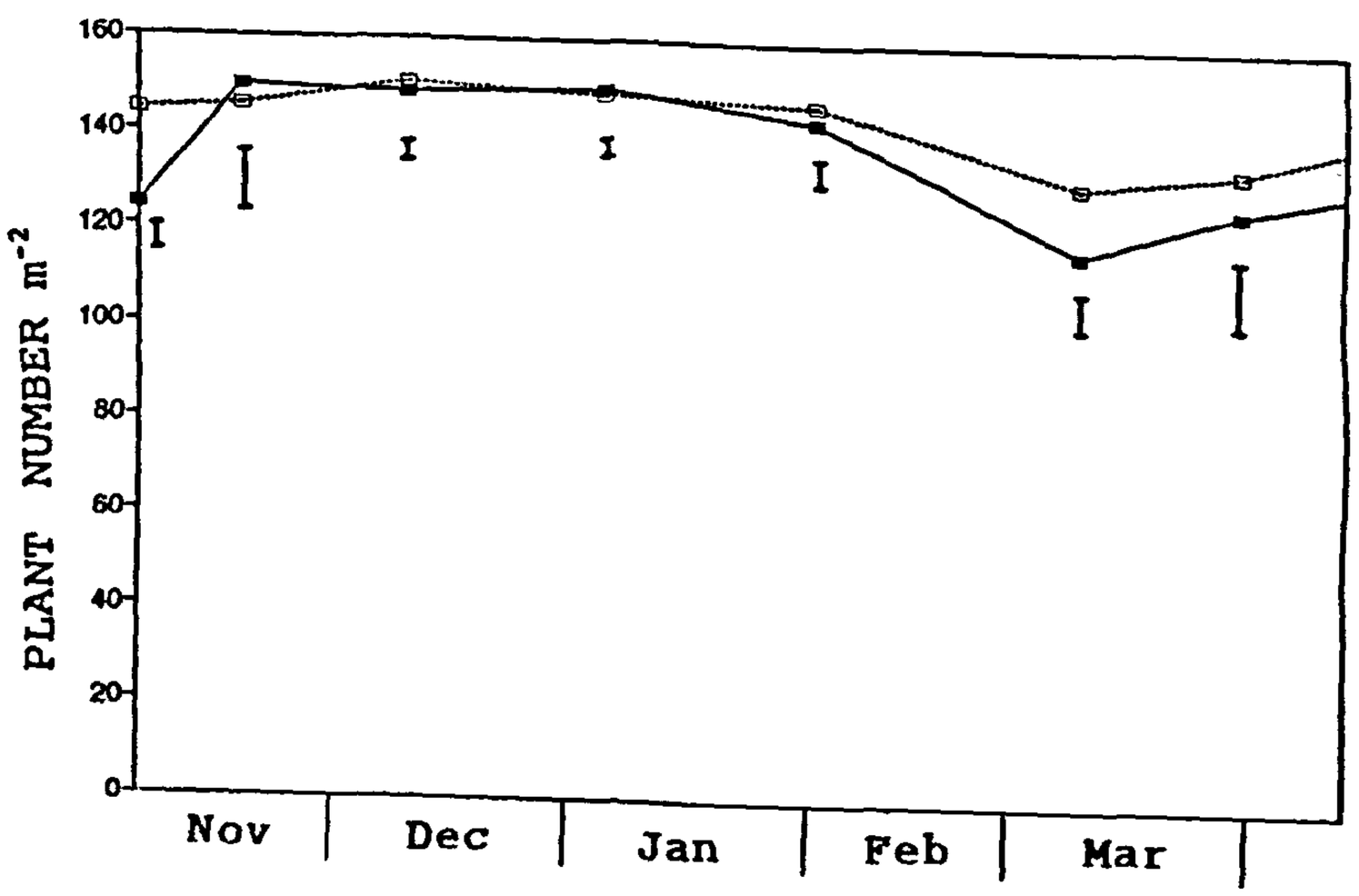

PLANT NUMBER m^{-2}
160
140
120
100
80
60
40
20
0
Nov
Dec
Jan
Feb
Mar

Fig. III.2. The effect of prochloraz on

(a) leaf number per m^2

(b) leaf number per plant

during vegetative development in the 1993 season:

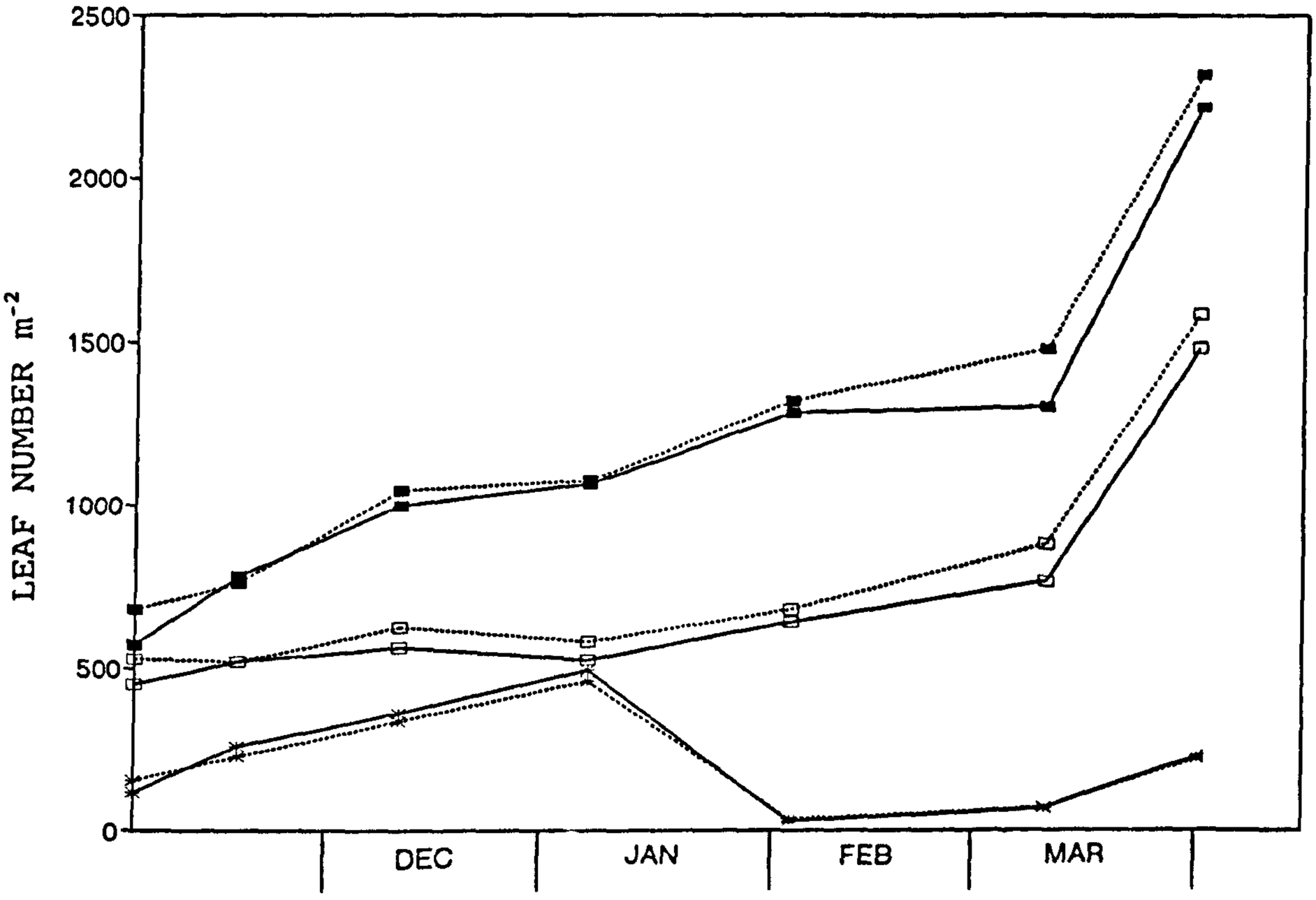
□ green leaves

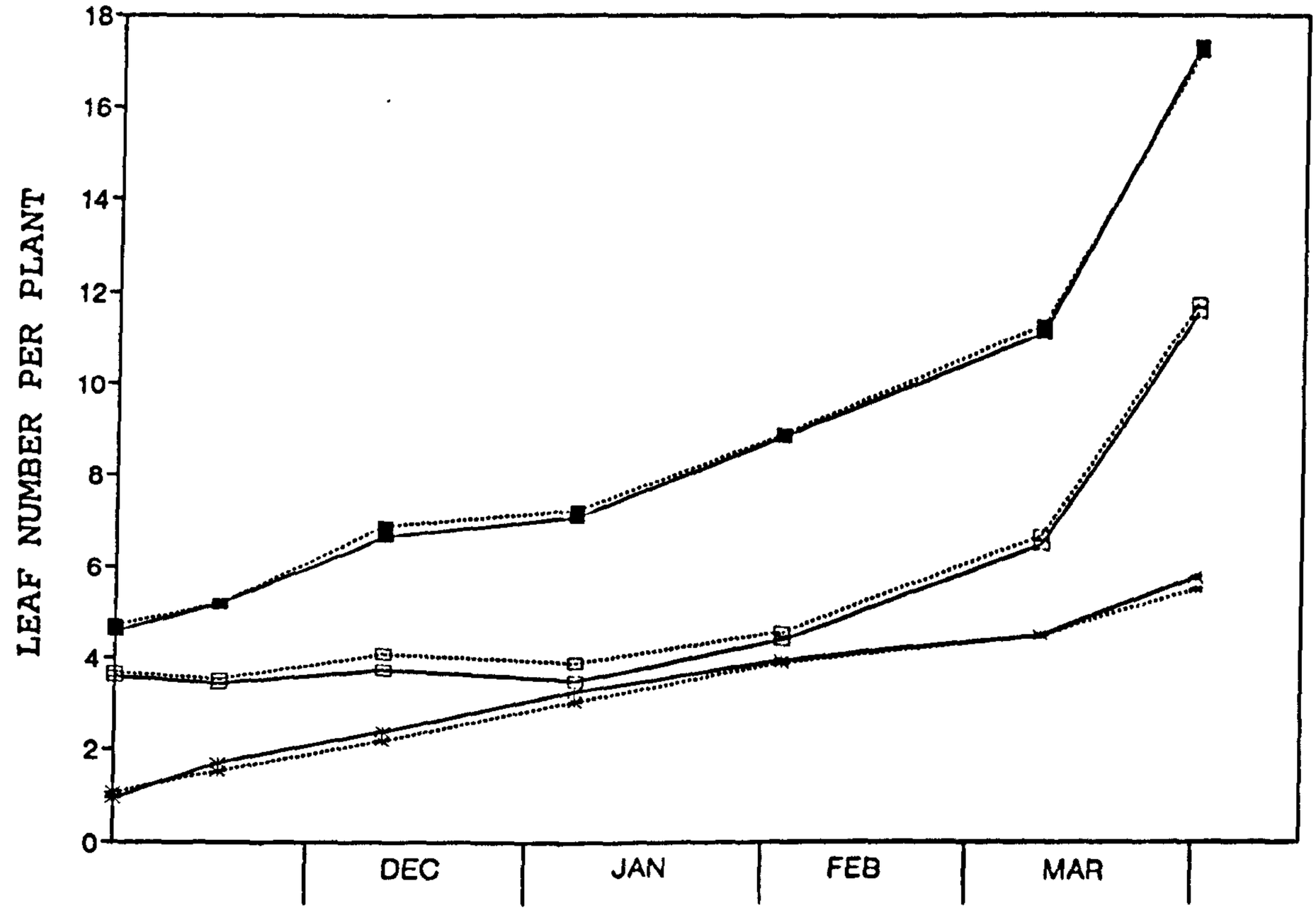
* senescing leaves and leaf scars

■ total leaves

Solid lines/ closed symbols = control

Broken lines/ open symbols = prochloraz-treated


LEAF NUMBER m-2
2500
2000
1500
1000
500
0
DEC
JAN
FEB
MAR


LEAF NUMBER PER PLANT
18
16
14
12
10
8
6
4
2
0
DEC
JAN
FEB
MAR

2. EFFECTS OF PROCHLORAZ AT FINAL HARVEST: 1992 and 1993

Table III.1. Effects of prochloraz on plant number per m^{-2} and leaf, stem and total dry matter at final harvest, 1992

		PLANT NUMBER PER m^2	DRY MATTER PER m^2			
			Leaf	Stem		Total
				> 80cm	< 80cm	
SPRING	0	86.5	2.17	354.6	151.6	1221
	1	89.1	2.68	335.7	146.2	1230
SUMMER	0	88.0	2.54	353.3	156.2	1249
	1	87.6	2.31	337.0	141.5+	1203
S.E.D.		4.96	0.734	14.31	6.56	32.5

(+ significantly different at $P < 0.10$)

Table III.2. Treatment means for the effects of prochloraz on plant number per m^{-2} and leaf, stem and total dry matter at final harvest, 1992

	PLANT NUMBER PER m^2	DRY MATTER PER m^2			
		Leaf	Stem		Total
			> 80cm	< 80cm	
CONTROL	91.7	2.30	163.1	375.8	1269
SPRING	84.2	2.78	149.3	330.7	1229
SUMMER	81.2	2.04	140.0	333.4	1174
SP + SU	94.0	2.57	143.1	340.7	1232
S.E.D.	7.01	1.038	9.27	20.24	45.9

Table III.3. Effects of prochloraz on pod and hull dry matter at final harvest, 1992

		POD DM (gm^{-2})			HULL DM (gm^{-2})
		Fertile	Shattered	Total	
SPRING	0	159	512	701	274.3
	1	203+	502	733	291.5
SUMMER	0	188	506	725	285.3
	1	174	508	709	280.5
S.E.D.		22.9	32.6	31.5	12.20

(+ significant at $P < 0.10$)

Table III.4. Treatment means for the effects of prochloraz on pod and hull dry matter at final harvest, 1992

	POD DM (gm^{-2})			HULL DM (gm^{-2})
	Fertile	Shattered	Total	
CONTROL	174	510	715	279.0
SPRING	203	502	734	291.7
SUMMER	144	514	686	269.7
SP + SU	203	503	732	291.3
S.E.D.	32.4	46.1	44.6	17.26

Table III.5. The effects of prochloraz on seed dry matter and components at final harvest, 1992

		SEED DM (gm^{-2})	1000-SEED WEIGHT (g)	SEED NO. PER POD	SEED NO. PER m^2	HARVEST INDEX
SPRING	0	426	5.810	14.74	73500	0.349
	1	442	5.976	14.34	74326	0.359
SUMMER	0	439	5.928	14.77	74172	0.352
	1	429	5.858	14.31	73346	0.356
S.E.D.		20.1	0.1167	0.638	3495.1	0.0130

Table III.6. Treatment means for the effects of prochloraz on seed dry matter and components at final harvest, 1992

	SEED DM (gm^{-2})	1000-SEED WEIGHT (g)	SEED NO. PER POD	SEED NO. PER m^2	HARVEST INDEX
CONTROL	436	5.863	14.82	74676	0.344
SPRING	442	5.993	14.71	73976	0.360
SUMMER	417	5.756	14.65	72324	0.354
SP + SU	441	5.960	13.96	74368	0.358
S.E.D.	28.4	0.1651	0.902	4942.8	0.0092

Table III.7. The effect of prochloraz on pod numbers at final harvest, 1992

		POD NUMBER m^{-2}			
		Fertile	Shattered	Yield-forming	Total
SPRING	0	1614	5038	5215	6651
	1	1946	4718	5510*	6665
SUMMER	0	1845	4788	5322	6632
	1	1715	4968	5403	6684
S.E.D.		198.4	334.3	148.0	289.6

Table III.8. Treatment means for the effects of prochloraz on pod numbers at final harvest, 1992

	POD NUMBER m^{-2}			
	Fertile	Shattered	Yield-forming	Total
CONTROL	1736	4978	5243	6713
SPRING	1954	4598	5401	6551
SUMMER	1492	5098	5187	6590
SP + SU	1939	4839	5618	6778
S.E.D.	280.6	472.7	209.2	409.5

Table III.9. The effect of prochloraz on combine yield at 9% moisture, combine seed 1000-seed weight and seed moisture content in 1992

		COMBINE YIELD (t ha^{-1})	1000-SEED WEIGHT (g)	SEED MOISTURE CONTENT (%)
SPRING	0	3.246	4.907	12.25
	1	3.199	4.983	12.66
SUMMER	0	3.252	4.940	12.48
	1	3.192	4.950	12.43
S.E.D.		0.749	0.102	0.578

Table III.10. Treatment means for the effect of prochloraz on combine yield at 9% moisture, combine seed 1000-seed weight and seed moisture content in 1992

	COMBINE YIELD (t ha^{-1})	1000-SEED WEIGHT (g)	SEED MOISTURE CONTENT (%)
CONTROL	3.215	4.874	12.14
SPRING	3.290	5.006	12.81
SUMMER	3.277	4.940	12.36
SP + SU	3.107	4.959	12.50
S.E.D.	0.1059	0.1020	0.817

Table III.11. Effects of prochloraz on plant number per m^2 and leaf, stem and total crop dry matter at final harvest, 1993

		PLANT NUMBER m^{-2}	DRY MATTER (g m^{-2})		
			Leaf	Stem	Total
AUTUMN	0	106.1	4.89	418.7	1251
	1	104.0	3.64+	441.5+	1304
SPRING	0	104.6	4.09	431.9	1242
	1	105.6	4.44	428.3	1313+
SUMMER	0	103.5	4.01	431.5	1262
	1	106.6	4.51	428.7	1293
S.E.D.		7.44	0.699	11.25	34.2

(+ significant at $P < 0.10$)

Table III.12. Treatment means for the effects of prochloraz on plant number per m^2 and leaf, stem and total crop dry matter at final harvest, 1993

	PLANT NUMBER m^{-2}	DRY MATTER (g m^{-2})		
		Leaf	Stem	Total
CONTROL	105.5	4.59	423.7	1218
AUTUMN	101.5	2.71	445.4	1241
SPRING	103.0	4.90	413.3	1223
SUMMER	110.0	4.43	426.5	1295
AU + SP	104.0	3.85	443.5	1367*
AU + SU	101.2	4.61	432.1	1214
SP + SU	106.0	5.63	411.5	1266
AU + SP + SU	109.2	3.37	444.8	1395*
S.E.D.	14.89	1.398	22.49	68.5

(* significantly different from control at $P < 0.05$; 31 total and 21 residual df)

Table III.13. Effects of prochloraz on pod and hull dry matter at final harvest, 1993

		POD DM (g m^{-2})		HULL DM (g m^{-2})
		Fertile	Total	
AUTUMN	0	389.0	811.0	295.4
	1	360.0	843.0	303.6
SPRING	0	383.0	793.0	284.6
	1	367.0	861.0*	314.4*
SUMMER	0	311.0	813.0	296.1
	1	439.0*	841.0	302.9
S.E.D.		56.9	27.5	10.86

(+, * significant at $P < 0.10$ and 0.05)

Table III.14. Treatment means for the effects of prochloraz on pod and hull dry matter at final harvest, 1993

	POD DM ($g\ m^{-2}$)		HULL DM ($g\ m^{-2}$)
	Fertile	Total	
CONTROL	429.0	777.0	281.2
AUTUMN	158.0*	785.0	284.7
SPRING	220.0	789.0	287.7
SUMMER	524.0	845.0	305.2
AU + SP	435.0	901.0*	330.9*
AU + SU	421.0	764.0	267.2
SP + SU	383.0	833.0	307.4
AU + SP + SU	428.0	922.0*	331.7*
S.E.D.	113.8	55.1	21.73

(* significantly different from control at $P < 0.05$; 31 total and 21 residual df)

Table III.15. Interactions between autumn and spring prochloraz applications for total pod DM and total crop DM per m^2 at final harvest, 1993

		TOTAL POD DM (g)		TOTAL CROP DM (g)	
AUTUMN	SPRING	0	1	0	1
0		811	811	1257	1244
1		774	912	1228	1381
S.E.D.		38.9		48.4	

Table III.16. Interactions between autumn and spring prochloraz for seed DM and seed number m^{-2} at final harvest, 1993

		SEED DM (g)		SEED NO. m^{-2} ($\times 10^{-3}$)	
AUTUMN	SPRING	0	1	0	1
0		514.7	511.3	77.7	77.4
1		485.4	577.4	72.8	86.8
S.E.D.		27.45		4.25	

Table III.17. Effects of prochloraz on pod numbers per m^2 at final harvest, 1993

		FERTILE	SHATTERED	YIELD-FORMING	TOTAL	EMPTY	ABSCISED	POTENTIAL
AUTUMN	0	2302	3072	4380	5372	39	6079	11490
	1	2143	3877	4548	6020+	40	6061	12121
SPRING	0	2187	3206	4223	5393	41	5928	11362
	1	2257	3742	4706*	5999+	38	6211	12249
SUMMER	0	1857	3830	4386	5687	32	5809	11528
	1	2587*	3119	4543	5705	47*	6331	12083
S.E.D.		339.7	605.6	176.1	333.8	6.56	304.7	570.5

(+, * significantly different from control at $P < 0.10$ and 0.05; 31 total and 21 residual df)

Table III.18. Treatment means for the effects of prochloraz on pod numbers per m^2 at final harvest, 1993

	FERTILE	SHATTERED	YIELD-FORMING	TOTAL	EMPTY	ABSCISED	POTENTIAL
CONTROL	2368	2550	4038	4918	35	5629	10582
AUTUMN	941*	5048+	4128	5989	24	5711	11723
SPRING	1505	3964	4329	5469	28	5640	11136
SUMMER	3039	2329	4679+	5368	41	6407	11815
AU + SP	2616	3758	5048**	6374*	42	6255	12671*
AU + SU	2401	2897	4046	5298	64*	5967	11330
SP + SU	2291	3444	4476	5735	53	6640	12428
AU + SP + SU	2616	3804	4972*	6420*	30	6310	12760*
S.E.D.	679.4	1211.2	352.3	667.7	13.11	609.4	1141.1

(+, *, ** significantly different from control at $P < 0.10$, 0.05 and 0.01; 31 total and 21 residual d.f.)

Table III.19. Effects of prochloraz on seed yield, components and harvest index, 1993

		SEED DM (gm^{-2})	1000-SEED WEIGHT (g)	SEED NO. PER POD	SEED NO PER m^2 ($x\ 10^{-3}$)	HARVEST INDEX
AUTUMN	0	513.0	6.612	19.93	77.5	0.410
	1	531.4	6.712	19.85	79.8	0.406
SPRING	0	500.0	6.676	19.74	75.2	0.402
	1	544.3*	6.648	20.04	82.1*	0.414*
SUMMER	0	514.3	6.670	19.71	77.6	0.407
	1	530.1	6.654	20.07	79.7	0.409
S.E.D.		19.41	0.1606	1.002	3.00	0.0060

(+, * significant at $P < 0.10$ and 0.05)

Table III.20. Treatment means for the effects of prochloraz on seed yield, components and harvest index, 1993

	SEED DM ($g\ m^{-2}$)	1000-SEED WEIGHT (g)	SEED NO. PER POD	SEED NO. PER m^2 ($x\ 10^{-3}$)	HARVEST INDEX
CONTROL	491.3	6.528	20.74	75.5	0.403
AUTUMN	498.2	6.700	18.61	75.4	0.401
SPRING	500.3	6.793	18.85	73.7	0.409
SUMMER	538.0	6.687	19.29	79.9	0.415
AU + SP	567.3+	6.661	20.64	85.7	0.415
AU + SU	472.6	6.788	20.33	70.2	0.388
SP + SU	522.2	6.439	20.84	81.0	0.412
AU + SP + SU	587.4*	6.701	19.82	87.9*	0.421
S.E.D.	38.82	0.3212	2.005	6.01	0.0121

(+, * significantly different from control at $P < 0.10$ and 0.05; 31 total and 21 residual df)

Table III.21. Effects of prochloraz and iprodione on combine yield, combine seed 1000-seed weight and seed moisture content, 1993

		COMBINE YIELD (t ha^{-1})	1000-SEED WEIGHT (g)	SEED MOISTURE CONTENT (%)
AUTUMN	0	3.677	6.216	11.68
	1	3.760	6.187	11.41
SPRING	0	3.637	6.161	11.44
	1	3.801^{+}	6.242	11.64
SUMMER	0	3.706	6.168	11.34
	1	3.731	6.235	11.75
IPRODIONE	0	3.456	6.058	11.30
	1	3.981***	6.345***	11.78
S.E.D.		0.0891	0.0632	0.291

(+, *** significant at P < 0.10 and 0.001; 63 total and 45 residual df)

Table III.22. Interactions between spring prochloraz and iprodione and between autumn and spring prochloraz applications for combine 1000-seed weight (g), 1993

	AUTUMN		IPRODIONE	
SPRING	0	1	0	1
0	6.123	6.199	5.946	6.376
1	6.309	6.174	6.169	6.314
S.E.D.		0.0893		

Table III.23. Treatment means for the effects of prochloraz and iprodione on combine yield at 9% moisture, combine seed 1000-seed weight and seed moisture content, 1993

	COMBINE YIELD (t ha^{-1})	1000-SEED WEIGHT (g)	SEED MOISTURE CONTENT (%)
CONTROL	3.336	5.878	11.48
AUTUMN	3.428	5.993	10.89
SPRING	3.265	6.161	11.81
SUMMER	3.342	6.006	11.25
AU + SP	3.623	6.021	11.65
AU + SU	3.351	5.907	11.27
SP + SU	3.649	6.313*	10.94
AU + SP + SU	3.656	6.180	11.14
IPRODIONE	3.895	6.249^{+}	11.60
AU + I	3.915*	6.432**	10.65
SP + I	4.125**	6.476**	10.76
SU + I	3.925*	6.360*	12.22
AU + SP + I	4.063**	6.132	11.83
AU + SU + I	3.903*	6.463**	12.14
SP + SU + I	3.880*	6.287*	13.34**
AU + SP + SU + I	4.143**	6.362*	11.66
S.E.D.	0.2519	0.1787	0.823

(+, *, ** significantly different from control at P < 0.10. 0.05 and 0.01; 63 total and 45 residual df)

Table III.24. Effects of prochloraz on combine yield at 9% moisture, combine seed 1000-seed weight and seed moisture content in plots sprayed with iprodione, 1993

		COMBINE YIELD (t ha^{-1})	1000-SEED WEIGHT (g)	SEED MOISTURE CONTENT (%)
AUTUMN	0	3.953	6.343	11.98
	1	4.006	6.347	11.57
SPRING	0	3.907	6.376	11.66
	1	4.053	6.314	11.90
SUMMER	0	3.999	6.322	11.21
	1	3.963	6.368	12.34*
S.E.D.		0.1231	0.0861	0.403

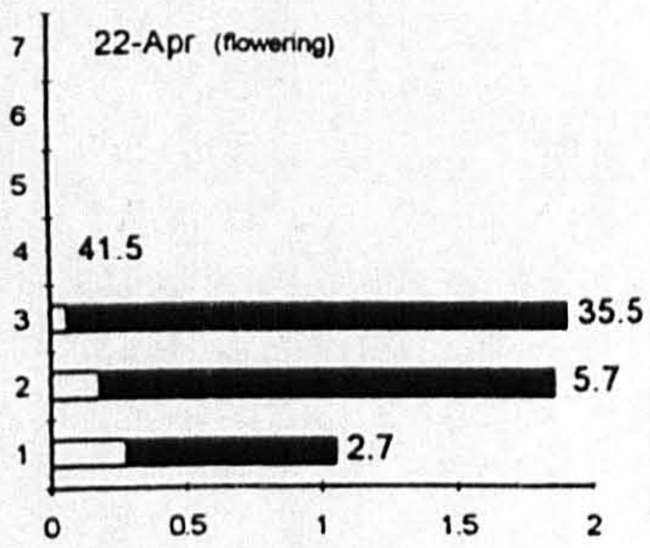
(* significant at $P < 0.05$; 31 total and 21 residual df)

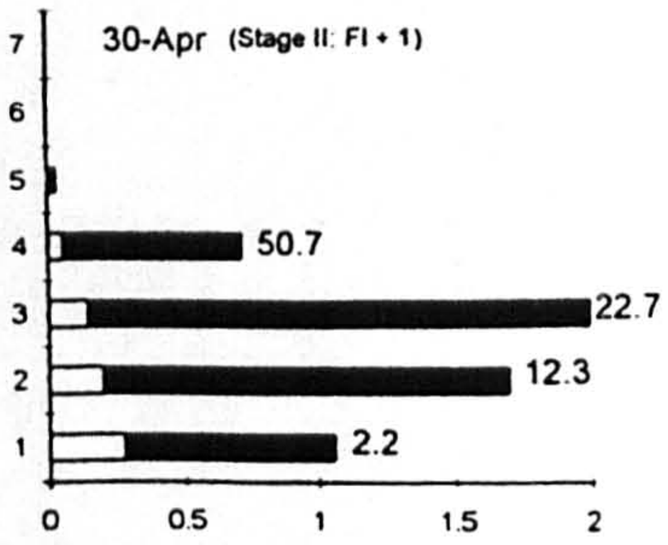
Table III.25. Interaction between summer prochloraz and iprodione for moisture content of combine seed (%), Season 3

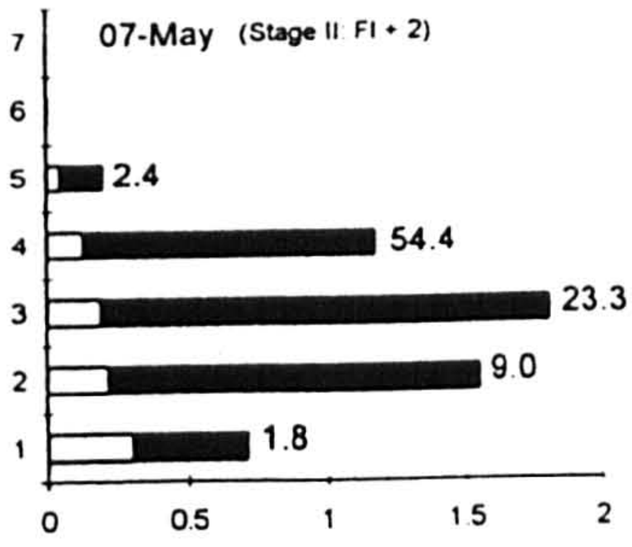
	IPRODIONE	
SUMMER	0	1
0	11.46	11.21
1	11.15	12.34
S.E.D.	0.412	

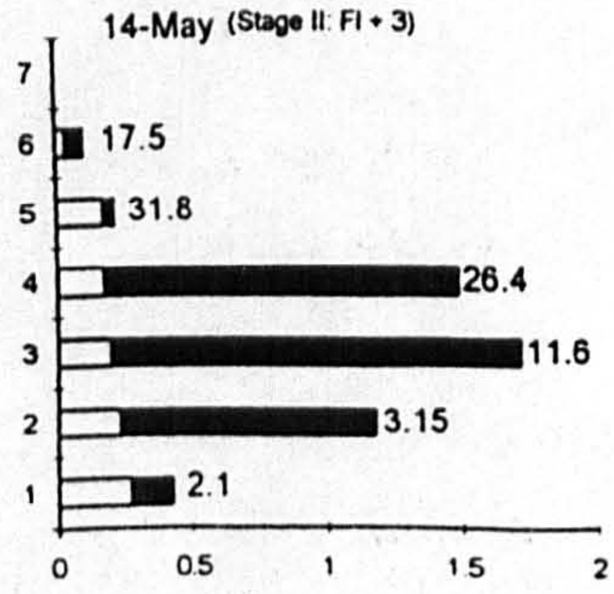
APPENDIX IV

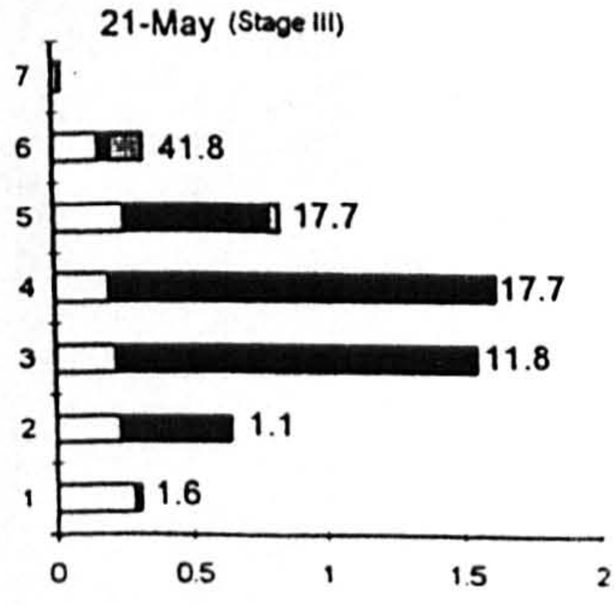
(a) 1991

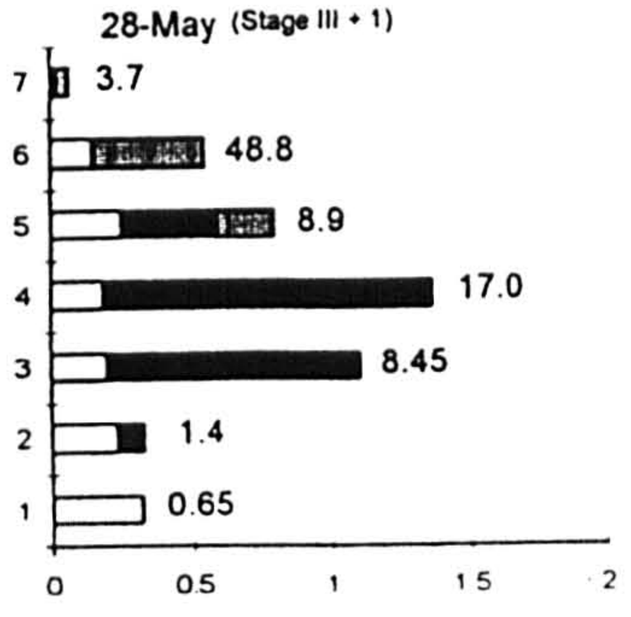


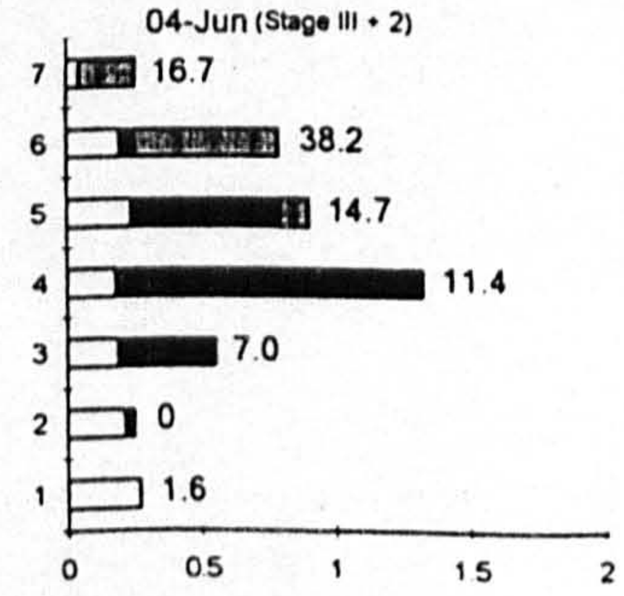


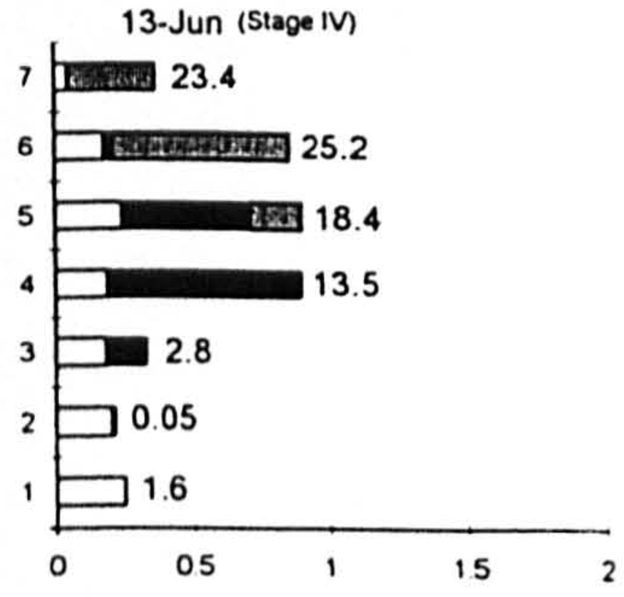


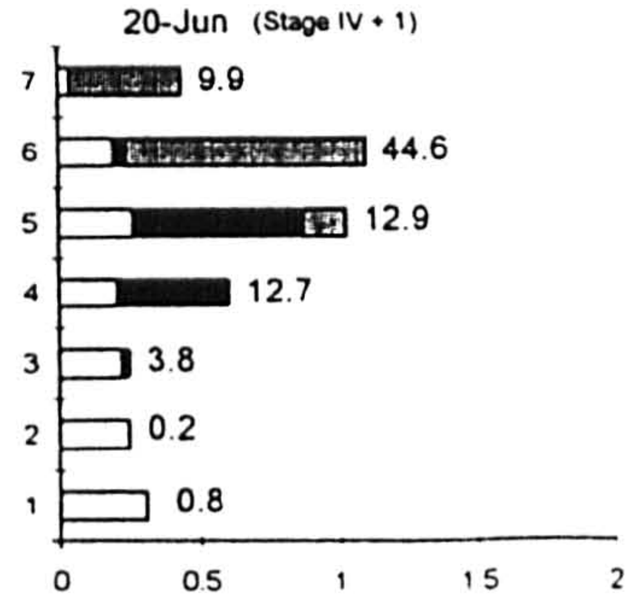


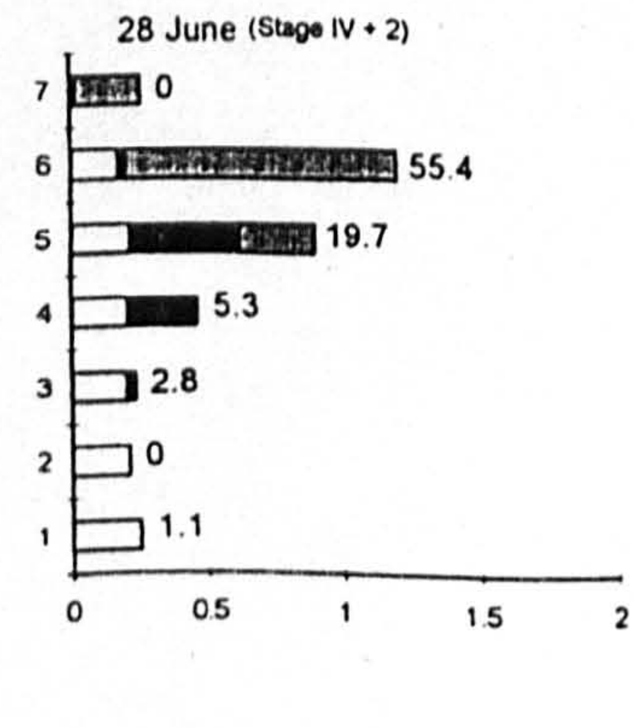


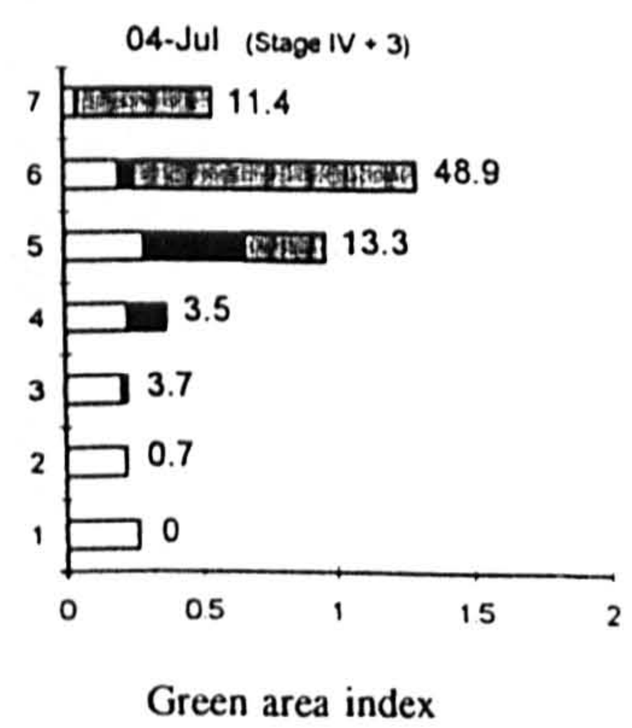


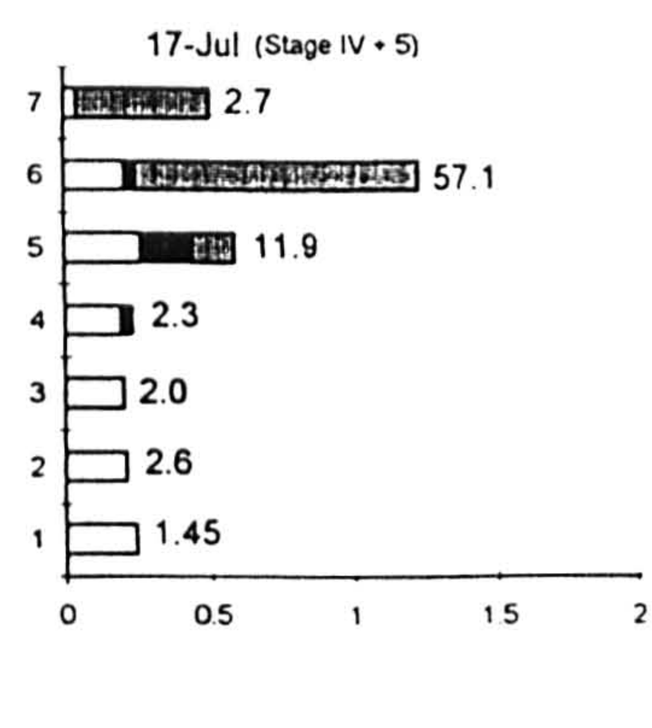










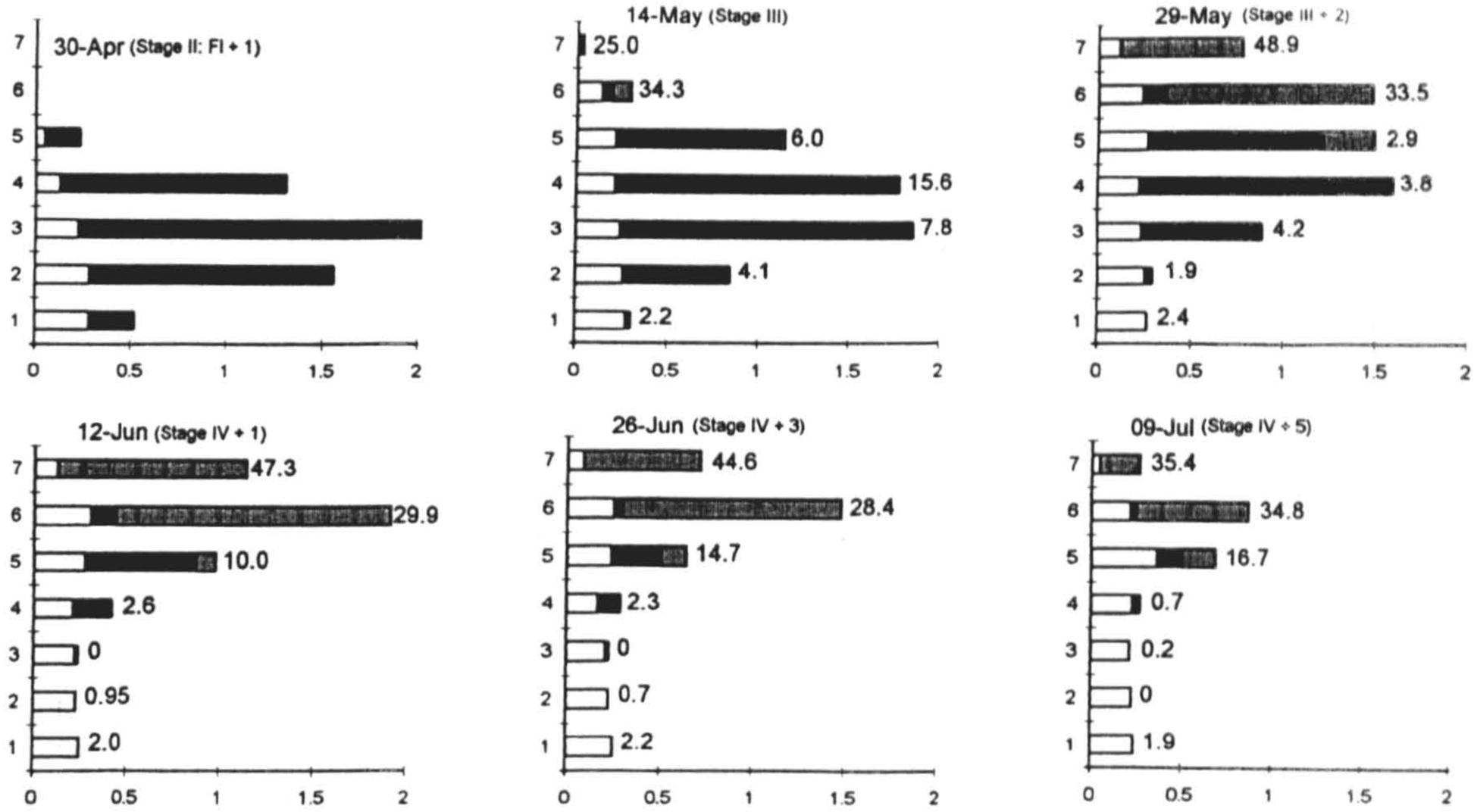


Green area index

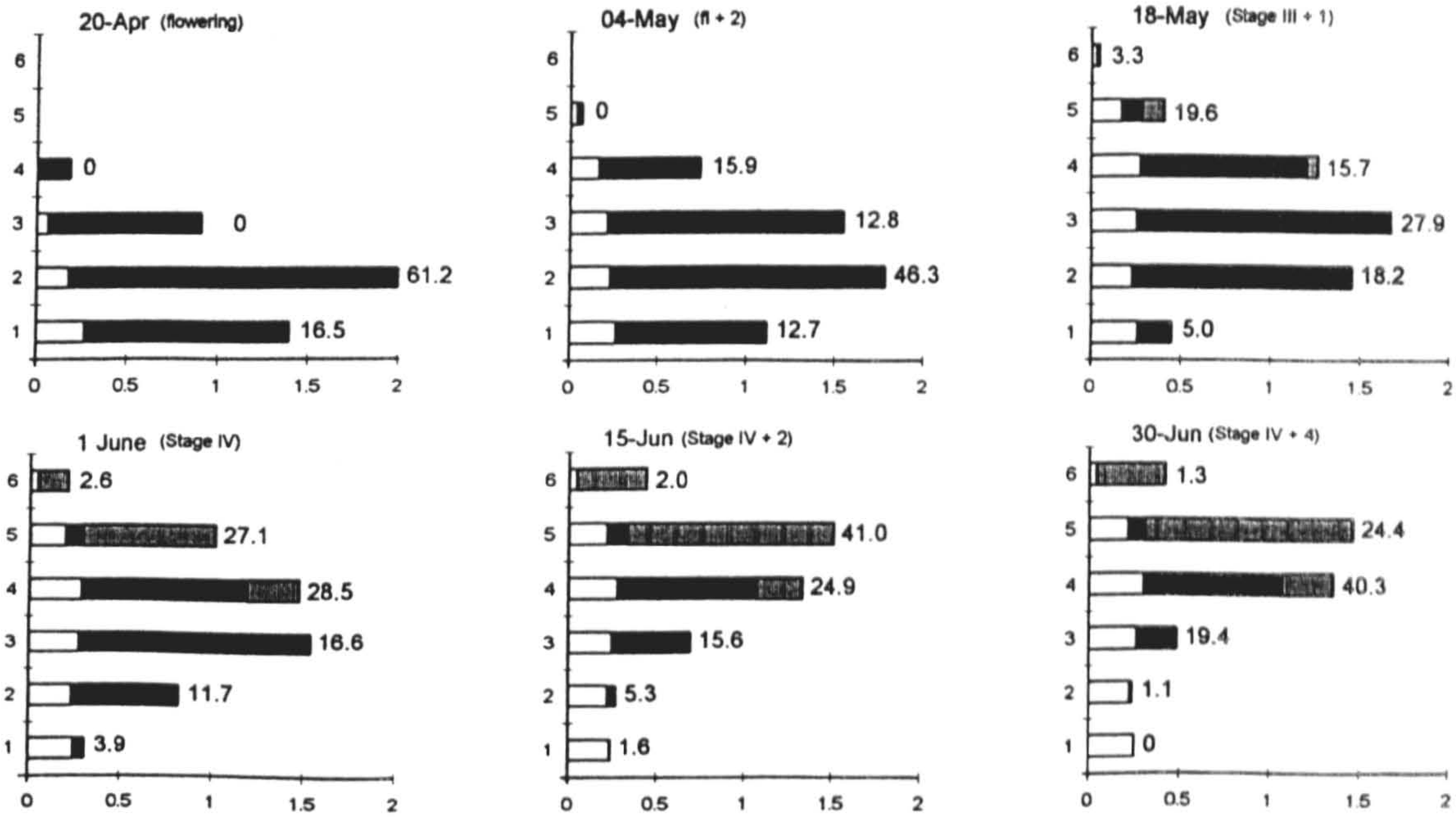
Fig. IV.1. Uncorrected data for radiation interception in the crop profile in relation to green area index: all seasons.

Contents: GAI in each layer of the profile (bars: □ stem, ■ leaf, ▒ pod); % of total incident radiation intercepted in each layer (figures next to bars); for reproductive development: (a) 1991, (b) 1992, and (c) 1993.

(b) 1992



(c) 1993



Green area index

Note: No radiation data are available for 30 April, 1992

(a) Control

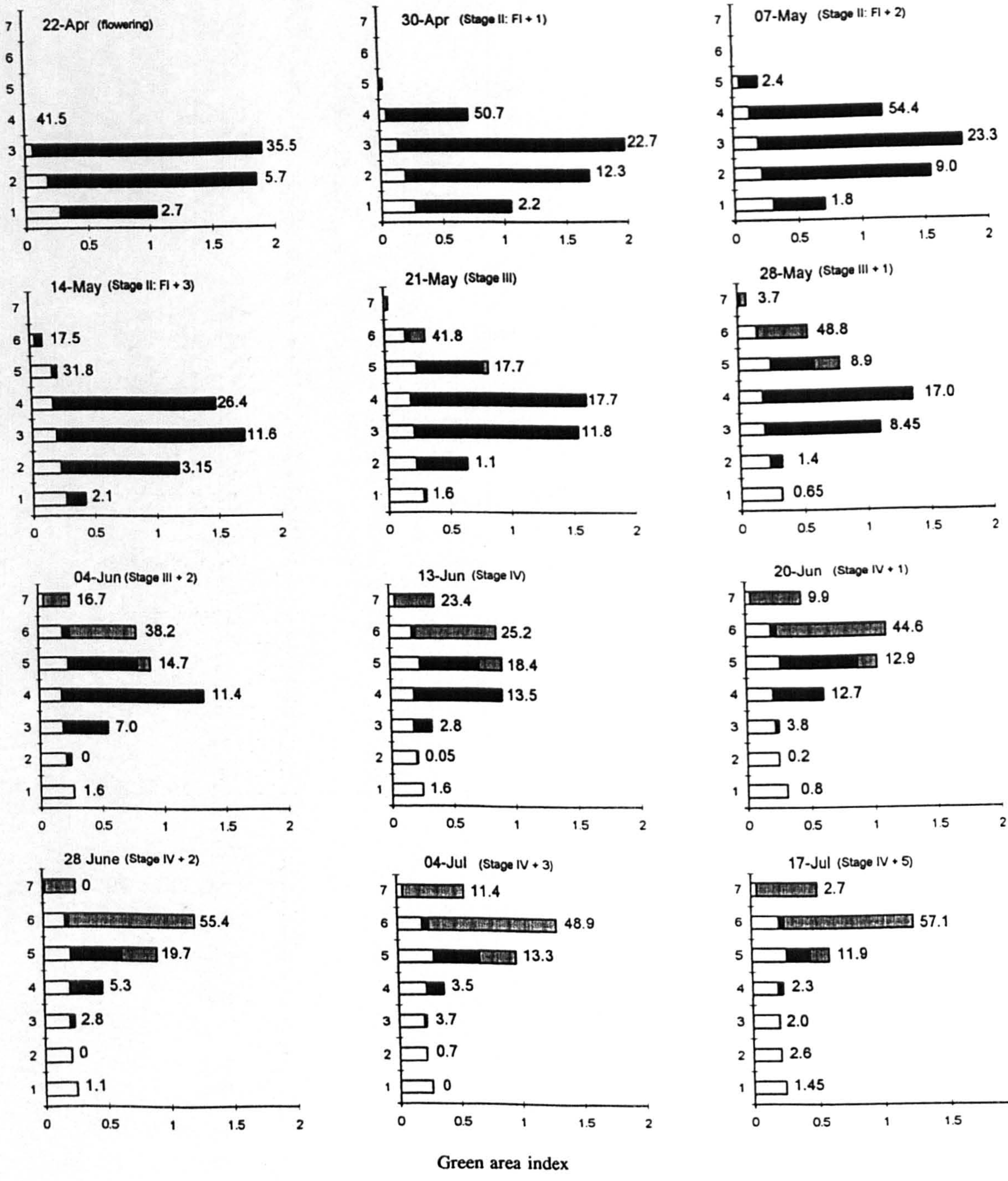
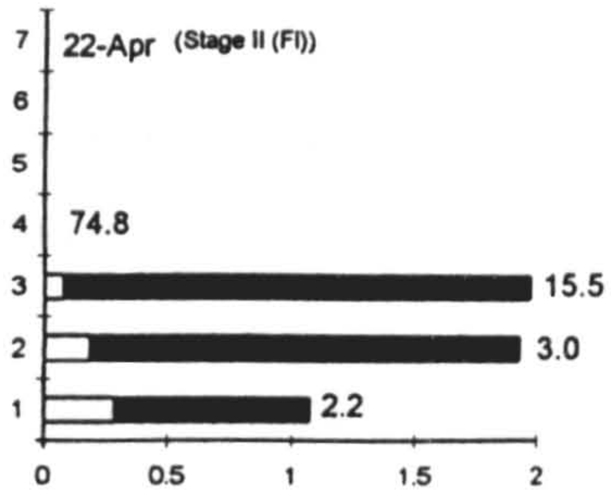
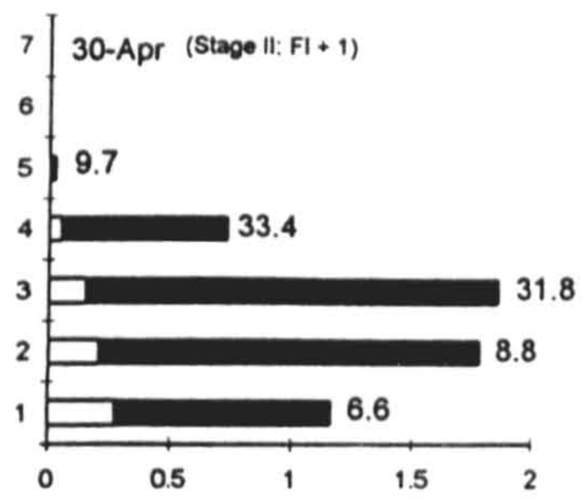
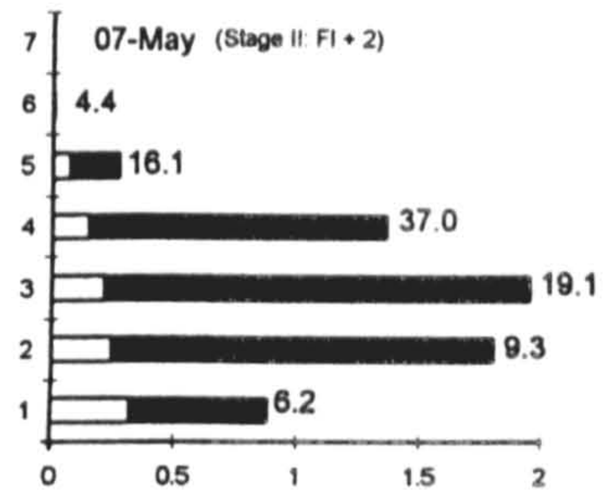


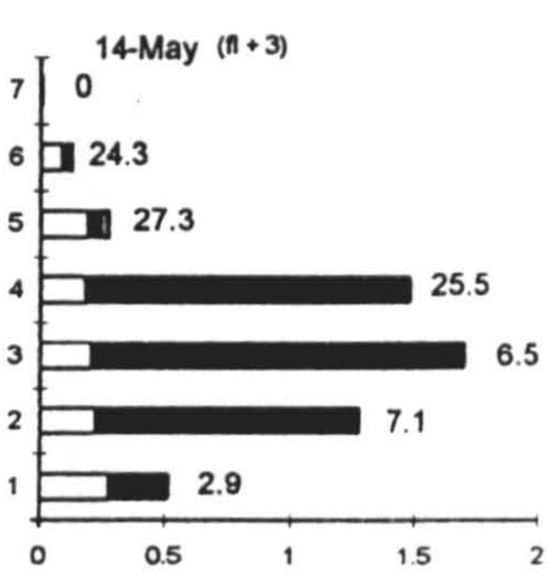
Fig. IV.2. Uncorrected data for radiation interception in the crop profile in relation to green area index: the effect of prochloraz in 1991.
Contents: GAI in each layer of the profile (bars: □ stem, ■ leaf, ▩ pod); % of total incident radiation intercepted in each layer (figures next to bars); for reproductive development: (a) 1991, (b) 1992, and (c) 1993.

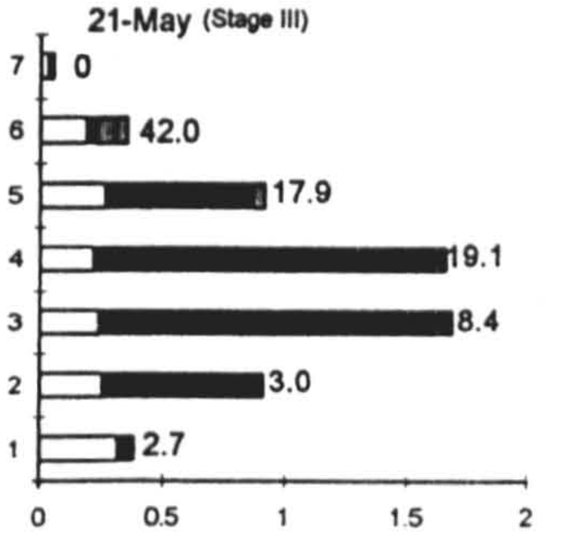
(b) Prochloraz-treated

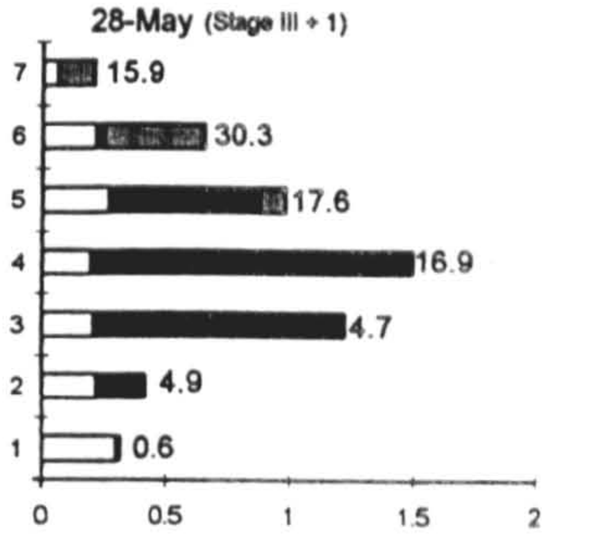


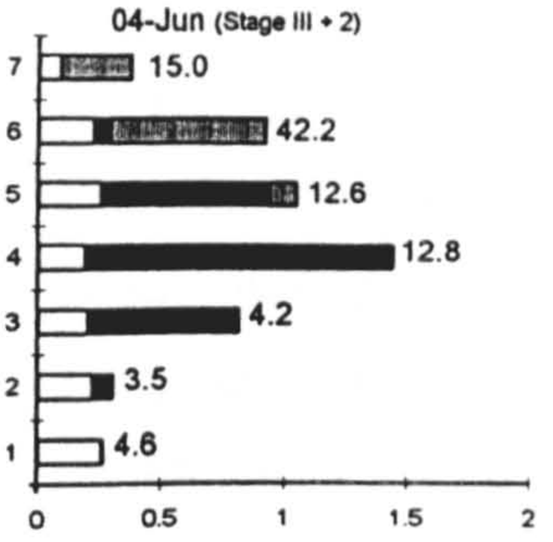


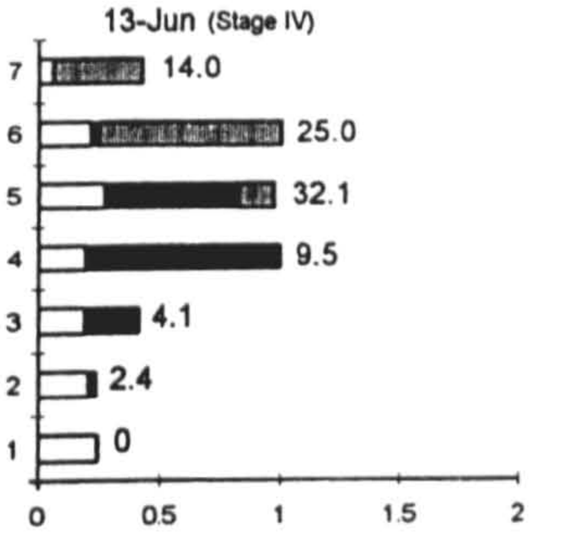


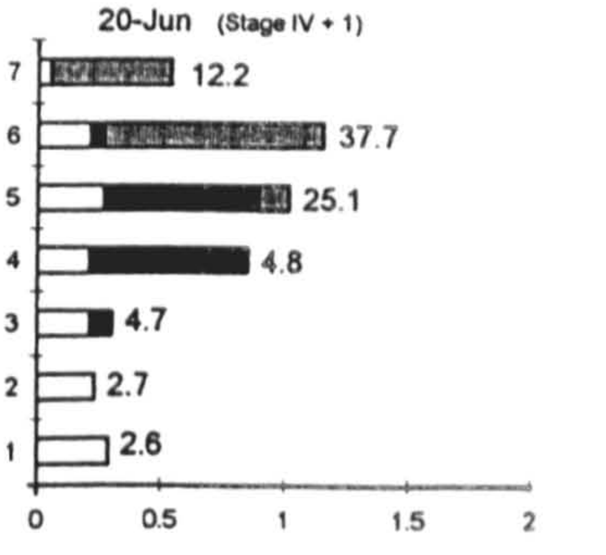


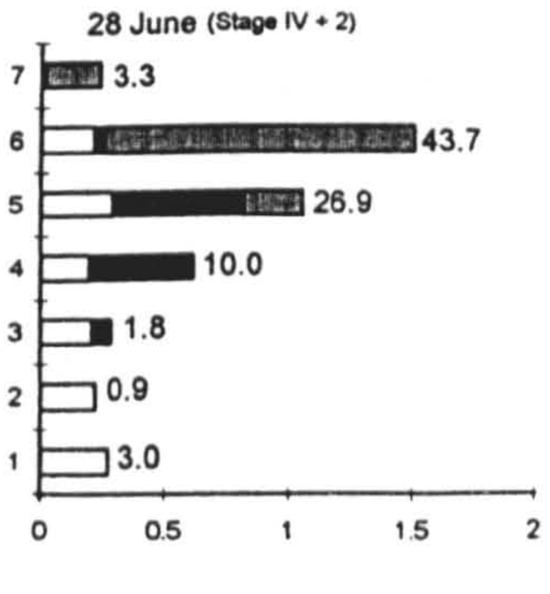


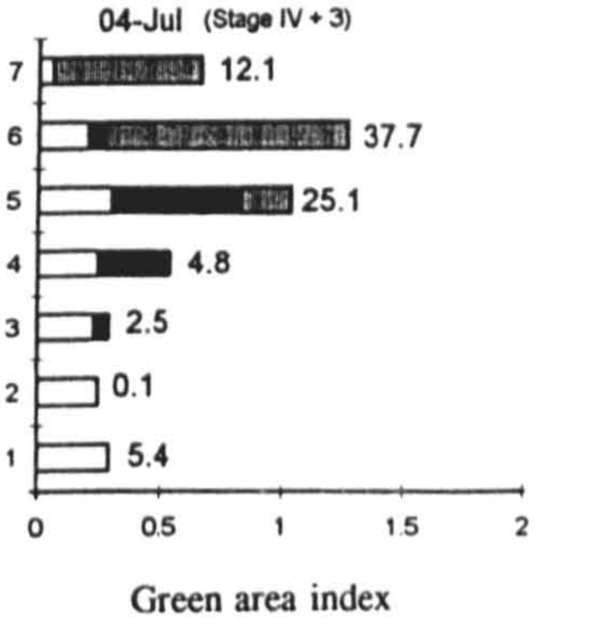


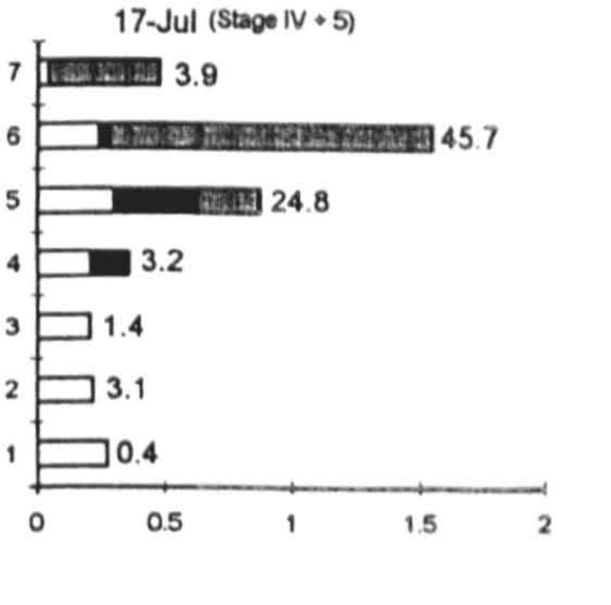












Green area index

Correction of solar radiation interception data in order to match interception and GAI data in the pod canopy:

1. The reduction of solar radiation down the crop profile was assumed to approximate to Beer's Law: $f = 1 - e^{-kG}$ where f = fractional interception, k = extinction coefficient and G = green area index.
2. Most of the misalignment was at the top of the crop. It was assumed that the pod canopies for both data sets had the same properties and therefore had the same extinction coefficient (k).
3. The proportion of radiation passing through the pod canopy was assumed to be the same in both $(1 - f_p)$.
4. k was calculated by substituting cumulative GAI (G_p) for the pod canopy and $(1 - f_p)$ into the Beer's Law equation.
5. The proportion of radiation passing through the top layer $(1 - f_7)$ was calculated by substituting GAI for the top layer (G_7) and k into the Beer's Law equation.
6. The proportion passing through the top two layers $(1 - f_{7+6})$ was calculated by substituting G_{7+6} and k into the equation. This procedure was repeated for the next layer.
7. The proportions of radiation intercepted by successive layers down the pod canopy were calculated from the difference between (1 - f) values, i.e. $f_7 = 1 - (1 - f_7)$, $f_6 = (1 - f_7) - (1 - f_6)$, and so on.
8. Original data were used for interception below the pod canopy.

k values for canopies in each season

1991

Stage	Interval	*k* value
II	7-14 May	0.69
	14-21 May	0.52
III	21-28 May	0.52
	28 May-4 June	0.48
	4-13 June	0.51
IV	13-20 June	0.46
	20-28 June	0.55
	28 June-4 July	0.46
	4-17 July	0.49
	17-29 July	0.67

1992

Stage	Interval	*k* value
III	14-29 May	0.74
	29 May-12 June	0.44
IV	12-26 June	0.48
	26 June-9 July	0.71
	9-16 July	0.95

1993

Stage	Interval	*k* value
II	22 April-4 May	0.34
II/III	4-18 May	0.21
III	18 May-1 June	0.28
IV	1-15 June	0.34
	15-30 June	0.39
	30 June-13 July	0.34

APPENDIX V

TABULATED SEDS FOR GROWTH ANALYSIS DATA

Table V.1. SEDs for the effect of prochloraz on DM (g m^{-2})and green area index in 1991

	Dry matter						Green area index			
	Leaf	Stem	Pod	Hull	Seed	Total	Leaf	Stem	Pod	Total
26 Jan	11.83	0.416	-	-	-	12.28	0.064	0.001	-	0.008
19 Mar	2.90	0.674	-	-	-	3.54	0.088	0.004	-	0.162
8 Apr	7.54	4.80	-	-	-	10.80	0.124	0.015	-	0.251
22 Apr	0.53	24.3	-	-	-	29.4	0.030	0.017	-	0.139
30 Apr	5.68	10.84	-	-	-	16.16	0.205	0.015	-	0.114
7 May	15.65	29.9	-	-	-	47.0	0.309	0.016	-	0.102
14 May	32.4	22.5	1.50	-	-	31.0	0.317	0.015	-	0.084
21 May	9.52	17.98	4.64	-	-	20.8	0.262	0.015	0.029	0.107
28 May	5.56	29.3	11.68	-	-	36.7	0.150	0.017	0.093	0.065
4 Jun	0.82	6.22	8.61	-	-	3.12	0.033	0.025	0.071	0.069
13 Jun	7.62	6.43	17.87	-	-	29.4	0.195	0.019	0.095	0.085
20 Jun	8.00	31.9	37.2	29.3	6.17	59.4	0.178	0.018	0.085	0.068
28 Jun	6.49	18.92	21.7	25.5	5.97	43.6	0.210	0.019	0.115	0.104
4 Jul	4.22	30.50	11.51	7.85	13.37	42.2	0.134	0.020	0.192	0.125
17 Jul	2.50	12.77	36.5	22.5	23.8	37.8	0.074	0.020	0.159	0.115
29 Jul	1.64	43.0	23.3	7.09	10.32	39.2	0.028	0.016	0.081	0.060

Table V.2. SEDs for the effect of prochloraz on DM (g m^{-2}) and green area index in 1992

	Dry matter						Green area index			
	Leaf	Stem	Pod	Hull	Seed	Total	Leaf	Stem	Pod	Total
30 Apr	9.83	17.01	-	-	-	25.60	0.316	0.094	-	0.406
14 May	8.21	14.82	2.75	-	-	7.77	0.030	0.116	0.018	0.096
29 May	7.45	12.35	30.2	-	-	27.60	0.233	0.075	0.111	0.288
12 Jun	5.26	27.70	77.3	43.7	26.4	90.20	0.160	0.095	0.356	0.287
26 Jun	4.91	16.78	54.0	21.5	32.3	71.40	0.145	0.044	0.191	0.365
9 Jul	1.98	32.70	89.8	21.6	66.2	90.30	0.078	0.097	0.139	0.121

Table V.3. SEDs for the effect of prochloraz on DM (g m^{-2}) and green area index in 1993

	Dry matter						Green area index			
	Leaf	Stem	Pod	Hull	Seed	Total	Leaf	Stem	Pod	Total
6 Nov	0.90	-	-	-	-	0.90	0.023	-	-	0.023
20 Nov	5.48	-	-	-	-	5.48	0.063	-	-	0.063
11 Dec	3.89	-	-	-	-	3.89	0.060	-	-	0.060
6 Jan	8.82	-	-	-	-	8.82	0.118	-	-	0.118
3 Feb	9.95	-	-	-	-	9.95	0.127	-	-	0.127
10 Mar	8.62	0.74	-	-	-	9.42	0.095	0.002	-	0.096
31 Mar	23.40	9.83	-	-	-	33.3	0.340	0.027	-	0.364
20 Apr	5.26	20.70	-	-	-	27.4	0.225	0.061	-	0.259
4 May	4.72	21.90	0.96	-	-	23.9	0.167	0.098	0.002	0.072
18 May	6.52	34.50	12.88	-	-	50.3	0.163	0.064	0.040	0.203
1 Jun	11.34	8.13	38.20	29.00	9.76	20.5	0.285	0.016	0.167	0.164
15 Jun	6.54	33.20	69.00	43.90	25.7	105.7	0.210	0.112	0.167	0.342
30 Jun	10.48	25.90	22.70	8.14	19.59	59.6	0.291	0.169	0.079	0.431
13 Jul	1.51	10.04	11.23	5.15	6.06	19.50	0.042	0.070	0.131	0.221

Table V.4. SEDs for the effect of prochloraz on pod numbers m^{-2}, seed number m^{-2} seed number per pod and 1000-seed weight (g) in 1991

	Pod numbers				Seeds		
	Fertile	Total	Abscised	Potential	Seed number m^{-2}	Seed number per pod	1000-seed weight
14 May	104.6	-	97.0	172.9	-	-	-
21 May	348.5	-	89.2	286.3	-	-	-
28 May	326.0	-	502.5	237.6	-	-	-
4 Jun	654.4	-	390.2	880.8	-	-	-
13 Jun	893.0	-	255.0	817.2	-	-	-
20 Jun	1157.7	-	709.2	1861.8	5.99	0.85	0.06
28 Jun	606.1	-	383.4	222.7	5.78	0.87	0.09
4 Jul	377.4	-	451.9	286.7	2.52	0.81	0.08
17 Jul	503.8	503.1	31.9	525.9	4.06	0.57	0.09
29 Jul	294.6	78.7	-	-	1.69	0.71	0.11

Table V.5. SEDs for the effect of prochloraz on pod numbers m^{-2}, seed number m^{-2}, seed number per pod and 1000-seed weight (g) in 1992

	Pod numbers				Seeds		
	Fertile	Total	Abscised	Potential	Seed number m^{-2}	Seed number per pod	1000-seed weight
14 May	138.7	-	635.2	739.6	-	-	-
29 May	1081.1	-	462.3	1490.8	-	-	-
12 Jun	688.4	-	555.0	1221.2	10772.4	1.454	0.070
26 Jun	345.1	379.2	272.9	626.2	5315.3	1.133	0.154
9 Jun	800.1	1337.8	1217.2	2474.1	22010.7	5.53	1.547

Table V.6. SEDs for the effect of prochloraz on pod numbers m^{-2}, seed number m^{-2}, seed number per pod and 1000-seed weight (g) in 1993

	Pod numbers				Seeds		
	Fertile	Total	Abscised	Potential	Seed number m^{-2}	Seed number per pod	1000-seed weight
4 May	128.4	-	538.6	1039.4	-	-	-
18 May	418.7	-	514.2	1065.7	-	-	-
1 Jun	712.1	-	443.9	291.4	2.42	2.26	0.069
15 Jun	926.8	-	249.8	1097.8	10.21	1.17	0.104
30 Jun	333.1	-	475.7	745.7	7.21	0.49	0.208
13 Jun	597.0	1337.8	43.7	589.6	1.40	1.27	0.175

APPENDIX VI

Table VI.1. Correlation matrix indicating correlation coefficients and levels of significance for relationships between seed yield, the components of yield, and harvest index over the three seasons 1991-1993.

	Pod number m^{-2}	Seed number per pod	1000-seed weight (g)	Seed number m^{-2}	Harvest index
Seed yield (g m^{-2})	0.366^{***}	0.446^{***}	0.298^{***}	0.815^{***}	0.828^{***}
Seed number per pod	-0.307^{**}	-	-	-	-
1000-seed weight (g)	-0.224^{*}	n.r.	-	-0.251^{*}	-
Seed number m^{-2}	-0.519^{***}	0.481^{***}	-	-	-
Harvest index	n.r.	0.706^{***}	0.176^{+}	0.722^{***}	-

+, *, **, *** significant at $P < 0.10$, 0.05, 0.01, and 0.001;
n.r. indicates no relationship;
- indicates not applicable.

APPENDIX VII

METEOROLOGICAL DATA FOR THE THREE SEASONS 1991-1993

Table VII.1. Mean monthly average temperatures (°C) with the long-term averages for 1921-1994

	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July
1990-91	18.7	13.3	12.3	7.0	4.5	2.95	1.85	8.2	7.85	11.0	16.15	17.45
1991-92	16.9	14.85	10.2	7.35	4.5	3.25	5.8	7.6	8.75	13.4	15.95	16.25
1992-93	15.9	13.4	7.8	7.1	3.4	5.7	4.9	6.8	9.5	11.4	14.8	15.3
Long-term average	16.3	12.7	9.7	9.7	6.3	5.1	3.3	7.9	8.5	10.1	14.7	18.3

Table VII.2. Average mean daily solar radiation (MJ m^{-2}) with the long-term averages for 1958-1994

	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July
1990-91	15.3	9.4	5.5	2.4	1.7	2.45	3.9	6.4	11.0	12.6	12.9	8.5
1991-92	14.9	11.1	5.1	2.7	1.6	2.1	4.4	6.7	11.5	18.9	17.7	15.1
1992-93	13.7	8.7	5.1	2.8	1.6	2.0	3.7	8.4	10.8	15.7	17.3	16.5
Long-term average	13.0	9.7	5.5	2.7	1.7	2.2	4.1	7.1	11.1	14.9	16.5	15.5

Table VII.3. Monthly rainfall (mm) with the long-term averages for 1916-1994

	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July
1990-91	38.6	31.9	62.7	44.1	67.9	47.1	26.7	36.6	55.8	11.1	60.7	54.4
1991-92	14.9	47.1	35.2	48.8	28.7	59.9	20.4	52.7	27.9	37.9	60.9	86.8
1992-93	57.8	77.9	68.2	78.0	39.0	49.6	6.5	9.6	65.7	45.5	71.7	80.7
Long-term average	60.0	58.0	52.0	58.0	55.0	52.0	41.0	45.0	40.0	47.0	47.0	51.0

APPENDIX VIII : PUBLICATIONS

From the

Proceedings of the ninth International Rapeseed Congress, Cambridge, 1995.

THE RELATIONSHIP BETWEEN CANOPY STRUCTURE AND YIELD IN OILSEED RAPE

S.C. MCWILLIAM, J.A. STAFFORD, R.K. SCOTT, G. NORTON, D.T.STOKES

Departments of Agriculture and Horticulture and Applied Biochemistry and Food Science, University of Nottingham, Sutton Bonington Campus, Loughborough, Leics, LE12 5RD, UK.

R. SYLVESTER-BRADLEY

ADAS, Anstey Hall, Maris Lane, Trumpington, Cambridge CB2 2LF, UK.

ABSTRACT

Both anecdotal evidence from growers and yield data from past experiments have indicated that thick, advanced crops of oilseed rape do not always yield as much as their thinner counterparts. This paper uses results from detailed measurements of growth and radiation interception made in two experiments to identify the likely mechanisms responsible for these observations.

INTRODUCTION

Yields of oilseed rape are notoriously variable; interestingly, farmers have reported similar or even better yields from sparse crops. Experiments examining the influence of plant establishment, sowing date and defoliation have also shown yield advantages following poor initial growth and the production of sparse and more open canopies (Mendham, Shipway & Scott, 1981; Spink, 1992). Table 1, reproduced from Jenkins and Leitch (1986) shows how the smaller biomass, fewer pods m^{-2} and lighter seeds of late sowings, were totally offset by a twofold increase in the number of seeds per pod.

TABLE 1. Yield components showing compensatory effect on seed number per pod.

Sowing Date	Yield (t/ha) 91% dm	Pods per m^2	Seeds per pod	1000 seed wt (g)	Harvest Index (%)	Total Biomass (t/ha)
10/9/82	4.82	7224	11	6.1	31	14.6
2/12/82	4.77	4703	20	4.9	35	13.1
7/9/83	4.35	11068	9	4.53	24	16.5
20/10/83	5.03	7208	19	3.68	30	15.4

The inference is that unlike crops such as sugar beet and cereals for which yield is strongly correlated with the amount of radiation intercepted and hence biomass produced, the yield of oilseed rape is more subtly linked with canopy architecture and the distribution of radiation within the canopy, particularly features which favour a high seed number per pod. This paper investigates the mechanisms that prevent thick crops from doing well while sometimes allowing sparse crops to do better.

EXPERIMENTAL

Plant population studies

A field experiment sown on 8 September 1992 examined the response of oilseed rape (cv. Libravo) when thinned in March to 7, 15, 30, 70 and 120 plants m^{-2}. Characteristically, lower populations compensated for fewer pods by retaining more seeds per pod (Table 2).

Between thinning in March and flowering in late April, biomass production was linked with green area index (GAI); higher populations had larger GAIs (Fig 1), intercepted more radiation and produced more biomass (Table 2). However, between flowering and harvest, the thicker canopies produced less biomass, despite maintaining larger GAIs (Fig 1) and intercepting more radiation (1370 MJ in 120 plants m^{-2}, but only 1220 MJ in 7 plants m^{-2}). Therefore, yield production seemed not to be linked with radiation interception by the whole crop. Examination of the pod layer in the 7, 15 and 120 plant m^{-2} canopies showed that the low densities (Fig 1) intercepted less radiation between flowering and maturity; 730MJ (120), 580MJ (15) and 540MJ (7). Thus, despite intercepting more radiation both in the pod layer and in the crop as a whole, the thicker crops used this radiation less efficiently, produced less growth after flowering resulting in greater loss of seeds and slightly smaller yields at harvest. The explanation for this must lie in the fate of intercepted radiation within the canopy.

TABLE 2. Yields and components from the plant population experiment

Plant Pop. m^{-2}	Yield(t/ha) 91% dm (SED=0.21 12df)	Pods per m^2	Seeds per pod	1000 seed wt (g)	HI (%)	Biomass (t/ha) Flowering	Harvest
7	3.6	4600	16	4.78	35	3.5	10.0
15	3.4	5300	15	4.49	33	5.0	10.0
30	3.7	6700	13	4.40	33	6.5	11.5
70	2.9	6200	10	4.84	27	8.4	11.0
120	3.0	6500	10	4.56	26	8.5	11.5

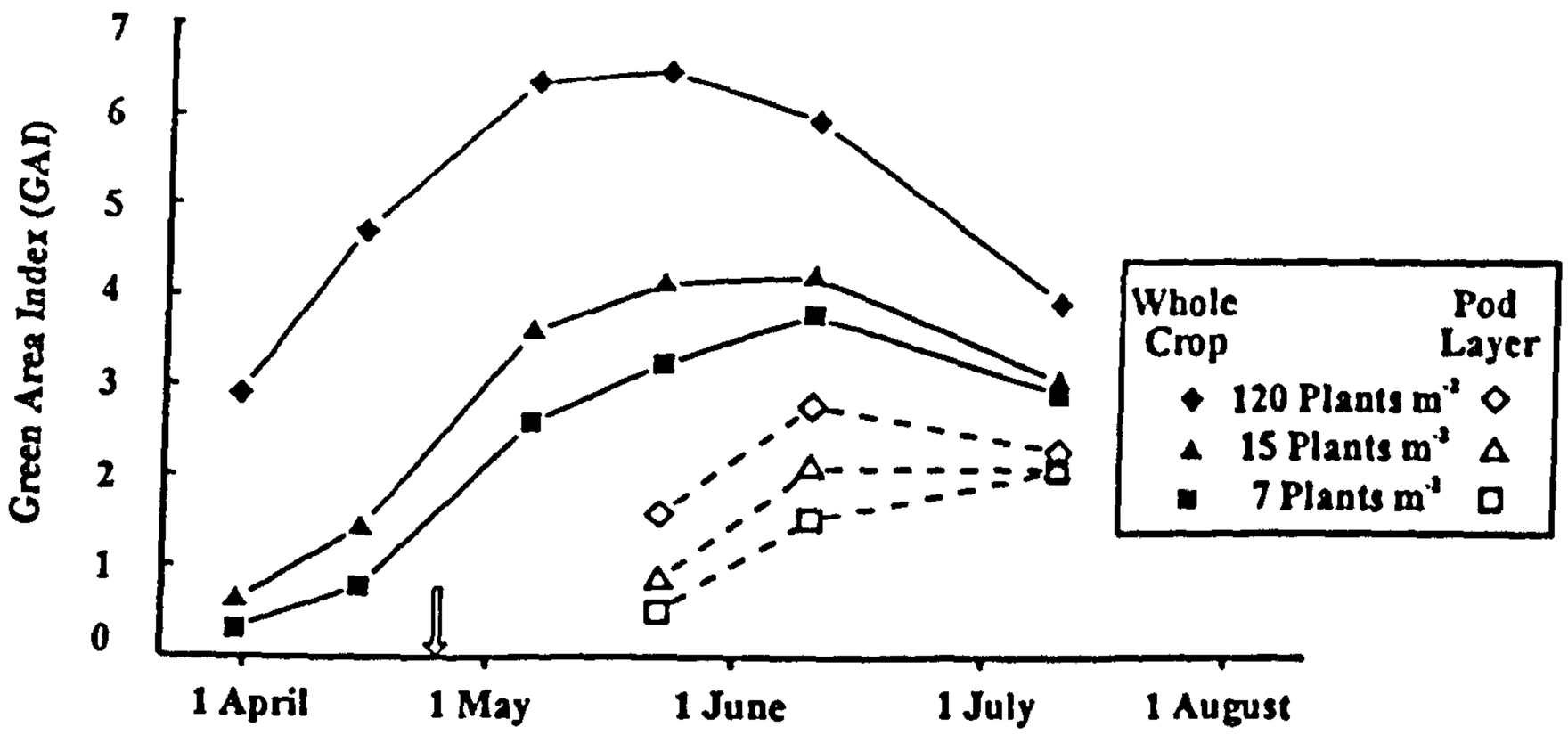


FIGURE 1. Green area index from 15 April to 8 July for whole crop and pod bearing layer from the 7, 15 and 120 plants m^{-2} populations; arrow indicates flowering.

Contrasting canopies in successive years

Following similar husbandry of autumn-sown Capricorn in 1992 & 1993, exceptionally

bright weather in May 1992 resulted in the growth of a much thicker pod canopy (GAI 6.8, 9500 pods m^{-2}) in late May compared with more normal conditions in 1993 (GAI 5.2, 6000 pods m^{-2}). Fig 2 shows a 'snap-shot' in mid June (early pod development) of the canopy profiles, with radiation penetration calculated for a typical day in June (incident radiation = 20 MJ m^{-2}). Pods set and seeds per pod at the end of May and those which were retained through to final harvest are represented diagrammatically for the different layers of the profile.

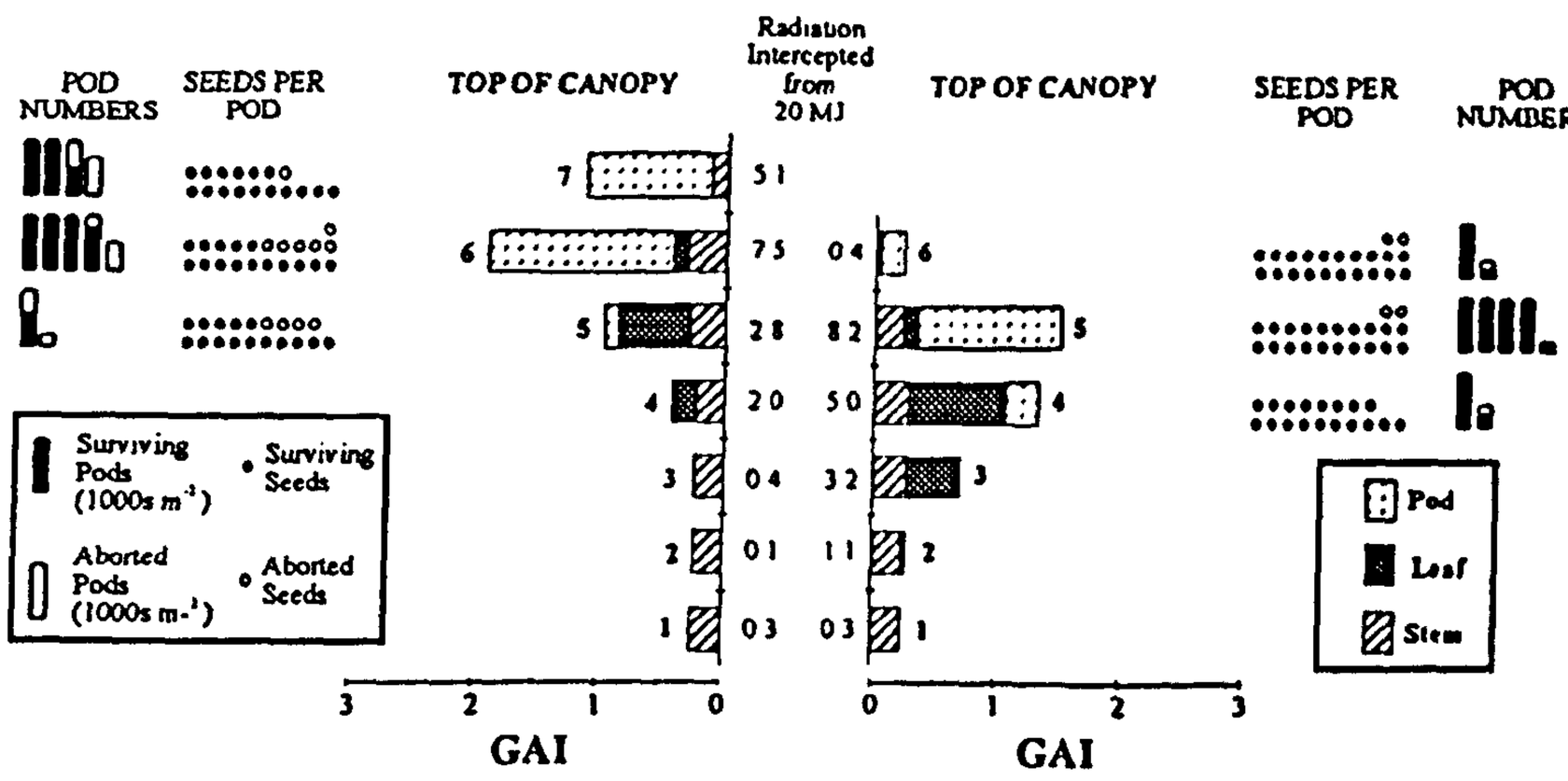


FIGURE 2. Diagrammatic representation of the canopies in 20cm layers showing the distribution and nature of the intercepting surface, radiation interception and fate of pods and seeds.

The thick crop resulted from 50% more pods setting. The top layer was well illuminated and few seeds per pod were lost. The pods lost in this layer were initiated late and almost certainly doomed not to survive, irrespective of radiation environment. In layer 6 of the thick crop, which was also dense, the shading from the top layer resulted in losses of pods and seeds per pod. Importantly, only one quarter of the radiation penetrated through to the lower layers (5 and 4) where the majority of leaves were situated. In contrast, the sparse crop allowed almost half the radiation to penetrate to the base of the pod layer and it seems that this better illumination and hence greater contribution to photosynthesis from lower leaves and pods is the likely causal mechanism leading to the maintenance of a high seed number per pod and the route through which sparse crops yield better than expected.

ACKNOWLEDGEMENTS

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EFFECTS OF PROCHLORAZ ON THE PHYSIOLOGY OF OILSEED RAPE

J.A. STAFFORD, G. NORTON, R.K. SCOTT, D.T. STOKES

Departments of Agriculture & Horticulture and Applied Biochemistry & Food Science, University of Nottingham, Sutton Bonington Campus, Loughborough, Leics. LE12 5RD.

K.J. DOUGHTY

Department of Plant Pathology, Rothamsted Experimental Station, AFRC Institute of Arable Crops Research, Harpenden, Herts. AL5 2JQ.

P.E. RUSSELL

AgrEvo UK Ltd., Chesterford Park, Saffron Walden, Essex CB10 1XL.

ABSTRACT

The effects of the imidazole fungicide prochloraz on the physiology of yield production were investigated in the winter oilseed rape variety Capricorn. Prochloraz was applied in autumn, spring and summer and crop growth assessed using stratified sampling. The chemical increased seed yield by 16% due largely to increased pod numbers m^{-2} and a slight increase in seed number per pod. Pod and seed abscission post-flowering were lessened probably through increased leaf persistence that utilised radiation passing through the pod layer more efficiently. These effects were not associated with the fungicidal activity of prochloraz.

INTRODUCTION

Experiments at Rothamsted Experimental Station have shown that applications of the imidazole fungicide prochloraz to oilseed rape sometimes produce yield increases which are not associated with reductions in disease incidence or severity (Bock *et al.*, 1991). A field experiment at Nottingham in 1990-91 was designed to further investigate a possible physiological response to prochloraz.

MATERIALS AND METHODS

Prochloraz (500g.a.i. ha^{-1} Sportak 45) was applied to replicated plots of Capricorn on 22nd November, 23rd April and 2nd July. Detailed analyses in a $1m^2$ area, harvested in 20 cm layers, were made of crop growth and development. Solar radiation interception was measured using tube solarimeters positioned in alternate rows at 20 cm intervals up the crop profile.

RESULTS AND DISCUSSION

Compared with unsprayed controls, prochloraz increased the seed yield (hand-harvested) by 16%, total pod (fertile + split) number m^{-2} by 14% and the number of yield-forming pods by 17% (Table 1). Mean seed number per pod was increased slightly (7%) but the average weight of individual seeds was not affected.

Table 1. Effect of prochloraz on seed yield and yield components

	Seed yield	Pod number m^{-2}		Seed number per pod	1000-seed wt
		Total	Yield-forming		
	(t ha^{-1})				(g)
Control	4.1	4527	4001	16.1	6.63
Prochloraz	4.8	5161	4668	17.2	6.68
S.E.D.*	0.14	340	378	1.09	0.08

(23 df)*

Treatment effects were not evident in late January but by mid-March leaf area index (LAI), stem area index and biomass were greater in prochloraz plots. These differences were maintained through to final harvest when total crop dry matter m^{-2} was increased by 13%because more seeds were retained. Yields reflected biomass production; there was no change in harvest index.

From flowering onwards, LAI declined from the base of the profile upwards in both treatments but more rapidly in the controls. Spraying with prochloraz increased the LAI within the pod canopy and in the layer below. The effect persisted when pods and seeds were developing in mid-late May and also during seed development in June and July. Prochloraz increased the potential number of pods, associated with the greater biomass at flowering (Mendham, Shipway & Scott, 1981) but the proportion of potential pods that set was not affected. The chemical treatment did not affect the initial number of seeds per pod but slightly improved their survival. This is unusual because following an increase in pod number, the extra shading in lower layers would normally result in a compensatory reduction in seed number per pod.

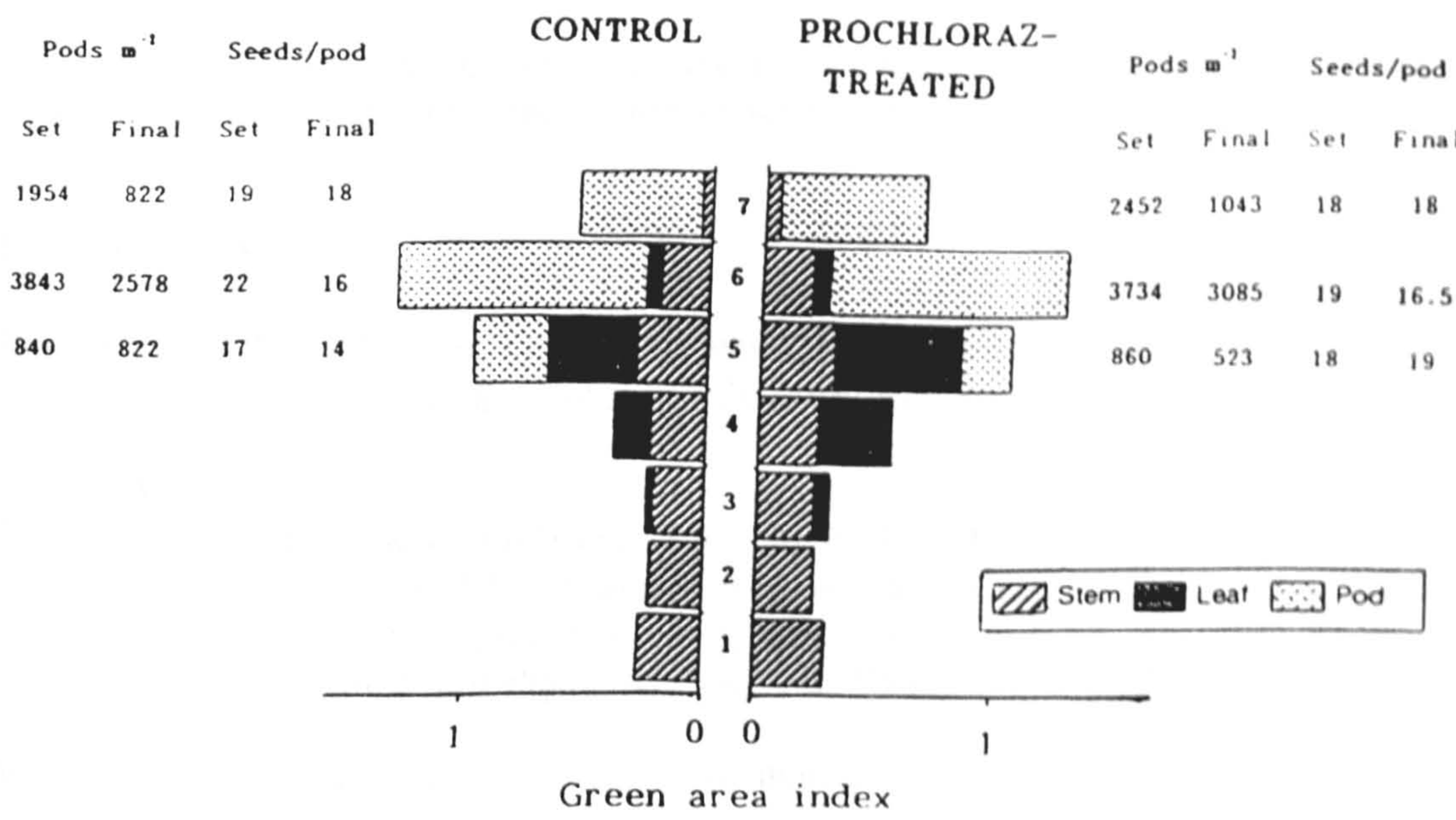

Fig. 1. Crop profiles in 20 cm layers on 4 July showing the components of green area index for each treatment and numbers of pods and seeds per pod set and at final harvest.

Prochloraz had only minor and transitory effects on disease incidence (light leaf spot (*Pyrenopeziza brassicae*) was slightly less in mid April but there was no effect in May; light stem and pod spot was reduced in early July). Thus the effects of prochloraz (which is structurally related to the growth regulatory triazoles used to modify growth in oilseed rape) on growth and yield are attributed to phytotonic rather than fungicidal properties. The effects were mediated through a change in the relationship between leaf and non-leaf photosynthesis which is important because on an area basis leaves are more efficient than pods and stems (Bilsborrow & Norton, 1988).

Fig. 1 represents the crop profiles divided into 20 cm layers on 4 July when thee top three layers formed the pod canopy. Prochloraz increased the LAI substantially in layer 5 and slightly in layer 6. It also maintained more leaf in layer 4 directly below the pod canopy. Thus more of the radiation penetrating through the pod canopy was intercepted by leaf in the prochloraz treatment compared with the control. Assimilates mostly move acropetally (Major & Charnetski, 1976) and it seems likely that photosynthesis by leaves at the base of the pod canopy promoted pod and seed survival in the treated crop. Prochloraz resulted in fewer seeds per pod being aborted in the lower layers of the canopy. However, the effect on seed number per pod was responsible for only a small proportion of the yield response, the majority of which was attributable to the production and retention of more pods in the upper and middle regions of the pod canopy.

In summary, prochloraz increased yield by improving leaf retention and radiation capture leading to improved assimilate supply during seed filling which favoured greater retention of both pods and seeds per pod.

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