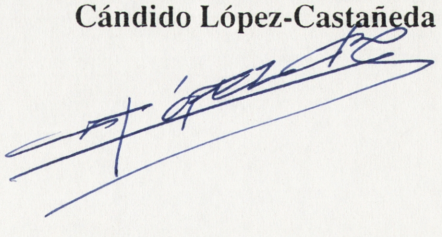
A COMPARISON OF GROWTH AND WATER-USE EFFICIENCY IN TEMPERATE CEREAL CROPS

A Thesis Submitted for the Degree of
Doctor of Philosophy
at the Australian National University

by

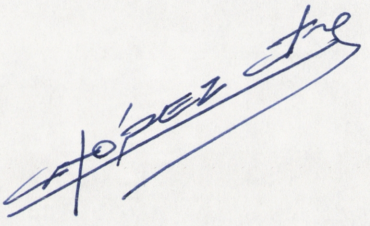
Cándido López-Castañeda



March 1992

STATEMENT

The work presented in this thesis is my own. Specific contributions and co-operative work with other are referred to in the acknowledgements.



Cándido López-Castañeda

Plant Environmental Biology Group
Research School of Biological Sciences
Australian National University
Canberra

ACKNOWLEDGEMENTS

I would like to thank Professor C.B. Osmond, Director, Research School of Biological Sciences, Australian National University, and Dr. W.J. Peacock, Chief, CSIRO, Division of Plant Industry, for allowing me to use the facilities of RSBS and of CSIRO to conduct this work.

I am especially grateful to Dr. Richard A. Richards and Professor Graham D. Farquhar for their helpful and enthusiastic supervision. Their encouragement and guidance are greatly appreciated.

Thanks are also due to Drs. Kerry Hubick, Tony Condon, Richard Williamson, Frank Dunin, Tony Fischer and Howard Rawson for helpful advice and fruitful discussions on various aspects of this work.

Staff at both the CSIRO, Division of Plant Industry and the Research School of Biological Sciences, provided excellent support in all aspects of this work. This included the use of field machinery for sowing and harvesting field trials and the introduction to scanning electron microscopy for exploring leaf epidermal cells.

Special thanks goes to Bernie Mickelson for his excellent technical help, advice, dedication and indefatigable support.

Field facilities and land preparation was generously provided by the New South Wales Department of Agriculture, Condobolin, and by Mr Alan Semmler 'Glenora', Moombooldool.

I am especially grateful to the field team comprising Richard, Tony, Bernie and Helena, not only for support in the field, but particularly in my final days in Australia.

The opportunity to do this work was provied by CONACYT and Colegio de Postgraduados at Chapingo, México. To them I shall be forever grateful.

Finally, to my family, Consuelo, Cinthya and Flerybeth. To them I owe special gratitude for the many sacrifices thay have made to enable me to complete this work.

ABSTRACT

The temperate cereals, bread wheat, durum wheat, triticale, barley and oats, are grown in Australia during the winter and spring. They are grown in the same regions and require similar agronomic practices. Phenotypically they are alike until the seed bearing structures emerge from stems at around anthesis. Thus, their comparison in the field is practical, although uncommon. In Australia, drought beginning around anthesis and continuing through grain filling is the principal edaphic factor limiting yields of these species. Hexaploid wheat or bread wheat, is the dominant species grown and accounts for 85% of the total temperate cereal grain production.

Studies were initiated to contrast bread wheat with durum wheat, triticale, barley and oats as each of these species has attributes that bread wheat may not possess, but if incorporated into bread wheat, may improve its yield in rainfed environments. Cultivars of bread wheat, durum wheat, triticale, barley and oats, adapted to rainfed areas in south-eastern Australia, were chosen for study. They were representative of commercial cereals grown in this region and covered a range of maturity times. Genotypes were grown at two sites in south-eastern Australia in three years. Aspects of their phenology were monitored as well as their growth and water use. The same genotypes were also grown in more precise conditions in pots either outside, in the glasshouse or in controlled environment cabinets.

Studies in field grown plants showed that barley had a 25% greater grain yield than the other species. Most of the yield advantage of barley was due to its higher above ground dry weight (AGDW) rather than to its higher harvest index (HI). The ranking in AGDW was barley > triticale > bread wheat > oats > durum wheat. When root biomass was included the advantage of barley was even greater as barley had an estimated 35% greater root length and mass than the other species. A remarkable feature of the higher biomass in barley compared to the other species was that it was achieved in a shorter time.

Although HI was not a major contributor to the yield advantage of barley, several important differences were found between genotypes and species in factors influencing HI. These were the rate of grain growth per unit ground area and the retranslocation of assimilates from the stem to the grain. The rate of grain growth per unit ground area in barley was 60% higher than in the other species. Bread wheat, triticale and oats were similar and about 30% higher than durum wheat. The greater grain growth in barley did not translate into a higher HI as the duration of grain growth was shorter. Stem weight at anthesis and maturity was determined in all genotypes at two sites to estimate retranslocation to the grain. Values averaged 25% (range 4 to 60%) and the amount was related to flowering time. Genotype rankings were similar in both years. At the driest site the amount of retranslocation was positively correlated with yield.

Differences among species and genotypes in AGDW and total biomass were not related to differences in soil water extraction. The amount of soil water extraction was greater in late flowering genotypes but differences in water extraction were independent of root length density.

Variation in AGDW was related to variation in water use efficiency and transpiration efficiency. Water use efficiency (WUE) was the main determinant of variation in yield. This was closely related to flowering time such that WUE declined by 0.67 kg $ha^{-1}mm^{-1}$ for each days delay in flowering. Variation in WUE was attributed to two factors. Firstly, to variation in transpiration as a proportion of evapotranspiration. This was greater in cultivars with the fastest leaf area development. Secondly, to the greater growth of the most vigorous lines when vapour pressure deficit (VPD) was low. The "effective transpiration", calculated by normalising transpiration for seasonal changes in VPD, was 26% higher in barley than the other species because of the greater growth by barley during the coolest periods. Variation in carbon isotope discrimination was not associated with variation in transpiration efficiency in these experiments.

The possible advantage of barley over the other species may have been due to it having a lower base temperature for growth. This was investigated by monitoring leaf extension but it was concluded that this could not account for the advantage of barley. Variation in relative growth rate between species was also eliminated as contributing to the higher AGDW of barley over the other species, as was tiller appearance rate, leaf appearance rate and the rate of utilisation of seed reserves.

Three factors were principally responsible for the greater early vigour in barley relative to the other species. Firstly, a larger and heavier embryo. This accounted for most of the variation in early plant weight among species. When seeds of the same kernel weight were examined, the barley embryo was found to be larger than the embryo of triticale which in turn was larger than that of the wheats and of oats. Secondly, barley leaves had a higher specific leaf area (SLA). This was found as soon as they emerged, giving barley a larger leaf area for a given leaf weight. Although this resulted in barley having a lower net assimilation rate, the greater area per plant more than compensated for this. A high specific leaf area was also associated with a high carbon isotope discrimination. Thirdly, and of least importance in these experiments, was a faster emergence time in barley. Barley emerged about 10^0C per day earlier than the other species.

It is concluded that for temperate cereals growing in mediterranean-type environments, increasing early vigour should result in an improved water-use efficiency and hence a higher biomass and a higher grain yield. For wheat, oats and triticale this could best be achieved by emulating barley. To do this it is proposed that selection for the size of the first leaf would integrate both embryo size and a high specific leaf area in a simple way.

CONTENTS

CHAPTER 1

INTRODUCTION, LITERATURE REVIEW AND EXPERIMENTAL OBJECTIVES

1.1 INTRODUCTION

The most important cultivated cereals in the cool, temperate region of the world are wheat (both bread wheat and durum wheat), barley, oats and triticale. They are grown in the same regions and require similar agronomic practices. They are also phenotypically very similar, having a similar vegetative morphology, leaf anatomy and are alike until the seed bearing structures emerge from the sheath of the last leaf of each stem or tiller around anthesis. All are inbreeding and have a basic chromosome number of seven.

Bread wheat is grown over a wider area than the other crops, primarily because it has a more marketable grain. In Australia, the area sown to wheat is about 11.4 Mha followed by barley 2.8 Mha, oats 1.3 Mha and triticale 0.23 Mha. In Australia, as in other parts of the world, production of these cereals is limited by rainfall. In fact in Australia, the yield of a well managed wheat crop is almost certainly limited by water in every region in every year. Further increasing wheat yields genetically in rainfed areas is therefore a major challenge to plant breeders. Passioura (1977) has shown that a yield increase in dry areas can only be achieved if transpiration, water-use efficiency or harvest index is increased. More simply, an increase in either biomass or harvest index will result in higher yield providing an increase in one does not result in a greater reduction in the other (Richards and Townley-Smith, 1987).

This study was conducted to contrast the growth and yield of different cereal species in water limited environments to determine whether they have specific yield characteristics that, if incorporated into wheat, may improve its yield in dry environments. The species chosen for contrast have a reputation as being either more drought resistant or having superior vegetative characteristics to wheat.

1.2 LITERATURE REVIEW

1.2.1 Temperate cereals

The most important winter and temperate spring cereals are common or bread wheat (*Triticum aestivum* L.), durum wheat (*T. turgidum* L. var. *durum*), barley (*Hordeum vulgare* L.) and oats (*Avena sativa* L.). Less important are triticale (*Tricosecale* Wittmack) and rye (*Secale cereale* L.) with triticale being the more important in Australia. All except triticale evolved millenia ago. Triticale was developed to combine the high yield of wheat with the high protein and adaptation to difficult environments of rye. Triticale developed from crosses between hexaploid

wheat and rye have been less promising that those between tetraploid (durum) wheat and rye. Triticales are often further categorized into complete (those that contain all 14 chromosomes from tetraploid wheat and 7 from rye) or incomplete (those that contain introgressions of the D-genome chromosomes either as substitutions or translocations).

1.2.1.1 Economic importance

Wheat is the world's most important crop and its production exceeds all other food crops. Its importance is derived from the properties of its gluten. In addition to its use for bread, large quantities of wheat are also used for noodles, pastry, animal feed as well as for industrial use. These, combined with its nutritive value and storage qualities, have made wheat a staple food for more than one third of the world's population.

Wheat is grown on about 227 Mha and total production is about 520 Mt. About 100 Mha of wheat are grown in the developing world and 127 Mha in developed countries (CIMMYT, 1989). Of the wheat area sown globally 27% is irrigated, 42% is in areas where annual rainfall exceeds 500 mm whereas 31% is in regions where annual rainfall below 500 mm. Durum wheat occupies 12% of the total area sown to wheat and most of this is rainfed (CIMMYT, 1989).

Wheat generally is used for human consumption but in a few countries, notably the USSR and Japan, imported wheat allows low-quality, local wheat to be used as animal feed. For the 1988-89 period, the world trade in wheat was estimated at 97 Mt (CIMMYT, 1989). The principal importers of wheat are eastern Europe and the USSR; an estimated 15 Mt or 15% of the global trade in wheat was imported by the USSR in 1988-89.

In Australia wheat production represents 13% of the total farm production. Over the last decade 11.4 Mha have been sown annually to wheat with production averaging 15.3 Mt each year (Australian Wheat Board, 1989). About 85% of this production is exported.

Barley has two principal uses. It is used in the malting, brewing and distilling industries; it is also largely used as feed for livestock to supply digestible energy. Barley harvested around the world between 1982-84 was about 79 Mha with 17 Mha grown in developing countries (ICARDA, 1986). In the developing countries (particularly in west Asia and north Africa) barley is grown by subsistence farmers who use both the grain and the straw for small ruminants and for human food. A large proportion of the crop is grown in marginal areas where it is often the only crop possible.

In Australia, barley occupies about 2.8 Mha and production has averaged 2.8 Mt (Bolt, 1989). It is mainly grown as a grain crop although in some areas it is used as fodder crop for grazing, with grain being subsequently harvested if conditions are suitable (Castles, 1991). Barley is often grown as a rotation crop with wheat, oats and pasture.

Oats are used extensively as a green fodder, hay and for livestock (Poehlman, 1987). Also the nutritional value of the oat kernel is high, being rich in protein and oil, thus making it a favoured grain for feeding horses, young stock or poultry, as well as a nutritional human food. In Australia oats are grown on about 1 Mha and production has average 1.3 Mt each year over the past decade (Bolt, 1989). It is confined to the more favourable cropping regions.

Triticale grain is largely utilized as a livestock feed (Poehlman, 1987; Bolt, 1989) and sometimes for grazing. Production over the last 5 years in Australia has averaged 0.23 Mt per year from an area of 156, 000 ha.

1.2.1.2 Growing-environments

The centre of origin of common wheat, durum wheat, barley, rye and oats is considered to be in southwestern Asia. As civilisations have developed these major crops have developed with them. Now wheat is a major crop on every continent except Antarctica and is grown widely in both tropical and temperate regions and with and without irrigation. Barley is grown widely in the driest margins and also where wheat can be grown as well as where it is wet. Oats are more likely to be grown in the less marginal zones. Unlike wheat, barley and oats are confined more to the temperate cropping zones.

In Australia, temperate crops, particularly wheat, grown during the winter and spring dominate crop production in southern Australia (Richards, 1991). Temperate crops are restricted to the southern and eastern parts of the continent (Fig. 1.1) in a narrow crescent known as the wheat-belt. Inland of the Great Dividing Range, the wheat-belt stretches in a curve from central Queensland through New South Wales, Victoria and southern South Australia. In Western Australia, the wheat-belt continues around the south west of the State and some way north up the western side of the continent. There are three climate regions in which cereals are grown in Australia. They are divided according to the amount and timing of precipitation: a southern winter rainfall region, a northern region of summer-dominant rainfall and a south-eastern region of high (greater than 550 mm) and evenly distributed rainfall (Perry and Hillman, 1991).

The southern winter rainfall region, which accounts for 70% of cereal production in Australia, includes Western Australia, South Australia, Victoria and southern New South Wales (Fig. 1.1). About 70% of annual rainfall is received typically during the growing season between May and September. The mean mid-winter temperatures are mild (12 to 15°C day 5 to 8°C night) and the mid-winter radiation levels are low (from 9 to 11 MJ m^{-2} day^{-1}).

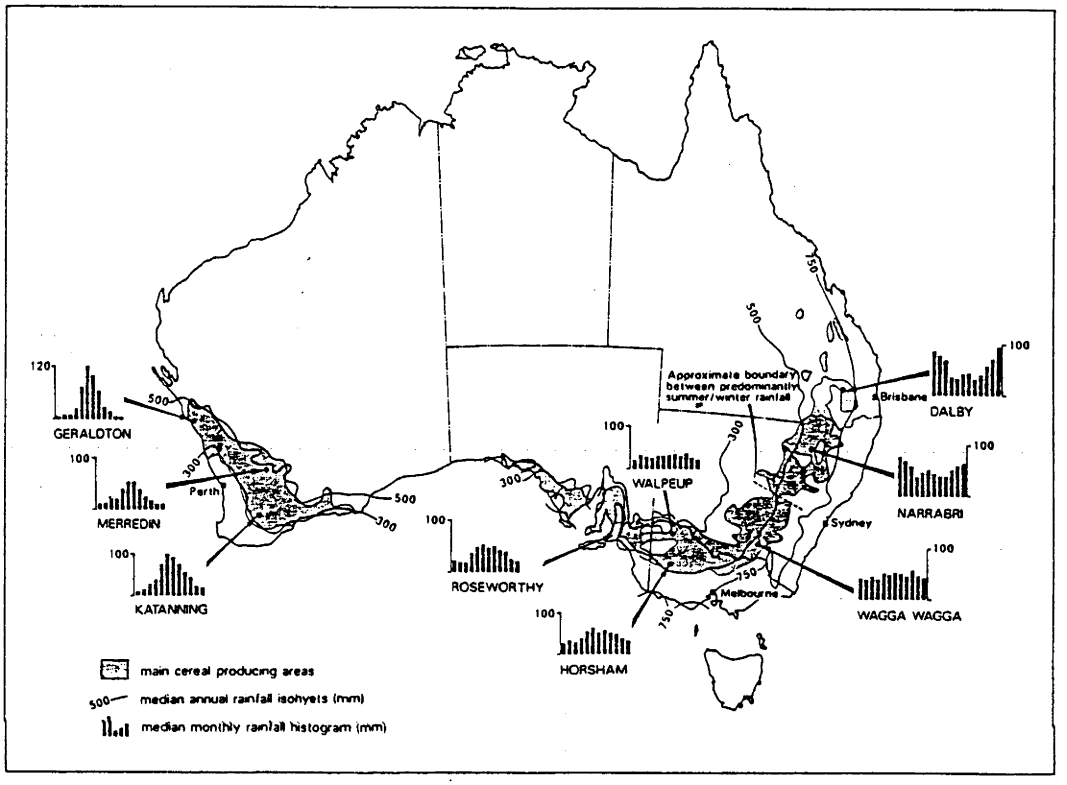


Fig. 1.1 Distribution of temperate cereal crops in Australia, as well as rainfall amount and ditribution at selected sites (Adapted from Perry and Hillman, 1991).

The northern summer rainfall region, extends from central NSW to Queensland and accounts for about 25% of cereal production. Rainfall is greater and increases in both amount and summer dominance to the north. Mean mid-winter temperatures are higher (15 to 19°C day/8 to 12°C night) than the southern region except at high elevation. Radiation frosts after ear emergence may cause severe damage and sowing dates and flowering times are adjusted to avoid flowering during the period of greatest risk of frost. The south-eastern region has high rainfall (over 500 mm) with significant amounts in both summer and winter. This region contributes less than 5% of Australia's wheat.

Crops of all species are typically sown from late autumn to early winter at a time when temperature, radiation and daylength are declining. Genotypes may be of spring habit or facultative, having a vernalisation requirement. Vegetative growth (tillering) occurs during the winter and stem elongation begins as temperature, radiation and daylength begin to increase again. Anthesis typically occurs when mean temperature is 15 °C in all species and in all regions. Thus, anthesis may range from August in the warmest region (central Queensland) to November in the coolest regions (south-eastern highlands). Pan evaporation may exceed rainfall in all except the coolest months in June, July and August. In some regions pan evaporation will always be higher than rainfall. Thus for well managed crops there will be a terminal drought in every region and in every year and drought will be the most important factor limiting yield. Other important limitations in some regions on some occasions will be frost during stem elongation, waterlogging in winter, salinity, and high temperature during grain filling.

The farming system in Australia typically involves a rotation which can include wheat, barley, oats or triticale. Thus, a reputation for performance related to drought resistance has been developed. Barley is considered the most drought tolerant followed by wheat and triticale and finally oats. A similar reputation was suggested by Fischer (1989) and was backed by data from field trials. These trials showed that barley was the most drought resistant followed by durum wheat, complete triticales, bread wheat, substituted triticales and finally oats. Results from CIMMYT's First International Drought Trial (7 sites) gave the following mean yields, for 12 cultivars each, of complete triticale 2.68 ton/ha, durum wheat 2.54 t/ha, bread wheat 2.32 t/ha and substituted triticale 2.30 t/ha (Fischer, 1989).

This order is also reflected in the regions where the cereals are grown and by crop introductions. Barley is typically found on the extreme margins where it may be the only crop that is grown. The grain is typically used for animal feed or for human consumption rather than for malting and in drier years the vegetative material is grazed because barley has a reputation for vigorous early growth (Sparrow and Doolette, 1975). Barley is also more likely to be better suited to lighter soils with a low waterholding capacity and to be sown after wheat as its yield does not decline as much as a late sown wheat. This contrasts with oats that are generally found in the wetter

regions. The drought resistance of durum wheats was also recognised as many of the first durum introductions into Australia were for their apparent superior performance over bread wheat (Matheson, 1975). The nature of the differences between cereals that is responsible for the variation in yield under drought is not known.

1.2.2 Yield of wheat, barley, triticale and oats

A number of studies have compared the yield of the different cereal species. In these studies it is often difficult to determine to what extent variation in crop duration may have contributed to differences. However, when barley is included in genotype evaluation in dry environments it often achieves a higher yield (Anderson, 1985; Siddique *et al.* 1989; Sheppard *et al.* 1985; Hadjichristodoulou, 1984; Acevedo *et al.* 1990). In a study by Fischer and Wood (1979) in north-west Mexico where irrigation was withheld before stem elongation the yield ranking was barley = bread wheat > durum wheat > triticale. The high yield in barley has also been found in more favourable environments (Puri *et al.* 1985) but not in others (Fischer and Wood, 1979).

Comparisons between triticale, durum wheat and bread wheats have shown variable results. Triticale has been superior in dry environments in North Africa and West Asia between 1970 and 1980 and there was little difference between durum wheat and bread wheat.

In trials in Syria, after barley, bread wheat or triticale were superior to durum wheat (Anderson, 1985) whereas in other trials, durum wheat has outyielded bread wheat (ICARDA, 1986). Durum wheats also typically yield more than bread wheat in north-west Mexico under irrigation and they yield more than bread wheat and triticale in the central north of India with irrigation. In dry environments in India bread wheat has yielded more than durums and triticales (Sinha *et al.* 1986), whereas in the northern wheatbelt of Australia triticale yields more than wheat in wetter areas (Sheppard *et al.* 1985).

1.2.3 Crop improvement

Genetic improvement in grain yield in water-limited environments has been less successful than in wetter environments. In general an improvement in yield by at least 1% per year has been found in most crops (Gifford, 1986) growing in relatively favourable environments. In dry environments yield gains may be half of this (Perry and D'Antuono, 1989). These gains have been achieved by traditional breeding methods where yield has been the unit of selection. Other relatively simple changes have occurred that have resulted in the yield increases. In dry environments better adaptation and yield have resulted from earlier flowering and reduced height (Richards, 1991).

To focus on ways to improve yield under drought Passioura (1977) proposed an identity in which yield is the product of three factors - the amount of usable water, water-use efficiency and harvest index. Assuming that strong negative interactions

between these factors are rare, an increase in any one should result in increased yield. Thus, any trait that increases the water passing through the crop by transpiration, the water-use efficiency or the proportion of total dry matter ending up in the grain should result in a higher yield .

The above identity can be modified slightly and expressed in a different way, viz:

$$Y = E_T \times T / E_T \times TE \times HI \qquad (1.1)$$

where Y is grain yield, E_T is the evaporation from soil and plant, T the amount of transpiration, TE the transpiration efficiency (T/biomass) and HI (yield/biomass) the harvest index. It shows that not only is the amount of water used (E_T) important but the proportion of this water actually used in transpiration. The difference between the above identity and that proposed by Passioura (1977) is that the term for water use efficiency has been expanded to include a component for transpiration efficiency TE and a term for the transpiration as a proportion of E_T. The latter is particularly important if evaporation from the soil surface is substantial as it often is in dry temperate cropping regions (Cooper *et al.* 1983).

Comparisons between the temperate cereals will be reviewed with respect to the above identity to determine how they may differ with respect to factors that may determine grain yield in water limited environments. Opportunities to improve each of these components have been reviewed before by Ludlow and Muchow (1988) and Richards (1991).

1.2.3.1 Evapotranspiration

Any differences in soil water extraction should increase transpiration and growth. It is likely that cereals have a sufficient root length density as they typically have a more prolific root system than, say, legumes (Hamblin and Tennant, 1987; Gregory, 1988) at all soil depths and particularly in the top 30 cm. Yet both extract the same amount of water. Thus any differences in water extraction between cereals is likely to depend on whether there are differences in rooting depth. Evidence of this is very scarce. Extraction of water deep in the soil profile generally depends on time taken to grow roots to depth, which in turn depends on anthesis time (Richards, 1991). The larger the interval between sowing and anthesis, the longer the time for root growth and the greater opportunity for roots to grow deep into the soil profile, providing water is available. In a study at a dry site several years in Western Australia where a single barley cultivar was tested with a number of wheats, E_T of barley, although the lowest, was not significantly less than the wheats. Part of the reasons for the low E_T in barley was that it had a shorter duration than the wheats (Siddique *et al.* 1990b; Siddique *et al.* 1989). Other trials in Western Australia also show a lower water extraction by barley than wheat particularly on heavier soils (Hamblin and Tennant, 1987). Differences in

water extraction between barley and wheat have also been noted by Gales *et al.* (1984) although in this example the crop duration for wheat was substantially longer than for barley. In India where bread wheat, durum wheat and triticale were compared, E_T was monitored to 150 cm depth and no differences between species were detected (Aggarwal *et al.* 1986).

1.2.3.2 Transpiration as a proportion of evapotranspiration

Any factor that reduces soil evaporation will increase T/E_T. Thus any factor that alters canopy growth may alter T/E_T. Barley is very different from wheat for many of these traits. For example, leaf appearance rate is considerably faster in barley than in wheat (Kirby *et al.* 1985; Cao and Moss, 1989a; Cao and Moss, 1989b) as is tiller appearance rate. Barley also has larger seedling leaves and larger leaf area early in the life of the crop compared to bread wheat, durum wheat and triticale (Rawson *et al.* 1988). In a study by Rawson *et al.* (1988) the durum wheats had the smallest leaf area at an early stage. Early ground cover which may integrate leaf appearance rate and tiller appearance rate is largest in barley followed by triticale and then both durum and bread wheats (Fischer and Wood, 1979). In Western Australia, the greater early ground cover of barley than wheat has also been noted by Siddique *et al.* (1990b) and Acevedo *et al.* (1990) in Syria. Part of the advantage in the greater early growth of barley may be that its seed size is greater than bread wheat and triticale. Seeds of durum wheats and barleys are often of a similar weight.

Germination of barley in the field has been observed to occur about 1 day earlier than in wheat (Russelle and Bolton, 1980). However, these authors also noted that barley requires a higher minimum temperature than wheat to emerge. However, once that minimum temperature has been exceeded barley requires fewer day degrees to emerge.

Evidence for the above factors increasing T/E_T is meagre, with Siddique *et al.* (1989) reporting the only study where this was higher in barley than in wheat.

1.2.3.3 Transpiration efficiency

An expression showing the various factors that may alter transpiration efficiency for above-ground production was given by Hubick and Farquhar (1989) and Richards (1991) as follows:

$$TE=(1-\phi_c)(1-r)P_a(1-P_i/P_a)/(1.6(e_i-e_a)(1+\phi_w)) \quad (1.2)$$

where e_i and e_a, and P_i and P_a are the intercellular and atmospheric vapour pressures for water and CO_2 respectively, r is the proportion of plant carbon in the roots, ϕ_c is the proportion of carbon fixed by the plant but respired at night, ϕ_w is the proportion of water lost fom the plants at night or through the cuticle (called residual transpiration, Clarke and Richards, 1988). This equation indicates that TE can be increased by

reducing either P_i/P_a, e_i-e_a, residual transpiration, the allocation of carbon to the roots or respiration.

No direct evidence exists that temperate cereals differ in respiration rate or residual transpiration rate and these factors will not be discussed further. Variation in e_i-e_a may arise either through the different timing at which growth occurs (higher TE when growth is under cool conditions) or by reducing the radiation load on the leaf surface. Evidence for barley growing at the time when e_i-e_a is low is evident in a number of studies because of the earlier maturity time typical of barley. Earlier maturity of barley than bread wheat, durum wheat or triticale has been reported in a number of studies (Siddique *et al.* 1990b; Fischer and Maurer, 1978; Puri *et al.* 1985; Hadjichristodoulou, 1987; Acevedo *et al.* 1990). Earlier maturity in triticale than in wheat without a penalty in biomass has also been noted (Ford *et al.* 1984).

Reducing root mass, provided there is no penalty to water or nutrient extraction, is another possible way to improve TE. Root-to-shoot ratio of the barley used in the study by Siddique *et al.* (1990a) was similar to that of the wheats, whereas in the more favourable sites in the study by Hamblin and Tennant (1987) barley had more roots in the top 1 m.

The value of P_i/P_a depends on the assimilation capacity in relation to stomatal conductance. An increased assimilation capacity, with no change in conductance, will reduce P_i/P_a and increase instantaneous transpiration efficiency. An integrated measure of P_i/P_a is the discrimination, Δ, against the stable isotope $^{13}CO_2$ relative to the more abundant $^{12}CO_2$ (Farquhar *et al.* 1982). Among bread wheats (Farquhar and Richards, 1984; Condon *et al,* 1987) and barleys (Hubick and Farquhar, 1989), TE has been negatively correlated with Δ.

Species differences in the ratio of photosynthesis to transpiration in flag leaves and ears of hexaploid and tetraploid wheats and barleys have not been found (Blum, 1985; Johnson *et al.* 1974; Rawson, 1986). Similarly no species differences in TE between bread wheat, durum wheat and barley were noted in plants grown in simulated canopies (Rawson *et al.* 1977) or as single plants (Salim and Todd, 1965), although in a glasshouse study the TE of barley was higher than for both wheat and oats (Salim and Todd, 1965).

Values of Δ, which should reflect variation in TE, also suggest there are differences for P_i/P_a and hence TE. Two durum wheats had similar, although high values of Δ, in relation to a larger number of wheats (Condon *et al.* 1990). Values in barley averaged 0.7‰ greater Δ in barley than in wheat at two sites (Acevedo *et al.* 1990) although the organ or stem level on which Δ was determined was not stated. High values of Δ suggest low TE.

1.2.3.4 Harvest index

The harvest index of a droughted crop can vary from close to the genetic potential of a particular genotype to zero when drought is so severe that plants do not reach anthesis. Thus Richards (1991) discussed factors that contribute to the HI genetic potential as well as those factors that alter HI under drought and could perhaps be modified genetically.

When there is a terminal drought, the HI depends strongly on how much of the total water supply is used after anthesis (Passioura, 1977). This will change with canopy development. If leaf area development is too fast then there may be no water available for grain filling and yield and harvest index will be low (Richards, 1983). The fast canopy development in barley discussed before may lead to a low HI if it results in greater water use before anthesis. However, this in turn may be countered by the shorter vegetative duration typical of barley.

As well as factors that influence leaf area development that in turn influence HI, there are factors in the post-anthesis period that may also be important. A notable one is the translocation of assimilate formed before or at anthesis, stored in the stem, and translocated to the grain during grain filling (Blum *et al.* 1983). In experiments using carbon-14 in both irrigated and droughted crops of wheat and barley, the pre-anthesis assimilate as a percentage of grain yield was 12 and 13% in irrigated barley and wheat crops and this increased to 17 and 22% in droughted barley and wheat crops (Bidinger *et al.* 1977).

1.2.3.5 Phenology

The phenology of a crop is generally the most important factor in determining yield and adaptation. Wheat, barley, triticale and oats all have genes that respond to daylength (photoperiod sensitive genes), low temperature (vernalisation sensitive genes) and to the accumulation of thermal time. Thus, variation in anthesis date can be extremely large within each species. Barley is generally acknowledged to be the earliest flowering species (see references earlier), although it is not known to what extent this reflects the place barley has in a farming system.

1.3 Experimental objectives

Bread wheat is the world's most important food crop. It is widely grown without irrigation. Other temperate cereals, namely barley, durum wheat, triticale and oats are less important. It is likely that these species have features different from wheat, as they have a different genetic and agronomic heritage. An understanding of these features may lead to ways to modify wheat in dry environments so as to improve its yield.

To determine the basic differences between the temperate cereals species, a number of well adapted genotypes with a range in phenology, were chosen for comparison. These were grown in conditions typical of those for cereals in south-

eastern Australia. These cultivars were grown at two sites over three years and their yields were determined. Differences in phenology, growth of leaf area, dry weight of shoots and roots, grain growth and water use were assessed. These provided basic data to:

1. Determine whether variation in grain yield between and within species is due to variation in above-ground dry weight or harvest index.
2. Determine if variation in phenology can contribute to differences in growth and yield.
3. Determine how leaf area development differs between and within species and whether this can lead to variation in above-ground dry weight.
4. Determine whether grain growth and retranslocation of assimilates after anthesis contribute to grain yield
5. Determine whether species differ in water use, water-use efficiency and the evaporation from the soil surface below them.

Substantial variation was found among and between species in several of these aspects. A major contributor to this variation was differences among species in early canopy growth. This was explored in detail in controlled pot experiments. The objective of these studies was to determine whether differences in germination, the utilization of seed reserves, growth rate and its components, could contribute to differences in early growth between species.

The ultimate objective was to devise ways to select wheat with an improved growth and yield in dry environments.

CHAPTER 2

VARIATION IN GRAIN YIELD AND AGRONOMIC CHARACTERISTICS

2.1 INTRODUCTION

The temperate cereals, bread wheat, durum wheat, triticale, barley and oats, are grown in Australia during the winter and spring. They are grown in the same regions and require similar agronomic practices. Phenotypically they are alike until the seed bearing structures emerge from the stems around anthesis. Thus, their comparison in the field is practical, although uncommon. In fact no previous study has been found that contrasts all these species. In Australia, drought beginning around anthesis and continuing through grain filling is the principal edaphic factor limiting yields of these species. Hexaploid wheat or bread wheat, is the dominant species grown and accounts for 85% of the total temperate cereal grain production. The large area sown to wheat probably reflects the greater market opportunities for wheat grain more than its better adaptation compared to other temperate cereal species.

This study was initiated to contrast bread wheat with durum wheat, triticale, barley and oats as each of these species have attributes that bread wheat may not possess, but if present, may improve its yield in rainfed environments. For example, durum wheat and barley are considered more drought tolerant than bread wheat (Acevedo *et al.* 1990), triticale may express the characteristics of rye that make it valuable in marginal environments (Lukaszeuski and Gustafson, 1987) and oats and barley have been selected for their biomass production for hay or grazing as well as for grain. The study was designed to explore whether there are features of these species that contribute to enhanced growth and yield over wheat that may then be used to improve the yield of wheat. If the attributes that contribute to a growth or yield advantage in one species can be identified then this should identify traits that, may improve the yield of wheat.

This chapter reports variation in yield and basic agronomic characteristics of high yielding, adapted genotypes of bread wheat, durum wheat, triticale, barley and oats. Later chapters report on growth, development and water use that may contribute to this variation. Experiments were sown at two locations in New South Wales that were chosen as being representative of a marginal dry environment (Condobolin) and a reliable but low rainfall site (Moombooldool).

2.2 MATERIALS AND METHODS

2.2.1 Field experiments

Six experiments were sown in late May or early June. They were at Condobolin, NSW (147° E, 33° S, elevation 189 m above sea level) in 1988, 1989 and 1990 and

Moombooldool, NSW (147° E, 34° S, elevation 170 m above sea level), in 1988, 1989 and 1990. Brief details are given in Table 2.1. Neighbour experimental designs were used in all experiments such that no genotype had the same neighbours at any site. Seeding rates were adjusted so that about 140 plants m^{-2} were established. Phosphorus and nitrogen fertiliser was banded with the seed at a rate of 15 kg/ha for both nutrients. An additional application of 15 kg/ha of nitrogen was applied to the experiment at Moombooldool in 1989 during early tillering as earliest formed leaves looked yellow after a period of wet, overcast days. Plots were 10 rows wide at both sites with 17 cm between rows and were 15 m long at Condobolin and 10 m long at Moombooldool. Weeds and diseases were controlled with chemicals as required. Each year a single application of Diclofop-methyl and Bromoxynil+MCPA was used to control grass and broad-leaf weeds at Moombooldool, whereas only Bromoxynil+MCPA was required at Condobolin to control broad-leaf weeds. One application of Bayleton® to control fungal diseases at Moombooldool was applied each year during stem elongation. There was no lodging.

Table 2.1. Years, sites and sowing dates of field experiments.

Year	Site	Experiment designation	Sowing date	Paddock history
1988	Condobolin	C88	May 27	Pasture
1988	Moombooldool	M88	June 9	Pasture
1989	Condobolin	C89	May 27	Pasture
1989	Moombooldool	M89	May 26	Pasture
1990	Moombooldool	M90	June 6	Pasture
1990[1]	Condobolin	C90	May 27	Pasture

[1] Seedlings of experiment C90 emerged poorly due to presumed residual herbicide effects from the previous year and thus this trial was abandoned.

Fifteen cultivars representing five temperate cereal species were grown. These are listed in Table 2.2 together with their origin and reasons for choosing them. All genotypes were well-adapted and high yielding in southern Australia. Where possible each species had genotypes with and without a requirement for vernalisation.

The day 50% of culms reached anthesis was recorded for each genotype at each site. At maturity crop height to the top spikelet in the spike or panicle was measured and a 1 m^2 hand harvest of all plant material above ground level was made from each plot in

all experiments. Fertile culms in the sample were counted and the sample dry weight determined. Samples were then threshed and the grain weighed. Harvest index (HI) was calculated as the ratio of grain weight to the total above-ground dry weight (AGDW).

Before machine harvesting to determine grain yield of each plot, 30 cm of plot ends and the outside rows were removed from all plots to eliminate border effects. The AGDW was determined from the quotient of plot yield and harvest index. Hundred grain weight was determined from the machine harvest grain sample. The yield components, culms m^{-2}, kernels m^{-2} and kernels $spike^{-1}$, were computed from the machine and hand harvest data.

Immediately, after harvest, soil cores were taken from experiments C89 (i.e. Condobolin 1989) and M90 (Moombooldool 1990) to calculate root length density and root dry weight. Cores were taken from all plots of plots of O'Connor, Ulandra, Meteor and Rosella in both experiments and from Dua in M90. Four soil cores were extracted from each plot, two over the planted rows and two between the rows. Additional cores were taken from bare soil plots to determine residual roots from the previous year.

In C89, 32 mm diameter intact cores were taken to a depth of 30 cm using a volumetric soil sampler. Roots in the 0 - 15 and 15 - 30 cm depths were washed from the soil using a 1 mm aperture sieve after dispersing clay particles with a detergent solution (Calgon). Counts of intersects of roots with the vertical and horizontal lines of a 5x5 mm grid were recorded following the method outlined by Tennant (1975). Root length density was estimated from the number of intersects x the length conversion factor for a 5x5 mm grid (0.3928). Dry weight of roots at each depth was calculated from the product of root length density and the root mass/length ratio (i.e. weight per unit length of root using the value of 0.19 mg cm^{-1} for each genotype). The mass per length ratio was determined by growing each genotype in pots to the 2 leaf stage. Roots were washed free of soil, then total length was measured and their dry weight determined. No differences were found in root mass per length between species or between genotypes and the value of 0.19 mg cm^{-1} was used, similar to that found by Siddique *et al.* (1990a) for Kulin wheat in the top 10 cm of soil for field grown plants. Below 10 cm, root mass per length in the field plants averaged 0.1 mg cm^{-1}. However, the cortex of older roots is often missing in field grown plants and the value of 0.1 may be an underestimate. The value of 0.19 was used in this study to estimate the weight of all roots.

Table 2.2. Genotypes grown in the field experiments.

Genotype	Origin	Year of release	Characteristics
***Hordeum vulgare* L.**			
Galleon	South Australia	1984	Two row, spring barley
O'Connor	Western Australia	1984	Two row, feed, spring barley
Ulandra	England, NSW Dept. of Agriculture	1987	Two row, postrate habit and high yielding winter barley
Malebo	NSW Dept. of Agriculture	1981	Six row winter barley for grazing and yield
***Triticum aestivum* L.**			
Kulin	Western Australia	1985	Semi-dwarf, high yielding spring wheat
Meteor	Cargill Seeds, NSW	1987	Semi-dwarf, high yielding, hybrid spring wheat
Hahn/Parula[a]	CIMMYT, Mexico	1985[b]	Semi-dwarf, high yielding spring wheat with small leaves
Rosella	NSW Dept.of Agriculture	1985	Semi-dwarf, high yielding winter wheat
M 3344	NSW Dept. of Agriculture	1985[c]	Semi-dwarf, high yielding winter wheat with 1B/1R translocation from rye
Triticum turgidum* var. *durum			
Altar 84	CIMMYT, Mexico	1984	Semi-dwarf, high yielding spring durum wheat
Carcomun	CIMMYT, Mexico	1985	Semi-dwarf, high yielding spring durum wheat
***Triticosecale* Wittmack**			
Dua (AT6-76)	CIMMYT, Mexico	1979	High yielding spring triticale
Currency	CIMMYT, Mexico South Australia	1983	High yielding spring triticale
***Avena sativa* L.**[d]			
Echidna	South Australia	1984	Dwarf high yielding spring oat
Hakea	NSW, Dept. of Agriculture	1987	Dual purpose winter oat

[a] Hahn/Parula was only grown in M88

[b] Year of seed obtained

[c] Not commercially released because of poor dough quality

[d] Oats were not grown in M88

Soil cores from M90 were taken immediately after grain harvest using a hydraulic corer. Cores were 40 mm in diameter and were taken to a depth of 150 cm. Soil cores were divided into segments of 0-10 cm and then every 20 cm up to 150 cm deep. Segments were soaked overnight in a Calgon solution and roots were washed using a hydro-pneumatic elutriation system (Smucker *et al.* 1982). Counts of intersects of roots and estimations of root length density, dry weight of roots at different depths and total dry weight of roots were made as in C89.

All data were analysed using the program SAFE (Lill *et al.* 1988) which utilizes the spatial analysis technique of Gleeson and Cullis (1987) to remove trend effects within replicates. Four autoregressive integrated moving average (ARIMA) models of spatial analysis and conventional randomized complete block analysis were compared. The analysis that gave the lowest mean standard error was selected for calculation of the least significant difference.

2.2.2 Meteorological data

At Condobolin data on maximum and minimum, and wet and dry bulb temperatures, rainfall, and wind speed were obtained from a weather station located less than 1 km from the experimental site and monitored by the NSW Department of Agriculture and Fisheries Research Station (Table 2.3). Solar radiation was extrapolated from a meteorological station of the NSW Department of Agriculture and Fisheries at Forbes located 90 km east from the experimental site. The photothermal quotient was calculated as the ratio of solar radiation to mean maximum and minimun temperature. Vapour pressure deficit (VPD) and potential evapotranspiration (E_p) were calculated from the weather data. Methods of calculation of these variables are given in appendix 1.

At Moombooldool rainfall was recorded at the experimental site and other weather data were obtained from CSIRO, Division of Water Resources at Griffith, 50 km west of Moombooldool. Temperatures at Griffith are higher than at Moombooldool and to correct for this maximum and minimum temperatures from a meteorological station of the NSW Department of Agriculture and Fisheries at Temora (110 km east from Moombooldool) were also used to estimate monthly and long-term means at Moombooldool (Table 2.4). The photothermal quotient was calculated as above and VPD was calculated as in appendix 1. The E_p was computed from the weather data from Griffith.

Table 2.3. Monthly observed and derived weather statistics at Condobolin.

	April	May	June	July	Aug.	Sept.	Oct.	Nov.
				Maximum temperature (°C)[a]				
Mean	24.9	19.0	15.6	14.7	16.5	20.2	24.7	28.6
1988	23.6	19.8	15.5	15.6	17.2	20.3	27.2	28.6
1989	24.0	19.8	14.9	13.9	15.0	20.5	24.7	29.1
				Mimimum temperature (°C)[a]				
Mean	9.5	6.0	2.9	2.1	3.4	5.2	9.0	12.4
1988	12.6	8.5	4.2	5.4	3.8	6.2	8.7	12.0
1989	12.3	9.2	4.4	3.9	3.1	3.4	8.4	12.9
				Solar radiation (MJ m^{-2} d^{-1})[b]				
Mean	17.6	13.1	10.0	11.1	13.6	18.5	24.6	28.6
1988	16.3	12.1	10.0	10.5	11.6	14.9	24.1	29.4
1989	15.5	10.6	9.8	8.8	13.6	20.3	23.6	26.2
				Photothermal quotient (MJ m^{-2} d^{-1} $°C^{-1}$)				
Mean	1.0	1.0	1.0	1.3	1.4	1.4	1.4	1.4
1988	0.9	0.9	1.1	1.1	1.2	1.2	1.4	1.5
1989	0.9	0.8	1.1	1.1	1.5	1.8	1.5	1.3
				Rainfall (mm)[c]				
Mean	29.6	35.4	33.9	30.6	33.2	27.3	40.1	37.1
1988	49.8	31.8	49.0	76.0	27.8	56.2	17.0	40.8
1989	53.2	56.6	49.0	42.5	21.8	8.6	20.6	32.8
				Potential evapotranspiration (mm d^{-1})[d]				
1988	4.2	2.5	1.8	1.8	3.3	5.0	7.3	8.1
1989	3.9	2.2	1.9	2.0	2.7	5.0	7.1	8.4
				Vapour pressure deficit (kPa)[d]				
1988	0.7	0.4	0.2	0.2	0.3	0.6	1.1	1.7
1989	0.6	0.3	0.2	0.2	0.3	0.8	1.2	1.8

[a] Long-term mean (34 years)

[b] Long-term mean (3 years)

[c] Long-term mean (72 years)

[d] Long-term mean not available

Table 2.4. Monthly observed and derived weather statistics at Moombooldool.

	April	May	June	July	Aug.	Sept.	Oct.	Nov.
Maximum temperature (°C)[a]								
Mean	23.2	18.1	14.5	13.7	15.4	18.4	22.1	26.3
1988	24.4	18.9	15.0	14.5	16.2	19.4	24.2	26.5
1989	22.4	18.3	13.7	12.8	13.4	18.5	22.2	27.7
1990	23.0	18.7	13.9	13.4	13.8	18.3	22.8	28.1
Minimum temperature (°C)[a]								
Mean	9.2	6.6	3.4	2.6	3.6	5.4	8.3	11.2
1988	11.4	8.6	4.2	4.9	3.4	5.8	7.5	10.7
1989	12.6	9.5	4.7	3.3	3.1	3.5	6.7	11.9
1990	12.6	6.4	4.3	6.3	4.4	5.3	7.5	11.0
Solar radiation ($MJ\ m^{-2}\ d^{-1}$)[b]								
Mean	14.3	9.8	7.8	8.4	11.5	15.3	19.5	24.3
1988	15.4	9.5	8.4	7.7	13.0	18.2	23.3	24.3
1989	13.3	8.8	7.7	8.2	11.2	17.2	21.7	25.3
1990	13.4	10.3	8.0	7.7	11.5	16.6	22.5	27.7
Photothermal quotient ($MJ\ m^{-2}\ d^{-1}\ °C^{-1}$)								
Mean	0.9	0.5	0.8	1.0	1.1	1.2	1.2	1.3
1988	0.9	0.7	0.9	0.8	1.4	1.5	1.5	1.3
1989	0.8	0.6	0.9	1.0	1.4	1.6	1.6	1.3
1990	0.8	0.9	0.9	0.8	1.3	1.4	1.5	1.5
Rainfall (mm)[c]								
Mean	42.0	44.0	32.0	29.0	38.0	37.0	47.0	27.0
1988	31.3	77.8	52.0	61.7	30.4	33.7	5.6	69.0
1989	34.9	74.2	39.6	43.7	38.6	14.9	25.4	24.1
1990	112.8	51.5	36.1	56.4	51.0	30.6	34.6	0.0
Potential evapotranspiration ($mm\ d^{-1}$)[b]								
Mean	3.9	2.2	1.5	1.7	2.4	3.6	5.2	7.2
1988	3.6	1.9	1.3	1.3	2.3	3.9	6.7	7.8
1989	2.5	1.4	0.8	1.0	1.5	3.3	5.7	7.5
1990	3.2	2.0	1.2	1.4	2.1	3.5	5.7	7.8
Vapour pressure deficit (kPa)								
1988	0.8	0.3	0.1	0.1	0.3	0.7	1.3	1.5
1989	0.5	0.2	0.1	0.1	0.2	0.6	1.1	1.8
1990	0.7	0.4	0.1	0.1	0.2	0.6	1.3	2.1

[a] Long-term mean (29 years at Griffith and 17 years at Temora) [b] and [c] Long-term mean (29 years at Griffith)

2.3 RESULTS

2.3.1 Weather at Condobolin and Moombooldool

Average rainfall during the period May to October, when rainfall is most effective, is 229 mm at Condobolin and 269 mm at Moombooldool. Rainfall during this interval was higher than average in 1988, there being 308 mm at Condobolin and 292 mm at Moombooldool, whereas in 1989 rainfall was above average at Condobolin (253 mm) but below average at Moombooldool (253 mm). Rainfall during this period in 1990 at Moombooldool was 373 mm. There was a terminal drought in every experiment and rainfall between reproductive development period and grain filling was less than average in each experiment except C88. Variation in above-ground dry weight was related to April to October rainfall (Fig. 2.1).

Condobolin was warmer than Moombooldool and received more solar radiation. Potential evapotranspiration and the vapour pressure deficit were also higher at Condobolin than at Moombooldool.

Maximum temperatures were higher than average in 1988 and either average or lower in 1989 and 1990. Minimum temperatures were in general higher than average at both sites each year except for August, September, and October when they were lower than average.

2.3.2 Variation among species

Barley had the highest grain yield in all experiments (Table 2.5). The yield of barley averaged over all environments was 25% higher than the mean for all the other species. The yield of bread wheat, durum wheat, triticale, and oats were generally similar although of these the yield of triticale tended to be highest.

The higher yield of barley was achieved because of both higher AGDW and HI. The AGDW of barley was 22%, 16%, 13%, and 2% higher than durum wheat, oats, bread wheat and triticale, respectively. The HI of barley was 8%, 9%, 12% and 16% higher than durum wheat, oats, bread wheat and triticale respectively. Barley, as a group, was the first to reach anthesis followed by triticale; the bread wheats as a group was the last to flower. Triticale was taller than the other species in all experiments (Table 2.5).

Barley had the greatest number of spikes m^{-2}, whereas triticale and durum wheat had the lowest number (Table 2.6). The number of kernels per spike was lowest in barley and wheat and highest in durum wheat, triticale and oats. For the two principal yield determinants, kernels m^{-2} and kernel weight, there were no consistent patterns between species. Barley had the highest values for kernel weight in all experiments at Moombooldool followed by triticale and durum wheat and at Condobolin, triticale had slightly heavier kernels than barley. Oats had the lowest kernel weight in all

experiments. The greater kernel weight of barley was the yield component contributing most to high yield.

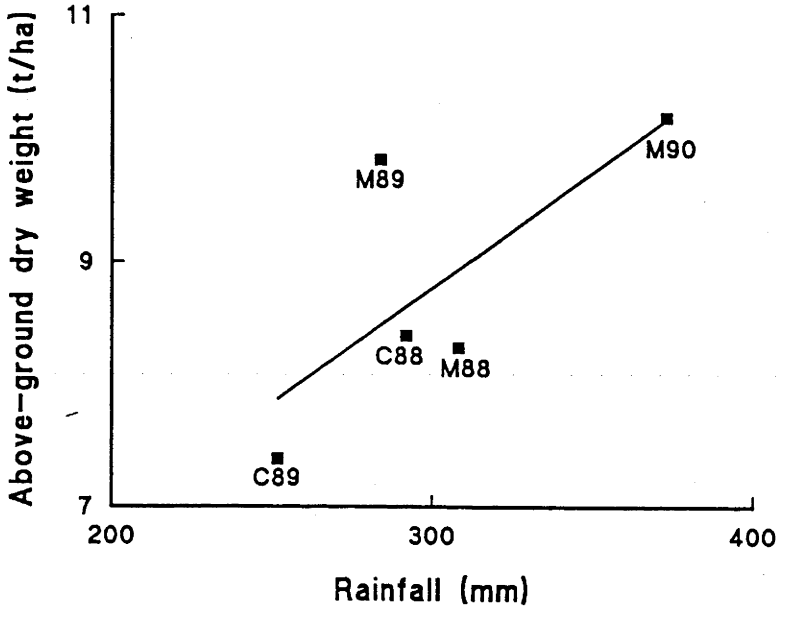


Fig. 2.1 Relationship between average above-ground dry weight for all genotypes at each site and April to November rainfall; Y=0.019X+3.13 (r=0.73, P<0.05).

Table 2.5. Anthesis (A, days after sowing, DAS), crop height (Ht), grain yield (GY), final above-ground dry weight (AGDW) and harvest index (HI) at each location.

Exp.	Species	Anthesis (DAS)	Ht (cm)	GY (gm^{-2})	AGDW (gm^{-2})	HI
C88	Barley	121	82	323	868	0.38
	Bread wheat	125	87	275	796	0.35
	Triticale	119	99	288	825	0.35
	Oats	125	75	285	828	0.34
	Lsd (P=0.05)	2	4	40	105	0.01
C89	Barley	124	69	312	861	0.36
	Bread wheat	134	69	213	642	0.33
	Durum wheat	134	68	216	620	0.35
	Triticale	127	84	270	891	0.30
	Oats	130	58	212	656	0.32
	Lsd (P=0.05)	3	2	27	45	0.02
M88	Barley	119	90	362	847	0.42
	Bread wheat	122	86	294	812	0.36
	Durum wheat	118	88	304	834	0.36
	Triticale	118	106	326	904	0.36
	Lsd (P=0.05)	1	3	38	86	0.03
M89	Barley	129	73	480	1065	0.45
	Bread wheat	138	75	391	979	0.40
	Durum wheat	138	80	364	865	0.42
	Triticale	133	96	375	1046	0.36
	Oats	134	67	380	885	0.43
	Lsd (P=0.05)	1	4	38	89	0.02
M90	Barley	122	88	404	1109	0.36
	Bread wheat	127	86	331	1004	0.33
	Durum wheat	126	85	298	876	0.34
	Triticale	124	102	328	1009	0.33
	Oats	128	82	346	1016	0.34
	Lsd (P=0.05)	1	4	29	103	0.02

Table 2.6. Yield components culms m^{-2}, kernels m^{-2}, kernels $spike^{-1}$ and kernel weight at each location.

Exp.	Species	Spikes m^{-2}	Kernels m^{-2}	Kernel $spike^{-1}$	Kernel weight (mg)
C88	Barley	398	9590	25	34
	Bread wheat	248	9803	40	29
	Triticale	145	8036	56	36
	Oats	260	12798	49	23
	Lsd (P=0.05)	46	1808	5	2
C89	Barley	435	9014	21	35
	Bread wheat	254	6185	26	35
	Durum wheat	165	6249	38	35
	Triticale	235	7249	31	38
	Oats	217	7802	35	27
	Lsd (P=0.05)	22	822	3	1
M88	Barley	331	7558	25	48
	Bread wheat	236	9508	41	31
	Durum wheat	170	8451	50	36
	Triticale	206	8219	49	40
	Lsd (P=0.05)	66	908	9	2
M89	Barley	546	10357	21	46
	Bread wheat	362	9741	27	40
	Durum wheat	233	8384	36	44
	Triticale	233	8410	36	45
	Oats	291	11974	42	32
	Lsd (P=0.05)	41	1157	4	2
M90	Barley	450	8334	20	48
	Bread wheat	297	8682	30	39
	Durum wheat	186	7297	40	41
	Triticale	179	7120	41	46
	Oats	291	10859	37	32
	Lsd (P=0.05)	39	1110	5	3

2.3.3 Variation within species

Substantial variation between genotypes within species was found for all measured traits. This variation was surprisingly similar in all environments and there was little evidence for genotype by environment interactions. Table 2.7 shows the yield of each genotype, expressed as a percentage of the site mean and averaged over all sites. Similar data for above-ground dry weight, harvest index, mature plant height and days to anthesis are also presented in Table 2.7. Mean values for each genotype in each experiment is given in appendix 1 (Tables 2.1 to 2.5).

Variation among barley and oat genotypes was greatest with less variation among genotypes of the other species. Most of this variation was associated with variation in the time of anthesis. Genotypes that flowered later inevitably had a lower grain yield (Fig. 2.2a) and harvest index (Fig. 2.2b); AGDW also declined with later anthesis date (Fig. 2.2c). From the regression of the mean percentage yield over all sites and the mean number of days between sowing and anthesis for all genotypes, there was a 3.5% yield loss for each day delay in anthesis.

Crop height was also important in determining variation in yield. With the exception of the late flowering Ulandra that did not reach its potential height, the tallest lines tended to have the lowest harvest indices (Fig. 2.3). This was evident in barley, triticale and oats, where there were substantial differences in height among genotypes, but not in either of the wheat species, in which all the genotypes were semi-dwarfs and there was little variation in mature plant height.

The two spring barleys and Ulandra had the highest number of culms m^{-2} followed by the two winter wheats (Table 2.8). Malebo, the only 6-row, barley had a higher kernel number per spike than the 2-row barleys. There was an inverse relationship between culms m^{-2} and kernels per culm ($r=-0.86$, $P<0.01$) when these yield components were averaged over all environments. Echidna oats had the highest number of kernels m^{-2} but the lowest kernel weight. There was less variation between species for kernel weight than for the other yield components.

2.3.4 Root length density and dry weight of roots

Data on roots were obtained for four cultivars in C89 and five in M90. Barley cultivars had a greater root length density than the wheat cultivars in C89 (Table 2.9) as well as in M90 (Table 2.10) and also higher than triticale in M90. The mean values for barley and wheat are shown in Fig. 2.4. The greatest difference occurred in the top 30 cm; barley had more roots at all depths above 80 cm. Root length density of Dua triticale was identical to the wheat cultivars at M90.

Assuming the root length density below 30 cm at C89 was similar to that obtained at M90 and in other studies (Gregory 1988; Siddique *et al.* 1990a), root weights were estimated assuming a root length density at C89 grading from 1.3 cm cm^{-3} at 40 cm to 0.1 cm cm^{-3} at 100 cm. The estimated root dry weights at C89 and M90 are given in

Table 2.11. The roots of barley were 40% heavier than wheat at C89 and over 30% heavier than wheat and triticale cultivars at M90. No differences in root weight within the wheat genotypes were found in either year. Ulandra barley had the heaviest roots at both sites. Although the roots of O'Connor barley were heavier than the two wheats and the triticale, they were in the same proportion to above-ground dry weight as in wheat at both sites. Thus with the exception of Ulandra, root/shoot ratio was the same in the barley and wheats in each experiment. Root/shoot ratio in Dua triticale was significantly higher than for the wheats and O'Connor barley in M90.

Table 2.7. Agronomic characteristics of genotypes averaged over all environments. Percentage values given are the % of the site mean and averaged over all sites.

Species	Anthesis %	Ht %	Yield %	AGDW %	HI %
Barley					
Galleon	92	93	126	107	118
O'Connor	93	102	138	118	110
Ulandra	107	77	84	95	89
Malebo	97	119	116	111	103
Bread wheat					
Kulin	97	99	99	93	106
Meteor	102	108	98	102	96
Hahn/Parula	99	93	99	98	103
Rosella	105	96	89	95	94
M 3344	106	90	82	91	90
Durum wheat					
Altar 84	101	102	88	86	104
Carcomun	101	95	90	93	103
Triticale					
Dua	97	110	97	101	97
Currency	100	128	101	107	90
Oats					
Echidna	98	75	116	99	119
Hakea	104	100	71	90	80
Mean over all experiments	**126** Days	**82** cm	**325** g m^{-2}	**882** g m^{-2}	**0.36**

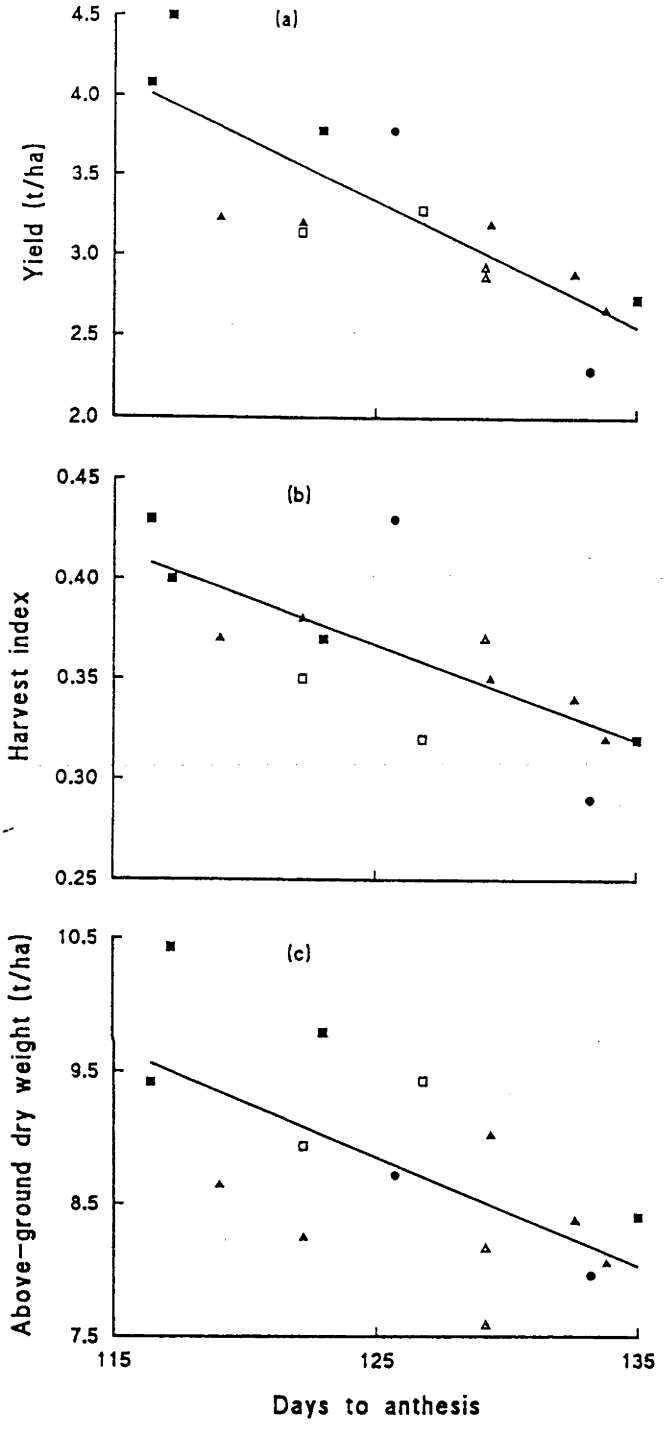


Fig. 2.2 Relationship between days to anthesis and (a) grain yield, (b) harvest index and above-ground dry weight for barley (■), bread wheat (▲), durum wheat (△), triticale (□) and oats (●) averaged over all sites. Relationship between:
Flowering time (x) and grain yield, GY=0.078x+13.1 (r^2=0.67, P<0.01).
Flowering time (x) and harvest index, HI=-0.0048x+0.96 (r^2=0.53, P<0.01).
Flowering time (x) and above-ground dry weight, AGDW=-0.082x+19.2 (r^2=0.44, P<0.01).

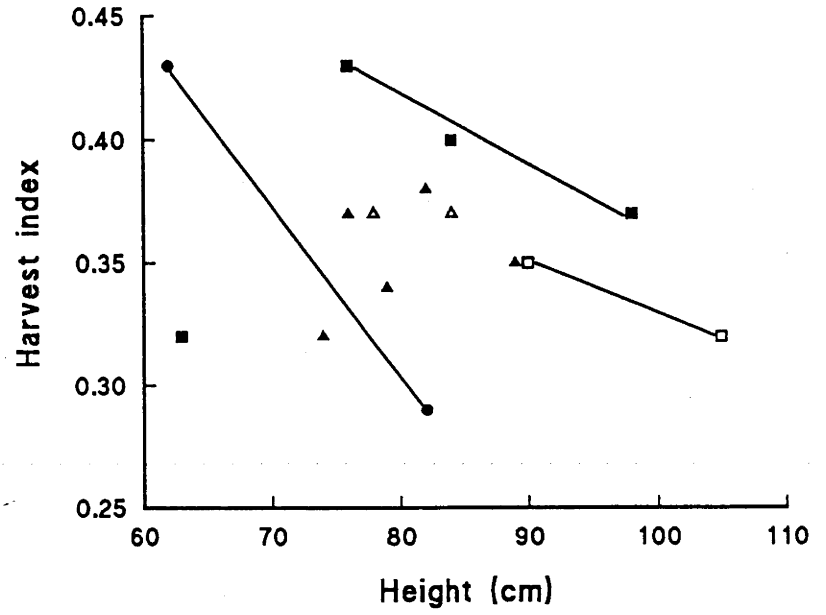


Fig. 2.3 Relationship between harvest index and mature crop height in barley (■), bread wheat (▲), durum wheat (△), triticale (□) and oats (●) averaged over all sites. Lines are fitted through barley (except Ulandra), triticale and oat genotypes.

Table 2.8. Culms m^{-2}, kernels m^{-2}, kernels $spike^{-1}$ and kernel weight averaged over all environments. Percentage values given are the % of each site mean aand averaged over all sites.

Species	Culms m^{-2} (%)	Kernels m^{-2} (%)	Kernel $spike^{-1}$ (%)	Kernel weight (%)
Barley				
Galleon	191	108	51	117
O'Connor	172	116	62	121
Ulandra	118	87	67	96
Malebo	96	98	91	120
Bread wheat				
Kulin	76	93	116	99
Meteor	94	107	103	91
Hahn/Parula	93	119	112	98
Rosella	100	96	91	90
M 3344	104	90	77	93
Durum wheat				
Altar 84	72	89	127	99
Carcomun	62	89	129	100
Triticale				
Dua	76	91	119	106
Currency	59	87	133	114
Oats				
Echidna	92	142	141	81
Hakea	80	100	114	72
Mean over all experiments	**299**	**8838**	**33**	**37**

Table 2.9. Root length density (cm cm^{-3}) for barley and wheat cultivars in the top 30 cm of soil at C89.

Genotypes	0-15 (cm)	15-30 (cm)
Barley		
O'Connor	7.1	2.6
Ulandra	8.1	2.7
Bread wheat		
Meteor	4.9	2.8
Rosella	3.7	2.2
Lsd (P=0.05)	2.2	0.6

Table 2.10. Root lenght density (cm cm^{-3}) for barley, wheat and triticale cultivars at M90 in the top 150 cm of soil.

Species	Depth (cm)							
	0-10	10-30	30-50	50-70	70-90	90-110	110-130	130-150
Barley								
O'Connor	4.3	1.5	1.1	0.7	0.6	0.2	0.1	0.1
Ulandra	5.8	1.4	1.3	1.1	0.9	0.4	0.1	0.1
Bread wheat								
Meteor	3.3	1.3	1.0	0.7	0.5	0.3	0.2	0.1
Rosella	2.9	1.2	1.0	0.7	0.5	0.2	0.1	0.1
Triticale								
Dua	3.4	1.4	1.0	0.8	0.4	0.2	0.1	0.1
Lsd (P=0.05)	0.6	0.3	0.2	0.2	0.2	0.1	0.1	0.1

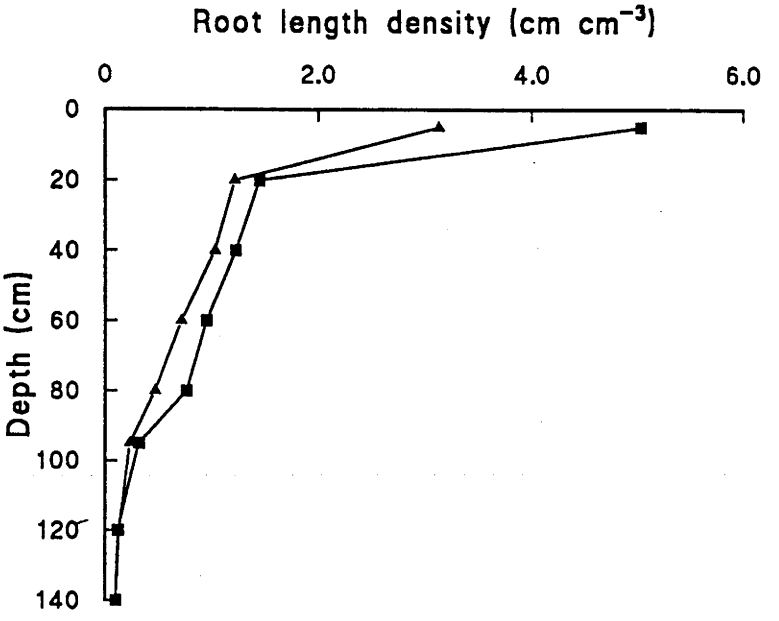


Fig. 2.4 Root length density of barley (■) and bread wheat (▲) at maturity in M90.

Table 2.11. Root dry weight, above-ground dry weight (AGDW) and root/shoot ratio (RSR) of barley, bread wheat and triticale at maturity in C89 and M90.

Exp.	Species	Roots ($g\ m^{-2}$)	AGDW ($g\ m^{-2}$)	TDW ($g\ m^{-2}$)	RSR
C89					
	Barley				
	O'Connor	318	934	1252	0.34
	Ulandra	351	670	1020	0.52
	Bread wheat				
	Meteor	261	649	910	0.40
	Rosella	208	636	843	0.33
	Lsd (P=0.05)	74	66	110	0.09
M90					
	Barley				
	O'Connor	252	1349	1601	0.19
	Ulandra	321	907	1228	0.35
	Bread wheat				
	Meteor	219	1199	1418	0.18
	Rosella	200	973	1174	0.20
	Triticale				
	Dua	221	913	1133	0.24
	Lsd (P=0.05)	37	175	186	0.04

2.4 DISCUSSION

High yielding, well adapted cultivars of barley, bread wheat, durum wheat, triticale and oats were evaluated in five rainfed environments to identify whether there are any outstanding features of these species that may suggest ways for their improvement. There were consistent differences in yield and agronomic characteristics among and within the species across all environments. Barley was the outstanding species. The average grain yield of barley was 25% higher than the other species in all environments and this was achieved by barley having a 13% higher AGDW and an 11% higher HI than the average of the other species. When the highest yielding barley is contrasted with the highest yielding wheat the difference in yield becomes larger. O'Connor barley yielded 39% more grain than Kulin wheat. This principally arose because AGDW of O'Connor was 27% higher than Kulin; the difference in HI between these cultivars was small. When root weight is also considered the difference in biomass

between barley and wheat increases. Averaged over the two environments where roots were measured, the weight of roots of Ulandra was 65% higher than Rosella that flowered two days earlier. Comparing species means, barley had 35% heavier roots than wheat and triticale and barley flowered about 3 days earlier.

Other studies in dry environments have also found barley to yield more grain and/or biomass than wheat. In these studies conditions were similar to those reported here, in that there was adequate water during the vegetative period but this was followed by a terminal drought. In rainfed experiments in south-western Australia, O'Connor barley had a 25% higher grain yield than the mean of numerous wheat cultivars at Merredin in 1987 (Siddique *et al.* 1989), whereas in 1988 at the same site, O'Connor yielded 19% higher (Siddique *et al.* 1990b). In the 1987 study, AGDW was 25% higher in O'Connor, whereas in 1988 there was no difference in AGDW between O'Connor and the wheat cultivars. At an irrigated site in north-western Mexico, the mean grain yield of six cultivars of barley in the drought treatment was no higher than the mean for bread wheat, durum wheat or triticale, but AGDW of barley was higher (Fischer and Wood, 1979). In the irrigated treatment barley yielded less grain and dry matter than wheat.

Some of the yield advantage in barley is due to the husk, which is attached to the kernel in both barley and oats. This contrasts with the naked kernel in bread wheat, durum wheat and triticale. The husk represents 8% of the harvested grain in barley and 30% in oats. Assuming these values and correcting for husk weight the mean grain yield of barley over all cultivars and environments was 17% higher than the other species while the HI of barley became the same as the other species except oats. Thus the higher yield of barley is due entirely to a higher AGDW. The mean AGDW for triticale over all environments was the same as for barley. However, the best barley had an 11% higher AGDW than the best triticale. Triticale had the lowest average HI, possibly because it was so tall, and therefore had a lower yield than barley.

The estimated dry weight of roots at maturity was very high considering the often quoted 10% of total dry weight. However, values were similar to those previously reported in dry environments in Western Australia (Hamblin *et el.*1990). At C89, the driest site, roots were estimated to form 28% of the total dry weight, whereas at M90, the wetter site, this value was 19%. The high values were principally due to the concentration of roots in the surface 15 cm and this was also the reason for the difference between the two sites. The largest difference for root weight and root length density within species occurred between Ulandra and O'Connor. Ulandra flowered about 18 days later than O'Connor and the extra nodal roots associated with more tillers and leaves (Klepper *et al.* 1984) in Ulandra, and typically found in the top 30 cm of soil, presumably accounts for this difference. The faster tiller and leaf appearance rate in O'Connor compared with the wheat and triticale (López-Castañeda, unpublished) and

hence more nodal root initials may also account for the higher root weight in O'Connor despite its earlier flowering.

Flowering and physiological maturity occurred earlier in barley than in the other species and so the higher AGDW and grain yield of barley were achieved in a shorter time and therefore before the onset of higher temperatures and vapour pressure deficits. Flowering time was negatively related to grain yield, HI and AGDW when all genotypes were considered. The association between early flowering and high HI was expected as earlier flowering lines should have avoided the detrimental effects of drought and high temperatures during or after flowering. Although, it should be pointed out that drought before anthesis was never severe in these experiments. Rainfall between April and October ranged from 253 to 373 mm and this contrasts with the long term average during the same interval of 230 mm at Condobolin and 270 mm at Moombooldool. In more typical drier years than when these experiments were conducted the negative relationship between flowering time and grain yield or harvest index may have been even greater. The inverse relationship between days to anthesis and AGDW (Fig 1c) was not expected. Barley dominates this relationship and when it is removed the relationship is not significant (r=-0.41). Nevertheless, within all species where the difference in flowering time was more than 3 days the latest flowering lines had less AGDW at maturity. Part of this difference in weight may be made up by more root growth in the later flowering lines; however, a penalty in growth is still evident.

The higher AGDW and biomass of barley could be achieved by several means. Firstly, barley may have a higher transpiration efficiency; that is, carbon gain per unit of water transpired may be higher in barley. Secondly, early leaf area or dry matter growth may be faster in barley which results in a lower proportion of evaporation from the soil surface and hence more water available for transpiration. Thirdly, the more extensive root system may extract more soil water than the other species. These factors will be explored in a subsequent chapters.

2.5 CONCLUSIONS

The relative performance of barley, bread wheat, durum wheat, triticale and oats was compared in rainfed environments to identify any outstanding features of these species that contribute to high grain yield. Drought was not a significant factor before head emergence but all the available water was used by maturity. Fifteen high yielding genotypes with a range of flowering times were evaluated in five rainfed environments where there was a terminal drought. Barley, which flowered earliest, had a 25% higher grain yield than the other species when averaged over all cultivars. However, the highest yielding barley had a 39% higher yield than the best wheat when averaged over all environments. There was little variation in the mean grain yield between the durum and bread wheats, oats and triticale but there was substantial variation within each species. After correcting for the husk enclosing the barley kernel the grain yield of

barley was 17% higher than the other species and 28% higher when the highest yielding barley was compared with the best wheat. With the exception of oats this higher yield was achieved by a higher above-ground dry weight (AGDW) rather than a higher harvest index. AGDW of barley averaged over all environments was 22%, 16%, 13% and 2% higher than durum wheat, oats, bread wheat and triticale respectively. Barley also had a more extensive and heavier root system than bread wheat and triticale. Root weight was estimated to be 35% greater, with most of the difference occurring in the top 15 cm, but differences occurred down to 90 cm. No differences were found in rooting depth.

CHAPTER 3

VARIATION IN GROWTH AND DEVELOPMENT IN FIELD GROWN PLANTS

3.1 INTRODUCTION

A comparison of bread wheat, durum wheat, barley, triticale and oats showed that barley had a 17% higher grain yield than the other species when averaged over five rainfed environments in south-eastern Australia (chapter 3). A yield difference of 39% was found when the highest yielding barley was contrasted with the highest yielding wheat. After correcting for the husk covering the barley kernel the yield advantage of barley was attributed to a higher above-ground dry weight rather than to a higher harvest index. Other important differences noted were that barley had a larger root mass and that triticale, like barley, had a high above-ground dry weight but its yield was less than in barley because of its lower harvest index. It is also noteworthy that both barley and triticale achieved the greater biomass in a shorter duration than the wheats and oats. The better performance of barley over wheat in dry areas has been found in other studies (Siddique *et al.*, 1989, 1990a & b) and farmers experience with the different temperate cereals would rank them for yield under drought as barley, complete triticale, durum wheat, bread wheat, substituted triticale and oats (Fischer, 1989).

The consistently higher above-ground dry weight achieved by barley and triticale compared to wheat has important implications for cereal improvement. It provides a clear demonstration that different cereal species with a similar morphology and phenology, when sown under the same conditions, can differ substantially in total biomass and this is responsible for greater yields. This contrasts with studies comparing old and new wheat and oat cultivars which, despite large differences in grain yield, there are no differences in above-ground dry weight (Austin *et al.*, 1980; Perry and D'Antuono, 1989; Wych and Stuthman, 1983); the increase in yield has occurred because of a greater harvest index. It is interesting to note than in barley newer varieties have both a greater biomass and harvest index (Riggs *et al.*, 1981, Wych and Rasmusson, 1983). As we approach the limit to the increase in harvest index ways to increase biomass and ways to modify the other cereals genetically must be identified.

This chapter explores variation between the species in the growth of leaf area as well as dry weight through the season. It also examines variation in the timing of reproductive development as this is a major difference between the species and of vital importance to adaptation in water limited environments (Richards, 1991).

3.2. MATERIALS AND METHODS

3.2.1 Phasic development

In C89 and M89 (see Table 2.1 for experiment legend) apex development was monitored periodically in ten plants of each genotype. The time of appearance of the first double ridge (DR) and of terminal spikelet was determined. Terminal spikelet (TS) formation is unambiguous in wheat and triticale. However, for barley the appearance of awn primordia was taken to indicate the completion of the spikelet initiation phase (Kirby and Appleyard, 1984) whereas stamen differentiation in the earliest formed spikelets was used in oats (Moncur, 1981). Anthesis (A) was recorded as the time when 50% of culms reached anthesis in all experiments. Physiological maturity (PM), recorded as the time when no green parts were present in a plot, was noted in experiments C89, M89 and M90. Intervals between successive phenological stages (DR, TS, A and PM) were calculated in both calendar days (CD) and thermal time (°Cd).

3.2.2 Crop growth

Two quadrat harvests (0.17 m^2 each) of above-ground plant parts were taken from each plot at regular intervals in experiments C88, M88, C89, M89 and M90. The two quadrat harvests from each plot were bulked. A subsample was taken, and in the pre-anthesis harvests, separated into leaves and stems (including leaf sheaths). The number of tillers per sample was recorded as well as the leaf number on the main stem. At the first harvest at M89 and C89 leaves from 30 plants were removed. The area of the first, second and third main stem leaves was determined as well as the total leaf area.

When ears emerged a subsample of 30 stems was taken from each quadrat bulk and separated into heads, dead leaves, green leaves and stems (including leaf sheaths). The area of leaves in samples was determined using a Delta-T Devices area measurement system, and oven dry weight of plant parts and of the bulk sample were determined. Leaf area index (LAI) was computed from the product of the sample specific leaf area ($m^2\ kg^{-1}$) and the total leaf weight per unit ground area. Stem density in the sample of 30 stems was determined in C89, M89 and M90 from the ratio of stem weight (not including the sheath) to stem length.

3.2.3 Crop growth indices

Relative growth rate (RGR) is defined as the rate of dry weight accumulation per unit of existing dry weight and crop growth rate (CGR) as the rate of dry weight accumulation per unit ground area (Warren Wilson, 1981). These indices were calculated, as suggested by Radford (1967), by substituting thermal time for calendar

time. Thermal time (T) was calculated in degree day units (°Cd) by summing the daily values of mean temperature (Russelle *et al.*, 1984). The daily values were calculated as:

$$T_i = [(T_{max}+T_{min})/2]-T_b \quad (3.1)$$

where T_i is the degree day for the i th day, T_{max} the maximum daily air temperature, T_{min} the minimum daily air temperature with a lower limit of 0 °C, and T_b, the base temperature below which no growth occurs (Cao and Moss, 1989), was set to 0 °C. The greatest T_{max} recorded from emergence to anthesis was less than 30 °C at both sites.

RGR was calculated from time T_1 to T_2 as:

$$RGR=(\log_e W_2-\log_e W_1)/(T_2-T_1) \quad (3.2)$$

where $\log_e W_1$ and $\log_e W_2$ are the natural log values of dry weight (g m^{-2}) at T_1 and T_2 respectively.

CGR was calculated from T_1 to T_2 as:

$$CGR=(W_2 - W_1) / (T_2 - T_1) \quad (3.3)$$

where W_1 and W_2 represent the dry weight (g m^{-2}) at T_1 and T_2.

Between anthesis and physiological maturity, 20 heads were randomly harvested from each plot on a regular basis. These were oven-dried and then weighed. The head growth rate (HGR) was determined during the linear phase of grain growth in M90 from regular harvests from just after anthesis to physiological maturity. There is no further increase in chaff weight (the head or spike without grains) after anthesis; any weight increase is in the growing kernels. Thus, HGR (mg $(°Cd)^{-1}$) of each genotype was taken as the slope of the relationship between head dry weight and the thermal time in successive harvests. The HGR (mg $(°Cd)^{-1}$) was used to calculate kernel growth rate (KGR) and grain growth rate (GGR). The GGR (mg m^{-2} $(°Cd)^{-1}$) was calculated from the product of HGR and the average number of spikes m^{-2} in M90, whereas KGR was calculated by dividing HGR by the number of kernels $spike^{-1}$ at M90 for each genotype.

3.3 RESULTS

3.3.1 Variation in development

Thermal time to reach different development stages was very similar at both C89 and M89 (Fig. 3.1). Minor exceptions occurred in that barley reached double ridge

earlier at M89, anthesis was somewhat earlier at M89 whereas physiological maturity was earlier at M89.

Variation in reproductive development within species was substantial and tended to mask major differences between species. Nevertheless, several consistent patterns emerged. Barley reached physiological maturity about 180 °Cd (*ca.* 10 days) before bread wheat, durum wheat and triticale and about 90 °Cd before oats (Table 3.1). The earlier maturity in barley arose because it generally had a shorter time interval to reach each developmental stage than the other species. The exception was between double ridge and terminal spikelet (taken as the appearance of awn primordia in barley) where barley tended to take a longer time (Table 3.2). This could be because the reproductive apex of barley does not have a terminal spikelet and the appearance of awn primordia, used as a surrogate for terminal spikelet, may over estimate the equivalent of terminal spikelet in barley. Other consistent differences between species were that triticale reached both double ridge and terminal spikelet very quickly but had the longest interval from terminal spikelet to anthesis and to physiological maturity. Variation in the duration between DR and A was small; mean range over C89 and M89 varied between 730 and 760 °Cd. Thus most of the variation in the time to reach anthesis was due to the interval between sowing and DR formation (Fig. 3.2a). The relationship between time to DR and time to flowering suggests that the period between DR and flowering is accelerated as floral initiation becomes later (Masle *et al.*, 1989; Stapper and Fischer, 1990). An alternative explanation to the apparent accelerated development to anthesis of plants with a long time to double ridge is that the longer daylength experienced by late flowering plants may also be important. However, this does not appear to be the case here as when photothermal time to flowering, calculated according to Masle *et al.* (1989), was plotted against photothermal time to double ridge, the same parabolic relationship was found. Thus it is likely that the interval between double ridge and anthesis is inversely related to the time to double ridge.

Data showing the thermal time and calendar time to reach each phenological stage for each genotype at C89, M89 and M90 are given in the appendix (Tables 3.1 to 3.3).

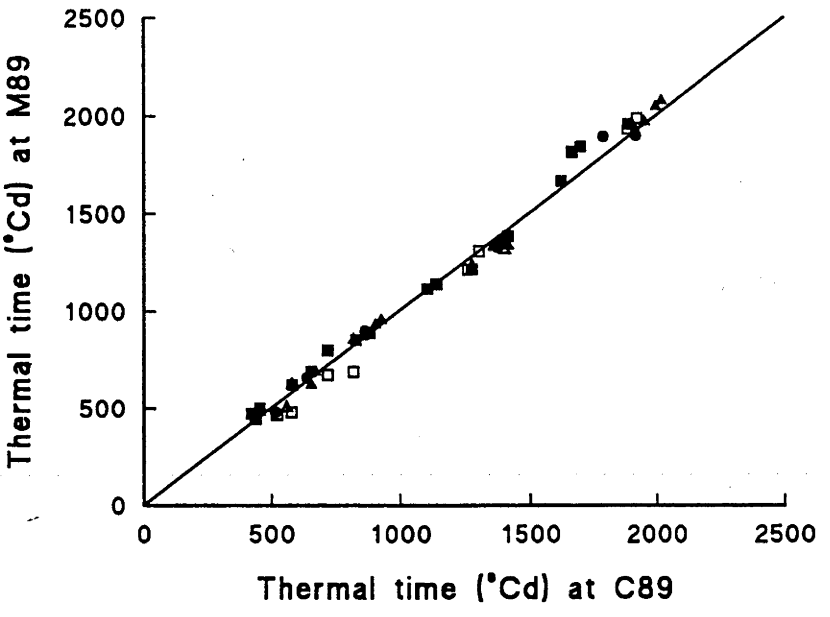


Fig. 3.1 Thermal time to reach each developmental stage in each genotype in M89 and C89. The line shows the 1:1 relationship.

Table 3.1. Degree and calendar days to double ridge (DR), terminal spikelet (TS), anthesis (A) and physiological maturity (PM).

Exp.	Species	DR	TS	A	PM
		°Cd (calender days)			
C89					
	Barley	473(47)	770(81)	1234(124)	1719(154)
	Bread wheat	607(63)	876(93)	1374(134)	1970(168)
	Durum wheat	616(64)	819(87)	1382(134)	1910(164)
	Triticale	549(57)	769(81)	1282(127)	1905(164)
	Oats	575(59)	846(90)	1326(130)	1853(161)
	Lsd(P=0.05)	20(2)	9(1)	8(1)	37(2)
M89					
	Barley	509(54)	807(91)	1214(129)	1823(169)
	Bread wheat	601(66)	902(101)	1330(138)	2009(178)
	Durum wheat	560(61)	851(96)	1322(138)	1931(174)
	Triticale	473(50)	680(76)	1263(133)	1965(176)
	Oats	568(62)	875(98)	1273(134)	1900(173)
	Lsd(P=0.05)	13(2)	16(2)	13(1)	33(2)
M90					
	Barley	-	-	1251(122)	1794(155)
	Bread wheat	-	-	1318(127)	1975(164)
	Durum wheat	-	-	1306(126)	1967(164)
	Triticale	-	-	1280(124)	2005(166)
	Oats	-	-	1335(128)	1846(157)
	Lsd(P=0.05)	-	-	15(1)	21(1)

The numbers between parentheses represent calendar days.

Table 3.2. Intervals between sowing and double ridge (S-DR), double ridge and terminal spikelet (DR-TS), terminal spikelet and anthesis (TS-A) and anthesis and physiological maturity (A-PM) in degree and calendar days.

Exp. Species	S-DR	DR-TS	TS-A	A-PM
	°Cd(calender days)			
C89				
Barley	473(47)	298(34)	464(42)	484(30)
Bread wheat	607(63)	268(30)	498(41)	596(34)
Durum wheat	616(64)	204(22)	562(47)	529(30)
Triticale	549(57)	220(24)	513(46)	623(37)
Oats	575(59)	270(30)	480(40)	527(31)
Lsd(P=0.05)	11(1)	14(2)	10(1)	39(2)
M89				
Barley	509(54)	297(36)	408(38)	609(39)
Bread wheat	601(66)	300(35)	428(37)	678(40)
Durum wheat	560(61)	291(35)	471(42)	609(37)
Triticale	473(50)	208(26)	582(57)	702(43)
Oats	568(62)	306(36)	398(35)	62(39)
Lsd(P=0.05)	13(2)	22(2)	23(2)	35(2)
M90				
Barley	-	-	-	543(32)
Bread wheat	-	-	-	656(37)
Durum wheat	-	-	-	661(38)
Triticale	-	-	-	725(41)
Oats	-	-	-	518(29)
Lsd(P=0.05)	-	-	-	30(2)

The numbers between parenthesis represent calendar days.

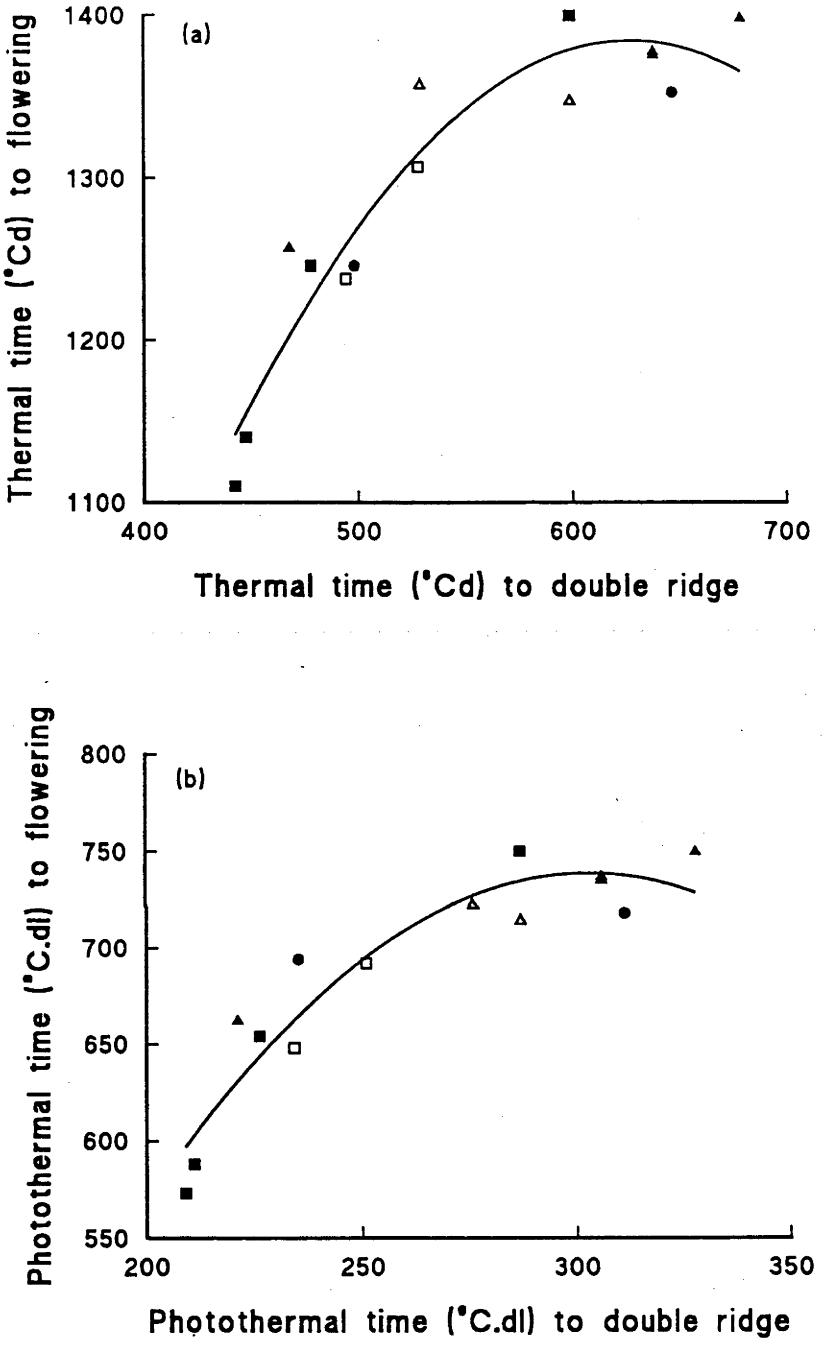


Fig. 3.2 Relationship between (a) thermal time and (b) photothermal time to reach double ridge and anthesis for each genotype at C89 and M89.

A sample of the variation evident within and between species is given in Fig. 3.3 where the intervals between each of the developmental stages are presented for the earliest and latest flowering wheat and barley and the mean value for triticale. The genotypes are placed in order of their time to reach double ridge. Little resemblance to this order was found in the intervals between the subsequent stages.

3.3.2 Variation in pre-anthesis growth

Characteristics of each species at the first detailed harvest in each experiment are given in Table 3.3. With the exception of M90, this harvest was made when the number of main stem leaves averaged 4.5 and leaf area index (LAI) was below 1.0. In almost every experiment barley had the highest LAI, developed main stem leaves fastest and hence had the shortest phyllochron interval, had produced the most tillers and with the exception of oats, had the highest specific leaf area (SLA). The above-ground dry weight (AGDW) of barley was also higher than the other species except triticale in all experiments. Averaged over all experiments barley and triticale had the same AGDW and this was about 50% greater than in the other species. The LAI of triticale was 17% less than for barley when averaged over all sites. Triticale contrasted with barley in that it had a longer phyllochron interval and thus fewer main stem leaves than bread wheat and barley. Also, triticale generally had fewer tillers than the other species at this first harvest.

Variation in plant characteristics to the beginning of reproductive development between species was much greater than the variation within species. Table 3.4 shows the same plant characteristics as in Table 3.3 for all genotypes at C89. Although there is some variation within species, notably Ulandra barley for most characteristics, variation within species was small.

Differences between species in leaf area were established from the time the first leaf had fully expanded and this difference was maintained as later leaves appeared. Fig 3.4 shows the cumulative leaf area of each species in 1989 (average of C89 and M89) after emergence. The leaf area at the final values at 330 °Cd comprises both main stem leaves and tillers whereas the earlier points represent leaf area of the main stem leaves as the contribution from tiller leaves is negligible. The first leaf of barley emerges earlier and it is larger than the other species. Although the cumulative area of the first two leaves of triticale and oats is greater than barley, triticale and oats have a slower leaf appearance time and barley maintains a higher leaf area. The difference in leaf area between barley and triticale, on the one hand, and the two wheat species, on the other, is large and begins from the appearance of the first leaf and continues through the tillering phase. The size of oat leaves were larger than bread and durum wheats whereas bread wheat had a significantly greater leaf area than durum wheat beginning from when leaf 2 had fully expanded.

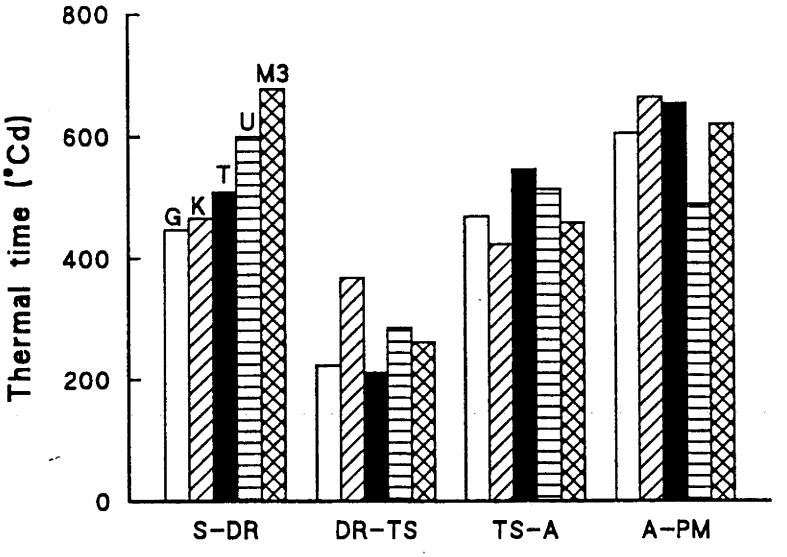


Fig. 3.3 The average interval between sowing and double ridge (S-DR), double ridge to terminal spiklet (DR-TS), terminal spiklet to anthesis (TS-A) and anthesis to physiological maturity (A-PM) for the earliest and latest barley (Galleon and Ulandra),bread wheat (Kulin and M3344) and the mean value for triticale at C89 and M89. Genotypes are placed in order of their time to reach the double ridge stage.

Table 3.3. Above-ground dry weight (AGDW, g m^{-2}), leaf area index (LAI), main stem leaf number (LNO), phyllochron interval (PI, (°Cd)$leaf^{-1}$), tillers m^{-2} (TNO) and specific leaf area (SLA, m^2 kg^{-1}).

Exp. Species	AGDW	LAI	LNO	PI	TNO	SLA
C88						
Barley	49	0.8	5.8	63	801	26.2
Bread wheat	31	0.4	4.9	74	488	22.5
Triticale	44	0.6	4.6	79	352	23.3
Oats	27	0.5	4.3	84	521	27.5
Lsd(P=0.05)	6	0.1	0.1	2	65	1.2
C89						
Barley	39	0.6	5.0	69	779	26.1
Bread wheat	23	0.3	4.2	82	544	20.3
Durum wheat	16	0.2	4.0	87	582	18.0
Triticale	30	0.4	3.9	88	545	22.6
Oats	23	0.4	3.9	88	658	26.0
Lsd(P=0.05)	5	0.1	0.3	5	79	1.8
M88						
Barley	48	0.7	5.9	73	799	23.2
Bread wheat	39	0.5	5.4	79	585	21.3
Durum wheat	37	0.5	5.0	85	462	22.3
Triticale	58	0.7	5.0	85	450	18.9
Lsd(P=0.05)	5	0.1	0.1	2	46	0.8
M89						
Barley	19	0.2	4.7	68	712	22.5
Bread wheat	16	0.2	4.0	80	556	19.8
Durum wheat	13	0.1	3.8	85	502	17.9
Triticale	23	0.3	4.1	79	558	21.4
Oats	14	0.2	3.9	82	550	23.3
Lsd(P=0.05)	3	0.05	0.2	5	57	1.6
M90						
Barley	151	2.4	7.2	76	878	24.6
Bread wheat	103	1.6	6.5	84	710	24.0
Durum wheat	59	0.9	6.0	91	570	25.0
Triticale	124	1.8	6.1	89	572	23.1
Oats	98	1.8	6.0	91	723	26.0
Lsd(P=0.05)	19	0.3	0.3	3	95	2.1

Table 3.4. Above-ground dry weight (AGDW, g m^{-2}), leaf area index (LAI), main stem leaf number (LNO), phyllochron interval (PI, (°Cd)$leaf^{-1}$)), tillers m^{-2} (TNO) and specific leaf area (SLA, m^2 kg^{-1}) in C89.

Genoytpe	AGDW	LAI	LNO	PI	TNO	SLA
Barley						
Galleon	42	0.7	5.0	68	770	28.2
O'Connor	44	0.7	5.0	69	793	25.4
Ulandra	31	0.4	4.7	73	777	23.8
Malebo	40	0.6	5.1	67	777	26.9
Bread wheat						
Kulin	20	0.2	4.0	87	457	24.3
Meteor	20	0.3	4.2	81	567	18.2
Rosella	24	0.3	4.5	77	557	19.9
M-3344	27	0.3	4.1	83	597	18.6
Durum wheat						
Altar84	15	0.2	3.7	93	553	18.0
Carcomun	16	0.2	4.3	81	610	17.9
Triticale						
Dua	28	0.3	4.0	87	603	22.8
Currency	33	0.4	3.9	89	487	22.5
Oats						
Echidna	23	0.3	3.8	91	673	26.6
Hakea	22	0.4	4.1	85	643	25.4
Lsd(P=0.05)	6	0.1	0.4	8	126	2.3

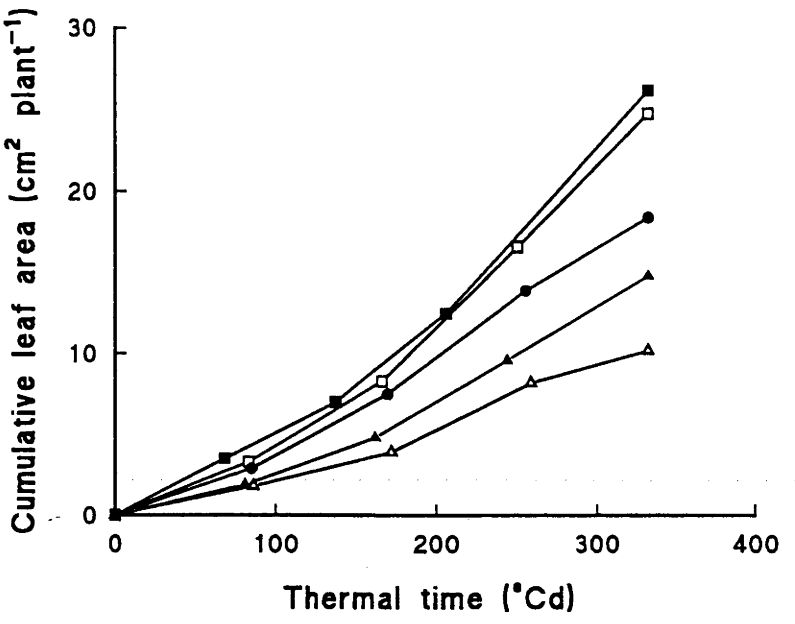


Fig. 3.4 Cumulative main stem leaf area for leaves one, two and three and total leaf area per plant at 330 °Cd after sowing for barley (■), bread wheat (▲), durum wheat (△), triticale (□) and oats (●). Values are averaged over C89 and M89 and are calculated from the leaf size of each fully expanded leaf and the phyllochron interval. The standard error for each of leaf 1, leaf 2, leaf 3 and total cumulative area is 0.21 cm^2, 0.25 cm^2, 0.44 cm^2 and 1.06 cm^2 respectively.

The most intensive sampling for LAI was made in 1988 (C88 and M88) and the development of leaf area for C88, which was typical for all experiments, is given in Fig 3.5. The LAI of barley was highest at all harvests up to anthesis. There was little difference between the two wheat species. Both triticale and oats had a higher LAI than wheat and there was evidence that triticale maintained its leaf area longer than the other species.

The most intensive sampling for AGDW was made in C89 and M89 and the results at these two sites, shown in Figs 3.6a and b, were representative of the other experiments. The AGDW was greatest at M89 and growth continued to physiological maturity. This contrasts with C89, which experienced a more severe terminal drought and no further accumulation of dry weight occurred after anthesis. Barley and triticale had the highest AGDW at all harvests at both sites and this was also true in the other experiments. Bread and durum wheats had the lower AGDW at most harvests at both sites; this was most apparent at M89. The dry weight of oats was consistently higher than for the wheats before anthesis but by maturity little difference in total AGDW between oats and wheat were found. Dry weight at anthesis varied between species. Although the bread wheat, durum wheat and oats reached anthesis later than barley and triticale, their AGDW at anthesis was less.

Crop growth rates (CGR) at M89 and C89 were greatest in barley and triticale up to anthesis (Figs 3.7a and b). Differences after anthesis were less. Despite the differences in AGDW and CGR, differences in relative growth rate (RGR) between species were not detected (Figs 3.8a and b). Thus, the differences in weight established early were maintained until physiological maturity.

3.3.3 Variation in post-anthesis growth

The head growth rate during the linear phase of growth was determined from regular harvests at M90. This is presented in Table 3.5 together with the coefficient of determination (r^2). The r^2 values were all over 0.95 except for Ulandra. The more relevant parameters, kernel growth rate (KGR) and grain growth rate (GGR) were determined using head growth rate, head number and kernel number. Both KGR and GGR were 75% greater in barley than in the other species. Bread wheat and triticale were similar and their GGR and KGR were about 15 to 20% greater than for oats and durum wheat. Variation in GGR between barley genotypes was large and was greater than the variation between genotypes in the other species.

The stem density at anthesis and physiological maturity for each genotype in M89 and C89 is given in Table 3.6. Stem density was always greater at anthesis and was maximal at the site with the greatest AGDW (M89).

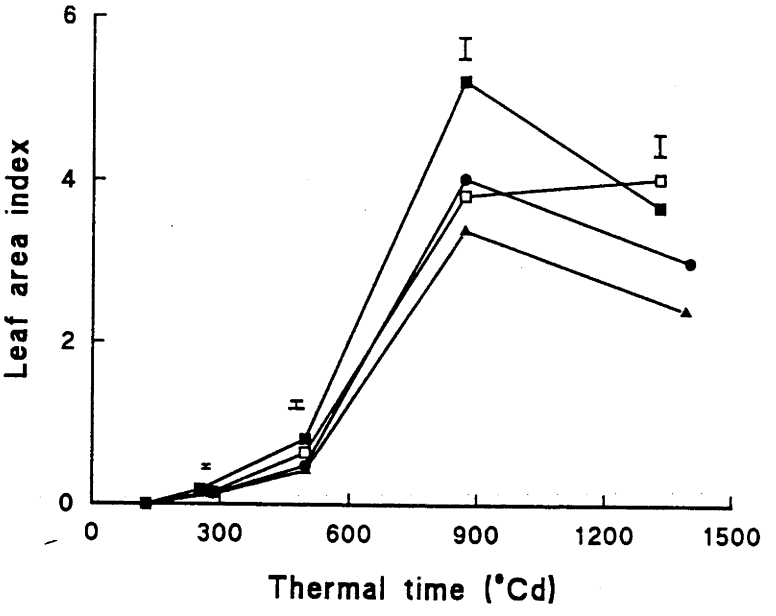


Fig. 3.5 Leaf area index for barley (■), bread wheat (▲), triticale (□) and oats (●) at C89 in relation to thermal time.

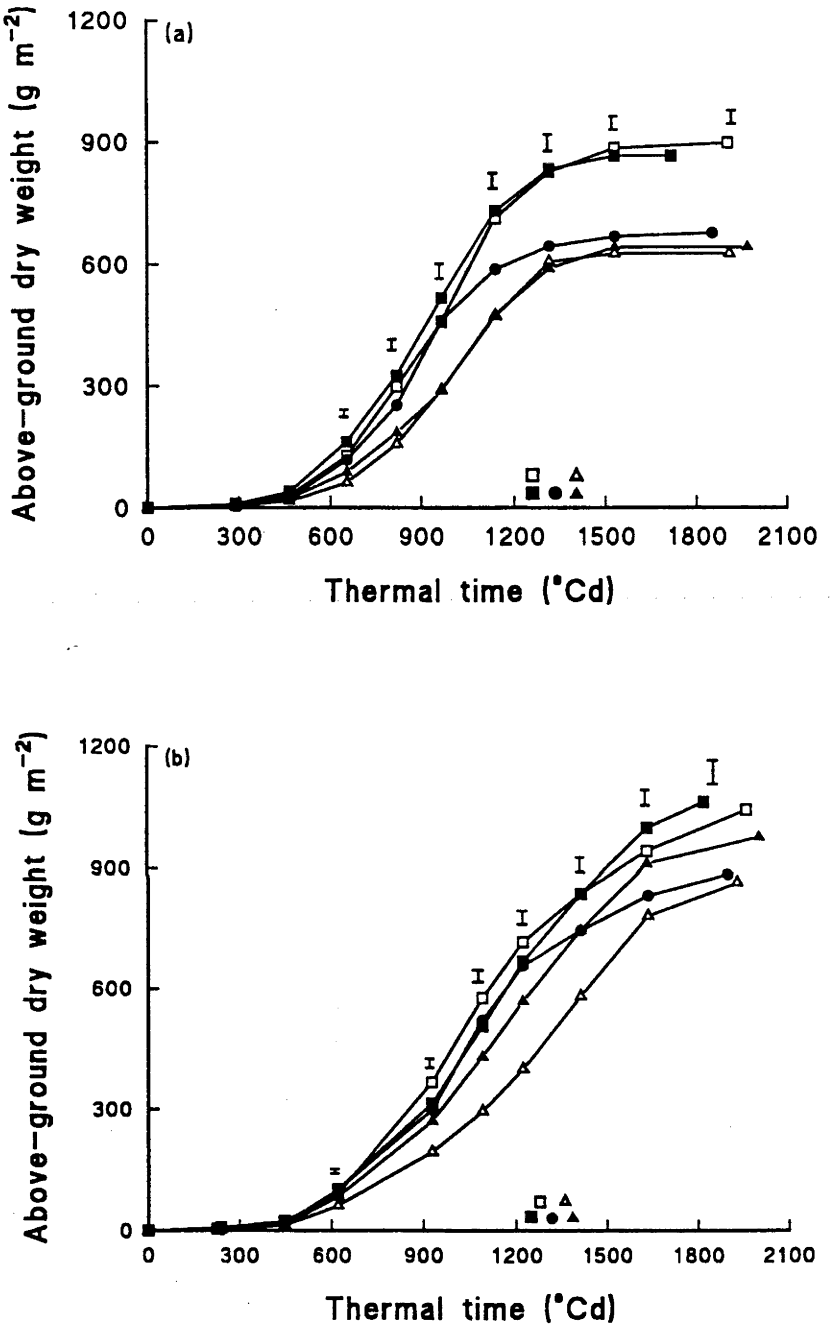


Fig. 3.6 Above-ground dry weight at a) C89 and b) M89 for barley (■), bread wheat (▲), durum wheat (△), triticale (□) and oats (●). Symbols on x-axis show the time to anthesis.

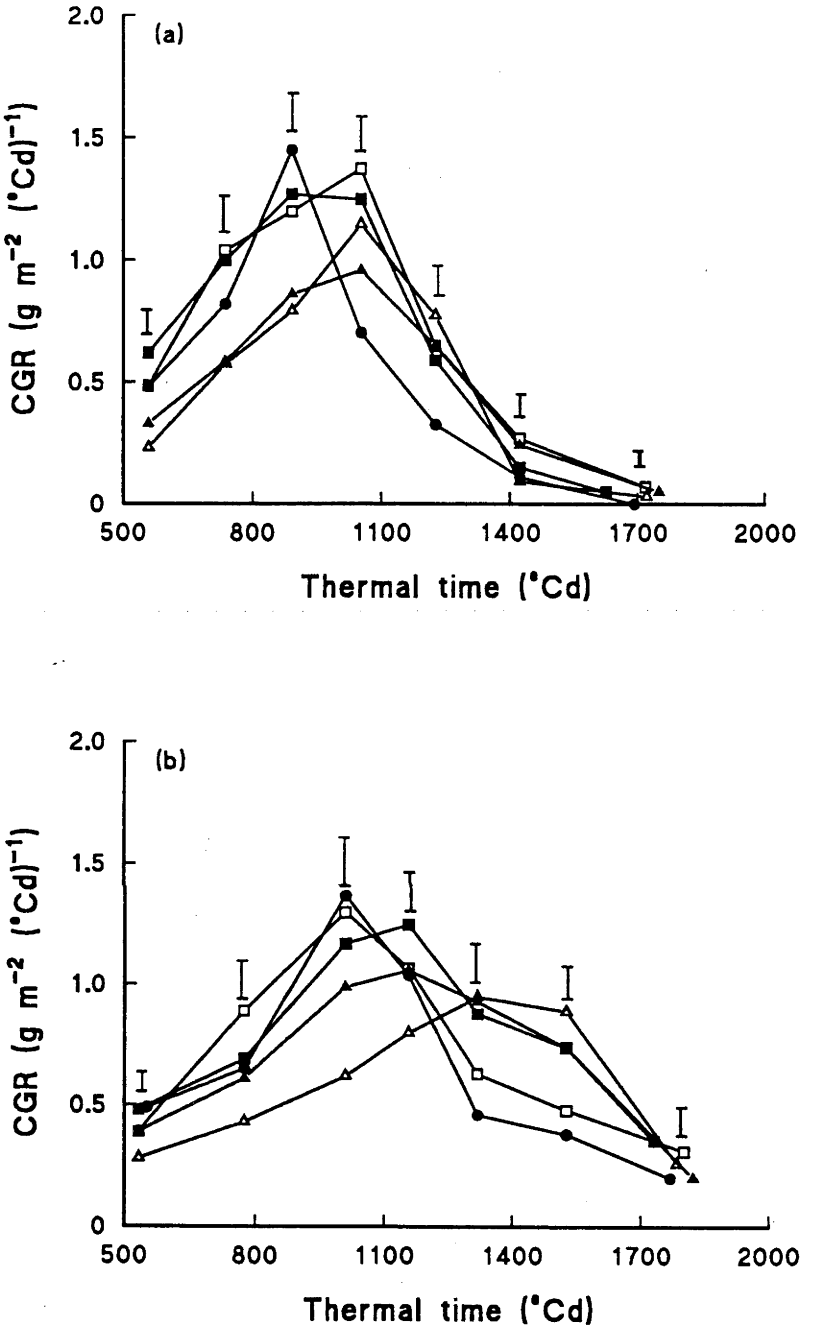


Fig. 3.7 Crop growth rate at a) C89 and b) M89 for barley (■), bread wheat (▲), durum wheat (△) and triticale (□) in relation to thermal time.

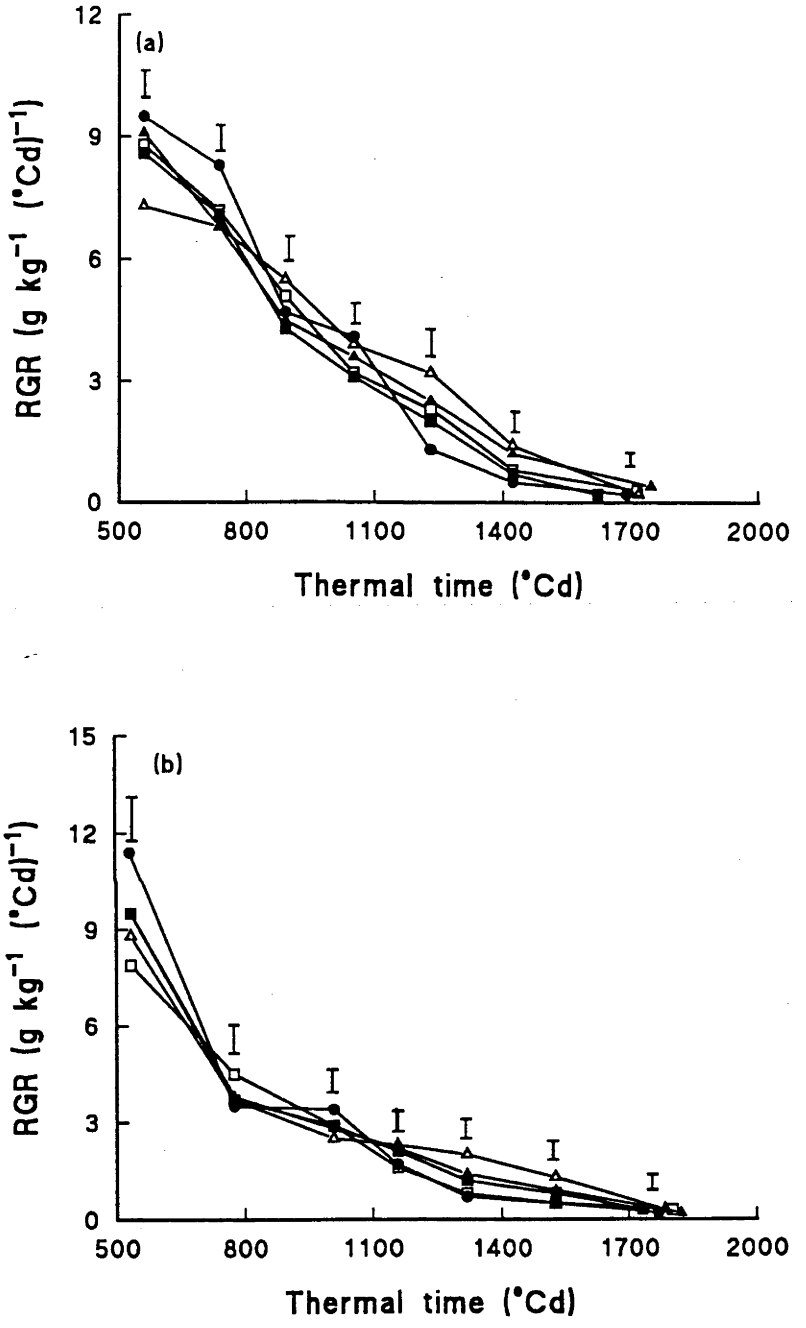


Fig. 3.8 Relative growth rate at a) C89 and b) M89 for barley (■), bread wheat (▲), durum wheat (△) and triticale (□) in relation to thermal time.

Table 3.5. Head growth rate (HGR, mg $(°Cd)^{-1}$) and r^2, grain growth rate (GGR, mg m^{-2} $(°Cd)^{-1}$) and kernel growth rate (KGR, mg $(°Cd)^{-1}$) in M90 during the linear phase of kernel growth.

Genotype	HGR	KGR	GGR
Barley			
Galleon	1.7(0.97)	0.126	1029
O'Connor	2.7(0.99)	0.145	1409
Ulandra	2.3(0.82)	0.107	906
Malebo	5.5(0.99)	0.206	1639
Bread wheat			
Kulin	3.6(0.99)	0.107	806
Meteor	2.3(0.99)	0.064	761
Rosella	2.3(0.96)	0.097	727
M-3344	2.4(0.97)	0.095	749
Durum wheat			
Altar 84	3.2(0.99)	0.080	541
Carcomun	3.5(0.99)	0.090	634
Triticale			
Dua	3.8(0.96)	0.096	695
Currency	3.9(0.96)	0.092	757
Oats			
Echidna	2.6(0.94)	0.058	788
Hakea	2.3(0.98)	0.077	619

As expected, triticale with the fewest stems, had heavier stems per unit length than barley which had the most stems.

The loss of stem weight per unit area (stem weight loss, SWL), which can estimate the storage and remobilisation of photosynthate was calculated from the product of (i) the change in stem density between anthesis and maturity, (ii) the stem length and (iii) the number of fertile spikes per m^2. This value is given in Table 3.6 for M89 and C89. Except for Dua triticale there was a good correspondence between genotypes at both sites, ($r=0.74$, $P<0.01$, excluding Dua) which indicates repeatable genotypic differences. Triticale had the greatest values when averaged over both sites and O'Connor barley and Meteor bread wheat also had large values. In barley, bread wheat and oats the latest flowering genotypes had the smallest change in stem weight.

3.4 DISCUSSION

Comparisons between the temperate cereals in development and in pre- and post-anthesis growth again showed that barley was the exceptional species. Although there were large differences within species in phenology, barley varieties were generally first to reach double ridge formation, anthesis and physiological maturity. Time from sowing to double ridge formation and from sowing to anthesis were inversely related to yield at M89 ($r = -0.60$ and $r = -0.78$ respectively) and at C89 ($r = -0.85$ and $r = -0.90$ respectively). Barley also produced leaves and tillers faster, leaf area and crop growth rate was greater (although triticale matched barley very closely in the accumulation of AGDW), and grain growth was also faster in barley. These differences were found in every experiment where these characters were investigated. They included the wetter environment where AGDW continued to increase after anthesis (M89) and the drier environment where there was little further increase in AGDW after anthesis (C89).

The earlier maturity in barley and the shorter grain growth period has been noted by others (Acevedo *et al.*, 1990, Yasuda, 1989). This makes barley quite remarkable compared to the other species in that despite its shorter growth duration its final AGDW is higher. What is the cause of this? It does not seem to arise from differences in growth rates as the relative growth rates were similar in all species, although this is difficult to measure precisely in field grown plants. The fast rate of leaf appearance and tiller appearance is sometimes thought to be responsible for faster absolute growth rates in cereals (Whan *et al.*, 1991). Both leaf area and tiller appearance were very high in barley. However, results here suggest this is unlikely to be important because triticale, with a similar absolute growth rate as barley, had among the lowest values for these characteristics. A high specific leaf area also has been proposed as an important trait for fast early growth (Rawson *et al.*, 1987). However, this alone cannot account for the higher AGDW in barley as the SLA in oats were comparable to that of barley. It seems likely that the higher AGDW of barley and triticale is established from the time the first leaves appear. The area of the first leaf in barley, for example, was twice that of durum wheat and bread wheat as well as being larger than triticale and oats.

Table 3.6. Stem density at anthesis (SD_A, mg cm^{-1}) and physiological maturity (SD_{PM}, mg cm^{-1}), also change in stem weight (SWL, g m^{-2}) between anthesis and physiological maturity for each genotype in M89 and C89.

	M89			C89		
	SD_A	SD_{PM}	SWL	SD_A	SD_{PM}	SWL
Barley						
Galleon	8.0	6.6	67.9	8.7	6.6	92.2
O'Connor	8.9	7.1	102.8	8.6	6.5	102.9
Ulandra	10.1	7.7	56.9	10.3	9.7	5.4
Malebo	16.6	13.2	103.6	14.0	11.7	73.2
Bread wheat						
Kulin	18.1	13.8	98.8	14.8	10.3	67.6
Meteor	15.5	11.6	120.7	13.1	9.0	137.5
Rosella	12.3	11.0	41.4	11.5	7.9	58.6
M3344	11.1	9.8	35.4	13.0	9.3	43.3
Durum wheat						
Altar84	15.5	13.6	33.0	16.0	11.7	42.9
Carcomun	17.9	15.1	54.0	15.8	11.8	43.0
Triticale						
Dua	24.9	16.6	177.8	17.7	14.4	65.2
Currency	24.2	17.7	139.5	21.4	15.6	100.9
Oats						
Echidna	16.7	11.9	65.5	13.4	8.3	53.6
Hakea	14.7	11.6	61.4	10.0	7.6	20.9

This will be investigated further in later chapters.

It is worth noting that although barley and triticale had a similar AGDW, leaf area index of barley was consistently greater. This may have been a result of its greater SLA and this may be an important advantage of barley over triticale in Mediterranean environments because of the likely reduced soil evaporation under barley. Presumably triticale has a higher net assimilation rate than barley to compensate for the reduced LAI.

Although most of the advantage in AGDW is already present by anthesis the grain yield of barley is also higher than the other species, despite the shorter duration for grain growth. This was possible because barley had a consistently higher rate of kernel growth (60% higher than for wheat) as well as a higher absolute growth rate of grain per unit ground area per unit of time. This was unexpected as barley, having a greater leaf area and dry weight, probably had less water available for grain filling. It was also unexpected as previously published values for kernel growth per °Cd (Gallagher *et al.*, 1976b) and estimated values for barley crops (Riggs and Gothard, 1976; Walpole and Morgan, 1971) are similar to those reported for wheat (Gallagher *et al.*, 1976b; Loss *et al.*, 1989; Sofield *et al.*, 1977). It is not known what contributes to this difference. The most likely reason is that the duration of growth in barley between anthesis and physiological maturity was shorter than in wheat and therefore grain growth in barley must be faster if yields are similar. However, this does not explain the lack of difference between barley and wheat, noted before in other studies, unless barley yields are very much lower. The published barley data comes from field experiments in the United Kingdom where temperatures during grain filling are declining and they are mostly from 2-row genotypes. Barley has a reputation for good performance in dry environments where temperatures during grain filling are increasing such as they were in these experiments. These factors may account for some of the differences. Another possible reason for the high values for grain growth in barley reported here is that values may be biased due to the growth of the husk. However, this is unlikely as earlier work shows that the husk does not increase in weight after anthesis (Porter *et al.*, 1950; Scott *et al.*, 1983).

Kernel growth rate at M90 was correlated with kernel weight ($r = 0.83$, $P < 0.001$) but not significantly associated with yield. Grain growth rate was significantly correlated with both grain yield ($r = 0.70$, $P < 0.01$ and $r = 0.80$, $P < 0.001$ when Malebo is excluded) and with kernel weight ($r = 0.72$, $P < 0.01$).

Higher grain yields must come about from either additional assimilation during grain filling, more remobilisation of reserves from the stem to the grain, or a combination of both of these. As well, it must occur in a shorter time in barley than in the other species. In C89 and M89 the weight loss from stems between anthesis and maturity, which presumably is due more to remobilisation of reserves to the grain than to respiration may also have contributed to yields. In the two years tested, weight loss

from the stems between anthesis and physiological maturity, as a percentage of total grain yield, ranged from 9 to 50% in M89 (mean 22%) and from 3 to 60% (mean 26%) at the drier site at C89. These values agree well with the 22% contribution of pre-anthesis assimilate to grain yield found in droughted crops of barley and wheat (Bidinger *et al.*, 1977). Stem weight loss per unit ground area in barley and wheat were similar at the two sites and higher than in durum wheat and oats but lower than in triticale. The change in stem weight was not correlated with grain yield at M89 ($r = 0.29$, $P > 0.05$) but was significantly correlated with yield at C89 ($r = 0.71$, $P < 0.001$, Fig 3.9). The hybrid wheat Meteor was the exception to this and when Meteor is excluded the relationship is stronger ($r = 0.88$, $P < 0.001$). There was evidence that the earliest flowering genotypes had the greatest loss of stem weight. The relationship between anthesis and stem weight was ($r = -0.50$ ($P = 0.10$)) at M89 and ($r = -0.68$ ($P < 0.01$)) at C89. It is evident that both the pre-anthesis and post-anthesis periods were important in determining yield in these experiments. The higher biomass in barley and triticale must be achieved by either a greater total transpiration or a greater transpiration efficiency (the ratio of biomass to transpiration). Although this will be the topic of the next chapter, it is clear from the results presented here that total transpiration is likely to be higher in barley. This would arise from its greater leaf area, established very early in the plants life, that would shade the soil surface more than the other species. In the experimental sites used here, which were characterised by a significant proportion of rainfall occurring during the vegetative period, this would reduce evaporation of water from the soil surface and increase the water available for transpiration. Post-anthesis events were also important. Grain growth rate was significantly correlated with grain yield at the one site this was examined. Loss of stem reserves were also significantly correlated with grain yield at the dry site in 1989.

3.5 CONCLUSIONS

Barley and triticale have superior AGDW at all stages of their growth compared to bread wheat, durum wheat and oats. This difference was established very early and was maintained through to maturity in both the lowest and highest yielding environments. Differences in dry weight were not associated with any apparent differences in relative growth rate. Barley and triticale were also the first to reach terminal spikelet (or its equivalent), anthesis and barley reached physiological maturity before the other species. Other advantages that were considered important for yield formation in these water limited environments were the faster and greater canopy growth of barley as well as its faster grain growth and high translocation of stem reserves to the grain.

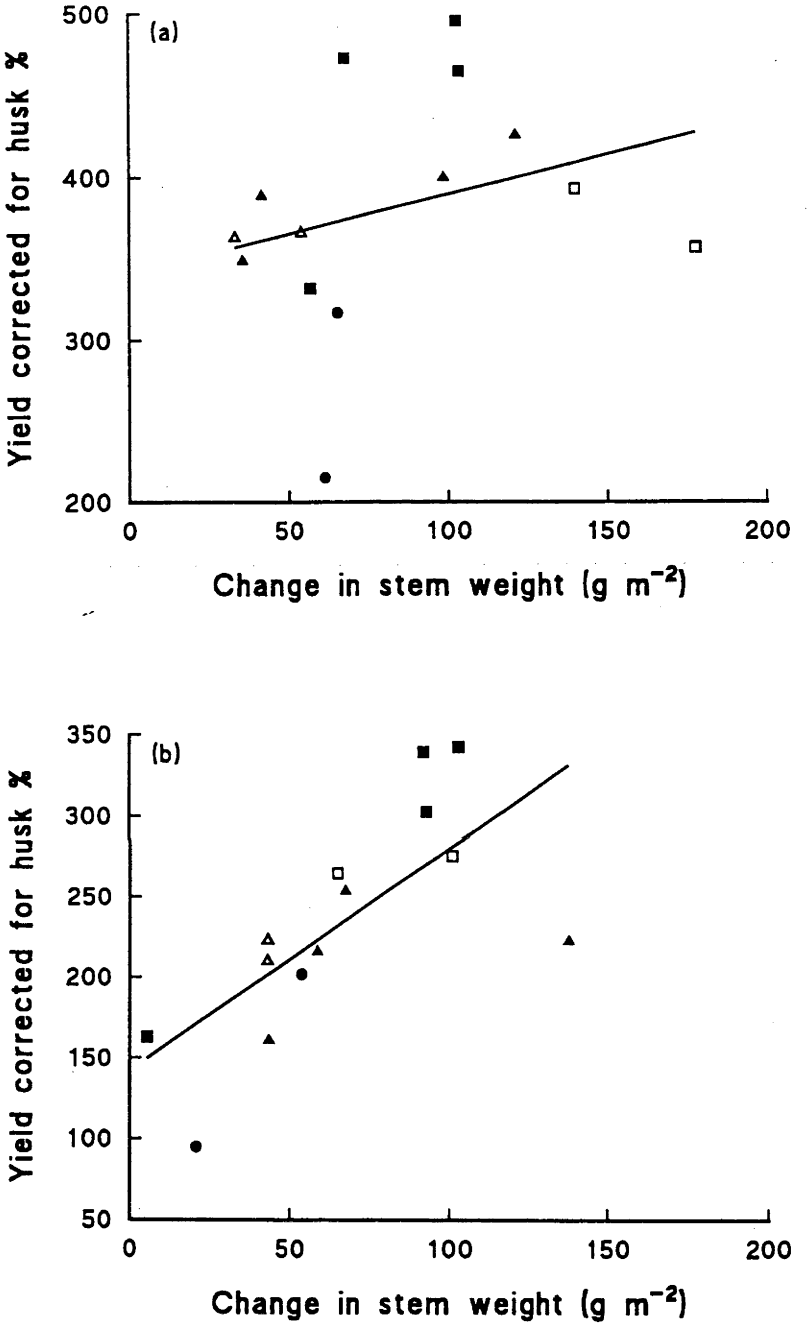


Fig. 3.9 Relationship between change in stem weight (g m^{-2}) between anthesis and physiological maturity and grain yield at a) M89 and b) C89 for barley (■), bread wheat (▲), durum wheat (△), triticale (□), oats (●). Grain yield of barley and oats has been corrected for husk weight.

CHAPTER 4

VARIATION IN WATER USE AND WATER-USE EFFICIENCY IN FIELD AND POT GROWN PLANTS

4.1 INTRODUCTION

The field experiments conducted in 1988, 1989 and 1990 have consistently shown the outstanding grain yield and dry weight accumulation of barley compared to the other species. The higher final AGDW in barley was associated with a faster development of leaf area and dry weight than the other species. In each of these experiments water supply was finite and was probably the main factor limiting growth and yield.

The higher AGDW of barley must be due to one or more of the following three factors. The first is that there may be variation in the extraction of soil water by roots which results in some genotypes having a higher evapotranspiration (E_T) or transpiration (T) than others and this results in more growth. The second is transpiration efficiency (TE), i.e. the amount of carbon fixed per unit of water transpired, and is represented by the ratio of dry matter to transpiration. The TE at a leaf level has been expressed by Farquhar and Richards (1984) as:

$$TE=P_a(1-P_i/P_a)/(1.6(e_i-e_a)) \qquad (4.1)$$

where P_i and P_a and e_i and e_a are the intercellular and atmospheric vapour pressure for CO_2 and water respectively. Thus, TE varies according to the ratio of P_i/P_a, of which carbon isotope discrimination is an integrated measure (Farquhar and Richards, 1984), and to the vapour pressure deficit (VPD) of the atmosphere. The importance of VPD in determining variation in water-use efficiency (WUE), i.e. the ratio of AGDW or biomass to evapotranspiration in cereal crops in southern Australia has been demonstrated by Perry (1987). The third factor that may account for variation in grain yield and AGDW is the amount of water lost by soil evaporation relative to transpiration. Genotypes may vary in their leaf area development such that some shade the soil and reduce the evaporation from the soil surface more than others. Equation 4.2, adapted from Richards (1991), expresses WUE in terms of its principal determinants, TE and the ratio of E_S (soil evaporation) to E_T (evapotranspiration);

$$WUE=(1-(E_S/E_T))TE \qquad (4.2)$$

In the environments in which the experiments reported here were conducted, the ratio of E_S to E_T can dominate variation in WUE. Typically E_S represents 40 to 50% of E_T but it can be higher (Cooper *et al.* 1983). This is because most of the rain falls

during winter when leaf area index is low and the soil surface is exposed to radiation and air turbulence which drives evaporation.

In this chapter the relative importance of the above three factors in determining variation in AGDW and grain yield will be investigated. There is evidence from the results in chapters 2 and 3 that each of the factors may be important. Barley had a greater root length density than the other species and may extract more soil water. Barley also developed a leaf canopy faster than the other species which should result in a lower E_S/E_T ratio and hence a higher WUE. Furthermore, barley accumulated AGDW faster than the other species during the coolest part of the year when VPD is lowest, which could result in a higher TE than the other species. Also, data on variation in carbon isotope discrimination, a surrogate for the ratio of P_i/P_a, will be presented together with the results of a pot experiment where measurements on TE can be made more precisely than in the field.

4.2. MATERIALS AND METHODS

4.2.1 Field grown plants

The field experiments and genotypes were the same as described in chapter 2.

4.2.1.1. Measurement of crop evapotranspiration

Crop evapotranspiration (E_T), or water use during the season, was determined for experiments C89, M89 and M90. Changes in the volumetric soil water content (θ_v) were monitored using a neutron probe (Troxler Model 3222A). A single access tube was installed in each of three replicates of two barleys (O'Connor and Ulandra), two bread wheats (Meteor and Rosella), one triticale (Dua), and one oat (Hakea). Three additional tubes were installed in unsown plots kept free of plants (bare soil) adjacent to each experiment. Access tubes were installed to a depth of 105 cm at Condobolin and 150 cm at Moombooldool. Soil below this depth was powder dry at both sites and previous experience at these sites has indicated water rarely goes beyond these depths. Neutron counts were taken at depths of 15, 25, 35, 45, 55, and then every 20 cm to the bottom of each tube. The volumetric water content of the 0-15 cm layer was determined gravimetrically from intact soil cores. Measurements were taken several times through the season corresponding to the dates of above-ground dry weight harvests (see chapter 3). For each plot the soil water content to 105 cm at Condobolin and 150 cm at Moombooldool was calculated by summing each depth measurement to give profile soil moisture (in mm of water) at each sampling time. E_T was calculated for each plot over each interval between soil moisture measurements from the water balance equation.

$$E_T = P - \Delta M - R - D \qquad (4.3)$$

where P is the precipitation during a given period of time (mm), ΔM (mm) is the change in profile soil water between each interval. Run-off (R) and drainage (D) below either 105 or 150 cm did not appear to occur at the sites and were assumed to be zero. Evaporation from bare soil, E_S, was determined from the access tubes installed in bare soil plots using equation 4.3. The above formulation treats precipitation as that reaching the crop, so that E_T includes direct evaporation of water from wet leaves following a rain event.

Measurements of θ_v began as soon as access tubes were installed. This was when plants had around 2 leaves on the main stem at C89 and M89 and 6 main stem leaves in M90. The E_T for the period prior to the first measurement of θ_v was estimated as 20 mm, 18 mm, and 44 mm for C89, M89 and M90 respectively. These values were calculated from the first and second soil moisture measurements in 1989 from the bare soil plots. They are equivalent to an E_T rate of 0.61 mm d^{-1} at M89 and 0.67 mm d^{-1} at C89. A value of 0.69 mm d^{-1} at M90 was used to calculate E_T between sowing and the first soil moisture reading.

The E_T was partitioned into components of soil evaporation, E_{SC}, and crop transpiration, T, using a model based on radiation penetration to the soil surface beneath the crop and evaporation from a bare soil surface (Cooper *et al.* 1983). The model is described in more detail in appendix 4 . Leaf canopy development at Moombooldool and Condobolin were the same and they also followed the same pattern each year (Fig. 3.4, chapter 3). As sampling for leaf area was most frequent at M88 and C88, these data were used to calculate light interception in the experiments reported here.

Crop WUE for above-ground dry weight (WUE_{AGDW}) and grain yield (WUE_{GY}) was computed for C89, M89 and M90 as the ratio of either AGDW or GY to E_T. Where root weights were estimated in C89 and M90, WUE for total biomass (WUE_B) was determined as the ratio of total biomass to E_T. Transpiration efficiency (TE) for the AGDW (TE_{AGDW}) and for biomass (TE_B) were calculated as the ratio of AGDW or biomass to the total transpiration (T) during the season.

4.2.1.2 Determination of carbon isotope discrimination

Carbon isotope discrimination, Δ, was determined from stem base samples removed at crop maturity in experiments C88, M88, C89, and M89, and the whole shoot at the 6-leaf stage in M90. The tissue in stem bases and of the shoot at the 6-leaf stage represent carbon fixed early in the life of the crop, when Δ values are stable and least affected by environmental factors (Condon and Richards, 1992). Samples were dried overnight in an oven at 80 °C and ground for determination of Δ in the laboratory following the procedure outlined by Condon *et al.* (1987).

The values of Δ were obtained as follows:

$$\Delta\,(‰) = (\delta_a - \delta_p)/(1+\delta_p) \qquad (4.4)$$

where δ_a is the air composition with respect to PeeDee Belemnite (PDB) with a value of -8‰(= - 8 x 10^{-3}) (Hubick *et al.* 1986), and δ_p is the composition of the plant material.

4.2.2 Pot grown plants

An experiment in large pots placed outside under natural conditions was conducted in Canberra (147°E, 35°S) between October 1989 and January 1990. The mean minimum and maximum temperatures for the duration of the experiment were 10.1 °C and 23.6 °C. The mean solar radiation and vapour pressure deficit were 26 MJ m^{-2} d^{-1} and 1.6 kPa. There were three barleys (Galleon, O'Connor and Ulandra), three bread wheats (Kulin, Meteor and Rosella), two durum wheats (Altar 84 and Carcomun), two triticales (Dua and AT 30) and two oats (Echidna and Hakea). Seeds of the late flowering cultivars (Ulandra, Rosella, AT 30 and Hakea) were pregerminated at 2 °C. Three seeds of each genotype were sown 3 cm below the soil surface in large pots (1 m tall and 10.3 cm diameter) containing a fertile soil. These were later thinned to one healthy plant per pot when the first leaf had fully expanded. A 4 cm cover of perlite was placed over the soil surface to prevent evaporation from soil. There were two water treatments - a control that was maintained near field capacity, and a droughted treatment, in which no water was applied after the time of sowing. In the control treatment, the weight of water lost from each pot in the previous week was added in three instalments over the next seven days. There were four replicates of each cultivar in each treatment. Pots were protected from rainfall with a moveable cover. Water use (transpiration) was determined by weighing each pot at weekly intervals in both the control and drought treatments from sowing to maturity. The date of anthesis of the main stem of each plant was recorded. Plants were harvested in January when they reached physiological maturity. Heads were separated from stems and leaves and were weighed separately. Roots were not extracted but the crown below the soil surface was included in the harvest sample. Total dry weight (DW) was recorded after oven-drying the plant samples at 80 °C for 48 h and plant transpiration efficiency (TE_{DW}) was calculated as the ratio of total DW (excluding roots) to total water use. In the drought treatment, seedlings of Ulandra barley were eliminated because of their poor growth

4.3 RESULTS

4.3.1 Potential and crop evapotranspiration

Accumulated potential evapotranspiration (E_p), crop water use (E_T) and transpiration (T) for Meteor bread wheat for C89, M89 and M90 are shown in Fig. 4.1a, 4.1b and 4.1c, respectively. The E_p at Condobolin (700 mm) was higher than at Moombooldool (500 mm).

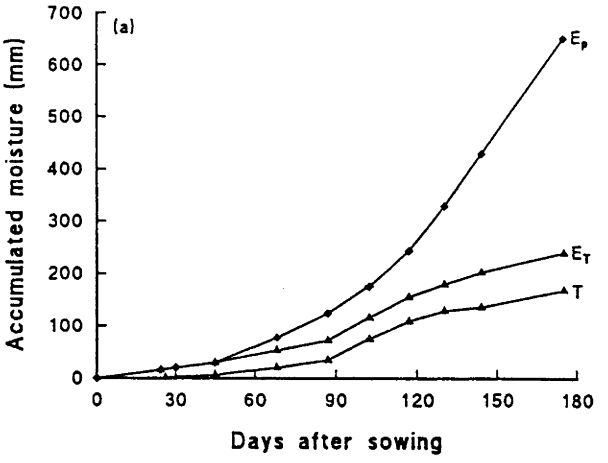


Fig 4.1a Accumulated potential evapotranspiration (E_p),crop water use (E_T) and transpiration (T) for Meteor (▲) bread wheat at C89.

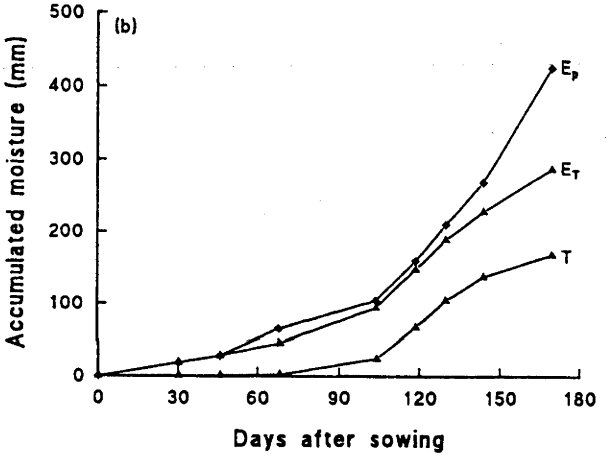


Fig 4.1b Accumulated potential evapotranspiration (E_p),crop water use (E_T) and transpiration (T) for Meteor (▲) bread wheat at M89.

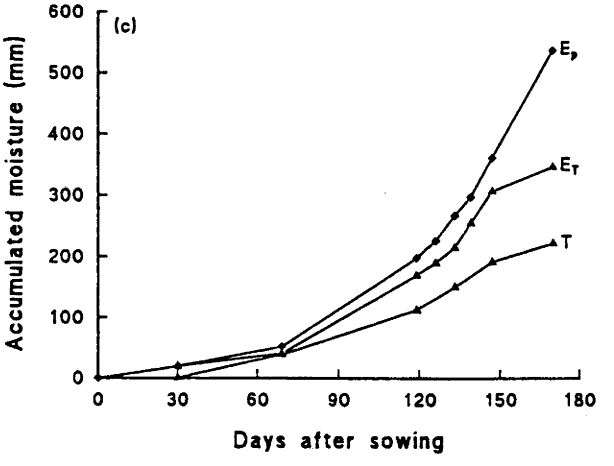


Fig 4.1c Accumulated potential evapotranspiration (E_p), crop water use (E_T) and transpiration (T) for Meteor (▲) bread wheat at M90.

The E_T was highest at M90 (326 mm) followed by M89 (282 mm) and C89 (241 mm). Variation in above-ground dry weight (AGDW) was closely related to E_T (mm) during the season ($AGDW=0.035(E_T)-0.73$, $r=0.95$, $P<0.05$). The slope of the line, 35 g m^{-2} mm^{-1}, is the average water-use efficency at these sites. It is very similar to values previously reported in southern Australia (Fischer and Kohn, 1966; Connor, 1975) and elsewhere (Table 1; Perry, 1987).

Crop transpiration (T) was highest at M90 (200 mm) and similar at M89 (167 mm) and C89 (174 mm). Evaporation from the soil surface averaged over all genotypes was higher at M89 and M90 than at C89. As a percentage of E_T, E_S was 28% at C89, 41% at M89 and 39% at M90 respectively.

4.3.2 Water use

Longer duration cultivars used more water than short duration cultivars in each experiment (Fig. 4.2) and genotypes in each species fitted the same general relationship. Hakea oats was the exception, using less water for a given anthesis date than the other genotypes.

Values for E_T for each genotype in each experiment are given in Table 4.1. At M89 and M90 the higher E_T in the later flowering genotypes was due to a greater extraction of water rather than capitalising on late rains as there was no rain during the period from physiological maturity of the earliest and the latest maturing lines. Some rain did fall at Condobolin during this time but it was insufficient to account for the variation in water use. For each day delay in flowering, water extraction increased by 0.52 mm, 1.81 mm and 0.90 mm at C89, M89 and M90 respectively.

The separation of E_T into E_S and T is also given in Table 4.1. The E_S was calculated to be about 20 mm lower in barley than in the other species at all sites. Whereas this resulted in a higher T in Ulandra, T in O'Connor was similar to the other genotypes because it had a lower E_T. When E_S is expressed as a percentage of E_T (Table 4.1), the E_S in barley was 5 to 10% less than in the other genotypes at each site. Table 4.1 shows that the percentage of water lost from the soil surface as a proportion of E_T ranged from 21% in Ulandra to 32% in Dua triticale at C89 and 36% in the two barleys to 44% in some of the other genotypes at both M89 and M90.

Fig. 4.3 and Fig. 4.4 present E_T, E_S and T for Ulandra and Rosella at C89 and M89 respectively. These genotypes were chosen as they represent a barley and a bread wheat with a similar anthesis date and total water use in two contrasting years. They show the consistently higher T in Ulandra from just after sowing to physiological maturity and the substantially lower E_S in Ulandra compared to Rosella. This also shows that T rose in C89 more quickly than in M89 and T rose faster in Ulandra than in Rosella as the former had a greater leaf area than the latter.

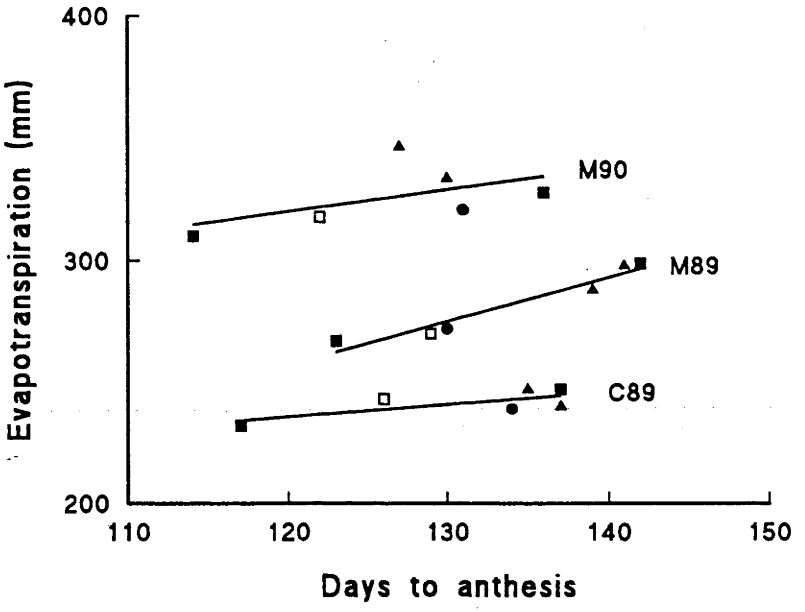


Fig 4.2 Relationship between crop evapotranspiration (E_T) and days to anthesis at each site. At C89 (E_T = 0.52(days)+173.8, r=0.82, P<0.05), at M89 (E_T = 1.81(days)+39.8, r=0.97, P<0.01) and at M90 (E_T=0.90(days)+221.8, r=0.53, n.s.).

Table 4.1. Water use (E_T), soil evaporation (E_S), transpiration (T) and the ratio of E_S/E_T.

Exp.	Genotype	E_T (mm)	E_S (mm)	T (mm)	E_S/E_T (%)
C89	**Barley**				
	O'Connor	232	57	175	25
	Ulandra	247	53	194	21
	Bread wheat				
	Meteor	240	72	168	30
	Rosella	247	75	172	31
	Triticale				
	Dua	243	76	167	32
	Oats				
	Hakea	239	70	169	29
	Lsd (P=0.05)	3	1	13	4
M89	**Barley**				
	O'Connor	267	99	168	37
	Ulandra	299	108	191	36
	Bread wheat				
	Meteor	288	119	169	41
	Rosella	298	128	170	43
	Triticale				
	Dua	270	120	150	44
	Oats				
	Hakea	272	120	152	44
	Lsd (P=0.05)	5	4	7	4
M90	**Barley**				
	O'Connor	310	106	204	34
	Ulandra	328	119	209	36
	Bread wheat				
	Meteor	347	125	222	36
	Rosella	334	139	195	42
	Triticale				
	Dua	318	129	189	41
	Oats				
	Hakea	321	140	181	44
	Lsd (P=0.05)	15	6	7	4

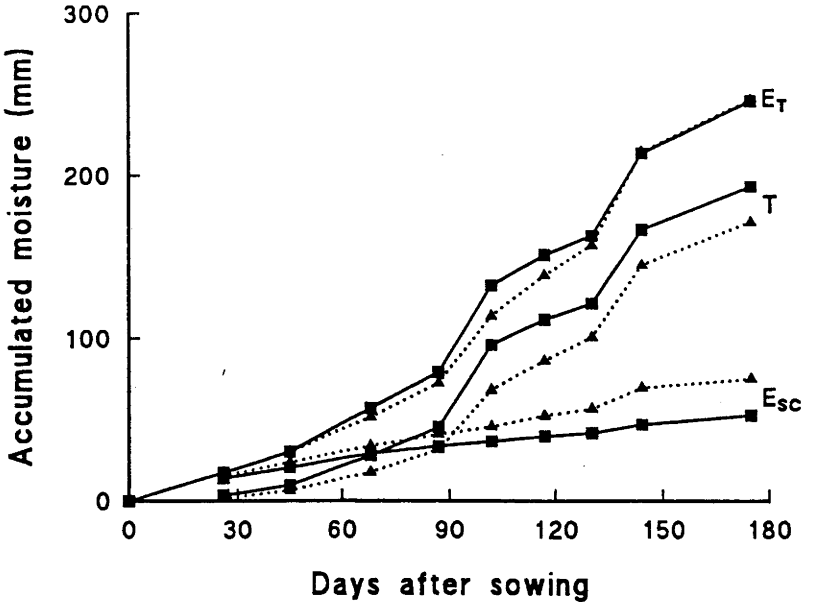


Fig 4.3 Crop water use (E_T), transpiration (T) and evaporation from soil under the crop (E_S) for Ulandra barley (■) and Rosella bread wheat (▲) at C89.

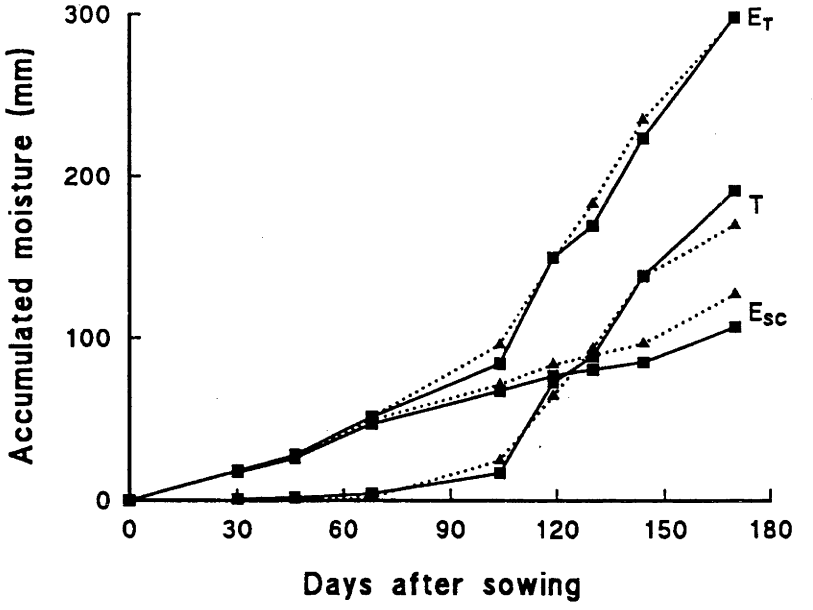


Fig 4.4 Crop water use (E_T), transpiration (T) and evaporation from soil under the crop (E_S) for Ulandra barley (■) and Rosella bread wheat (▲) at M89.

4.3.3 Water use efficiency and transpiration efficiency

Water-use efficiency for AGDW (WUE_{AGDW}) and for grain yield (WUE_{GY}) and transpiration efficiency for AGDW (TE_{AGDW}) are presented in Table 4.2. Values at Moombooldool were higher than at Condobolin. O'Connor barley had a 37% higher WUE_{AGDW} and a 70% higher WUE_{GY} than the other genotypes when averaged over the three sites. Other noteworthy values were for Dua triticale that had a significantly higher WUE_{AGDW} than the other genotypes (except O'Connor) at C89 and the hybrid wheat Meteor that consistently had high values for WUE_{AGDW} and WUE_{GY} at M89 and M90. The WUE_{GY} for Hakea oats was lowest at all sites.

Values for water-use efficiency (WUE) in these experiments were negatively related to the time of anthesis. All sites fit the same general relationship. Fig. 4.5 shows WUE for above-ground dry weight (AGDW) and grain yield (GY) in relation to the number of days after the begining of anthesis. O'Connor, the first to reach anthesis, was taken as day one at each site. The WUE for AGDW decreased by 0.67 kg ha^{-1} mm^{-1} whereas WUE_{GY} decreased by 0.39 kg ha^{-1} mm^{-1} for each day delay in flowering. The TE for AGDW was also negatively related to anthesis date at all three sites. The two trials at Moombooldool had similar values for TE and were about 12 kg ha^{-1} mm^{-1} higher than at C89 (Fig. 4.6). For each days delay in anthesis, TE_{AGDW} declined by 0.87 kg ha^{-1} mm^{-1} at Moombooldool and 1.03 kg ha^{-1} mm^{-1} at Condobolin.

The greater root mass at Condobolin accounted for much of the difference between sites (Table 4.3). For those genotypes in which roots were measured the mean values of TE based on above-ground dry weight (AGDW) were 41.1 kg ha^{-1} mm^{-1} at C89 and 52.4 kg ha^{-1} mm^{-1} at M90. When roots were included, TE values were 59.3 kg ha^{-1} mm^{-1} and 64 kg ha^{-1} mm^{-1} at C89 and M90 respectively. The mean value of TE was still c. 10% greater at M90, presumably because of the cooler conditions at Moombooldool.

The TE in the pot experiment was lower than in the field (Table 4.4). This reflects the higher vapour pressure deficit during this experiment. The TE was higher in the drought treatment than in the control. O'Connor also had the highest TE in the drought treatment in the pot experiment. It was significantly higher than all other genotypes except Galleon barley. Although TE of O'Connor and Galleon was also high in the control treatment, differences between genotypes were generally not significant. Only the extreme winter lines that flowered last, Ulandra, Rosella and Hakea had significantly lower TE values than the other genotypes.

Most of the variation in TE in pots could also be ascribed to differences in anthesis date. Analysis of the TE data using flowering time as a covariate (Table 4.4) resulted in fewer differences in TE. Rosella and Hakea in the drought treatment and Rosella and Ulandra in the control treatment were the only genotypes significantly lower than O'Connor and Galleon barley after adjustment for flowering time. These genotypes presumably had more root mass than the earlier lines and this could account

Table 4.2. Water-use efficiency for above-ground dry weight (WUE_{AGDW}, kg ha^{-1} mm^{1}), water-use efficiency for grain yield (WUE_{GY}, kg ha^{-1} mm^{-1}) and transpiration efficiency (TE_{AGDW}, kg ha^{-1} mm^{-1}).

Exp.	Genotype	WUE_{AGDW}	WUE_{GY}	TE_{AGDW}
C89	**Barley**			
	O'Connor	40.5	16.1	53.8
	Ulandra	27.2	7.2	34.6
	Bread wheat			
	Meteor	27.0	9.3	38.7
	Rosella	25.9	8.8	37.3
	Triticale			
	Dua	36.6	10.9	53.2
	Oats			
	Hakea	28.0	5.7	39.8
	Lsd (P=0.05)	3.3	1.9	5.5
M89	**Barley**			
	O'Connor	42.6	20.2	68.0
	Ulandra	30.3	12.0	47.4
	Bread wheat			
	Meteor	36.7	14.8	62.6
	Rosella	33.3	13.0	58.3
	Triticale			
	Dua	36.3	13.2	65.5
	Oats			
	Hakea	29.5	11.3	52.8
	Lsd (P=0.05)	5.9	2.5	9.4
M90	**Barley**			
	O'Connor	43.5	16.5	66.1
	Ulandra	27.7	8.6	43.4
	Bread wheat			
	Meteor	34.5	11.1	54.0
	Rosella	29.2	9.0	49.9
	Triticale			
	Dua	28.7	10.1	48.3
	Oats			
	Hakea	30.2	8.2	52.3
	Lsd (P=0.05)	8.0	1.3	4.0

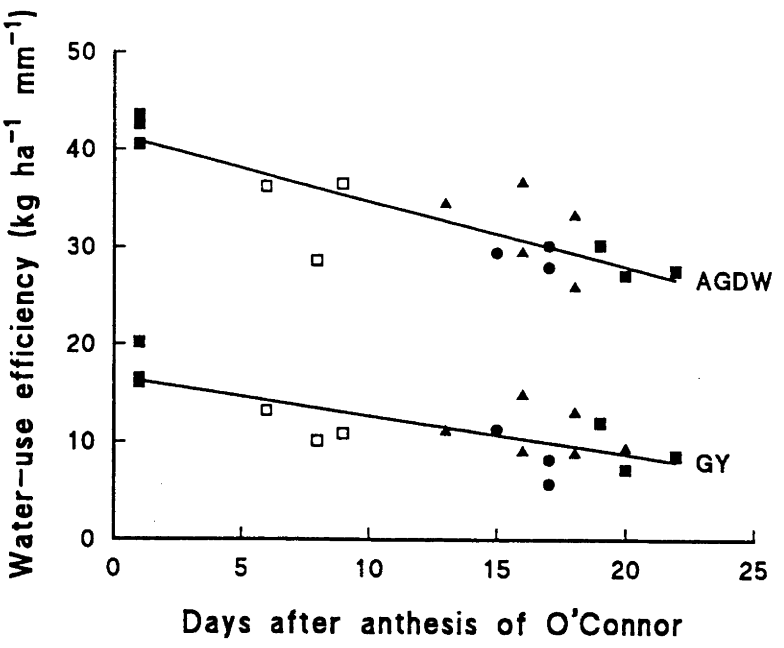


Fig 4.5 Relationship between water-use efficiency for above-ground dry weight (WUE_{AGDW}) and grain yield (WUE_{GY}) and days to anthesis taking the flowering date of O'Connor barley as day one at each site. (WUE_{AGDW} = 0.67(days)+415, r=-0.85, P<0.01) and (WUE_{GY} =- 0.39(days)+16.6, r=-0.75, P<0.01).

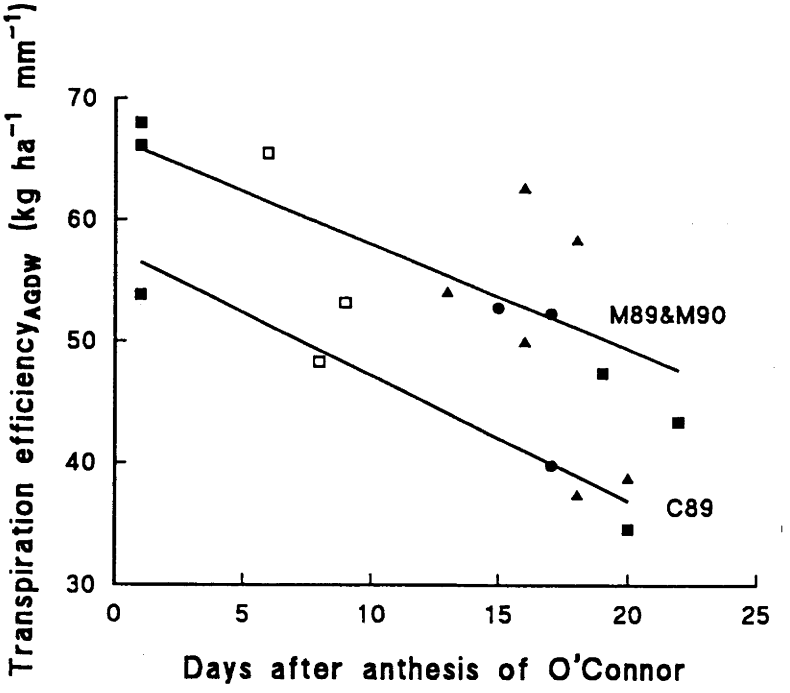


Fig 4.6 Relationship between transpiration efficiency of the above-ground dry weight (TE_{AGDW}) and days to anthesis taking the flowering date of O'Connor barley as day one at all sites. At C89 (TE_{AGDW} = 1.03(days)+57.5, r=-0.94, P<0.01) and at M89&M90 (TE_{AGDW} = 0.87(days)+66.7, r=-0.74, P<0.01).

Table 4.3. Water-use efficiency of total biomass (roots + above-ground dry weight, WUE_B) and transpiration efficiency of total biomass (roots + above ground dry weight, TE_B).

Exp.	Genotype	WUE_B	TE_B
		(kg ha^{-1} mm^{-1})	
C89	**Barley**		
	O'Connor	55.8	74.3
	Ulandra	42.9	54.7
	Bread wheat		
	Meteor	39.4	56.4
	Rosella	35.9	51.4
	Lsd (P=0.05)	4.5	8.7
M90	**Barley**		
	O'Connor	51.6	78.5
	Ulandra	37.4	58.7
	Bread wheat		
	Meteor	40.8	63.9
	Rosella	35.2	60.2
	Triticale		
	Dua	35.2	59.9
	Lsd (P=0.05)	4.6	7.0

Table 4.4. Dry weight (DW) of above-ground parts and transpiration efficiency (TE_{DW}) in well watered (control) and droughted plants (drought) grown in pots.

Genotype	Control			Drought		
	DW	TE_{DW}	$^{*}TE_{DW}$	DW	TE_{DW}	$^{*}TE_{DW}$
	(g.plant^{-1})	(kg ha^{-1} mm^{-1})		(g.plant^{-1})	(kg ha^{-1} mm^{-1})	
Barley						
Galleon	14.0	29	28	5.5	39	36
O'Connor	13.6	29	28	5.5	39	36
Ulandra	5.8	15	16	-	-	-
Bread wheat						
Kulin	16.1	29	28	5.2	35	35
Meteor	15.1	27	27	4.9	34	35
Rosella	10.6	18	20	3.7	26	28
Durum wheat						
Altar 84	18.4	29	29	4.8	35	36
Carcomun	16.1	27	27	4.9	32	33
Triticale						
Dua	14.8	27	26	5.1	34	35
AT 30	16.4	27	28	4.5	31	33
Oats						
Echidna	16.7	27	26	4.9	37	35
Hakea	12.8	23	23	4.7	32	32
Lsd (P=0.05)	3.6	3	6	0.8	4	4

$^{*}TE_{DW}$ is the transpiration efficiency for above-ground dry weight corrected by anthesis time using covariate analysis.

for much of the difference in TE. Similar results were found for the field grown plants when TE was adjusted for anthesis date. Ulandra barley, Rosella bread wheat and Hakea oats, the late genotypes, had significantly lower TE than O'Connor barley and Dua triticale (Table 4.2).

4.3.4 Carbon isotope discrimination

Significant and substantial variation was found in carbon isotope discrimination in the different environments and between genotypes. Table 4.5 presents the mean values of Δ for all genotypes at each environment. It shows that values of Δ determined in stem bases at maturity (M88, M89, C88 and C89) were lower than Δ values determined on the whole shoot at the 6-leaf stage (M90). The higher Δ at M90 presumably arose because the tissue sampled at that stage represents the carbon fixed during the winter when water was not limiting growth and vapour pressure deficit (VPD) was at its lowest. The Δ determined on stem bases is representative of the carbon fixed at around the time of stem elongation. At this time temperatures and VPD are increasing and there may be some stomatal closure due to water stress.

Variation between species in Δ was smaller than between cultivars. However, the Δ of barley averaged over all sites was higher than in bread wheat, durum wheat and oats. Triticale was similar to barley. Within species the early cultivars had higher Δ than the late cultivars and anthesis date was negatively associated with Δ across all gonotypes (Fig. 4.7) (Δ=0.12(days)+35.4, r=-0.94, P<0.01).

4.4 DISCUSSION

In the Introduction, three factors were suggested as possible causes of the greater AGDW of barley. These were variation in either evapotranspiration (E_T), in the proportion of total E_T that is transpiration (T) or in the transpiration efficiency (TE).

4.4.1 Evapotranspiration

There was no evidence that total water use by barley was greater than for the other species. Variation in anthesis date among genotypes was the dominant factor influencing total water use. For field-grown plants, E_T increased by an average of 1.0 mm for each days delay in anthesis. O'Connor barley, the earliest flowering genotype, used the least water. Ulandra barley and Rosella wheat, the last genotypes to flower, used the most. Variation in anthesis date was also the dominant factor influencing E_T in the study by Siddique *et al.* (1990b) in Western Australia in which they compared 10 bread wheats and one barley (O'Connor). In that study, total soil water extraction was strongly correlated with days to anthesis. O'Connor and early flowering wheats extracted the least soil water, late flowering wheats extracted the most. In the present study the greater E_T of late flowering genotypes was also largely the result of greater extraction of soil water. Greater water extraction by late flowering genotypes may be

Table 4.5. Carbon isotope discrimination, (Δ), for five environments (M88, M89, M90, C88 and C89) and the cultivar mean over all environments, assessed from the stem base at maturity, except M90 where whole shoot at 6-leaf stage was measured.

Genotype	$\Delta x10^3$					
	M88	M89	M90	C88	C89	Cultivar Mean
Barley						
Galleon	20.8	21.0	23.2	21.0	20.8	21.4
O'Connor	21.0	21.9	23.3	20.9	20.1	21.4
Ulandra	19.8	18.4	21.7	19.8	18.0	19.5
Malebo	20.7	20.4	23.4	20.3	19.6	20.9
Bread wheat						
Kulin	20.4	20.8	22.1	21.2	20.1	20.9
Meteor	20.2	20.4	22.1	19.6	18.8	20.2
Rosella	19.2	19.3	22.0	18.9	17.7	19.5
M 3344	19.7	18.8	22.2	19.0	17.3	19.4
Durum wheat[a]						
Altar 84	20.2	19.5	22.9	-	18.6	20.2
Carcomun	20.0	20.2	22.7	-	19.7	20.6
Triticale						
Dua	20.5	21.1	22.6	20.5	20.2	21.0
Currency	20.6	21.3	23.0	20.5	19.7	20.8
Oats[a]						
Echidna	-	20.1	23.3	20.3	19.1	20.7
Hakea	-	18.4	22.1	19.2	17.1	19.1
Mean of all environments	20.2	20.1	22.6	20.1	19.1	20.4
Lsd (P=0.05)	0.7	0.4	0.3	0.7	1.0	0.3

[a] These cultivars were only grown in four of the five field experiments.

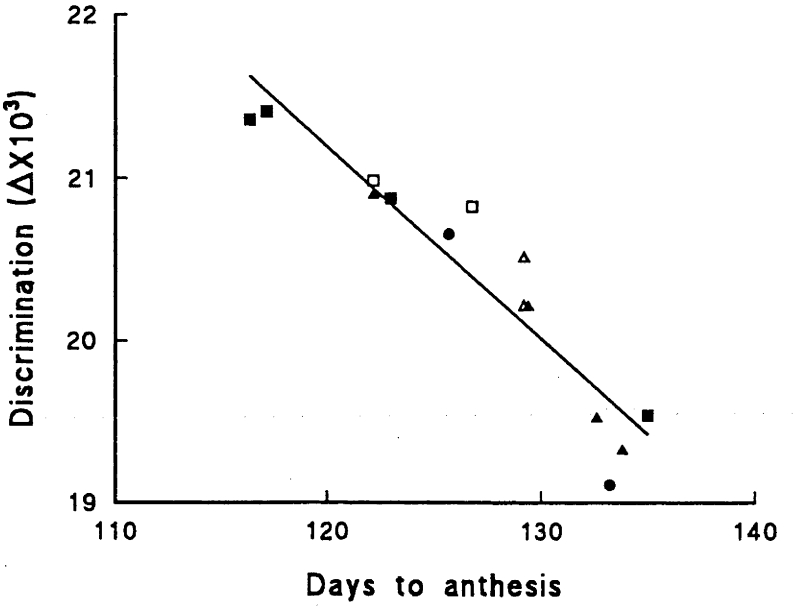


Fig 4.7 Relationship between carbon isotope discrimination (Δ) and days to anthesis for barley (■),bread wheat (▲),durum wheat (△),triticale (❑) and oats (●) across five field environments (C88,C89,M88,M89,M90). (Δ = -0.12(days)+35.4, r=-0.94, P<0.01).

due to the presence of more roots (Passioura, 1977). Root weight and root length density were high for Ulandra (chapter 2) but not for Rosella, which had the least roots. This indicates that a more important factor in allowing late genotypes to extract more soil water is the maintenance of a transpiring canopy longer into the season (Richards, 1991).

4.4.2 Water-use efficiency

Since the greater AGDW by barley and triticale was not due to greater E_T, the difference must be in greater WUE. Water-use efficiency depends on both TE and the ratio of soil evaporation as a proportion of evapotranspiration (equation 4.2). A lower soil evaporation relative to evapotranspiration was a consistent feature of the two barleys in each of these experiments. Averaged over the three experiments for which it was calculated (C89, M89 and M90), the ratio of E_S/E_T was 0.31 for the barleys, 0.37 for the bread wheats and 0.39 for Dua triticale and Hakea oats. Siddique *et al.* (1990b) also observed lower E_S/E_T for O'Connor barley (0.34) compared to the wheats they grew (average 0.39 for wheats with similar flowering date to O'Connor). The results described in chapter 3 indicate that the lower E_S/E_T for barley resulted from faster leaf area development. Barley had the highest leaf area index (LAI), developed main stem leaves fastest and hence had the shortest phyllochron interval, produced the most tillers and with exception of oats had the highest specific leaf area (SLA).

These results indicate that reducing E_S as a proportion of E_T contributes to greater WUE by barley. It meant that T was always high for Ulandra barley, but T was still only intermediate for O'Connor, which produced the most AGDW. This indicates that variation in TE was also important, especially for O'Connor. Table 4.6 compares O'Connor with the other genotypes for TE_{AGDW} and T as a proportion of E_T averaged over the three field experiments. It shows that TE was the most important factor contributing to differences between O'Connor and Ulandra. A higher TE and also a higher T relative to E_T accounted for the better performance of O'Connor compared to Rosella, Dua and Hakea. It was notable that Meteor, the only hybrid wheat in the study, was more like barley in having a high ratio of T/E_T.

The higher TE of O'Connor relative to all other genotypes could arise in several ways. According to equation (4.1), high TE of leaf gas exchange may result from either a lower e_i-e_a and/or a lower P_i/P_a. Carbon isotope discrimination (Δ) is an integrated measure of P_i/P_a (Farquhar *et al.* 1982), so if P_i/P_a is the dominant factor then Δ should be negatively related to TE. This was not found. In fact Δ averaged over all experiments was positively associated with TE_{AGDW} at each site (C89, r=0.89, P<0.01; M89, r=0.87, P<0.01; M90, r=0.60, P<0.05). The value of Δ was also significantly associated with final AGDW at maturity (Fig.4.8) (AGDW (%)=8.42(Δ)-72.5, r=0.70, P<0.01). This has also been found in field grown plants in wheat (Condon *et al.* 1987; Ehdaie *et*

Table 4.6 Comparison between O'Connor barley and the other genotypes for TE_{AGDW} and transpiration (T) relative to soil evaporation (E_S). Values are the percentage by which O'Connor exceeds the other genotypes.

Genotypes		TE_{AGDW} (%)	T/E_T (%)
O'Connor *versus*			
	Ulandra	50	0
	Meteor	23	6
	Rosella	31	10
	Dua	14	11
	Hakea	30	11

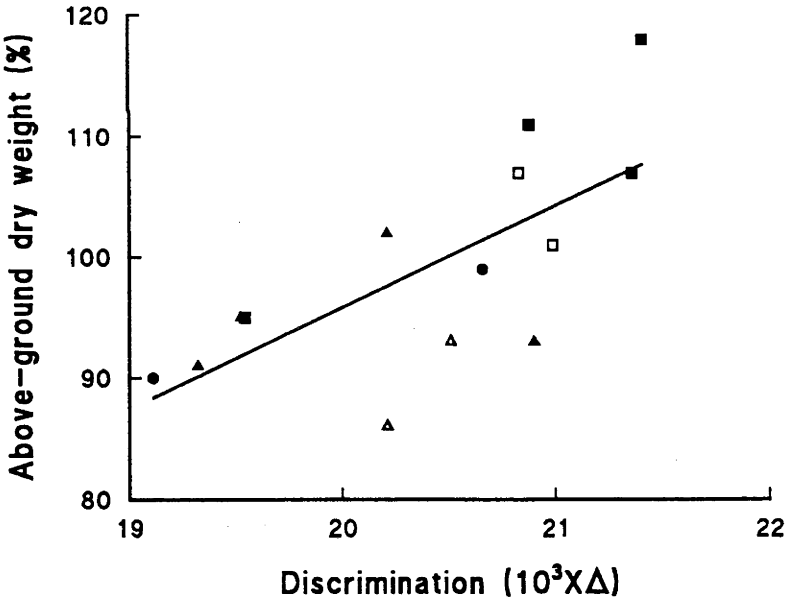


Fig 4.8 Relationship between final above-ground dry weight (AGDW) at maturity and carbon isotope discrimination (Δ) for barley (■), bread wheat (▲), durum wheat (△), triticale (❑) and oats (●) across five field environments. (AGDW = 8.42(Δ)-72.5, r=0.70, P<0.01)

al. 1991), barley (Craufurd *et al.* 1991) and crested wheat grass (Read *et al.* 1991). In these latter studies water use, soil evaporation and root biomass were not determined, which may account for the positive associations they observed. However, water use and soil evaporation were measured here. Root biomass was also measured but accounting for root biomass had little impact on the relationship between TE and Δ. The slope of the relationship between TE_{AGDW} and Δ at C89 (Fig. 4.9) indicates that TE_{AGDW} increased by 43% with a change in mean Δ from 19.5 x 10^{-3} to 21.5 x 10^{-3}. For the same change in Δ, there was still a 43% increase in TE_B. In other words the relationship between TE_B and Δ was still strongly positive ($r=0.97$, $P<0.01$), not negative as might be expected from leaf gas exchange theory.

Two factors may account for this positive relationship. The first, which will almost certainly be important, is the greater growth by barley (and hence greater T) when VPD is low. The influence of seasonal changes in VPD can be accounted for by calculating, for each genotype, an "effective transpiration" (=transpiration/average VPD) for each of the periods between soil water measurements. This procedure, based on the analysis presented by Sinclair *et al.* (1983), is similar to that used by Hubick and Farquhar (1989) in accounting for differences in VPD between two glasshouse experiments with different barley genotypes. Because of data limitations the calculations were only possible for C89. At this site, when summed over the whole season, the values of "effective transpiration" were 458, 403, 345, 323, 346 and 347 $mm.kPa^{-1}$ for O'Connor, Ulandra, Meteor, Rosella, Dua and Hakea respectively. On average, the value for the barleys was 26% greater than for the other species. This means that transpired water was used 26% more effectively in producing dry matter in the barleys than in the other species. Fischer (1981) pointed out that growth during the winter months is cheap in terms of transpirational cost. In these experiments, by maximising its early growth, barley achieved a greater "effective transpiration" than the other species, and thereby a higher TE. When this advantage is accounted for in calculating TE_B, the strong positive relationship between TE_B and Δ is largely eliminated (Fig. 4.9). Nevertheless, the relationship between TE_B and Δ is still not negative.

This may be due to yet another factor, the effect of boundary layer conductance on transpiration from field plots. In calculating "effective transpiration" it was assumed that the driving force for transpiration was VPD. This is not strictly the case. The true driving force is e_i-e_a. This will be proportional to VPD if e_i (the vapour pressure inside the leaf) is constant, but this will only occur if leaf temperature is constant. If variation in Δ is the result of variation in stomatal conductance, then leaf temperature is unlikely to be constant. In the field, genotypes with low conductance will tend to have hotter canopies because of the greater influence of the boundary layer on leaf gas exchange. A hotter canopy means that transpiration will be driven faster per unit conductance, reducing any gain in TE from lower conductance (Cowan and Troughton, 1971; Jarvis

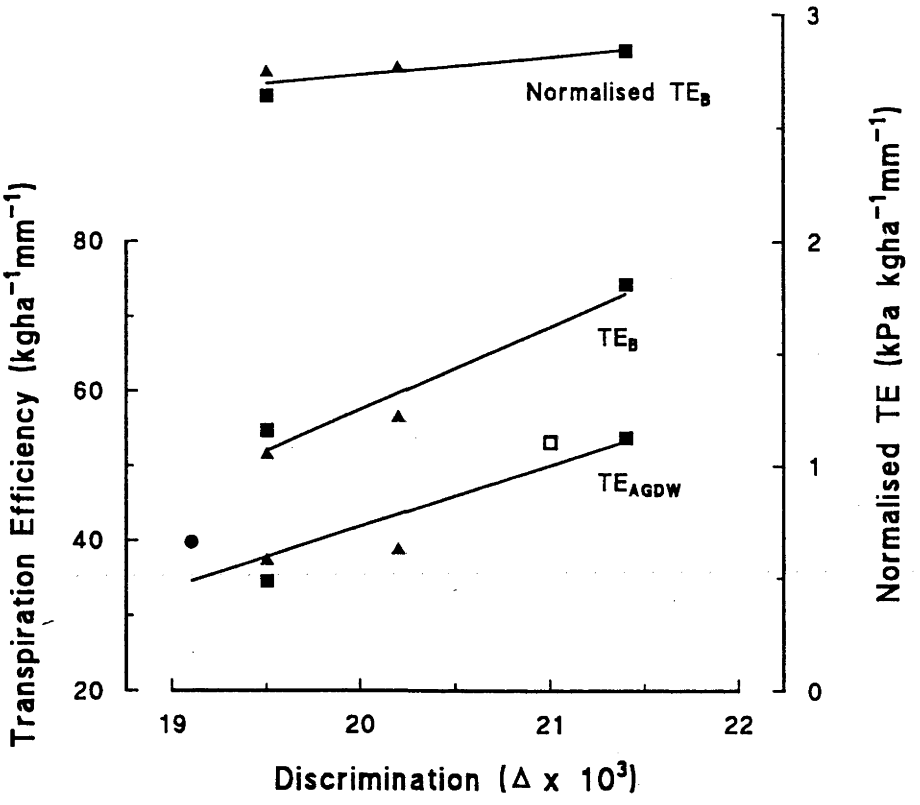


Fig 4.9 Relationships between transpiration efficiency at C89 and carbon isotope discrimination (Δ, mean of all sites) for barley (■), bread wheat (▲), triticale (❑) and oats (●). Transpiration efficiency was calculated on the basis of above-ground dry weight (TE_{AGDW} = 8.15Δ-121.05, r=0.89, P<0.01), on the basis of total biomass (TE_B=11.09Δ-164.29, r=0.97, P<0.01) and with TE_B normalised for seasonal variation in VPD (Normalised TE_B=0.0793Δ+1.148, r=0.86, P<0.01).

and Mc Naughton, 1986; Cowan, 1988). Little is known of the stomatal conductance in these species, but given the large range in Δ values, it is likely that conductance is lower and hence the field canopies warmer in Ulandra and Rosella than in O'Connor and Meteor (Condon *et al.* 1990).

4.4.3 Flowering time

Variation in anthesis date among genotypes was an important factor influencing water use, water-use efficiency and its component transpiration efficiency, and also carbon isotope discrimination in the three field experiments. It was also a dominant factor influencing transpiration efficiency in the pot experiment. However, anthesis date was not related to the proportion of soil evaporation to evapotranspiration.

Even though for field grown plants total water use increased by an average of 1.0 mm for each days delay in anthesis, this was more than offset by lower WUE_{AGDW} and WUE_{GY}. These declined by 0.67 and 0.39 kg ha^{-1} mm^{-1} for each days delay in flowering respectively. The TE_{AGDW} declined by 0.95 kg ha^{-1} mm^{-1} d^{-1} for each days delay in flowering. These effects can be attributed to the rapid rise in VPD in the latter part of the growing season. Similar results were obtained for wheat grown at Tamworth by Doyle and Fischer (1979), who varied flowering date by manipulating sowing time. O'Connor barley, which flowered earliest, consistently had the highest WUE for both grain yield and above-ground dry weight. This presumably accounts for O'Connor having the highest grain yield and AGDW in all experiments (chapter 2). It is likely that all barley lines evaluated in chapter 2, that also had high yields, achieved these because of their higher WUE rather than a higher total E_T.

The strong negative association between Δ and flowering time was unexpected. A link between early flowering and grain Δ has been noted in barley (Craufurd *et al.* 1991), but this has not been found in isogenic populations of wheat differing in flowering time (Virgona and Richards, unpublished data), or in breeding populations of wheat segregating for both Δ and flowering time (Condon and Richards, unpublished). What was most unexpected was the very tight association found (r=-0.94) and that all genotypes fitted the same relationship. This association may have arisen in a number of ways. It may be a result of the time and plant material sampled or it may be due to intrinsic physiological differences between genotypes, or may be due to genetic linkage or pleiotropy. The sampled material in four of the five environments came from stem bases taken at maturity. These were expected to be representative of carbon laid down early in the life of the plant before vapour pressure deficit (VPD) rises and before drought occurs that may induce stomatal closure (Condon and Richards, 1992). Stem elongation occurs after terminal spikelet formation in wheat and triticale or its equivalent in barley and oats. There was large variation among genotypes in reaching this stage (chapter 3) and it coincided with the rapid rise in VPD and dry matter growth. The Δ values at M90, from whole plants at the 6-leaf stage were not as closely

associated with flowering time as the stem bases (r=-0.46, n.s.) and were 2 to 3 x 10^{-3} greater than for stem base material indicating that plants were less stressed at M90. It is also notable that the difference in Δ between whole plant Δ values at M90 and stem bases at both Moombooldool (M88 and M89) and Condobolin (C88 and C89) were consistently greater in the late flowering than in the early flowering lines.

The alternative explanation for the association between anthesis and Δ is that there has been unconscious selection for faster growth in genotypes of short duration so as to compensate for the shorter duration and the requirement to maintain grain yield. This is best achieved by producing a canopy as fast as possible so that there will be a large assimilatory surface. This could be achieved by investing in large thin leaves with a low assimilation capacity rather than in smaller, thick leaves with a high assimilation capacity. If this was the case, Δ would be negatively related to flowering time as was found, providing there was not a corresponding decrease in stomatal conductance with early flowering. This seems highly unlikely and the reverse is more likely, i.e. a high conductance in early flowering lines. Later flowering lines have a longer opportunity to develop their leaf area and, when they do, a high assimilation capacity would be favoured. This is consistent with these lines having a low Δ.

A further possible explanation is that the genes for flowering time are linked with those for Δ. This seems highly unlikely considering the few major genes regulating flowering time in wheat (Pugsley, 1983) and barley (Nilan, 1964) and the presumably many genes that influence photosynthetic capacity and stomatal conductance, but should be tested. However, there is also the possibility that the genes that regulate flowering time may program the future exchange of CO_2 for water. This could occur after emergence from the ground, when the plant integrates the change in daylength and temperature, both of which control flowering time. If conditions are not conducive to flowering a water conservation strategy is imposed resulting in low Δ in plant tissue. On the other hand, if conditions are conducive to flowering, rapid biomass accumulation and water spending are programmed, resulting in high Δ in plant tissue.

4.5 CONCLUSIONS

Results presented in this chapter show that the main factor contributing to the greater AGDW of barley was its greater water-use efficiency (WUE). Total E_T was no greater in barley than in the other species. Variation in E_T was largely accounted for by variation in anthesis date. Longer duration lines used more water than short duration genotypes in each experiment and cultivars within each species fitted the same general relationship. The higher E_T in the late flowering lines was achieved using a greater extraction of water from the soil profile.

Water-use efficiency and TE were both negatively associated with anthesis date, but for barley WUE and TE were greater for a given anthesis date. This was achieved largely as a result of faster leaf area development by barley. The separation of E_T into

transpiration (T) and soil evaporation (E_S) showed that E_S in barley was about 20 mm lower than in the other genotypes at all sites. Whereas this resulted in a higher T in the late flowering Ulandra, T of the early variety O'Connor was similar to the other genotypes, as it had lower total E_T.

More rapid leaf area development by barley also contributed to greater TE because it resulted in a greater proportion of the total transpiration occurring when VPD was lower. When seasonal changes in VPD were accounted for, "effective transpiration" was 26% greater in barley than in the other species. This effect was greater for the early-flowering O'Connor than for the late-flowering Ulandra. When averaged over the three experiments, WUE for above-ground dry weight (WUE_{AGDW}) and grain yield (WUE_{GY}) in O'Connor barley (husked kernel) was 37% and 70% higher, respectively, than for all other genotypes.

Variation in P_i/P_a among genotypes, measured as variation in Δ, had little influence on TE. The value of Δ was negatively related to anthesis date across all cultivars. This meant that mean VPD was also negatively related to Δ, negating any advantage in TE that may have resulted from low Δ.

All these results point to the dominant contribution of faster leaf area development to the greater WUE and biomass production of barley relative to the other species. The following chapters explore factors responsible for this higher early growth and faster canopy development.

CHAPTER 5

VARIATION IN EARLY GROWTH AND LEAF AREA DEVELOPMENT

5.1 INTRODUCTION

Studies on field grown plants presented in earlier chapters established than barley was more vigorous that bread wheat, durum wheat, triticale and oats. This was consistent across genotypes, field sites and years. The faster growth of barley accounted for its greater yield of biomass and grain and for its greater water-use efficiency.

The following chapters explore the factors responsible for barley's growth advantage, under more precisely monitored conditions than are possible in the field. This chapter describes three experiments designed to determine firstly whether the differences in growth between barley and bread wheat also occur in plants grown in pots in contrasting environments and secondly whether differences in relative growth rate and/or differences in the base temperature at which growth occurs can account for the greater growth of barley compared to wheat in the field. In the experiments investigating variation in growth rate, regular destructive harvests were made so that the important components that contribute to growth rate could be determined. Whereas, in the experiment investigating the effect of temperature on growth, leaf extension, considered to be a more sensitive indicator of growth, was monitored. In this latter experiment genotypes of all species grown in the field experiments were evaluated.

5.2. MATERIALS AND METHODS

5.2.1 Growth analysis

5.2.1.1 Experimental

Two experiments were planted on September 1, 1988 in Canberra (147°E, 35°S). One experiment was placed outside under natural conditions (Outdoors) and the other was kept in a glasshouse. Three spring barleys (Galleon, O'Connor and Beecher, a six row barley), two long season or winter barleys (Ulandra and Malebo), three spring bread wheats (Kulin, Meteor and Hahn Parula) and two winter bread wheats (Rosella and M3344) were sown. The mean kernel weight for bread wheat was 35 mg and 38 mg for the husked barley kernels; the husk of the barley kernel weighed 3 mg. Twenty eight seeds of each cultivar were planted at a constant depth (3 cm) in a large plastic pot (20 cm tall and 25 cm diameter) containing a standard, fertile potting mix. These were thinned to 20 uniform plants per pot after emergence. All pots were well watered during the experiment. There were four replicate blocks in the glasshouse and outside.

5.2.1.2 Dry weight and leaf area

Five harvests were made in each experiment from each pot. The average leaf number on the main stem for barley at each harvest was as follows with the number for bread wheat given in parentheses. In the glasshouse experiment leaf number was 2.3(2.0), 2.8(2.4), 3.5(2.9), 4.1(3.4) and 4.4(3.8), whereas for plants grown outside leaf number was 1.7(1.5), 2.9(2.4), 3.9(3.1), 4.3(3.7) and 4.7(4.3). At each harvest, taken on the same day for all genotypes in each experiment, four plants were harvested from each pot so that mutual competition and shading between plants in pots were negligible. Plants were cut off at the seed. At each harvest leaf and tiller number per plant were recorded and then plants were partitioned into leaves, leaf sheaths and below-ground stems or leaf sheaths. Leaf area (LA) was measured with an area measurement system (Delta T-Devices LTD, Burwell, Cambridge, England). Dry weight of leaves, leaf sheaths and below-ground stems were determined after oven-drying for 48 h at 80°C and total shoot dry weight (W_s) was calculated. Total plant nitrogen was determined on the whole shoot of glasshouse and outdoors grown plants on one occasion (harvest 4 + harvest 5 combined) using the microKjeldahl method (Lang, 1958).

5.2.1.3 Data analysis

Relative growth rate (RGR, day^{-1}) and its components net assimilation rate (NAR, $g\ m^{-2}\ day^{-1}$) and leaf area ratio (LAR, $m^2\ kg^{-1}$) were calculated according to Hunt (1982) (and see appendix 5). The RGR for each genotype or/and species was taken from the slope of the relationship between $\log_e$ shoot dry weight (W_s) and harvest time (in days); a linear relationship accounted for more than 95% of the variation in all genotypes both in the glasshouse and outdoors. The values of LAR were calculated for each harvest and values of NAR were derived from NAR=RGR/LAR. The LAR was separated into specific leaf area (SLA, $m^2\ kg^{-1}$) and leaf weight ratio (LWR, $g\ g^{-1}$) for each harvest. Differences between genotypes were tested as suggested by Poorter and Lewis (1986). Relative leaf expansion rate (RLER) for each genotype was calculated as the linear regression of $\log_e$ leaf area against time.

Relative growth rate, r ($10^{-6}\ s^{-1}$), and its components assimilation rate, A ($\mu mol\ C\ m^{-2}\ s^{-1}$) and shoot carbon to leaf area, ρ ($mol\ C\ m^{-2}$) were also calculated following Masle and Farquhar (1988) as follows:

$$r=(1/M \cdot dM/dt)=(Al(1-\phi))/\rho \qquad (5.1)$$

where M represents the total plant carbon, A is the assimilation rate ($\mu mol\ C\ m^{-2}\ s^{-1}$), l is the light period as a proportion of the day, ϕ is the proportion of losses by respiration during day-time fixation (mol C/mol C) and ρ ($mol\ C\ m^{-2}$) is the ratio of total plant carbon, M, to photosynthetic area.

The leaf emergence rate (LER, leaf(°Cd)$^{-1}$) and tiller emergence rate (TER, tiller(°Cd)$^{-1}$) were calculated from the cumulative thermal time in each environment using 0 °C as the base temperature. The phyllochron interval ((°Cd)leaf^{-1}) was calculated as the reciprocal of the leaf emergence rate.

5.2.1.4 Carbon isotope discrimination

Carbon isotope discrimination (Δ) was determined on all replicates of glasshouse grown plants on two occasions (harvest 1 + harvest 2 combined and harvest 4 + harvest 5 combined) and on plants grown outdoors (harvest 4 + harvest 5). Shoots were oven-dried at 80 °C over night and ground for determination of Δ in the laboratory according to Condon *et al.* (1987).

The values of Δ were calculated as presented by Farquhar and Richards (1984) and as outlined in chapter 4.

5.2.2 Effect of temperature on leaf extension

5.2.2.1 Experimental

Two wooden flats 60 cm length x 30 cm width containing a fertile potting mix were planted with twelve genotypes of barley, bread wheat, durum wheat, triticale and oats used in the field experiments (chapter 2, Table 2.2). Planting was arranged in a nearest neighbour design with five replications in each flat giving a total of ten replications. Barley seeds were sown two days after the other species on July 5, 1991 as barley emerges faster than the other species. Seeds of a similar weight were planted in the glasshouse (18°C day and 8°C night with no supplementary lighting) and four days after the first planting flats were moved outdoors.

Leaf blade expansion was measured daily with a ruler beginning with leaf one and ending, at the termination of the experiment, with leaf three on most plants. Flats were moved between the glasshouse and outdoors and on several occasions from outdoors to a cold room with lights during the day so as to vary temperature over each interval of measuremnent. Temperatures every two hours were obtained from glasshouse monitoring and from the Bureau of Meteorology and averaged over the daily measurement period. Negative values were recorded as 0°C when calculating average temperatures during the growth period.

5.3 RESULTS

5.3.1 Growth analysis

5.3.1.1 Growth conditions

Mean maximum and minimum temperatures outside were 16°C and 4°C and day/night temperatures in the glasshouse averaged 25°C/15°C. The average daily radiation for the experiments was 18.7 MJ m^{-2}. The seedlings grown in the glasshouse emerged about 4 days before the seedlings grown outdoors. Relative growth rates (RGR) of barley and bread wheat were higher in the glasshouse (mean RGR=0.180 day^{-1}) than outdoors (mean RGR=0.147 day^{-1}).

5.3.1.2 Dry weight and leaf area

Barley had about 40% more W_s and about two times greater LA than bread wheat from the first harvest, when there were two main stem leaves, to the termination of the experiments, when there were about four leaves on the main stem, in the glasshouse (Fig. 5.1a and Fig. 5.1b) and outdoors (Fig. 5.1c and Fig. 5.1d).

Differences in W_s and LA between genotypes within species were significant and values at the first and last harvest are given in Tables 5.1 and 5.2. There was no overlap between barley and wheat genotypes for shoot weight or leaf area.

Leaf emergence rate and tiller emergence rate were also faster in barley than bread wheat in both environments (Table 5.3). Tiller emergence was 2-fold greater outdoors than in the glasshouse but the relative difference in tiller emergence rate between species remained about the same.

5.3.1.3 Relative growth rate

The relative growth rate for barley and bread wheat were the same in the glasshouse and the same in plants grown outdoors (Fig. 5.2a and Fig. 5.2b). The RGR of barley and bread wheat in the glasshouse were 0.182 g g^{-1} d^{-1} and 0.177 g g^{-1} d^{-1} respectively whereas outdoors values for barley were 0.146 g g^{-1} d^{-1} and 0.149 g g^{-1} d^{-1} for wheat.

The partitioning of relative growth rate (RGR) into net assimilation rate (NAR) and leaf area ratio (LAR) at the first harvest showed that barley had an almost two fold higher LAR than bread wheat in both the glasshouse and outside (Table 5.4). However, this was counter balanced by a two fold higher NAR in wheat relative to barley. Variation within each species in LAR and NAR was small relative to variation between barley and wheat. Further partitioning of LAR into SLA and LWR indicate that although both are greater in barley, SLA contributes most to the greater LAR of barley (Table 5.4). These results were consistent in both the glasshouse and outside experiments.

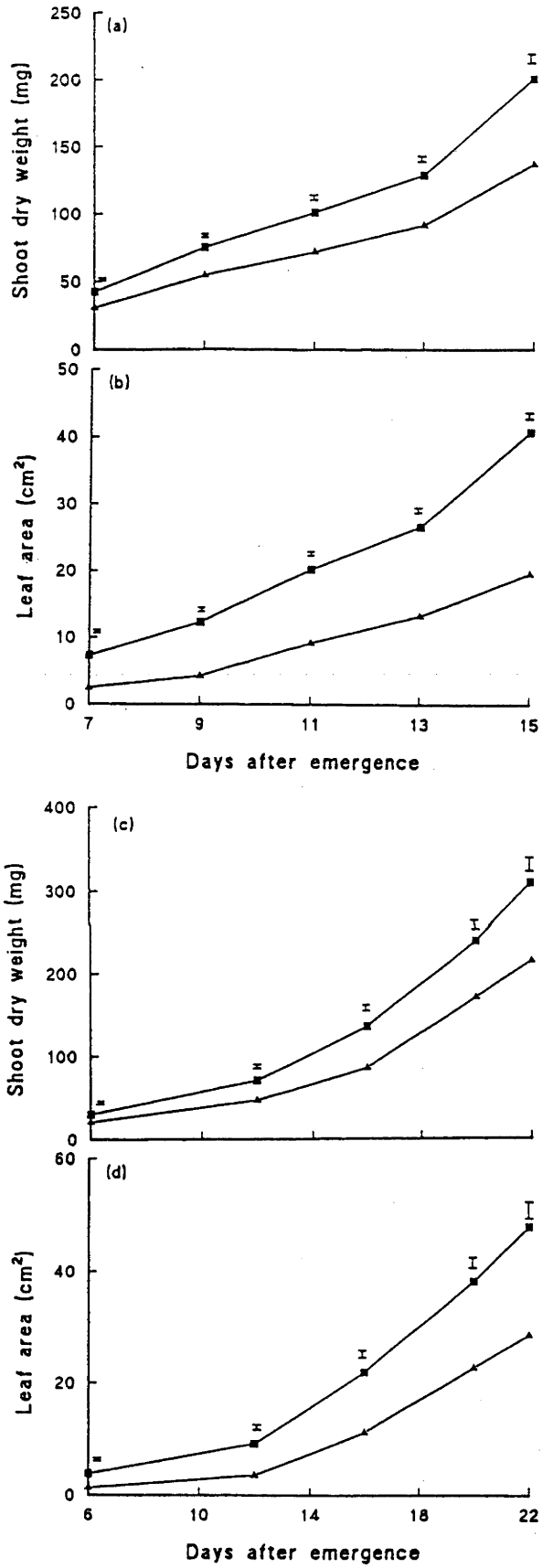


Fig 5.1 a) Shoot dry weight and b) leaf area of barley (■) and bread wheat (▲) grown in glasshouse, c) shoot dry weight and d) leaf area of barley (■) and bread wheat (▲) grown outdoors. Error bars show the standard errors.

Table 5.1. Dry weight of shoot (W_S, mg), leaf area (LA, cm^2) and leaf number (LNO) for all genotypes at the first harvest in the glasshouse and outdoors.

Genotype	Glasshouse			Outdoors		
	W_S	LA	LNO	W_S	LA	LNO
Barley						
Galleon	42.1	6.3	2.2	29.5	3.4	1.9
O'Connor	41.5	7.8	2.4	32.0	4.4	1.7
Ulandra	37.5	6.4	2.2	26.4	2.9	1.8
Malebo	50.0	8.4	2.4	35.0	4.6	1.7
Beecher	41.9	7.8	2.2	28.2	4.2	1.5
Mean	**42.6**	**7.3**	**2.3**	**30.2**	**3.9**	**1.7**
Bread wheat						
Kulin	28.1	2.6	1.8	20.2	1.6	1.3
Meteor	31.6	2.4	1.9	22.3	1.6	1.5
Hahn/Parula	27.4	2.3	1.9	20.4	1.2	1.5
Rosella	31.9	2.5	2.1	17.3	0.9	1.5
M 3344	35.5	2.8	2.0	24.1	1.6	1.6
Mean	**30.9**	**2.5**	**2.0**	**20.8**	**1.4**	**1.5**
s.e. (Genotypes)	4.6	0.8	0.1	1.8	0.2	0.1

Table 5.2. Dry weight of shoot (W_s, mg), leaf area (LA, cm^2) and leaf number (LNO) for all genotypes at the final harvest in the glasshouse and outdoors.

Genotype	Glasshouse			Outdoors		
	W_s	LA	LNO	W_s	LA	LNO
Barley						
Galleon	190	33	4.6	293	45	4.7
O'Connor	215	42	4.6	304	50	4.8
Ulandra	170	35	4.2	241	33	4.8
Malebo	222	48	4.4	413	62	4.8
Beecher	211	47	4.3	293	52	4.5
Mean	**201**	**41**	**4.4**	**309**	**48**	**4.7**
Bread wheat						
Kulin	111	15	3.3	209	29	3.8
Meteor	136	20	3.8	239	34	4.2
Hahn/Parula	134	18	3.9	207	26	3.9
Rosella	155	24	4.2	192	25	4.1
M 3344	152	21	4.1	229	30	4.2
Mean	**138**	**20**	**3.9**	**215**	**29**	**4.0**
s.e. (Genotypes)	17	3	0.1	25	4	0.2

Table 5.3. Leaf (LER, 10^{-3}leaf(°Cd)$^{-1}$) and tiller (TER, 10^{-3} tiller (°Cd)$^{-1}$) emergence rates and phyllochron interval (PI, (°Cd) leaf^{-1}) for all genotypes in the glasshouse and outdoors.

Genotype	Glasshouse			Outdoors		
	LER	TER	PI	LER	TER	PI
Barley						
Galleon	17.5	9.7	54.8	15.7	25.5	60.6
O'Connor	15.7	13.9	60.8	17.3	22.6	54.3
Ulandra	14.9	15.7	63.1	16.1	27.6	58.4
Malebo	14.6	16.8	66.3	17.2	28.2	54.2
Beecher	14.4	11.0	68.1	16.9	19.0	54.7
Mean	**15.4**	**13.4**	**59.2**	**16.6**	**24.6**	**55.6**
Bread wheat						
Kulin	10.8	5.9	88.0	14.2	13.5	68.8
Meteor	13.1	6.6	71.3	14.6	18.4	65.6
Hahn/Parula	13.4	11.8	71.8	13.7	21.2	71.1
Rosella	15.1	15.6	59.7	13.9	19.7	67.5
M 3344	13.3	12.5	62.9	14.6	18.5	65.1
Mean	**13.1**	**10.5**	**64.5**	**14.2**	**17.3**	**66.2**
s.e. (Genotypes)	0.9	1.6	4.3	0.9	1.7	3.4

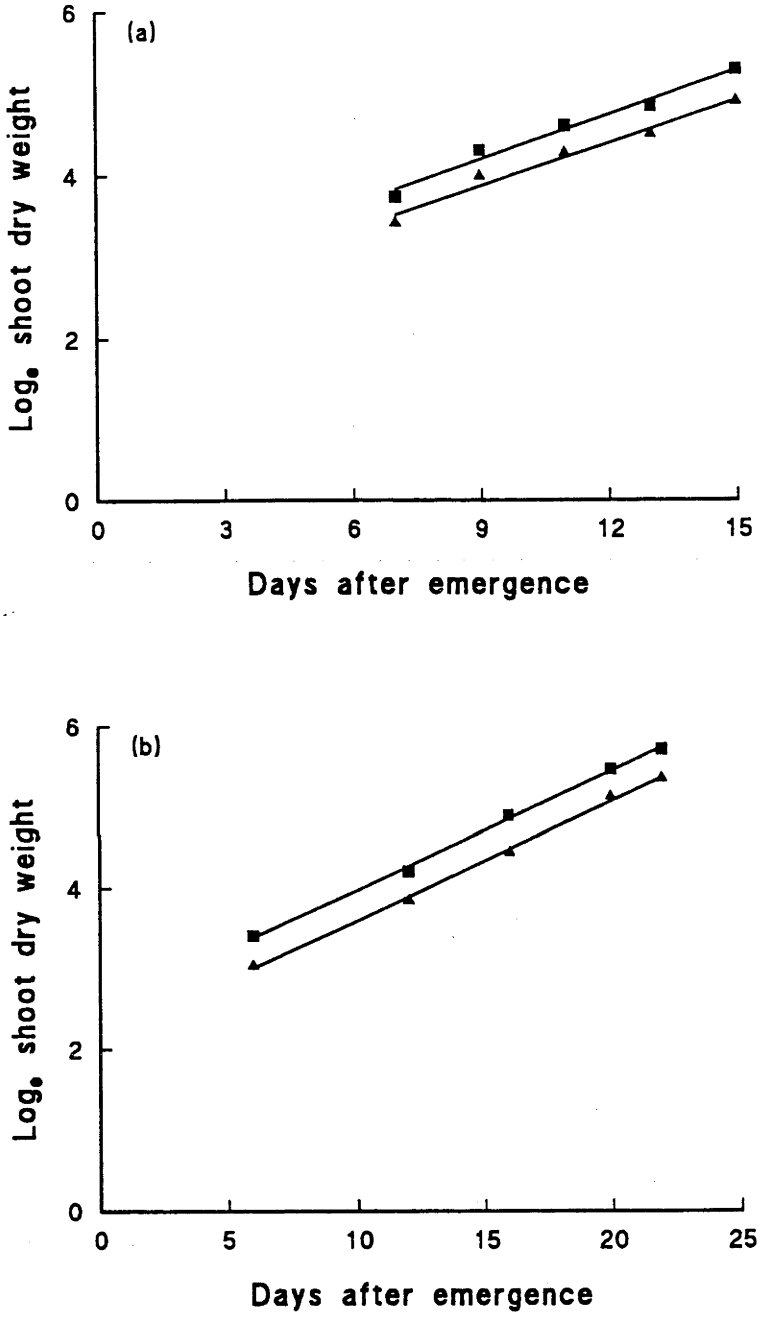


Fig 5.2 a) Log$_e$ shoot dry weight for barley (■) (Y_B = 0.183(t)+2.55, r = 0.99) and bread wheat (▲) (T_W = 0.178(t)+2.26, r=0.99) grown in glasshouse. The difference between intercepts is 0.342±0.06.

b) Log$_e$ shoot dry weight for barley (■)(Y_B = 0.146(t)+2.52, r = 0.99) and bread wheat (▲) (Y_W = 0.149(t)=2.10, r = 0.99) grown outdoors. The difference between intercepts is 0.386±0.06.

Table 5.4. Relative growth rate (r, 10^{-6} s^{-1}) and (RGR, day^{-1}) estimated over the duration of the experiments. Net assimilation rate (NAR, g m^{-2} d^{-1}), leaf area ratio (LAR, m^2 kg^{-1}), specific leaf area (SLA, m^2 kg^{-1}) and leaf weight ratio (LWR, g g^{-1}) for all genotypes at the first harvest in the glasshouse and outdoors.

Genotype	r	RGR	NAR	LAR	SLA	LWR
Glasshouse						
Barley						
Galleon	2.04	0.18	12.1	1.5	2.5	0.60
O'Connor	2.22	0.19	10.7	1.8	2.9	0.62
Ulandra	2.13	0.18	11.2	1.6	2.6	0.63
Malebo	1.98	0.17	10.1	1.7	2.7	0.62
Beecher	2.19	0.19	10.4	1.8	2.8	0.65
Mean	**2.11**	**0.18**	**10.9**	**1.7**	**2.7**	**0.62**
Bread wheat						
Kulin	1.94	0.17	18.3	0.9	1.6	0.57
Meteor	2.04	0.18	24.7	0.7	1.3	0.55
Hahn/Parula	2.14	0.19	23.8	0.8	1.4	0.55
Rosella	2.20	0.19	25.0	0.8	1.4	0.54
M 3344	1.92	0.17	22.0	0.8	1.3	0.58
Mean	**2.05**	**0.18**	**22.7**	**0.8**	**1.4**	**0.56**
s.e. (Genotypes)	0.10	0.01	0.6	0.1	0.1	0.01
Outdoors						
Barley						
Galleon	1.70	0.15	12.9	1.2	2.1	0.55
O'Connor	1.63	0.14	10.3	1.4	2.5	0.55
Ulandra	1.59	0.14	11.8	1.2	2.1	0.55
Malebo	1.79	0.16	12.0	1.3	2.4	0.54
Beecher	1.72	0.15	9.9	1.5	2.6	0.59
Mean	**1.69**	**0.15**	**11.4**	**1.3**	**2.3**	**0.56**
Bread wheat						
Kulin	1.77	0.15	17.2	0.9	1.7	0.53
Meteor	1.71	0.15	19.0	0.8	1.5	0.51
Hahn/Parula	1.72	0.15	22.0	0.7	1.4	0.49
Rosella	1.76	0.15	21.1	0.7	1.5	0.48
M 3344	1.64	0.14	22.2	0.6	1.2	0.54
Mean	**1.72**	**0.15**	**20.3**	**0.8**	**1.5**	**0.51**
s.e. (Genotypes)	0.10	0.01	1.1	0.1	0.1	0.01

Differences between species in NAR and LAR became less with consecutive harvests. Values for the final harvest are given in Table 5.5. The smaller difference was due to a greater decrease in NAR and a corresponding increase in LAR in wheat relative to barley in later harvests (Table 5.5). This was found in both the glasshouse and outdoors experiments. Fig. 5.3a, b, c and d present data for *A* and ρ in both the glasshouse and outdoors at each harvest respectively. They show the greater change in *A* and ρ in wheat than in barley. This decline in *A* and ρ was associated with the greater increase in SLA in wheat than in barley in both experiments.

Carbon isotope discrimination was about $0.6x10^{-3}$ ‰ greater in barley than in wheat with little overlap between genotypes within species in both experiments (Table 5.5). Nitrogen contents in wheat and barley shoots in both experiments were not significantly different (mean = 5.4% N). Assuming leaf blades did not differ from leaf sheaths in N content per unit weight, leaf nitrogen per unit area would be inversely related to SLA.

Relative leaf expansion rate calculated over the duration of the experiments was greater in wheat than in barley. Values for wheat in the glasshouse were 0.26 $m^2 m^{-2} d^{-1}$ and 0.20 $m^2 m^{-2} d^{-1}$ outdoors compared to barley which was 0.20 $m^2 m^{-2} d^{-1}$ in the glasshouse and 0.16 $m^2 m^{-2} d^{-1}$ outdoors.

5.3.2 Temperature and leaf extension

Twenty four hour mean temperatures varied from a low of 3 °C to a high of 20 °C. The median 24-hour temperature was 7 °C. Table 5.6 presents the slope of the line between temperature and leaf extension per day (mm $(°Cd)^{-1}$) and the estimated temperature (°C) at which leaf extension ceased.

A linear relationship between temperature and leaf extension accounted for about 95% of the total variation (Table 5.6). Oats and barley had the lowest leaf extension per °C per day whereas triticale and bread wheat had the greatest leaf extension rates. There was little difference between species in the temperature at which growth ceased between species although temperatures were slightly higher in barley than in the other species.

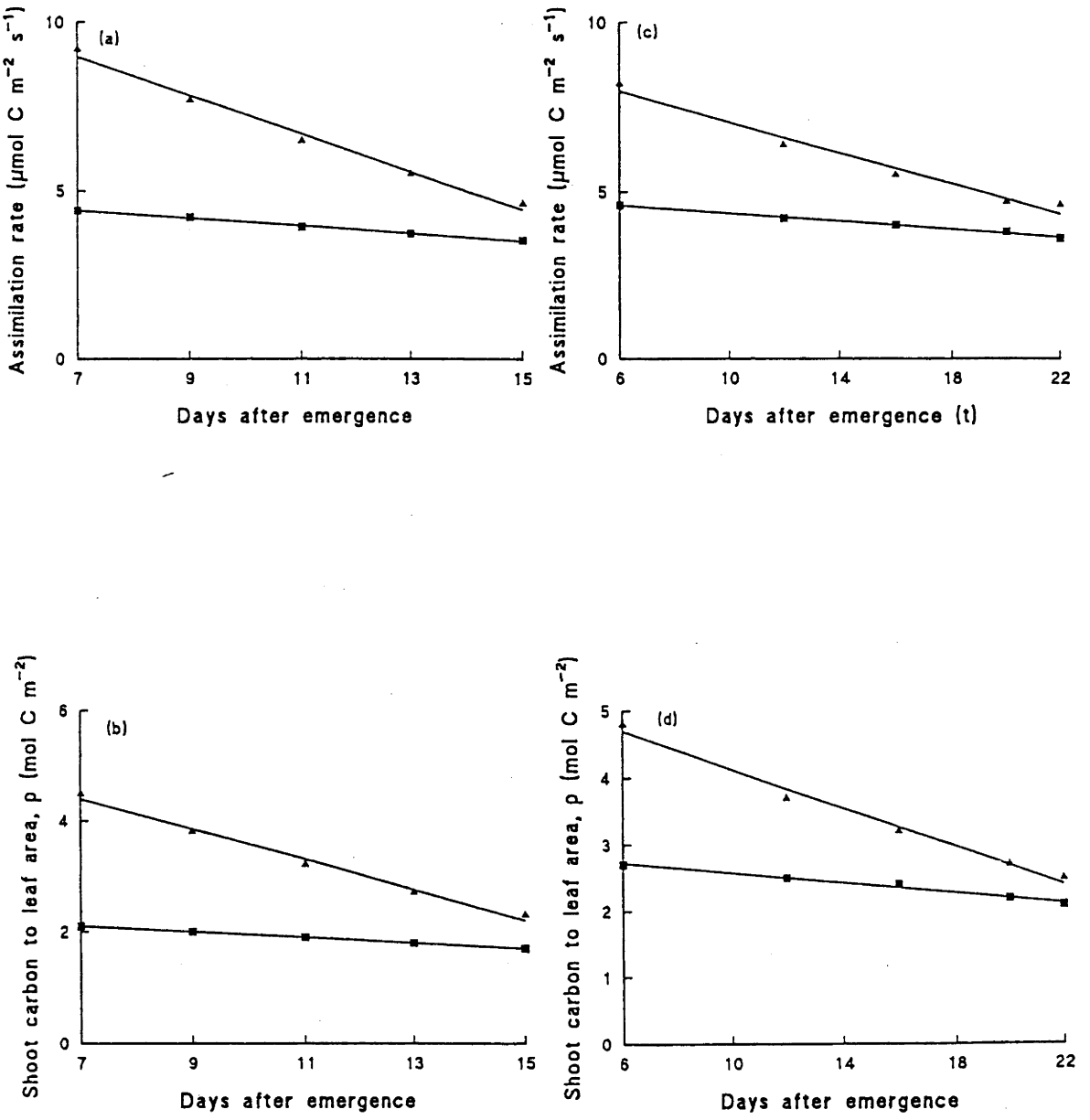


Fig. 5.3 Assimilation rate versus time in barley (■) and bread wheat (▲) grown in the glasshouse (a), and outdoors (c), and the ratio of shoot carbon to leaf area versus time in the glasshouse (b) and outdoors (d).

Table 5.5. Net assimilation rate (NAR, g cm^{-2} day^{-1}), leaf area ratio (LAR, m^2 kg^{-1}), specific leaf area (SLA, m^2 kg^{-1}) and leaf weight ratio (LWR, g g^{-1}) and carbon isotope discrimination (Δ) for all genotypes at the final harvest in the glasshouse and outdoors.

Genotype	NAR	LAR	SLA	LWR	$\Delta x10^{-3}$
Glasshouse					
Barley					
Galleon	9.4	1.9	3.2	0.59	20.95
O'Connor	9.9	1.9	3.1	0.62	20.49
Ulandra	8.5	2.1	3.3	0.65	21.05
Malebo	7.6	2.3	3.5	0.65	21.03
Beecher	7.9	2.4	3.4	0.65	21.12
Mean	**8.7**	**2.1**	**3.4**	**0.63**	**20.93**
Bread wheat					
Kulin	10.8	1.6	2.5	0.61	20.26
Meteor	10.8	1.6	2.7	0.61	20.22
Hahn/Parula	12.7	1.5	2.4	0.60	20.74
Rosella	11.0	1.7	2.8	0.62	20.55
M 3344	11.7	1.8	2.4	0.59	20.09
Mean	**11.4**	**1.6**	**2.6**	**0.61**	**20.37**
s.e. (Genotypes)	0.6	0.1	0.1	0.01	0.18
Outdoors					
Barley					
Galleon	9.1	1.6	2.8	0.58	20.75
O'Connor	8.2	1.7	2.9	0.58	20.71
Ulandra	9.6	1.4	2.5	0.58	20.66
Malebo	10.1	1.5	2.6	0.59	20.65
Beecher	8.1	1.8	2.9	0.62	20.79
Mean	**9.0**	**1.6**	**2.8**	**0.59**	**20.71**
Bread wheat					
Kulin	10.4	1.5	2.5	0.59	19.93
Meteor	10.0	1.5	2.5	0.59	20.19
Hahn/Parula	11.0	1.4	2.3	0.59	20.27
Rosella	11.1	1.4	2.3	0.60	19.68
M 3344	10.5	1.4	2.3	0.58	19.96
Mean	**10.6**	**1.4**	**2.4**	**0.59**	**20.00**
s.e. (Genotypes)	0.4	0.1	0.1	0.01	0.15

Table 5.6. Leaf extension (LE, mm $(°Cd)^{-1}$) and estimated temperature when leaf extension ceased (°C) for cultivars of barley, bread wheat, durum wheat, triticale and oats. The r^2 values are for the linear relationships between leaf extension and temperature.

Genotype	LE	r^2	Temperature when LE=0
Barley			
Galleon	0.89	0.96	0.6
O'Connor	0.73	0.91	0.7
Ulandra	1.00	0.93	0.5
Bread wheat			
Kulin	1.06	0.96	0.3
Meteor	1.06	0.95	0.3
Rosella	1.00	0.94	0.1
Durum wheat			
Altar 84	0.96	0.93	0.0
Carcomun	0.86	0.92	1.3
Triticale			
Dua	1.01	0.95	0.1
Currency	1.15	0.96	0.1
Oats			
Echidna	0.65	0.96	-0.5
Hakea	0.66	0.95	0.3

5.4 DISCUSSION

The greater dry weight, leaf area, leaf emergence rate and tiller emergence rate of barley relative to wheat, previously found in field grown plants in chapter 3, were also found in plants grown in pots in a glasshouse and outdoors. The magnitude of the differences in dry weight and leaf area between the species grown in these experiments and in the field experiments were similar. That is, above-ground dry weight was 40% greater in barley than wheat whereas leaf area at the final harvest (main stem leaves) was two times greater in barley than in wheat.

Contrary to expectations there were no differences in RGR between the species and hence RGR cannot account for the substantial differences in growth between barley and wheat. The RLER of wheat was greater than that of barley over the duration of the experiment. Barley and wheat achieved the same RGR in different ways. The NAR was

higher in wheat whereas LAR was higher in barley and variation in SLA was largely responsible for the variation in NAR and LAR (Fig. 5.4a and Fig.5.4b). The SLA over the duration of the experiments changed more in wheat than in barley and NAR changed more in wheat than in barley per unit change in SLA. This accounted for the smaller difference in NAR and LAR between wheat and barley at the final harvest. The greater increase in SLA in wheat presumably also accounts for the higher RLER in wheat than in barley.

Carbon isotope discrimination (Δ) was determined in leaf material and there is evidence in wheat that plants with low Δ and hence a high water-use efficiency (Farquhar and Richards, 1984), may be slower growing (Condon *et al.* 1987; Richards and Condon, 1992). This was found to be true in both the glasshouse and outdoors experiment. The relationship between Δ and dry weight at final harvest in the glasshouse and outside was $r=0.64$ ($P<0.05$) and $r=0.71$ ($P<0.05$) respectively, whereas the relationship between Δ and leaf area was $r=0.72$ ($P<0.05$) in the glasshouse and $r=0.78$ ($P<0.01$) outside. Variation in Δ was attributed to variation in SLA (Fig. 5.5). Plants with a high SLA have less nitrogen per unit leaf area and hence presumably less RuBP carboxylase which results in a lower assimilation rate and a higher carbon isotope discrimination.

The relationship between leaf extension and temperature in the different species was similar. Although triticale and bread wheat had a faster longitudinal extension rate than barley and oats, the expansion of total leaf area may not differ greatly as the latter species have broader leaves. There was no evidence that barley has a lower base temperature for growth than the other species, which may have partly accounted for its greater crop growth during the winter in the field experiments. On the contrary, barley leaves ceased growth at a higher temperature than the other species and this is consistent with the requirement of a higher temperature for germination in barley than in wheat (Russelle and Bolton, 1980). The similar growth difference between barley and wheat in the warmer glasshouse experiment and in the cooler outdoors experiment also support the conclusion that the temperature response in the different species was generally similar.

The similar RGR in both wheat and barley despite the heavier and larger plants of barley at each harvest and the similar response to temperature indicate that factors between germination and the appearance of the second main stem leaf are responsible for the greater growth in barley. Important factors in barley could therefore be earlier emergence and/or a larger above-ground biomass at emergence or just after. The latter could arise from a larger embryo as care was taken to use seeds of a similar weight, or to a greater allocation of stored seed reserves to the shoot than to the roots. Evidence for a larger shoot at emergence of barley comes from extrapolation of the linear relationship between $\log_e$ dry weight versus time in the glasshouse (Fig. 5.2a) and outdoors (Fig. 5.2.b) experiments. The estimated dry weight at emergence in the

glasshouse experiment was 12.8 mg in barley and 9.6 mg in wheat whereas values outdoors were 12.4 mg and 8.2 mg in barley and wheat respectively. A larger plant size due entirely to an earlier emergence and variation in embryo size has been reported in other crop species. In tomatoes Alvarado *et al.* (1987) found that a greater plant dry weight, leaf area and ground cover was due entirely to an earlier emergence rather than to an increased relative growth rate. In carrots, variation in size of seedlings at emergence was directly related to variation in embryo length (Gray and Steckel, 1983) and embryo size has also been found to account for hybrid vigour in maize (Ashby, 1930, 1932) and tomatoes (Ashby, 1937)

Another important factor in barley is the higher leaf area per unit leaf mass (SLA). The relative difference in SLA between barley and wheat was greatest at the first harvest in these experiments when two main stem leaves had fully expanded. For the same leaf mass, barley had an average leaf area 75% greater than wheat at this time. Although this may not result in increased carbon assimilation, as it is counterbalanced by a low net assimilation rate, in field grown plants, where fast canopy growth is important to reduce evaporation from the soil surface, a high SLA of first formed leaves should result in more transpiration relative to soil evaporation and hence to a higher total biomass at maturity.

5.5 CONCLUSIONS

The greater shoot dry weight and leaf area in barley than in bread wheat observed in field grown plants was confirmed in pot experiments.

There was no evidence that more growth at low temperature in barley could account for the observed differences in the field. There was also no evidence that differences in relative growth rate could account for the greater weight and leaf area of barley. Much of the difference in weight was attributed to a greater shoot weight at emergence or an earlier emergence of barley. The difference in leaf area was due to the above and to a higher specific leaf area in barley.

Variation in emergence time, the allocation of seed reserves to root and shoot and to embryo size will be investigated in the following chapters.

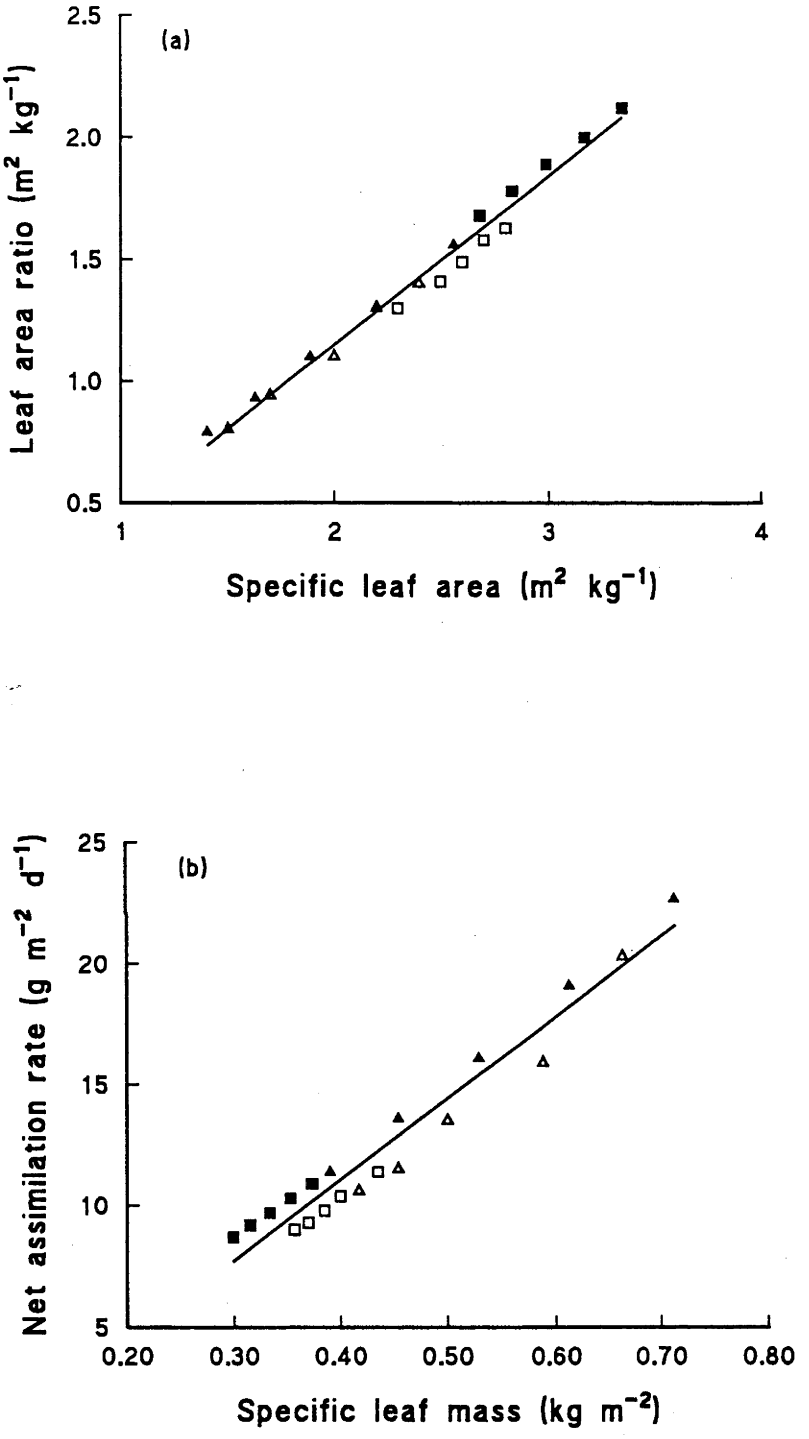


Fig. 5.4 Relationship between a) leaf area ratio (LAR) and specific leaf area (SLA) and b) net assimilation rate and the inverse of specific leaf (i.e. specific leaf mass, SLM) in barley (■) and bread wheat (▲) grown in both glasshouse (closed symbols) and outdoors (open symbols). Relationship between:
LAR and SLA: $Y_{LAR} = 0.69(SLA)-0.02$ ($r = 0.99$, $P<0.01$).
NAR and SLM, $Y_{NAR} = 33.6(SLM)-2.35$ ($r = 0.80$, $P<0.01$).

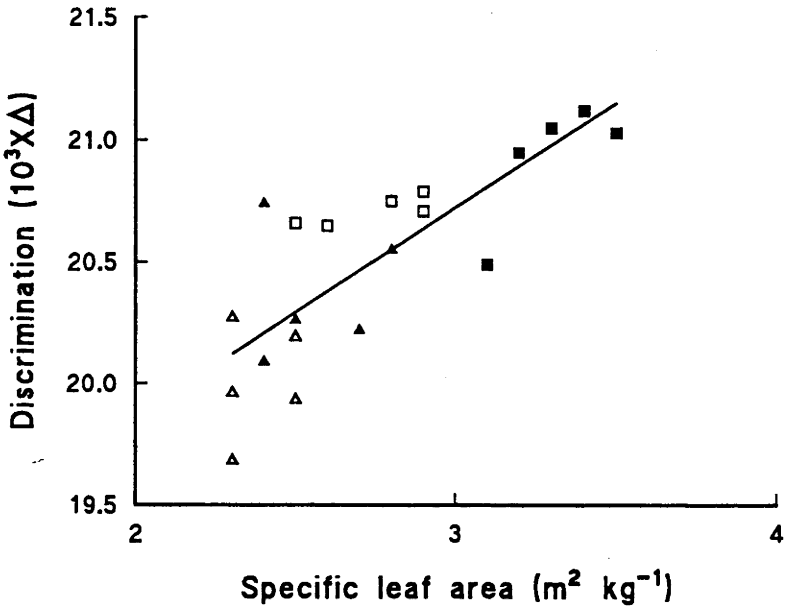


Fig. 5.5 Relationship between specific leaf area and carbon isotope discrimination at final harvest in barley (■, □) and bread wheat (▲, △) grown in both glasshouse (closed symbols) and outdoors (open symbols). Relationship: Discrimination = 0.86(SLA)+18.1 ($r=0.80$, $P<0.01$).

CHAPTER 6

VARIATION IN GERMINATION AND SEEDLING EMERGENCE

6.1 INTRODUCTION

Pot studies described in chapter 5 confirmed the greater vigour of barley compared to wheat that was found in field grown plants grown during the winter. In pot experiments conducted in a glasshouse and outdoors the shoots of barley plants were 40% heavier and the leaf area two-fold greater than bread wheat. Two hypotheses were tested in chapter 5, to see whether they could account for the differences in vigour. The first was to test whether differences in the relative growth rate between wheat and barley accounted for the differences in vigour. The second was to test whether barley may continue growing at a lower base temperature than wheat.

Neither of these hypothesis were proven. Instead it was concluded that the differences in growth between barley and wheat arise between germination and the appearance of the second main stem leaf. This chapter explores factors during this time that may account for differences in vigour between temperate cereal species. It is proposed that the following factors may be important: (i) emergence time and the differential depletion of seed reserves, (ii) a greater shoot biomass formed from seed reserves and attributed to either a larger embryo or a larger plumule relative to radicle in the embryo. Earlier emergence would result in earlier carbon fixation and faster attainment of net carbon gain. A greater shoot biomass should result in a larger photosynthetic organ on which exponential growth can build.

6.2 MATERIALS AND METHODS

6.2.1 Experimental

The experiment was planted in a growth cabinet (Conviron, model PGW 36) in September 1989. Seeds of all genotypes were from field grown plants in 1988 except Meteor (from Cargill seeds in 1986) and AT 30 (from University of New England, Armidale, 1986). Ninety six seeds of the same weight were selected for each genotype; the husked seeds of barley and oats weighed 38 mg and 46 mg whereas the naked seeds of bread wheat, durum wheat and triticale weighed 35 mg. The husk weight for a 38 mg barley kernel was found to be 3 mg whereas for 46 mg oat kernel it was 11 mg. Three seeds of each genotype were sown per pot at a constant depth (3 cm) in a fertile potting mix. Pots were 20 cm tall and 8 cm diameter. The cultivars used in this experiment are shown in Table 2.2 (chapter 2). AT 30, a winter triticale, was used instead of Currency. The cultivars were assigned positions in the growth cabinet using a neighbour design such that no genotype had the same neighbour in any replicate. There were four replications in a randomized block design.

6.2.2 Growth conditions

The growth cabinet was maintained at a constant temperature of 5°C night/15°C day, and a mean thermophotoperiod of 11 h. The daily radiant flux density was 12 mol m^{-2}, and the relative humidity was 80%. All pots were well watered during the experiment. All replicates were periodically moved inside the growth cabinet to reduce any environmental variation effects on plant growth.

Thermal time was calculated in degree day units (°Cd) by summing the daily values of mean temperature (Russelle *et al.* 1984) as indicated in crop growth indices (chapter 3).

6.2.3 Emergence and harvests

The time the coleoptile of each seedling was first visible was recorded. From this data the thermal time to 95% emergence and the regression of % of emerged seedlings against thermal time during the linear phase of emergence were calculated. The slope of this regression was taken as the rate of seedling emergence (% seedlings $(°Cd)^{-1}$).

Regular harvests of three seedlings per pot including roots and shoots were made from germination to the time when there were around two leaves on the main stem in all genotypes. There were eight harvests during the experiment. The first harvest (H1) was made 4 days after sowing just after germination of all genotypes. Four more harvests were made around the time of emergence, 7 (H2), 9 (H3), 10 (H4) and 11 (H5) days after sowing. The last three harvests were made at 15 (H6), 19 (H7) and 28 (H8) days after sowing. Total root length was determined for each plant using a ruler.

6.2.4 Dry weight and leaf area

Shoot dry weight (W_s), root dry weight (W_r) and seed dry weight were determined at each harvest. Samples were oven-dried at 80°C and dry weight was recorded after 48 h. Leaf area was measured using a leaf area measurement system (Delta-T Devices, Cambridge, England). Leaf number on the main stem was also recorded at each harvest. No tillers emerged during the experiment.

6.2.6 Growth analysis

Relative growth rates for whole plant (RGR, $(°Cd)^{-1}$), shoot (RGR_s, $(°Cd)^{-1}$) and roots (RGR_r $(°Cd)^{-1}$) from emergence to the leaf 2 stage were calculated as in chapter 5. The RGR was partitioned into its components net assimilation rate (NAR, g m^{-2} $(°Cd)^{-1}$) and leaf area ratio (m^2 kg^{-1}). A further partition of LAR into specific leaf area (SLA, m^2 kg^{-1}) and leaf weight ratio (LWR, g g^{-1}) was made at each harvest. The ratio of root to shoot (RSR, W_r/W_s) was calculated for all harvests.

6.3 RESULTS

6.3.1 Emergence

Barley seedlings were the first to emerge (Table 6.1). They emerged about 10 °Cd before bread and durum wheats and about 15 °Cd earlier than triticale and oats. Barley also had a shorter thermal time to reach 95% emergence being about 10 °Cd less than bread wheat, triticale and oats and about 15 °Cd less than durum wheat.

The rate of seedling emergence (RSE) during the linear phase was highest in oats (Table 6.1). Barley had the same rate as bread wheat and triticale whereas durum wheat had the lowest rates. The r^2 values for the relationship between emergence and thermal time were generally greater than 0.95. These results indicate that most variation in emergence between species was due to an earlier emergence rather than to a faster rate of seedling emergence.

6.3.2 Seed mass depletion and the beginning of autotrophic growth

The reduction in seed mass in all species before germination was similar (Fig. 6.1). Between germination and emergence the reduction in seed mass of barley began earlier and was greater than in the other species. This difference was maintained to the completion of the experiment. There was evidence that the initial seed weight declined more in barley and oats than in the other species. Barley was also first to become autotrophic (Fig. 6.2). This occurred about 50 °Cd after emergence.

6.3.3 Plant sizes

The increase in shoot, root and whole plant (excluding seed) weight of each species is shown in Fig. 6.3. Barley had the greatest weight at all times. Root and shoot growth varied somewhat in the other species such that by the final harvest the shoot weight of triticale was greatest but its root growth was lowest. The root weight of oats differed from the other species in that it was lowest around emergence time but was high at the final harvest.

Leaf area after emergence is shown in Fig. 6.4. Barley leaf area was substantially greater than in all the other species at all harvests. Triticale leaf area was next highest and durum wheats were least. Root length was also greater in barley (Fig. 6.5) whereas length in oats was least. It was notable that prior to emergence barley initiated about five seminal roots whereas the other species initiated only three. The additional roots in barley probably account for the faster increase in root length observed in barley compared to the other species (Fig. 6.5).

Root to shoot ratio (RSR) declined with time (Fig. 6.6). The species were generally similar except that oats had the lowest RSR at emergence and about the highest at the final harvest whereas the RSR ratio for triticale was lowest at the final harvest.

Table 6.1 Time to first emergence (TFE, °Cd), time to 95% seedling emergence (T95%, °Cd) and rate of seedling emergence during the linear phase (RSE, % seedlings (°Cd)$^{-1}$).

Genotype	TFE	T95%	RSE
Barley			
Galleon	99	122	4.2
O'Connor	101	123	3.8
Ulandra	98	119	4.2
Bread wheat			
Kulin	108	133	3.1
Meteor	110	132	3.8
Rosella	108	127	4.6
Durum wheat			
Altar 84	110	140	3.1
Carcomun	112	134	2.9
Triticale			
Dua	113	127	3.3
AT 30	119	130	3.1
Oats			
Echidna	112	129	5.0
Hakea	114	129	4.6
s.e.	3	5	0.3

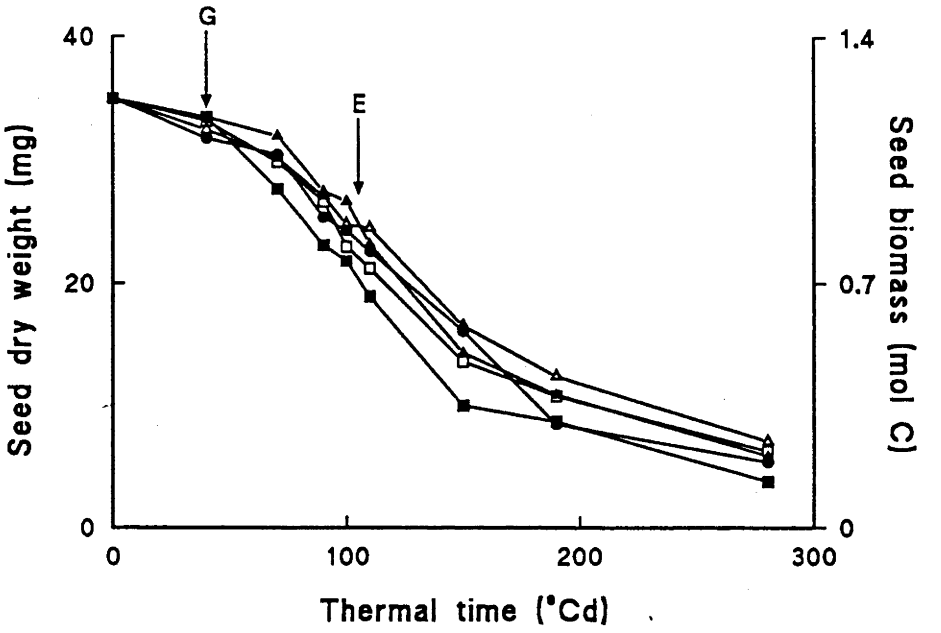


Fig. 6.1 Depletion of seed weight in barley (■), bread wheat (▲), durum wheat (△), triticale (□) and oats (●). Germination (G) and emergence (E) are marked. The values for the standard error of the means (s.e.) at 40, 70, 90, 100, 110, 150, 190 and 280 °Cd after sowing are 0.15, 0.12, 0.15, 0.20, 0.13, 0.28, 0.38 and 0.14.

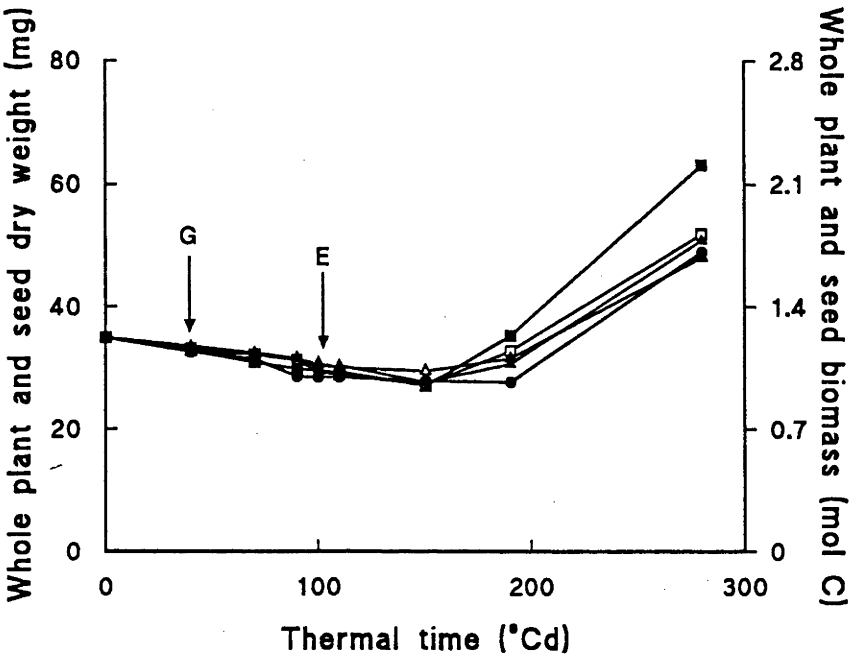


Fig 6.2 Whole plant dry weight including shoot,roots and seed for barley (■), bread wheat (▲) , durum wheat (△), triticale (□) and oats (●). Germination (G) and emergence (E) are marked. The values for the standard error of the means (s.e.) at 40, 70, 90, 100, 110, 150, 190, and 280 °Cd after sowing are 0.14, 0.14, 0.16, 0.14, 0.12, 0.45, 0.50 and 0.54.

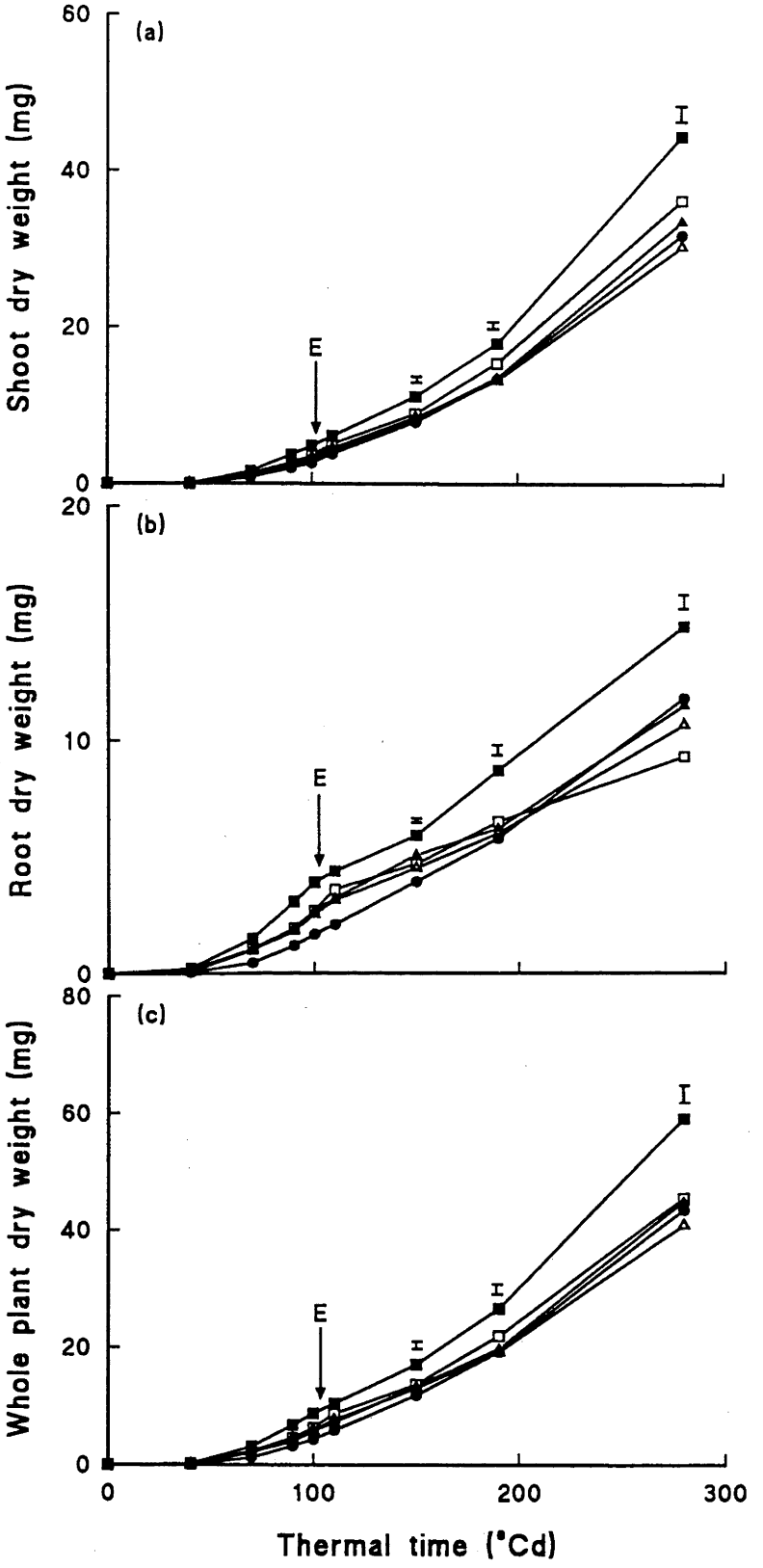


Fig 6.3 Shoot (a), root (b) and shoot + root (c) dry weight in barley (■), bread wheat (▲), durum wheat (△), triticale (□) and oats (●). The arrow shows the time of emergence in barley. Vertical bars represent the standard error of means.

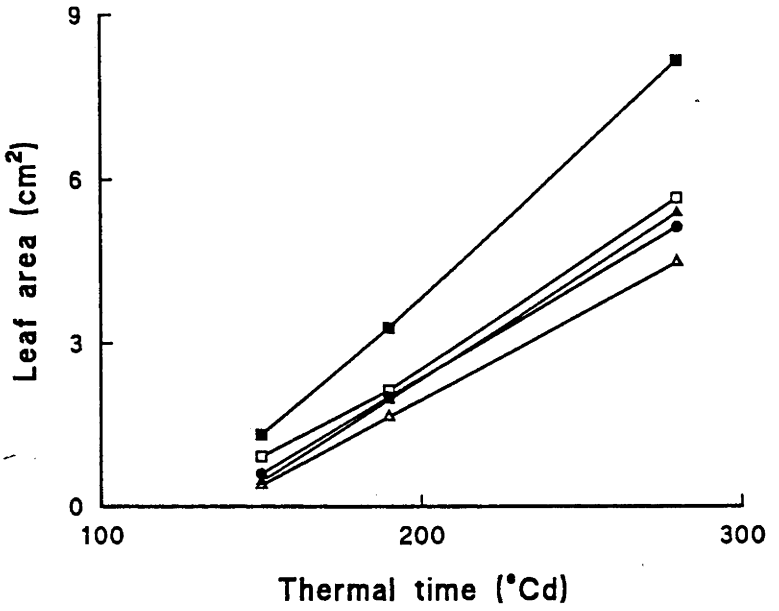


Fig 6.4 Leaf area for barley (■),bread wheat (▲), durum wheat (△), triticale (□) and oats (●). The values for the standard error of means (s.e.) at 150, 190 and °Cd after sowing are 0.02, 0.03 and 0.08.

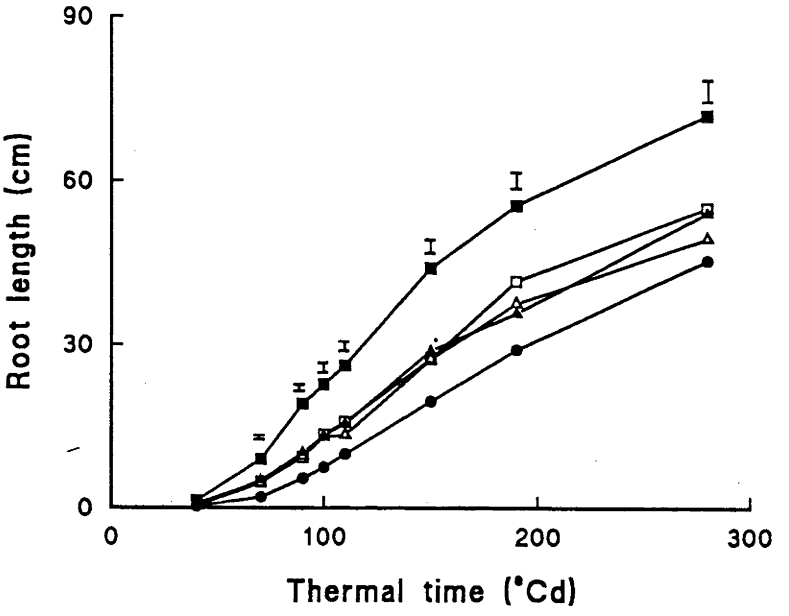


Fig 6.5 Root length for barley (■), bread wheat (▲), durum wheat (△), triticale (□) and oats (●). Vertical bars represent the standard error of the means.

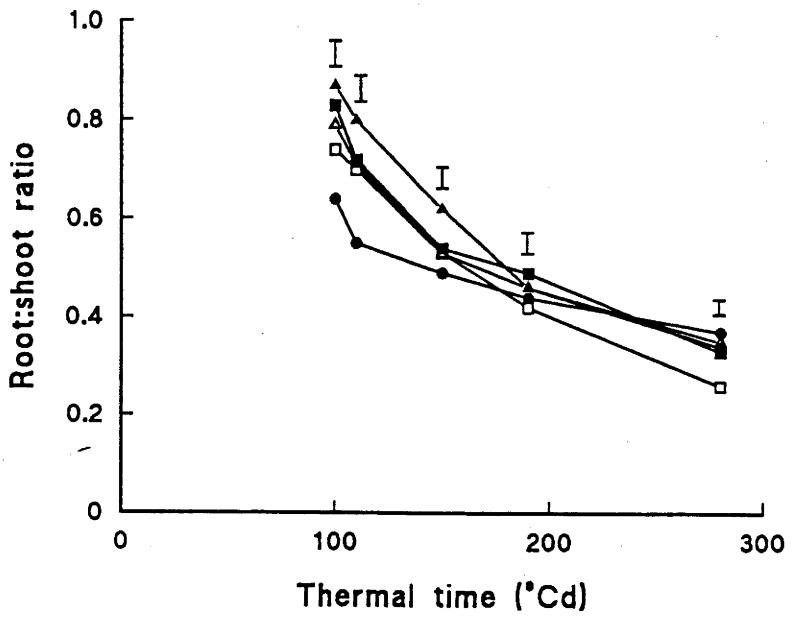


Fig 6.6 Root to shoot ratio for Barley (■), bread wheat (▲),durum wheat (△), triticale (□) and oats (●). Vertical bars represent the standard error of the means.

Table 6.2 Dry weight of whole plant excluding the seed (W, mg), shoot (W_s, mg) and roots (W_r, mg), root:shoot ratio (RSR, W_r/W_s), length of roots (RL, cm), leaf area (LA, cm^2) and leaf number (LNO) at the final harvest.

Genotype	W	W_s	W_r	RSR	RL	LA	LNO
Barley							
Galleon	59.4	45.6	13.8	0.29	74.5	8.3	2.4
O'Connor	62.8	45.3	17.5	0.39	75.1	8.8	2.4
Ulandra	55.9	42.6	13.3	0.32	66.7	7.5	2.4
Bread wheat							
Kulin	44.7	32.8	11.9	0.37	48.6	5.1	1.8
Meteor	45.0	33.2	11.8	0.36	56.2	4.9	2.3
Rosella	45.5	34.8	10.7	0.31	57.8	6.2	2.4
Durum wheat							
Altar 84	40.4	29.3	11.1	0.38	56.2	4.3	1.9
Carcomun	41.6	31.5	10.1	0.32	42.9	4.7	1.9
Triticale							
Dua	50.0	40.0	10.0	0.25	51.5	4.8	2.0
AT 30	41.2	32.6	8.6	0.27	58.7	4.5	2.3
Oats							
Echidna	45.2	32.9	12.3	0.37	45.3	5.4	1.7
Hakea	42.1	30.9	11.2	0.36	45.8	4.9	1.6
s.e.	4.2	3.1	1.5	0.03	0.7	0.7	0.2

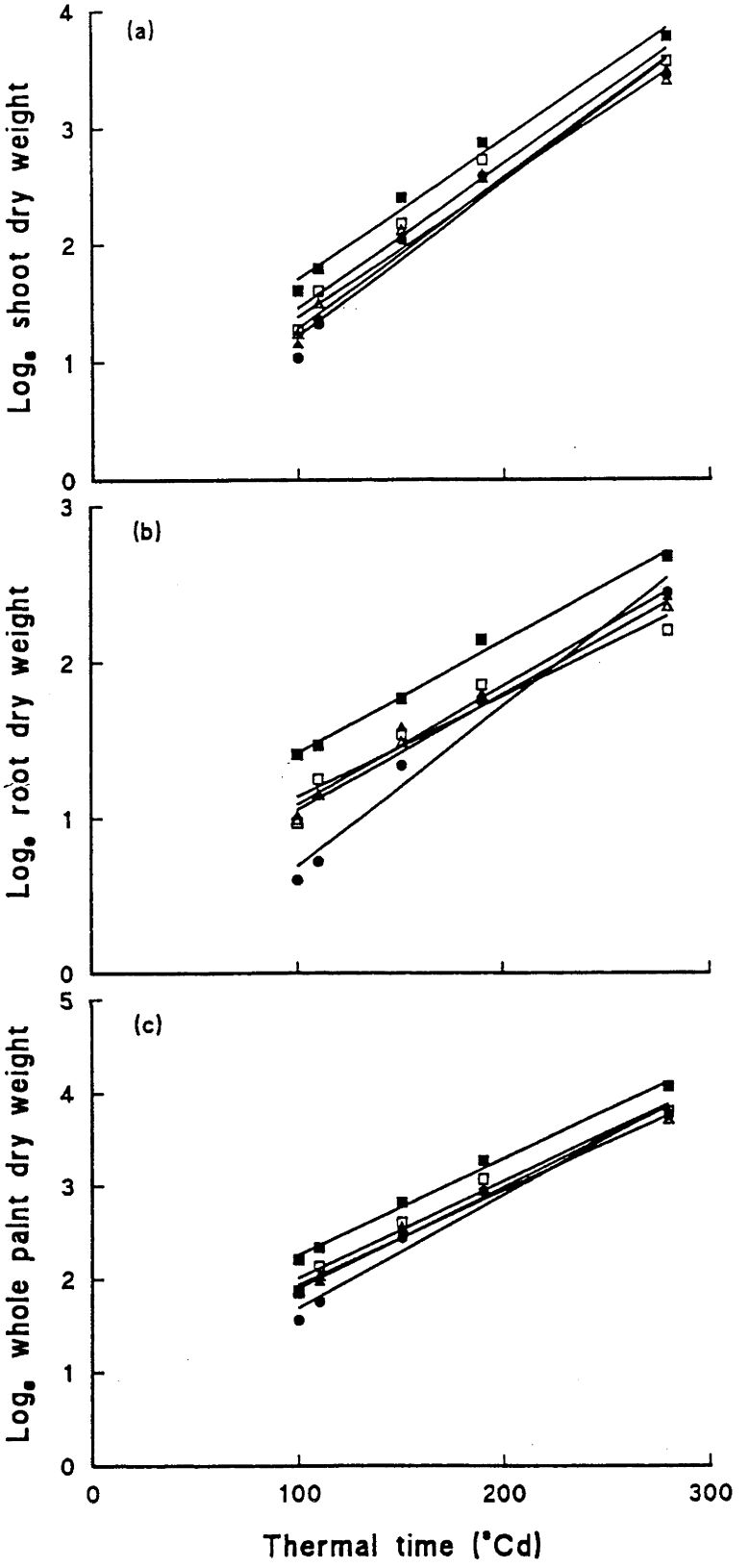


Fig. 6.7 Relationship between thermal time and a) $\log_e$ shoot, b) $\log_e$ root and c) $\log_e$ whole plant (excluding seed) for barley (■), bread wheat (▲), durum wheat (Δ), triticale (o) and oats (●). See text for regressions.

The variation between genotypes in plant size at the final harvest is given in Table 6.2. Variation within species for these plant characteristics was not substantial. The main exceptions were for plant weights in triticale and the root weight of O'Connor barley.

6.3.4 Relative growth rate

The RGR on a total dry weight basis and the RGR_s and RGR_r between emergence and the leaf 2 stage were similar for each species (Fig. 6.7). The only exception was the higher RGR in the oat roots. The relationship between thermal time and $\log_e$ shoot was: for barley (Y_B = 0.0121(°Cd)+0.47), bread wheat (Y_{BW} = 0.013(°Cd)-0.06), durum wheat (Y_{DW} = 0.0119(°Cd)+0.17), triticale (Y_T = 0.0125(°Cd)+0.02) and oats (Y_O = 0.0134(°Cd)-0.14). The relationship between thermal time and $\log_e$ root was: for barley (Y_B = 0.0073(°Cd)+0.66, bread wheat (Y_{BW} = 0.0078(°Cd)+0.25, durum wheat (Y_{DW} = 0.0076(°Cd)+0.27, triticale (Y_T = 0.0066(°Cd)+0.47 and oats (Y_O = 0.0106(°Cd)-0.40. The relationship between thermal time and $\log_e$ whole plant (excluding seed) was: for barley (Y_B = 0.0106(°Cd)+1.12), bread wheat (Y_{BW} = 0.0112(°Cd)+0.71), durum wheat (Y_{DW} = 0.0105(°Cd)+0.85), triticale (Y_T = 0.0108(°Cd)+0.85) and oats (Y_O = 0.0125(°Cd)+0.40). The RGR, RGR_s and RGR_r were also similar for each genotype (Table 6.3). The partitioning of RGR into its components NAR, LAR, SLA and LWR showed there was little variation in LWR but that SLA may have contributed to some variation in NAR and LAR (Table 6.4).

Table 6.3. Relative growth rate of whole plant (RGR, $(°Cd)^{-1}$), shoot (RGR_s, $(°Cd)^{-1}$) and roots (RGR_r, $(°Cd)^{-1}$) for each genotype.

Genotype	RGR	RGR_s	RGR_r
Barley			
Galleon	0.0099	0.0114	0.0065
O'Connor	0.0109	0.0124	0.0083
Ulandra	0.0107	0.0125	0.0072
Bread wheat			
Kulin	0.0115	0.0134	0.0082
Meteor	0.0111	0.0128	0.0080
Rosella	0.0113	0.0132	0.0075
Durum wheat			
Altar 84	0.0104	0.0115	0.0081
Carcomun	0.0105	0.0123	0.0070
Triticale			
Dua	0.0117	0.0135	0.0074
AT 30	0.0098	0.0115	0.0058
Oats			
Echidna	0.0117	0.0127	0.0096
Hakea	0.0133	0.0140	0.0116
s.e.	0.0010	0.0010	0.0010

Table 6.4 Net assimilation rate (NAR, g m^{-2} $(°Cd)^{-1}$), leaf area ratio (LAR, m^2 kg^{-1}), specific leaf area (SLA, m^2 kg^{-1}) and leaf weight ratio (LWR, g g^{-1}) at the final harvest.

Genotype	NAR	LAR	SLA	LWR
Byrley				
Galleon	0.8	1.3	3.2	0.45
O'Connor	0.8	1.4	3.4	0.42
Ulandra	0.7	1.5	3.4	0.45
Bread wheat				
Kulin	1.0	1.1	2.7	0.42
Meteor	1.0	1.1	2.5	0.42
Rosella	0.9	1.2	2.5	0.46
Durum wheat				
Altar 84	0.8	1.3	3.0	0.42
Carcomun	0.9	1.2	2.1	0.55
Triticale				
Dua	1.0	1.2	2.5	0.46
AT 30	0.8	1.3	2.7	0.46
Oats				
Echidna	0.9	1.3	2.9	0.43
Hakea	1.2	1.1	2.8	0.39
s.e.	0.1	0.1	0.2	0.02

6.4 DISCUSSION

Differences in plant characteristics around germination and emergence account for the higher dry weight and leaf area of barley compared to the other species. These differences were independent of initial seed weight as the kernels sown all weighed 35 mg. In barley, germination and the utilization of seed reserves began about 30 °Cd earlier than in the other species (Fig. 6.1), although differences in emergence time were only of the order of about 10 °Cd - 15 °Cd. The rate of utilization of seed reserves, although not calculated, is likely to be the same for each species (Fig. 6.1, slope of the lines between harvest 2 and harvest 6 are similar).

The earlier emergence of barley cannot account for all of the difference in early growth. The weight of shoot and root in barley at emergence time was also greater than the other species. Table 6.5 presents the estimated weight of shoots, roots and plants (excluding the seed) at 50% emergence. Values at the time of 50% emergence of each genotype were calculated from the emergence data and RGR of each genotype. Both shoot and root weight were about 50% greater in barley than in wheat (Table 6.5). This corresponds with the magnitude of the difference in weight between wheat and barley in other experiments and it must be due to barley having a larger embryo or a faster utilization of seed reserves before emergence.

The larger embryo is favoured as both leaf area and root length just after emergence were larger in barley. Both these factors indicate more cell primordia in the barley embryo and cannot be accounted for by the faster utilization of seed reserves as no differences in rate of utilization could be detected (0.048 and 0.060 mg $(°Cd)^{-1}$ in barley and wheat respectively).

It was proposed earlier that the faster growth of barley may be due to a larger plumule relative to radicle in the embryo. This seems unlikely as the ratio of root to shoot at 50% emergence was similar in barley, both wheat species and triticale. The root-to-shoot ratio was significantly lower in oats, although this was short lived as the RGR for oat roots was faster than the other species and by the 2 leaf stage there was little difference between oats and the other species.

The relative contribution of the earlier emergence of barley to its higher plant dry weight, assuming that all species emerged at the same time as barley, was about 20%. The embryo size may have contributed about 80% of the variation in plant dry weight between species. Studies in other species have also found that earlier emergence and larger embryo may influence growth and final plant size. In tomatoes an earlier emergence resulted in a greater plant dry weight, leaf area and ground cover with no effects on relative growth rate (Alvarado *et al.* 1987). The same has been found for the *Rht* genes in wheat (Richards, 1992). Also, variation in the size of carrot seedlings at emergence was found to be directly related to variation in embryo length (Gray and Steckel, 1983). These results agree with the present findings in that the earlier

emergence and larger embryo in barley compared with the other species were the factors responsible for its greater early vigour.

Differences between species in NAR and LAR were less in this experiment than those reported in chapter 5. Variation in SLA which was responsible for variation in NAR and LAR earlier was correspondingly less. The likely reason for this is the lower light intensity in the cabinet used in this experiment relative to values in the two experiments under sunlit conditions. From Fig. 5.4a and Fig. 5.4b a change in SLA from 2.6 m^2 kg^{-1} in wheat to 3.3 m^2 kg^{-1}in barley corresponds to a change of about 25% in LAR and 20% in NAR. These values closely match the 25% lower value of NAR and LAR in barley and wheat respectively.

6.5 CONCLUSIONS

Barley had a higher dry weight than bread wheat, durum wheat, triticale and oats because it emerged earlier and it had a greater biomass at emergence than the other species. Is is likely that the greater biomass at emergence in barley was due to a larger embryo relative to the total seed size as all plants in these studies were derived from seed of the same weight. Differences between species in embryo size will be explored in the following chapter.

Table 6.5 Estimated biomass of shoot (W_s, mg), root (W_r, mg), whole plant, excluding the seed (W_p, mg) and root to shoot ratio (RSR, W_r/W_s) at 50% emergence of each genotype.

Genotype	W_s	W_r	W_p	RSR
Barley				
Galleon	6.5	4.9	11.4	0.75
O'Connor	7.6	5.0	12.6	0.66
Ulandra	5.9	4.7	10.6	0.80
Bread wheat				
Kulin	4.3	3.3	7.6	0.77
Meteor	4.6	3.3	7.9	0.72
Rosella	4.5	3.3	7.8	0.73
Durum wheat				
Altar 84	5.2	3.2	8.5	0.62
Carcomun	4.9	3.4	8.3	0.69
Triticale				
Dua	4.8	3.2	8.0	0.67
AT 30	3.8	3.5	7.3	0.92
Oats				
Echidna	4.5	2.7	7.2	0.60
Hakea	4.1	2.1	6.2	0.51
s.e.	0.2	0.1	0.3	0.05

CHAPTER 7
VARIATION IN EMBRYO AND LEAF EPIDERMAL CHARACTERISTICS

7.1 INTRODUCTION

Results presented in chapter 6 showed that the root and shoot dry weight in barley at the time of emergence was greater than bread wheat, durum wheat, triticale and oats. Furthermore, the leaf area and root length just after emergence was two-fold larger in barley than in the other species. Those results were for seedlings with the same weight. They suggest that, for a given seed weight, the embryo size is greater in barley than in the other species and that this is largely responsible for the greater vigour consistently found in barley. Faster utilisation of seed reserves was discounted in chapter 6 as being important in determining differences in vigour.

This chapter examines variation in embryo size and leaf epidermal characteristics of the first and second leaf, among barley, bread wheat, triticale and oats. Leaf epidermal characteristics were examined to provide indirect evidence of differences in cell numbers in the embryo: many of the cells forming the first two mains stem leaves are already present in the dormant seed (Lersten, 1987). Leaf epidermal characteristics were also examined to determine whether variation in the arrangement of cells in the leaves may account for variation in leaf area.

7.2 MATERIALS AND METHODS

7.2.1 Embryo characteristics

Eight genotypes shown in earlier studies (chapter 6) to have contrasting seedling dry weight and leaf area were chosen here. Genotypes were: Galleon, O'Connor, Ulandra and Malebo barleys; Kulin, Meteor and Rosella bread wheats; Dua triticale and Echidna oat.

Seeds were weighed to identify ten seeds with variation of less than 0.5 mg in each of three different sizes (25±0.5 mg, 35±0.5 mg and 50±0.5 mg) for all genotypes. The husk was removed from seeds of barley and oats before weighing. The embryo from each seed was extracted using a light microscope, scalpel, forceps and mini-spatulas. The minispatulas were modified to have a scalpel like-blade on each edge.

The embryo of cereal seeds occupies a dorsi-ventral position in the proximal portion of the grain (Bradbury *et al.*, 1956). This position of the embryo in the kernel makes its extraction relatively easy. The dissection of the embryo was made holding the seed with forceps and removing the covering layers with a scalpel. Then the embryo was detached from the kernel using the mini-spatula. The remaining layers of pericarp and scutellum attached to the coleoptile and coleorhiza were removed using the mini-spatula. Further dissection of the embryo was made by removing the coleoptile to expose the first leaf in the embryo. Scanning electron micrographs of leaf 1 in the

embryo were taken for barley and bread wheat.

Immediately after dissection, the weight (W_e) of each embryo was determined using a balance with precision of 1 mg. Length and width of coleoptile and coleorhiza were then determined using a light microscope on each excised embryo. The excised embryos were stored in plastic vials for a few days before examination in a scanning electron microscope (Stereoscan 360, Cambridge Instruments, England).

To prepare embryos for examination in the stereoscan, embryos were adhered with nail varnish to an aluminium stub 12.5 mm in diameter and then coated in gold using a Polaron E5000 SEM Coating Unit. Photographs of embryos were taken using an accelerating voltage of 20 kV and secondary electron imaging.

7.2.2 Leaf epidermal characteristics

Epidermal characteristics of fully expanded leaves were determined for the same genotypes as in 7.2.1, except that Dua triticale was substituted with Currency triticale. Three seeds of 35 mg in each genotype were planted in pots 15 cm tall and 8 cm diameter. There were four replicated blocks for each genotype. Plants were grown in a growth cabinet (Conviron, model PGW 36) under a mean temperature of 5°C/night and 15°C/day and a mean daily radiant flux density of 13.9 mol m^{-2}. The photothermal period was 11 h and the relative humidity was 80%. All plants were well watered during the experiment.

When the main stem leaf 3 of each plant had fully expanded, the length and breadth of leaf 1 and leaf 2 were measured with a ruler. The leaf area was determined as length x breadth x 0.8. Impressions of the adaxial surfaces were also taken from leaves using permagum impression material (Elastomeric Vinyl Polysiloxane, low viscosity). Ten minutes after application when the paste had dried, the impression was peeled away from the leaf and clear nail varnish was applied to the paste impression. The varnish impression (positive) was peeled away from the paste impression and adhered to a 12.5 mm aluminiun stub and coated in gold in the same way as the embryos.

Length and width measurements of epidermal cells were then made from scanning electron microscope images. Counts of epidermal cell number and of the number of cells across the width were determined in four fields 0.429 mm^2 in the middle of each leaf and on 12 plants of each genotype. Because the number of cells wholly within each field was small, number of epidermal cell ends within each field was also recorded. The average cell length could then be determined according to Hardham and Gunning (1978), using the following relationship:

$$L = 2Na/T$$

where L is the average cell length (mm), a is the field length (mm), N is the number of rows of cells across the field width, T is the total number of cell ends per field and 2

represents the two ends of each cell. The average cell width was calculated by dividing the field width by the number of rows of cells across the field width. The total cell number per leaf was estimated by multiplying the average cell number per field x the area of the whole leaf (cm^2) and dividing this product by the field area (0.00429 cm^2).

7.3 RESULTS

7.3.1 Variation in embryo size

The embryo of barley was heavier than the embryo of the other species in all seed size classes. Averaged over the three seed sizes, the barley embryo was about 90% heavier than that in bread wheat and oats and about 15% heavier than triticale (Table 7.1). Embryo weight was closely related to seed weight (Fig. 7.1) and there was evidence that the embryo size may increase more in barley for a given increase in seed size than in the other species, although data from more genotypes would be required to confirm this. Embryo size as a percentage of seed size was 1.7, 1.5, 0.9 and 0.9 for barley, triticale, bread wheat and oats respectively.

The embryo length in barley was about 20% greater than in bread wheat and oats (Table 7.1). Triticale embryo length was generally similar to barley. Differences in embryo width between species were smaller than differences in embryo length. The embryo width in barley was about 10% greater than in bread wheat and oats, whereas the embryo width in triticale was similar to that in barley (Table 7.1). Fig. 7.2 shows scanning micrographs of embryos extracted from seeds of barley (cv. O'Connor), bread wheat (cv. Kulin), triticale (cv. Dua) and oat (cv. Echidna). These micrographs show details of differences between species in embryo size and the two visible parts of the embryo, the coleoptile and the coleorhiza. Both the length and width of the coleoptile and coleorhiza in barley are greater than in bread wheat and oats. Triticale is similar to barley in these characteristics. The embryo length in intact seeds of barley, bread wheat, triticale and oats was positively correlated ($r=0.96$, $P<0.01$) to the weight of excised embryos (Fig. 7.3).

Removal of the coleoptile in the embryo exposed a larger first leaf in barley than in bread wheat (Fig. 7.4). This leaf is about 30% longer in barley than in bread wheat and it is folded over itself in such a way that its width is about two times greater in barley than in bread wheat. Leaf 2 was about 30% of the length of leaf 1 in both species and hence is larger in barley than in bread wheat. In addition, the coleorhiza envelopes three conspicuous seminal axes in barley but only one in wheat.

Table 7.1. Mean weight (mg), length (mm) and width (mm) of embryos from seeds of 25 mg, 35 mg and 50 mg weight for barley, bread wheat, triticale and oats.

Species	Weight	Length	Width
25 mg			
Barley	428	2.04	0.78
Bread wheat	219	1.69	0.74
Triticale	383	1.89	0.80
Oats	214	1.75	0.68
s.e.	11	0.04	0.02
35 mg			
Barley	621	2.14	0.86
Bread wheat	333	1.82	0.82
triticale	582	2.19	0.83
Oats	300	1.89	0.73
s.e.	15	0.06	0.03
50 mg			
Barley	860	2.38	1.00
Bread wheat	500	2.03	0.96
Triticale	674	2.33	0.94
Oats	467	2.01	0.76
s.e.	23	0.08	0.05

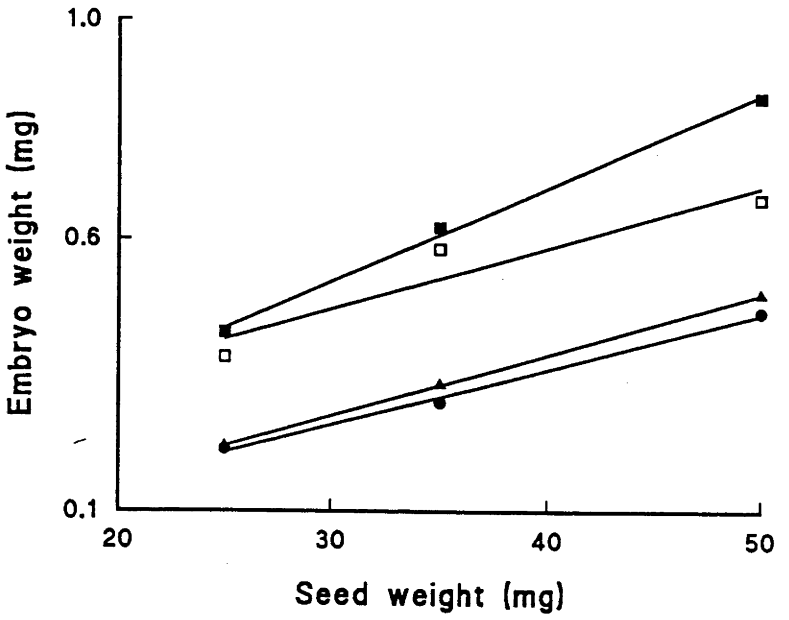


Fig. 7.1 Relationship between embryo weight and seed weight for barley (■), bread wheat (▲), triticale (□) and oats (●).

Relationship between embryo weight (W_e) and seed weight (S) for:

barley, W_e=0.017(S)+0.01 (r=0.96, P<0.01),

bread wheat, W_e=0.011(S)-0.06 (r = 0.95, P<0.01),

triticale, W_e=0.011(S)+0.14 (r = 0.95, P<0.01),

oats, W_e=0.010(S)-0.05 (r = 0.99, P<0.01).

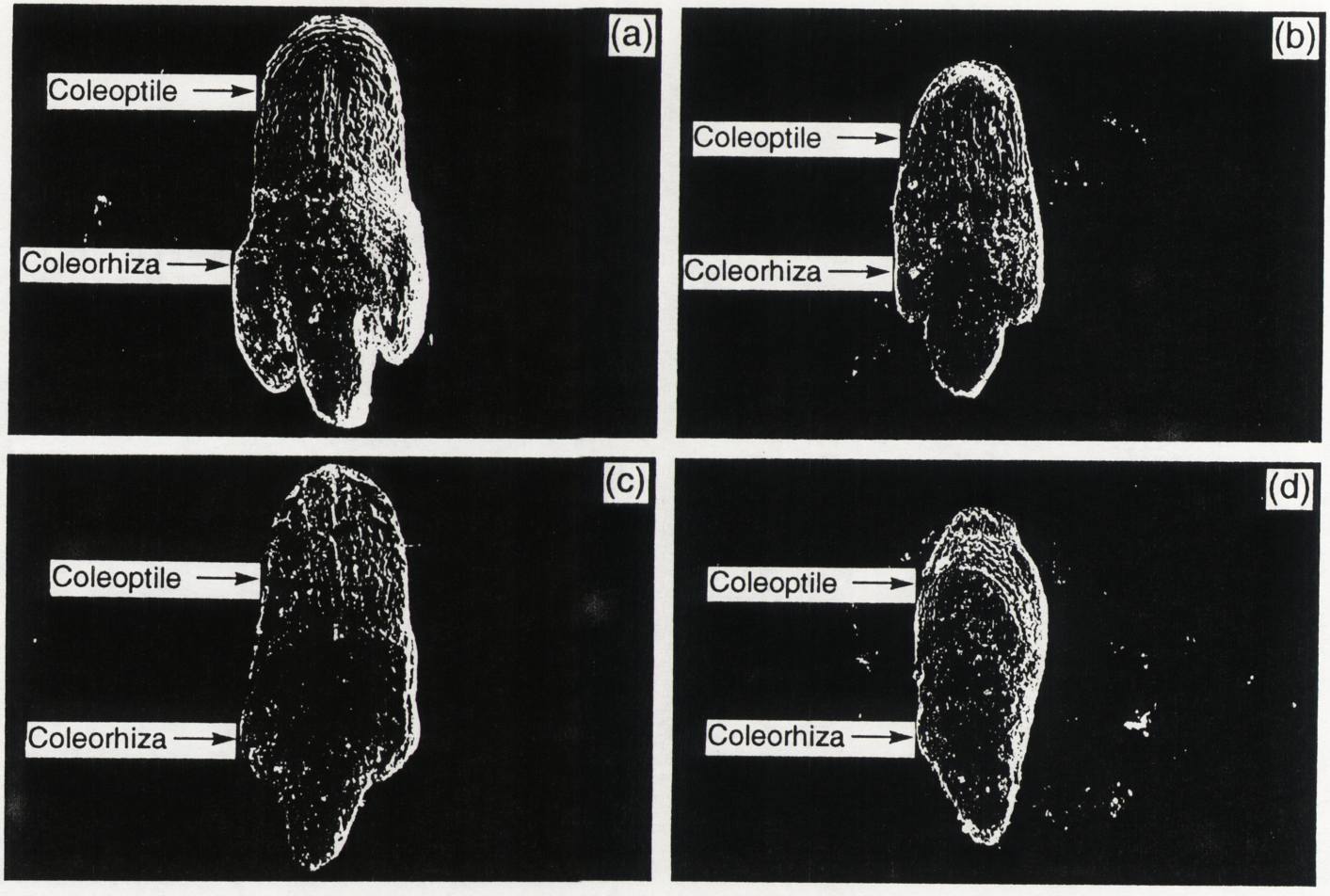


Fig. 7.2. Scanning electron micrographs of excised embryos from (a) barley, (b) bread wheat, (c) triticale and (d) oats. All seeds were the same weight (35 mg). Magnification x 35.

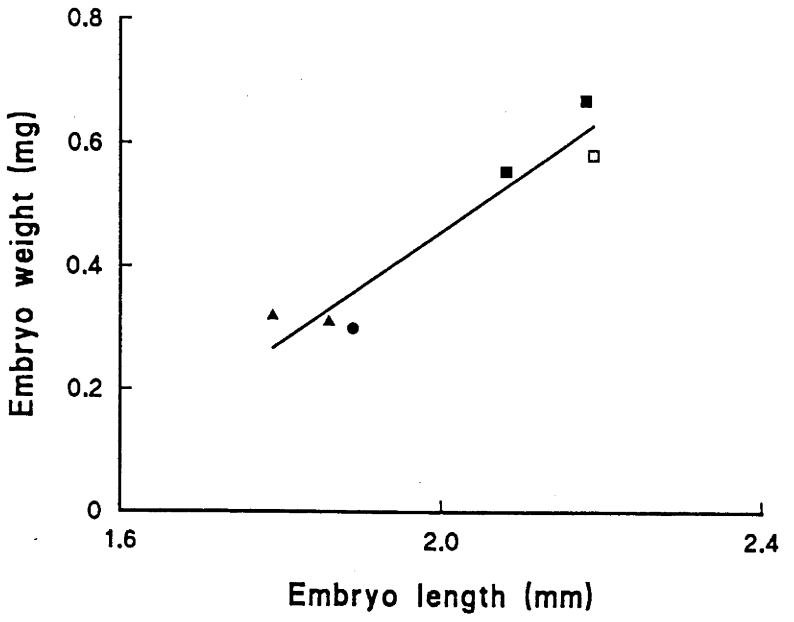


Fig. 7.3 Relationship between embryo length in intact seeds and weight of excised embryos for barley (■), bread wheat (▲), triticale (□) and oats (●). All seeds were the same weight (35 mg). Relationship between embryo length and embryo weight (W_e); W_e=0.91(mm)-1.36, (r = 0.96, P<0.01).

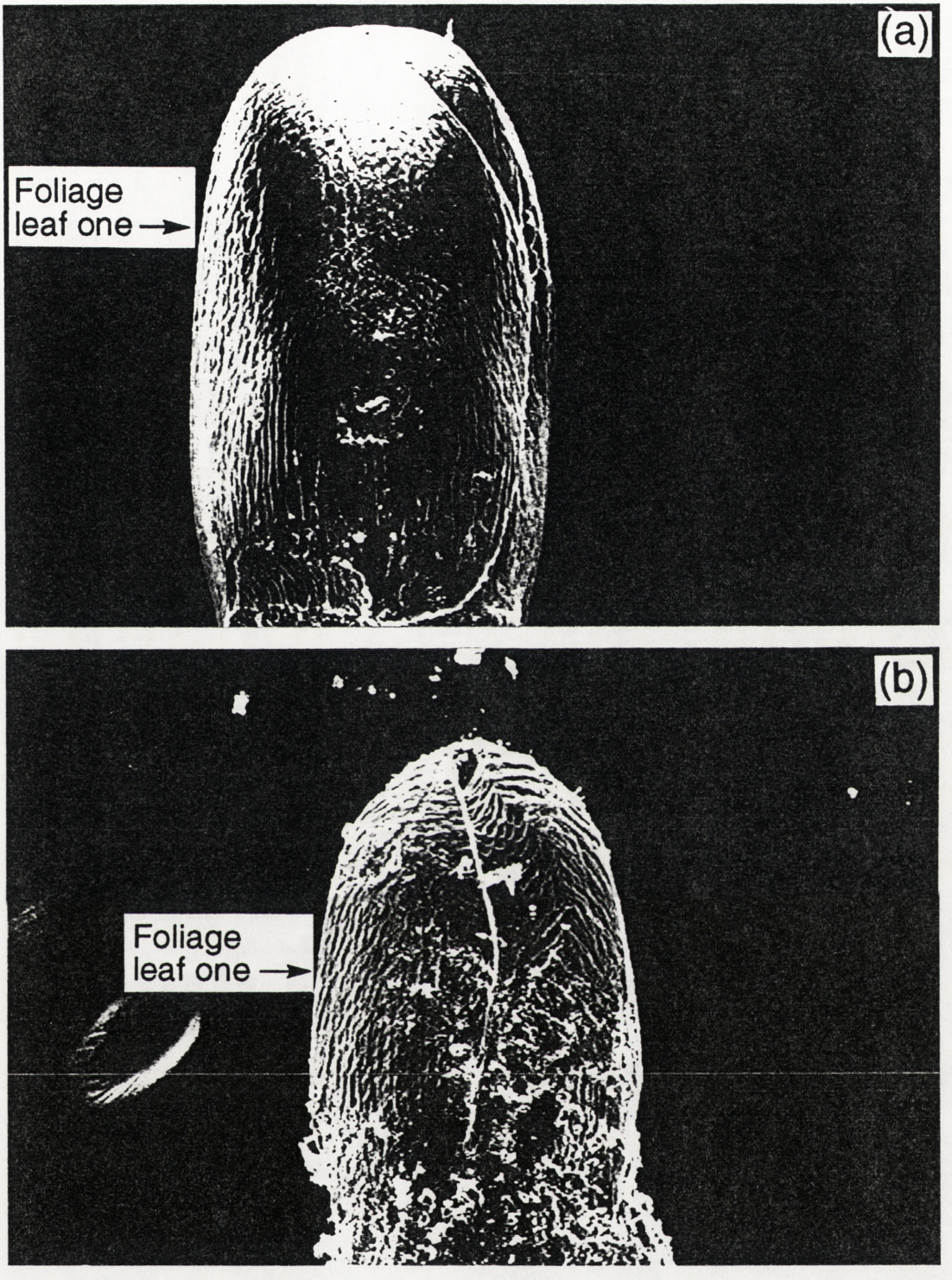


Fig. 7.4. Scanning electron micrographs of the first leaf in the embryo from (a) barley and (b) bread wheat. Both seeds were the same weight (35 mg). Magnification x 100.

Differences between genotypes in weight, length and width of embryo are given in Table 7.2. O'Connor and Meteor had the heaviest embryos in barley and bread wheat respectively. Variation between genotypes in length and width of embryo was smaller than differences in weight.

7.3.2 Variation in leaf epidermal characteristics

The length, width and area of leaves 1 and 2 that were used to examine epidermal cells are given in Table 7.3. The length of leaves of all species was generally similar although Currency triticale had longer leaves than the other genotypes. Most variation between genotypes was in leaf width and this accounted for most of variation in leaf area. Barley had the widest leaves, followed by oats, triticale and then wheat.

Variation in leaf width was mainly due to more rows of cells in barley and to more rows and wider cells in oats (Table 7.4). The cell dimensions of wheat and barley were generally similar. Oat epidermal cells, on the other hand, were significantly longer and wider than in the other species. Cell length in triticale was greater than in wheat and barley but width was the same. This variation in cell dimensions resulted in significant variation between species in cell number per unit area (Table 7.4). Total epidermal cell number on the adaxial surface of leaves 1 and 2 was greatest in barley and lowest in oats. Wheat and triticale had similar epidermal cell numbers per leaf. Differences in cell characteristics between genotypes within each species were significant but relatively small compared to the differences between species.

7.4 DISCUSSION

Results from earlier chapters predict that most of the variation in early vigour is attributed to embryo size. Fig. 7.5 shows the relationship between embryo weight and (a) root + shoot dry weight and (b) leaf area, in plants described in chapter 6. The significant positive relationship confirms the importance of embryo weight in determining early vigour; about 90% of variation in leaf area and plant weight was acounted for. Similar results have been reported before in maize (Ashby, 1930, 1932), tomato (Ashby, 1937), subterranean clover (Black, 1957) and carrot (Gray and Steckel, 1983). It was not found in wheat (Bremner *et al.*, 1963) where the embryo and endosperm of one genotype was varied by seed size and surgery.

Embryo size also varied with seed size as expected and there was evidence that the embryo mass may increase more in barley than in the other species as seed mass increases. Length and breadth of the intact embryo were determined to assess whether they may be closely related to embryo weight and could be used to screen large populations of plants for embryo size and hence vigour. Length was easier to measure than width and would be an effective alternative to weight in screening for a large embryo size. This will be discussed further in the following chapter.

Table 7.2 Mean weight (mg), length (mm) and width (mm) of embryos from seeds of 25 mg 35 mg and 50 mg weight for all genotypes.

Species	Weight	Length	Width
25 mg			
Barley			
Galleon	435	2.03	0.77
O'Connor	466	2.18	0.83
Ulandra	400	1.89	0.79
Malebo	411	2.05	0.77
Bread wheat			
Kulin	234	1.69	0.73
Meteor	236	1.76	0.75
Rosella	187	1.63	0.76
Triticale			
Dua	383	1.90	0.80
Oats			
Echidna	214	1.75	0.68
s.e.	14	0.05	0.02
35 mg			
Barley			
Galleon	647	2.08	0.94
O'Connor	670	2.18	0.86
Ulandra	555	2.08	0.76
Malebo	610	2.22	0.89
Bread wheat			
Kulin	319	1.79	0.77
Meteor	371	1.86	0.90
Rosella	310	1.81	0.80
Triticale			
Dua	582	2.19	0.83
Oats			
Echidna	300	1.89	0.73
s.e.	19	0.07	0.04

Cont.

Table 7.2 continued.

50 mg			
Barley			
Galleon	819	2.45	0.96
O'Connor	968	2.33	1.03
Ulandra	788	2.25	1.01
Malebo	864	2.51	0.97
Bread wheat			
Kulin	474	1.94	0.92
Meteor	577	2.13	0.97
Rosella	448	2.03	0.98
Triticale			
Dua	674	2.33	0.94
Oats			
Echidna	467	2.01	0.76
s.e.	27	0.10	0.07

Table 7.3. Dimensions of fully expanded main stem leaves 1 (L1) and 2 (L2).

Genotype	Length (cm)		Width (cm)		Area (cm^2)	
	L1	L2	L1	L2	L1	L2
Barley						
O'Connor	11.6	17.5	0.71	0.76	6.6	10.6
Ulandra	10.4	18.4	0.75	0.84	6.3	12.5
Malebo	11.6	20.2	0.75	0.86	6.9	13.9
Bread wheat						
Kulin	11.8	20.2	0.43	0.54	4.1	8.8
Rosella	12.3	17.7	0.44	0.56	3.9	7.9
Triticale						
Currency	15.1	22.4	0.43	0.61	5.2	11.0
Oats						
Echidna	12.1	19.8	0.63	0.77	6.1	12.2
s.e.	0.6	0.8	0.02	0.02	0.4	0.8

Table 7.4. Epidermal cell characteristics on adaxial surface of fully expanded leaves 1 (L1) and 2 (L2).

Genotype	Number of rows		Cell length (μm)		Cell width (μm)		Cell number per leaf x 10^3		Cell number cm^{-2}
	L1	L2	L1	L2	L1	L2	L1	L2	L1+L2*
Barley									
O'Connor	228	241	247	243	32	32	113	177	16.8
Ulandra	254	264	229	233	30	32	117	218	17.8
Malebo	239	262	254	256	32	33	114	213	15.7
Bread wheat									
Kulin	147	173	253	266	30	32	71	138	16.1
Rosella	135	161	267	244	33	35	61	121	15.5
Triticale									
Currency	131	176	311	320	33	35	74	142	13.3
Oats									
Echidna	161	193	387	444	39	41	58	105	8.9
s.e.	8	10	12	12	1	1	6	13	0.4

*Mean of leaves 1 and 2.

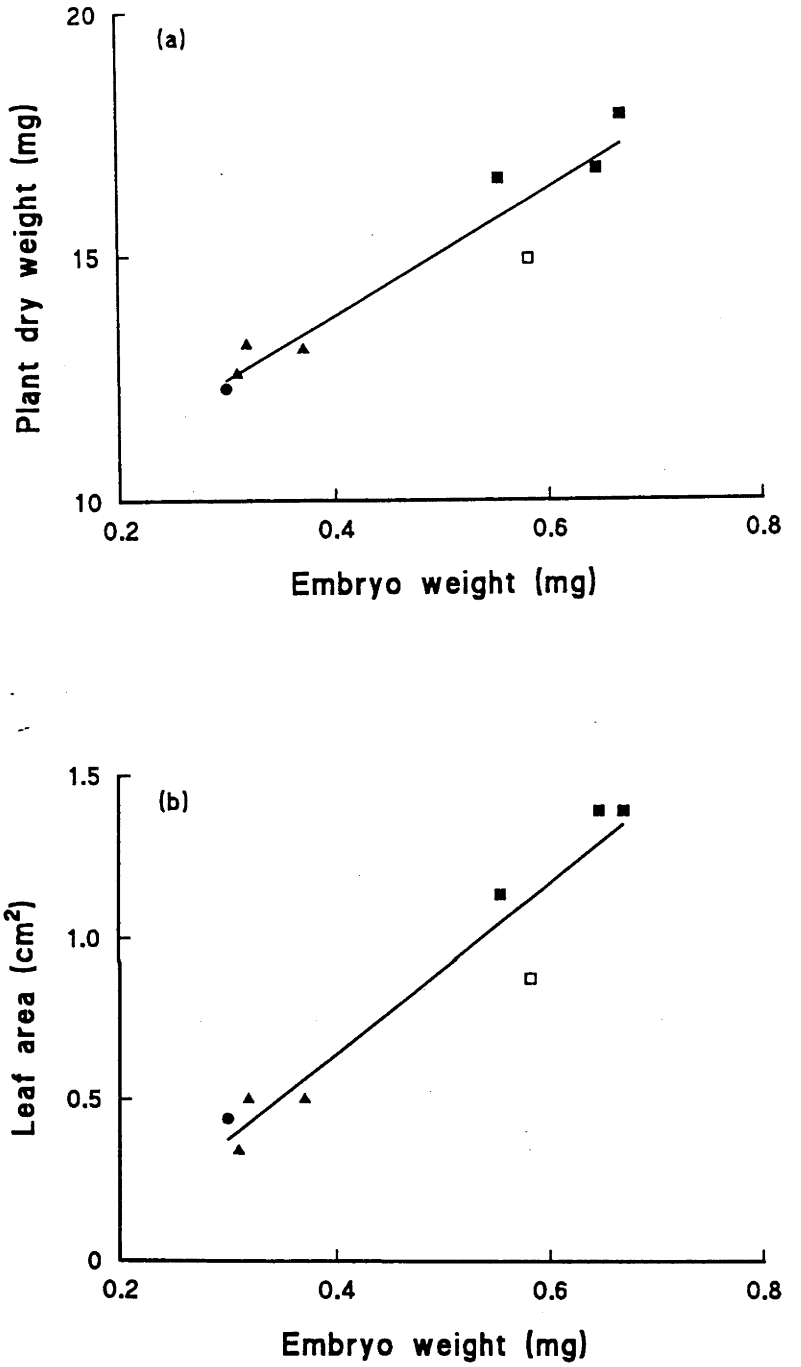


Fig. 7.5 Relationship between embryo weight and (a) plant dry weight including shoot and root, (b) leaf area, before leaf 1 had fully expanded for barley (■), bread wheat (▲), triticale (□) and oats (●). Plant weight and leaf area data at harvest 6 from experiment described in chapter 6. Relationship between:

embryo weight (W_e) and plant dry weight (W); $W=13.1(W_e)+8.6$ ($r = 0.96$, $P<0.01$).

embryo weight (W_e) and leaf area (LA); $LA=2.7(W_e)-0.42$ ($r = 0.96$, $P<0.01$).

Epidermal cell characteristics on the adaxial surface of the first and second main stem leaves were examined. This was firstly to provide an indirect measure of differences in cell number in the embryo, as most of the cells of the first leaf are already present in the embryo and secondly to examine whether there are differences in the arrangement of cells that may account for differences in leaf area. Cells in oats and triticale leaves were larger than in wheat and barley. These data on cell dimensions, when considered with the previous results showing that there are no differences in the relative growth rate of the shoot, indicates variation in the rate of cell division in leaves. As cell number per unit leaf area differs by a factor of two between the species (Table 7.4) presumably the rate of cell division in oats and triticale leaves is less than in wheat and barley and this is compensated for by a greater cell expansion. Embryo weight was associated with epidermal cell number on the adaxial leaf surface (Fig. 7.6); although triticale did not fit this relationship. One reason for triticale being different is that a different genotype was used to determine cell number (Currency) and embryo size (Dua). However, this is unlikely to be the main explanation as leaf size of Currency was large and matched with a large embryo size. Other reasons are: cell number on the adaxial surface is only a crude estimate of variation in cell number in leaves in the embryo, variation between abaxial and adaxial surface, mesophyll cells or cell volume in the embryo.

The arrangement of leaf cells clearly differed between genotypes. The number of rows of cells across the breadth of the leaf varied substantially among genotypes and this accounted for most of the variation in leaf width, which in turn was responsible for variation in the area of each fully expanded leaf. The meristematic zone is at the base of the cereal leaf and the number of rows of cells across the width of the leaf is one indicator of the size of the meristematic region. Clearly the meristematic zone in barley leaves is expected to be larger than it is in the other species. This is likely to be also true for the roots. More seminal axis are visible in the embryo of barley than in the other species and more axes initiate in barley. Thus if the seminal axes are of a similar size, the meristematic zone in the early formed roots is greater in barley then in the other species.

7.5 CONCLUSIONS

Variation in embryo weight accounted for about 90% of variation in plant dry weight and leaf area when seeds of the same weight were compared. The area of the first formed leaves was generally associated with the number of rows of cells across the breadth of the leaf and hence the size of the meristematic zone. Cell dimensions were larger in oats and triticale than in the other species.

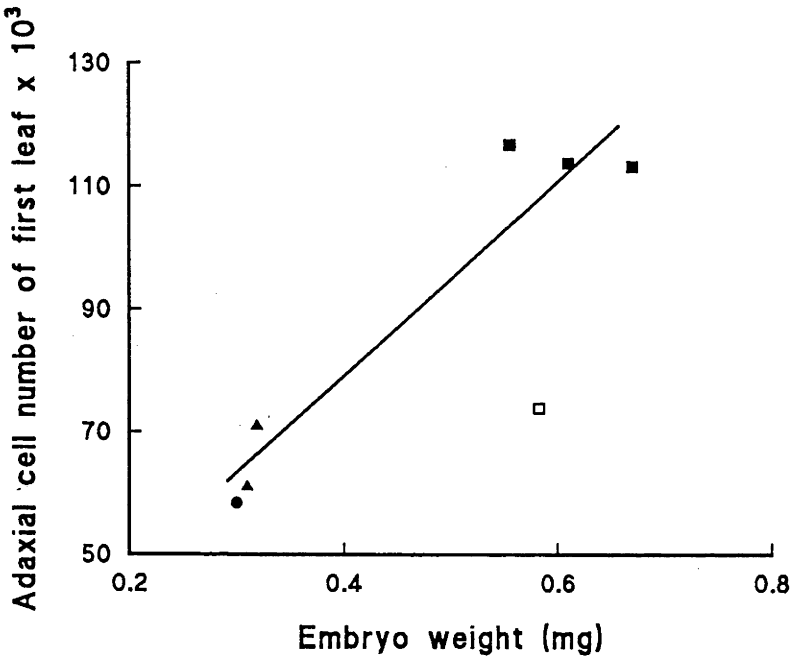


Fig 7.6 Relationship between embryo weight and adaxial cell number of first fully expanded leaf for barley (■), bread wheat (▲), and oats (●). Relationship between embryo weight (W_e) and adaxial cell number of first leaf (ACNFL); ACNFL=160.9(W_e)+14.9 (r = 0.96, P<0.01).

CHAPTER 8

GENERAL DISCUSSION

8.1 INTRODUCTION

Plant breeders are facing increasing pressures to improve yields in all cropping zones. This challenge is probably greatest in the drier regions because yields of temperate cereals growing in rainfed areas are increasing at only about half the rate that they are in wetter areas. At the same time opportunities to genetically modify crops in these regions are becoming increasingly more difficult. For example, in wheat at least, there is no evidence that biomass has increased despite intensive plant breeding efforts over the last century. All of the increase in yield has occurred because of the increase in harvest index (HI). As the limits to harvest index approach the increase in HI will taper off and the challenge to increase the more formidable component of yield, above-ground dry matter (AGDW), will increase.

The aim of the work presented in this thesis was to contrast the growth and yield of bread wheat, the most important single grain crop around the world, with other temperate cereals namely, durum wheat, triticale, oats and barley. Each of these cereals have been highly bred for maximum grain yield or biomass yield. These species were contrasted to determine whether they may yield or grow better than bread wheat, or each other, so as to determine whether attributes possessed by one may be approriate for the other in dry areas. No previous study is known where the growth and yield of these different species have been contrasted in the same conditions.

The emphasis in this study was placed on contrasting the growth of leaf area and weight in rainfed Mediterranean-type environments. These environments are such that the crop is sown in late autumn, at a time when rainfall is common, but then diminishes as evapotranspiration begins to increase and the crop begins reproductive development. Anthesis and grain filling is generally at a time when the effects of drought become chronic and irreversible.

Emphasis was placed on the development of leaf area rather than on water relations of the crop as there is increasing evidence that this is by far the most important determinant of yield in dry environments. The development of leaf area is deemed important as firstly, water use is a function of leaf area, and secondly, a leaf canopy may be important to shade the soil thereby conserving water that may otherwise be lost by soil evaporation. Furthermore, there is growing evidence that plants have an early warning system whereby they can sense deteriorating soil moisture conditions and slow their leaf area development (Passioura, 1988).

8.2 EXPERIMENTAL

Cultivars of bread wheat, durum wheat, triticale, oats and barley that were well adapted to rainfed areas in south-eastern Australia, were chosen for study. They represent genotypes with a range in maturity time common among commercial cultivars grown in this region. Most were bred for their high grain yield whereas others were bred for both grazing and grain, or just for hay production, in the case of an oat genotype.

Genotypes were grown at two sites in south-eastern Australia in three years. Aspects of their growth and water use were monitored as well as their phenology. To assess the important characteristics that may contribute to yield under drought, an extension of the identity proposed by Passioura (1977) was followed. This is:

$$Y = E_T \times T/E_T \times TE \times HI$$

where Y is grain yield, E_T is evapotranspiration, T is transpiration from the crop, TE is the transpiration efficiency and HI the harvest index.

The same genotypes were also grown in more precise conditions in pots either outside, in the glasshouse, or in controlled environment cabinets.

8.3 RESULTS AND DISCUSSION

The yield of barley was 25% greater than the other species when averaged over all environments. The yield advantage of barley was even more pronounced when the best yielding barley was contrasted with the best yielding wheat, triticale or oats. Some of this advantage was attributed to the husk. However, even after correction for husk weight the yield of barley was still substantially greater than the other species. Most of this yield advantage was due to a higher AGDW than to a higher HI. The ranking in AGDW was barley > triticale > bread wheat > oats > durum wheat. If root biomass is also included, the advantage in barley is even more marked as barley had an estimated 35% greater root length and mass than the other species. Most of this root mass was in the top 15 cm of soil although differences down to 90 cm were found. A remarkable feature of the higher biomass in barley, compared to the other species, was that it was achieved in a shorter time. Thus instead of differences in biomass between genotypes being confounded by differences in crop duration (Waddington *et al.* 1987), in this study the highest biomass was achieved by the shortest duration cultivars. In general, earlier flowering lines reached double ridge earlier, flowered earlier and physiological maturity was also earlier.

For the improvement of durum wheat, oats and bread wheat the results presented here are very encouraging as evidence in historic sets of these species have indicated little change in AGDW (Austin *et al.* 1980; Wych and Stuthman, 1983; Waddington *et al.* 1986; 1987; Perry and D'Antuono, 1989). Here, for species sown at the same time under identical circumstances, quite substantial differences in AGDW were found. This

gives promise that an understanding of how these differences arise may highlight ways to increase AGDW and grain yield in the different species.

Although HI was not a major contributor to the yield differences between the species, several important differences were found between genotypes in factors influencing HI. These were grain growth and the retranslocation of assimilates from the stem to the grain. The rate of grain growth per unit ground area in barley was 60% higher than in the other species. Bread wheat, triticale and oats were similar and grain growth was about 30% higher than in durum wheat. Although greater grain growth in barley did not translate into a higher HI, as the duration of growth was shorter, it demonstrated the potential that is possible providing the right conditions are maintained. The loss in stem wheat between anthesis and physiological maturity was used to estimate retranslocation of assimilate from the stem. This averaged 25% at each of two sites, a value similar to that reported by Bidinger *et al.* (1977). However, the variation among genotypes was substantial, ranging from 3% to 60%. This last value is similar to values found in droughted wheats in large pot experiments by Richards and Townley-Smith (1987). The ranking among cultivars from site to site was consistent and at the driest site the loss of dry matter from stems was positively associated with grain yield. The late maturing cultivars lost less dry matter from stems than earlier flowering cultivars.

From the identity above, differences in AGDW must arise in one or more of the follow ways:

(i) a higher E_T by more extraction of water from the soil by roots,

(ii) a higher proportion of T/E_T, which could arise if soil evaporation was less and plants used this water saving for transpiration,

(iii) a higher TE, which could arise either by a lower ratio of P_i/P_a at the leaf level or more growth when e_i-e_a is low, as it is when temperate cereal crops are grown in winter. Other factors that may also be important in accounting for variation in TE, but were not measured, were respiration and residual transpiration.

In all experiments where soil water use was monitored the differences in E_T or soil water extraction between species were not great. In fact the early flowering barleys extracted less water than the later flowering varieties. It was found that for each days delay in flowering an extra 1 mm of water was extracted. This was similar to results reported by Siddique *et al.* (1990b). It was also found that root mass was not related to soil water extraction as O'Connor barley, which extracted the least amount of water, had among the largest root mass. Thus a greater soil water extraction cannot account for the improved yields.

Despite a slightly lower E_T in barley, T was generally greater and T/E_T sustantially greater in barley than in the other species. This was achieved because of the greater and faster canopy cover in barley than in the other species and was observed in

all field experiments. In addition to the faster leaf area growth, and partly as a result of it, the growth during the cooler months was also greater in barley than in the other species. This greater growth of barley is at a time when e_i-e_a is low and growth is most efficient (Sinclair *et al.* 1983; Richards, 1991). To determine the contribution of the greater transpiration and growth when it is cool, tranpiration during different time intervals was normalised for vapour pressure deficit (VPD) during the same intervals (Sinclair *et al.* 1983; Hubick and Farquhar 1989). This indicated that transpiration per unit ground area in barley was effectively 26% greater than the other species because of the greater transpiration when it is cool. Flowering time again proved important in accounting for the variation in TE and water use efficiency (WUE). The WUE_{AGDW} declined by 0.67 kg ha^{-1} mm^{-1} for each days delay in flowering whereas TE declined by 0.95 kg ha^{-1} mm^{-1} for each days delay in flowering. The importance of flowering time in determining variation in yield in other Mediterranean environments has also been found by Siddique *et al.* (1990b) and Craufurd *et al.* (1991).

To determine whether differences in P_i/P_a may also account for differences in transpiration efficiency, carbon isotope discrimination (Δ) was also measured (Farquhar *et al.* 1982). Whereas a negative relationship between Δ and TE was expected, a positive relationship was observed. This has also been noted in cereals grown in the field (Condon *et al.* 1987, Craufurd *et al.* 1990; Ehdaie *et al.* 1991). Taking root mass into account did not alter the relationship. Normalising transpiration by correcting it for the change in VPD throughout the season changed the relation between Δ and TE from a positive association to one where there was no relationship. This suggests that other, unknown, factors are important in the relationship between Δ and transpiration efficiency that negates the expected negative relationship. One such factor could be due to scaling up to crop canopies in the field, as boundary layer conductances to water vapour are very much lower for field grown plants than for isolated plants and hence canopy gas exchange is less dependent on differences in stomatal conductance (Cowan and Troughton, 1971; Jarvis and McNaughton, 1986; Cowan, 1988). Another explanation may be that genotypes with low Δ have a higher respiratory loss than genotypes with a high Δ. It is also possible that the time of measurement of Δ prevented a true assessment of the relationship between Δ and transpiration efficiency in the field. Values of Δ were determined at maturity in field grown plants. The stem base was chosen as this represented carbon laid down as early in the life of the plant as is possible from a harvest at maturity. In view of the earlier flowering in barley and the relationship between Δ and flowering time, the Δ value from these stem bases may have been lower in the later flowering genotypes because of the time the stem base material formed. This may also have contributed to the lack of relationship between Δ and TE.

The field experiments established the superiority of barley compared to the other species and its greater water use efficiency, due to its greater growth during the cool winter months and greater canopy development which reduced soil evaporation. The

question then to resolve is what contributes to the variation in early growth? It was not possible to determine this in the field and so experiments were conducted in pots in more precise conditions.

Results in pots were similar to those in the field in that early leaf area of barley was about 2-fold greater than wheat and that differences in dry weight were about 40% greater in barley than in wheat. In these experiments the seeds sown all had the same weight. No differences in relative growth rates were detected in any of the experiments contrasting the different species. Considerable variation was found in parameters that may, initially at least, seem important in determining differences in leaf area development (Whan *et al.* 1990; Acevedo *et al.* 1991). Thus, barley had a faster leaf appearance rate and tiller appearance rate but these did not account for the differences between species.

Another factor proposed to account for the differences in growth during winter was that the base temperature may be lower in barley than in the other species, allowing more growth when it is cool. No evidence was found for this and in fact growth at low temperatures tended to be less in barley than the other species. This finding supports that of Russelle and Bolton (1980).

Evidence from these experiments pointed to several factors that may account for differences in growth. These were a faster emergence from the soil, a faster utilisation of seed reserves, a faster beginning of autotrophic growth and/or to a larger embryo and hence starting capital. Although barley emerged about 10 °C d^{-1} before the other species the larger embryo was found to be the main factor responsible for the variation in early growth. The embryo size of barley was larger than triticale which in turn was substantially larger than both wheat and oats. This finding contrasts with that of Bremner *et al.* (1983),who noted that the endosperm was more important than the embryo in the early growth of a single variety of wheat. However, the results of Ashby (1930; 1932; 1937) in maize and tomato, and of Black (1957) in clover, all show the importance of embryo size in determining variation in early growth rather than differences in relative growth rates.

Another feature of barley that was important in its early leaf area growth was its higher leaf area relative to leaf weight i.e. specific leaf area. Although this resulted in barley having a lower net assimilation rate compared to wheat, its greater leaf area more than compensated for this reduction in net assimilation rate. With time, the specific leaf area of wheat converged towards barley. A notable difference in leaf structure between barley and the other species was that the leaf width of barley was greater, although oats were similar to barley. Barley and oats had more rows of cells across the width of the leaf and hence a wider meristematic zone at the base of the leaf. Thus the absolute leaf expansion rate of barley must be greater than wheat and triticale and this may be related to its higher specific leaf area.

Carbon isotope discrimination was positively correlated with specific leaf area

which in turn was correlated with leaf area. This was not unexpected as plants with a high SLA presumably also have less photosynthetic machinery per unit leaf area and hence a lower assimilation rate per unit leaf area. The association between Δ and SLA may partly account for the positive relationship between Δ and AGDW observed in field grown plants when it is wet (Condon *et al.* 1987). A similar relation between Δ and SLA has been noted in peanuts (Wright *et al.* 1988), although in this case no negative relationship with early growth was observed.

8.4 CONCLUSIONS

This study has identified several opportunities to improve the early canopy development and greater early growth of temperate cereals. The advantage in barley and to a lesser extent in triticale, is that it begins with a larger embryo and starting capital which, in the absence of differences in relative growth rate, results in a substantially larger plant at all times whilst water is available. Other advantages in barley were that its early formed leaves have a high SLA and hence for the same weight of leaf, a greater leaf area. Barley also germinates first.

Selection to improve the vigour of temperate cereals could firstly be based on embryo weight or size. However, selection for embryo weight is unrealistic as it was found that selection for *in situ* embryo length and width is unlikely to be effective as small differences among genotypes are unlikely to be detected. Instead it is suggested that the area of the first leaf would be the most effective selection criterion for faster early growth. This would integrate the two important components of vigour *viz*: size of the embryo and specific leaf area. It could be easily done as it requires only a ruler or a leaf area machine. It is also appealing as the measurement is non destructive to the plant and can be conducted at a very early stage of plant development. It therefore satisfies several of the requirements for a selection criterion: i.e. it is fast, cheap, non-destructive and the same plant can be used as the unit of selection or for hybridisation. Information is now required on the genetic control and heritability of this trait and whether genotype x environment interactions may be important.

Thus for temperate cereals growing in mediterranean-type environments the opportunities to increase yield would seem to be very good. Genetic improvement in early canopy development, that would result in less evaporation from the soil surface and more transpiration, as well as greater growth when VPD is lowest and hence growth is cheapest, would seem a very promising avenue to pursue.

REFERENCES

Acevedo, E., Perez-Marco, P. and van Oosterom, E., 1990. Physiology of yield of wheat and barley in stressed environments. *In:* Proc. Intern. Congress Plant Physiology. New Delhi, India, February 15-20, 1988. Society for Plant Physiology and Biochemistry (Eds. S.K. Sinha, P.V. Sane, S.C. Bhargava and P.K. Agrawal). pp. 117-126.

Acevedo, E., Craufurd, P.O., Austin, R.B. and Perez-Marco, P., 1991. Traits associated with high yield in barley in low-rainfall environments. J. Agric. Sci. Camb., 116: 23-36.

Aggarwal, P.P., Singh, A.K., Chaturvedi, G.S. and Sinha, S.K., 1986. Performance of wheat and triticale cultivars in a variable soil-water environment. II. Envapotranspiration, water use efficiency, harvest index and grain yield. Field Crops Res., 13: 301-315.

Allen, S.J., 1990. Measurement and estimation of evaporation from soil under sparse barley crops in northern Syria. Agric. For. Meteorol., 49: 291-309.

Alvarado, A.D., Bradford, K.J. and Hewitt, J.D., 1987. Osmotic priming of tomato seeds: effects of germination, field emergence, seedling growth and fruit yield. J.Amer. Soc. Hort. Sci., 112: 427-432.

Anderson, W.K., 1985. Grain yield responses of barley and durum wheat to split nitrogen application under rainfed conditions in a Mediterranean environment. Field Crops Res., 12: 191-202.

Ashby, E., 1930. Studies in the inheritance of physiological characters. I. A physiological investigation of the nature of hybrid vigour in maize. Ann.Bot., 44: 457-467.

Ashby, E., 1932. Studies in the inheritance of physiological characters. II. Further experiments upon the basis of hybrid vigour and upon the inheritance of efficiency index and respiration rate in maize. Ann Bot., 46: 1007-1032.

Ashby, E., 1937. Studies in the inheritance of physiological characters. III. Hybrid vigour in the tomato. Part 1. Manifestations of hybrid vigour from germination to the onset of flowering. Ann Bot., N.S. 1: 11-41.

Austin, R.B., Bingham, J., Blackwell, R.D., Evans, L.T., Ford, M.A., Morgan, C.L. and Taylor, M., 1980. Genetic improvement in winter wheat yields since 1900 and associated physiological changes. J. Agric. Sci. Camb., 94: 675-689.

Australian Wheat Board, 1989. Wheat Industry. *In:* Australian agriculture: the complete reference on rural industry. Ed. Julian Cribb, Vol. 2 . Camberwell, Victoria. Australia. pp. 247-264.

Bidinger, F., Musgrave, R.B. and Fischer, R.A., 1977. Contribution of stored pre-anthesis assimilate to grain yield in wheat and barley. Nature, 270: 431-433.

Black, J.N., 1957. The early vegetative growth of three strains of subterranean clover (*Trifoliun subterranean* L.) in relation to size of seed. Aust. J. Agric. Res., 8: 1-14.

Black, T.A., Tanner, C.B. and Gardner, W.R., 1970. Evaporation from a snap bean crop. Agron. J., 62: 66-69.

Blackman, V.H., 1919. The compound interest law and plant growth. Ann. Bot., 67: 137-144.

Blum, A., Poiarkova, H., Golan, G. and Mayer, J., 1983. Chemical desiccation of wheat plants as a simulator of post-anthesis stress. I. Effects on translocation and kernel growth. Field Crops Res., 6: 51-58.

Blum, A., 1985. Photosynthesis and transpiration in leaves and ears of wheat and barley varieties. J. Exp. Bot., 36: 432-440.

Boesten, J.J.T.I. and Stroosnijder, L., 1986. Simple model for daily evaporation from fallow tilled soil under spring conditions in a temperate climate. Neth. J. Agric. Sci., 34: 75-90.

Bolt, C., 1989. Coarse grains industry. *In:* Australian agriculture: The complete reference on rural industry. Ed. Julian Cribb, Vol.2. Camberwell, Victoria, Australia. pp. 265-277.

Bradbury, D., Cull, I.M. and McMasters, M.M., 1956. Structure of the mature wheat kernel. I. Gross anatomy and relationships of the parts. Cereal Chem., 33: 329-342.

Bremner, P.M., Eckersall, R.N. and Scott, R.K., 1963. The relative importance of embryo size and endosperm size in causing the effects associated with seed sizein wheat. J. Agric. Sci., 61: 139-145.

Cao, W. and Moss, D.N., 1989. Temperature effect on leaf emergence and phyllochron in wheat and barley. Crop Sci., 29: 1018-1021.

Cao, W. and Moss, D.N., 1989a. Daylength effect on leaf emergence and phyllochron in wheat and barley. Crop Sci., 29: 1021-1025.

Castles, I., 1991. Agricultural industries. *In:* Year book Australia. Ed. by The Australian Bureau of Ststistics, Canberra. ASS Catalogue No. 1301.0 pp. 396-400.

CIMMYT, 1989. CIMMYT world wheat facts and trends 1987-1988. The wheat revolution revisited: Recent trends and future challenges. CIMMYT, Mexico, 1989. 57p.

Clarke, J.M. and Richards, R.A., 1988. The effects of glaucousness, epicuticular wax, leaf age, plant height and growth environment on water loss rates of excised wheat leaves. Can. J. Plant Sci., 68: 975-982.

Condon, A.G., Richards, R.A. and Farquhar, G.D., 1987. Carbon isotope discrimination is positively correlated with grain yield and dry matter production in field grown wheat. Crop Sci., 27: 996-1001.

Condon, A.G., Farquhar, G.D. and Richards, R.A., 1990. Genotypic variation in carbon isotope discrimination and transpiration efficiency in wheat. Leaf gas exchange and whole plant studies. Aust. J. Plant Phsiol., 17: 9-22.

Condon, A.G. and Richards, R.A., 1992. Broad-sense heritability and genotype x environment interaction for carbon isotope discrimination in field-grown wheat. Aust. J. Agric. Res., (In Press).

Condon, A.G., Richards, R.A. and Farquhar, G.D., 1992. The effect of variation in soil water availability, vapour pressure deficit and nitrogen nutrition on carbon isotope discrimination. Aust. J. Agric. Res., (In Press).

Connor, D.J., 1975. Growth, water relations and yield of wheat. Aust. J. Plant Physiol., 2: 353-366.

Cooper, J.P.M., Keatinge, J.D.H. and Hughes, G., 1983. Crop evapotranspiration : A technique for calculation of its components by field measurements. Field Crops Res., 7: 299-312.

Cowan, I.R. and Troughton, J.H., 1971. The relative role of stomata in transpiration and assimilation. Planta, 97: 325-336.

Cowan, I.R., 1988. Stomatal physiology and gas exchange in the field. *In:* Flow and transport in the natural environment: Advances and applications. Eds. W.L. Steffen and O.T.Denmead. Springer-Verlag Publishers, Berlin, 1988. pp. 160-172.

Craufurd, P.Q., Austin, R.B., Acevedo, E. and Hall, M.A., 1991. Carbon isotope discrimination and grain yield in barley. Field Crops Res., 27: 301-313.

Doyle, A.D. and Fischer, R.A., 1979. Dry matter accumulation and water use relationships in wheat crops. Aust. J. Agric. Res., 30: 815-829.

Dunin, F.X. and Reyenga, W., 1978. Evaporation from a themeda grassland. I. Controls imposed on the process in a sub-humid environment. J. Appl. Ecol., 15: 317-325.

Ehdaie, B., Hall, A.E., Farquhar, G.D., Nguyen, H.T. and Waines, J.G., 1991. Water-use efficiency and carbon isotope discrimination in wheat. Crop Sci., 31: 1282-1288.

Farquhar, G.D., O'Leary, M.H. and Berry, J.A., 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Aust. J. Plant Physiol., 9: 121-137.

Farquhar, G.D. and Richards, R,A., 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. Aust. J. Plant Physiol., 11: 539-552.

Fischer, R.A. and Kohn, G.D., 1966. The relationship between evapotranspiration and growth in the wheat crop. Aust. J. Agric. Res., 17: 255-267.

Fischer, R.A. and Maurer, R., 1978. Drought resistance in spring wheat cultivars. Grain yield responses. Aust.J. Plant Physiol., 29: 897-912.

Fischer, R.A. and Wood, J.T., 1979. Drought resistance in spring wheat cultivars. III. Yield associations with morpho-physiological traits. Aust. J. Agric. Res., 30: 1001-1020.

Fisher, R.A., 1920. Some remarks on the methods formulated in a recent article on 'The quantitative analysis of plant growth'. Ann. Appl. Biol., 7: 367-372.

Fischer, R.A., 1981. Optimizing the use of water and nitrogen throught breeding of crops. Plant and Soil, 58: 249-278.

Fischer, R.A., 1989. Cropping systems for greater drought resistance. *In:* Drought resistance in cereals. Ed. by F.W. Baker. C.A.B. International, U.K. pp. 201-211.

Ford, M.A., Austin, R.B., Gregory, R.S. and Morgan, C.L., 1984. A comparison of the grain and biomass yields of winter wheat, rye and triticale. J. Agric. Sci. Camb., 103: 395-403.

Gales, K., Ayling, S.M. and Cannell, R.Q., 1984. Effects of waterlogging and drought in winter wheat and winter barley grown on a clay and sandy loam soil. Plant and Soil, 80: 67-78.

Gallagher, J.N., Biscoe, P.V. and Scott, R.K., 1976a. Barley and its environment. IV. Growth and development in relation to yield. J. Appl. Ecol., 13: 563-583.

Gallagher, J.N., Biscoe, P.V. and Hunter, B., 1976b. Effects of drought on grain growth. Nature, 264: 541-542.

Gallagher, J.N. and Biscoe, P.V., 1978. Radiation absorption, growth and yield of cereals. J. Agric. Sci. Camb., 91: 47-60.

Gifford, R.M. 1986. Partitioning of photoassimilate in the development of crop yield. *In:* Phloem transport. Alan R. Liss, Inc., pp. 535-549.

Gleeson, A.C. and Cullis, B.R., 1987. Residual maximum likehood (REML) estimation of a neighbour model for field experiments. Biometrics, 43: 277-288.

Gray, D. and Steckel, J.R.A., 1983. Some effects of umbel order and harvest date on carrot seed variability and seedling performance. J. Hort. Sci., 58: 73-82.

Gregory, P.J., 1988. Root growth of chickpea, faba bean, lentil, and pea and effects of water and salt stresses. *In:* World Crops: Cool Season Food Legumes. Ed. by R.J.Summerfield. Kluwer Academic Publishers. pp. 857-867.

Hadjichristodoulou, A., 1984. Performance of triticale in comparison with barley and wheat in a semi-arid Mediterranean region. Expl. Agric., 20: 41-51.

Hadjichristodoulou, A., 1987. The effects of optimum heading date and its stability on yield and consistency of performance of barley and durum wheat in dry areas. J. Agric. Sci. Camb., 108: 599-608.

Hamblin, A. and Tennant, D., 1987. Root length density and water uptake in cereals and grain legumes: how well are they correlated ? Aust. J. Agric. Res., 38: 513-527.

Hamblin, A.P., Tennant, D. and Perry, M.W., 1990. The cost of living in stressful environments: Dry matter partitioning with changes in seasonal supply of water and nitrogen to dryland wheat. Plant and Soil, 122: 47-58.

Hardham, A.R. and Gunning, B.E.S., 1978. Structure of cortical microtubule arrays in plant cells. J. Cell. Biol., 77: 14-34.

Hubick, K.T., Farquhar, G.D. and Shorter, R., 1986. Correlation between water-use efficiency and carbon isotope discrimination in diverse peanut *(Arachis)* germplasm. Aust. J. Plant Physiol., 13: 803-816.

Hubick, K.T. and Farquhar, G.D., 1989. Carbon isotope discrimination and the ratio of carbon gained to water lost in barley cultivars. Plant, Cell and Environment. 12: 795-804.

Hunt, R., 1982. Plant growth curves. Edward Arnold (Publishers) Limited. pp. 248.

ICARDA, 1986. Cereal improvements program. Annual Report 1986. ICARDA. Aleppo, Syria. pp. 229.

Jarvis, P.G. and McNaughton, K.G., 1986. Stomatal control of transpiration: scaling up from leaf to region. Adv. Ecol. Res., 15: 1-49.

Johnson, R.R., Frey, N.M. and Moss, D.N., 1974. Effect of water stress on photosynthesis and transpiration of flag leaves and spikes of barley and wheat. Crop Sci., 14: 728-731.

Kirby, E.J.M. and Appleyard, M., 1984. Cereal development guide. Arable Unit, National Agricultural Centre, Stoneleigh, Kenilworth, Warwickshire CV82LZ, England, pp. 95.

Kirby, E.J.M., Appleyard, M. and Fellowes, G., 1985. Effect of sowing date and variety on main shoot leaf emergence and number of leaves of barley and wheat. Agronomie, 5: 117-126.

Klepper, B., Belford, R.K. and Rickman, R.W., 1984. Root and shoot development in winter wheat. Agron. J., 76: 117-122.

Lang, C.A., 1958. Simple microdetermination of Kjeldhl nitrogen in biological materials. Anal. Chem., 30: 1692-1694.

Lersten, N.R., 1987. Morphology and anatomy of the wheat plant. *In:* Wheat and wheat improvements - Agromony monograph no. 13. (2nd Ed.). U.S.A. p.33-75.

Lill, W.J., Gleeson, A.C. and Cullis, B.R., 1988. Relative accuracy of a neighbour method for field trials. J. Agric. Sci. Camb., 111: 339-346.

Loss, S.E., Kirby, E.J.M., Siddique, K.H.M. and Perry, M.W., 1989. Grain growth and development of old and modern Australian wheats. Field Crops Res., 21: 131-146.

Ludlow, M.M. and Muchow, R.C., 1988. Critical evaluation of the possibilities for modifying crops for high production per unit of precipitation. *In:* Drought research priorities for the dryland tropics. Ed. by F.R. Bidinger and C. Johansen. ICRISAT, Patancheru, India. pp. 179-211.

Lukaszeuwski, A.J. and Gustafson, J.P., 1987. Cytogenetics of triticale. Plant Breed. Reviews, 5: 41-93.

Matheson, E.M., 1975. Exploration and explotation of genetic variation. *In:* Australian field crops. Vol.1. Wheat and other temperate cereals. Ed. by A.Lazenby and E. Matheson. Angus and Robertson Publishers. Sydney, Australia. pp. 153-182.

Masle, J. and Farquhar, G.D., 1988. Effects of soil strength on the relation of water-use efficiency and growth to carbon isotope discrimination in wheat seedlings. Plant Physiol., 86: 32-38.

Masle, J., Doussinault, G., Farquhar, G.D. and Sun, B., 1989. Foliar stage in wheat correlates better to photothermal time than to thermal time. Plant, Cell and Environment. 12: 235-247.

Moncur, M.W., 1981. Floral initiation in field crops: An atlas of scanning electron micrographs. Division of Land Use Research, C.S.I.R.O., Canberra, A.C.T. pp. 135.

Nilan, R.A. 1964. The cytology and genetics of barley 1951-1962. Monographic Supplement No. 3, Research Studies, Washington State Uni., Vol 32, No. 1.

Passioura, J.B., 1977. Grain yield, harvest index and water use of wheat. J. Aust. Inst. Agric. Sci., Sept.-Dec. 1977. 43: 117-120.

Passioura, J.B., 1988. Root signals control leaf expansion in wheat seedlings growing in drying soil. Aust. J. Plant Physiol., 15: 687-693.

Perry, M.W., 1987. Water-use efficiency of non-irrigated field crops. Proc. of the 4th Aust. Agron. Conference. La Trobe Uni., Melbourne, Victoria. August 1987. Aust. Society of Agronomy., pp. 83-99.

Perry, M.W. and D'Antuono, M.F., 1989. Yield improvement and associated characteristics of some Australian spring wheats introduced between 1860 and 1982. Aust. J. Agric. Res., 40: 458-472.

Perry, M. and Hillman, B., 1991. The wheat book. Dept. of Agric. Western Australia. Bulletin 4196. pp. 182.

Poelhman, J.M., 1987. Breeding field crops. AVI Publishing Company, Inc. Westport, Connecticut, U.S.A. pp. 724.

Poorter, H. and Lewis, C., 1986. Testing differences in relative growth rate: A method avoiding curve fitting and pairing. Physiol. Plant., 67: 223-226.

Porter, H.K., Pal, N. and Martin, R.V., 1950. Physiological studies of plant nutrition. XV. Assimilation of carbon by the ear of barley and its relation to the accumulation of dry matter in the grain. Ann. Bot., 14: 55-68.

Pugsley, A.T., 1983. The impact of plant physiology on Australian wheat breeding. Euphytica, 32: 743-748.

Puri, Y.P., Qualset, C.O., Miller, M.F., Baghott, K.G., Jan, C.C. and De Pace, C., 1985. Barley, wheat and triticale grain yield in relation to solar radiation and heat units. Crop Sci., 25: 893-900.

Radford, P.J., 1967. Growth analysis formulae: Their use and abuse. Crop Sci., 7: 171-175.

Rawson, H.M., Bagga, A.K. and Bremner, P.M., 1977. Aspects of adaptation by wheat and barley to soil moisture deficits. Aust. J. Plant Physiol., 4: 389-401.

Rawson, H.M., 1986. Gas exchange and growth in wheat and barley in salt. Aust. J. Plant Physiol., 13: 475-489.

Rawson, H.M., Gardner, P.A. and Long, M.J., 1987. Sources of variation in specific leaf area in wheat grown at high temperature. Aust. J. Plant Physiol., 14: 287-298.

Rawson, H.M., Richards, R.A. and Munns, R., 1988. An examination of selection criteria for salt tolerance in wheat,barley and triticale. Aust. J. Agric. Res., 38: 759-772.

Read, J.J., Johnson, D.A., Asay, K.H. and Tieszen, L.L., 1991. Carbon isotope discrimination, gas exchange and water-use efficiency in crested wheatgrass clones. Crop Sci., 31: 1203-1208.

Richards, R.R., 1983. Manipulation of leaf area and its effect on grain yield in droughted wheat. Aust. J. Agric. Res., 34: 23-31.

Richards, R.A. and Townley-Smith, T.F., 1987. Variation in leaf development and its effect on water use,yield and harvest index of droughted wheat. Aust J.Agric Res., 38: 983-992.

Richards, R.A., 1991. Crop improvement for temperate Australia: Future opportunities. Field Crops Res., 26: 141-169.

Richards, R.A., 1992. The effect of dwarfing genes in spring wheat in dry environments. II. Growth, water use and water-use efficiency. Aust. J. Agric. Res., (In Press).

Richards, R.A. and Condon, A.G., 1992. Challengers ahead in using carbon isotope discrimination in plant breeding programs. *In:* Perspectives on carbon and water relations from stable isotopes. Ed. J.R. Ehlinger, A.E. Hall, G.D. Farquhar and I. Ting. Academic Press.

Riggs, T.J. and Gothard, P.G. 1976. The development of barley grain: comparisons between cultivars for growth rate and a-amylase activity. J. Agric. Sci. Camb., 86: 603-608.

Riggs, T.J., Hanson, P.R., Start, N.D., Miles, D.M., Morgan, C.L. and Ford, M.A., 1981. Comparison of spring barley varieties grown in England and Wales between 1880 and 1980. J. Agric. Sci. Camb., 100: 383-391.

Ritchie, J.T., 1972. Model for predicting evaporation from a row crop with incomplete cover. Water Resour. Res., 8: 1204-1213.

Russelle, M.P. and Bolton, F.E., 1980. Soil temperature effects on winter wheat and winter barley emergence in the field. Agron. J., 72: 823-827.

Russelle, M.P., Wilhelm, W.W., Olson, R.A. and Power, J.F., 1984. Growth analysis based on degree days. Crop Sci., 24: 28-32

Salim, M.H. and Tood, G.W., 1965. Transpiration patterns of wheat, barley and oat seedlings under varying conditions of soil moisture. Agron. J., 57: 593-596.

Scott, W.R., Appleyard, M., Fellowes, G. and Kirby, E.J.M., 1983. Effect of genotype and position in the ear on carpel and grain growth and grain weight of spring barley. J. Agric. Sci. Camb., 100: 383-391.

Sheppard, J.A., Keys, P.J. and Fearon, P.H., 1985. A comparison of the yield of barley,wheat and triticale. Queensland Agric. J. Brisbane: Dept. Primary Industries. Jan.-Feb. 1985. pp.37-40.

Siddique, K.H.M., Belford, R.K., Perry, M.W. and Tennant, D., 1989. Growth development and light interception of old and modern wheat cultivars in a Mediterranean-type environment. Aust J. Agric. Res., 40: 473-487.

Siddique, K.H.M., Belford, R.K. and Tennant, D., 1990a. Root:shoot ratios of old and modern, tall and semi-dwarf wheats in a Mediterranean environment. Plant and Soil., 121: 89-98.

Siddique, K.H.M., Tennant, D., Perry, M.W. and Belford, R.K., 1990b. Water use and water use efficiency of old and modern wheat cultivars in a Mediterranean-type environment. Aust. J. Agric. Res., 41: 431-447.

Sinclair, T.R., Tanner, C.B. and Bennett, J.M., 1983. Water-use efficiency in crop production. BioScience, 34: 36-40.

Sinha, S.K., Aggarwal, P.K., Chaturvedi, G.S., Singh, A.K. and Kailasnathan, K., 1986. Performance of wheat and triticale cultivars in a variable soil water environment. I. Grain yield stability. Field Crops Sci., 13: 289-299.

Smucker, A.J.M., McBurney, S.L., and Srivastava, A.K., 1982. Quantitative separation of roots from compacted soil profiles by the hydropneumatic elutriation system. Agron. J., 74: 500-503.

Sofield, I., Evans, L.T., Cook, M.G. and Wardlaw, I.F., 1977. Factors influencing the rate and duration of grain filling in wheat. Aust. J. Plant Physiol., 4: 785-797.

Sparrow, D.H.B. and Doolette, J.B., 1975. History and development of the Australian barley crops. *In:* Australian field crops. Vol. 1. Wheat and other temperate cereals. Ed. by A. Lazenby and E.M Matheson. Angus and Robertson Publishers. Sydney, Australia. pp. 431-480.

Stapper, M. and Fischer, R.A., 1990. Genotype, sowing date and plant spacing influence on high-yielding irrigated wheat in southern New South Wales. I. Phasic development , canopy growth and spike production. Aust. J. Agric. Res., 41: 997-1019.

Tanner, C.B. and Jury, W.A., 1976. Estimating evaporation and transpiration from a row crop during incomplete cover. Agron. J., 68: 239-243.

Tennant, D., 1975. A test of a modified line intersect method of estimating root length. J. Ecol., 63: 995-1001.

Waddington, S.R., Ransom, J.K., Osmanzai, M. and Saunders, D.A., 1986. Improvement in the yield potential of bread wheat adapted to northwest Mexico. Crop Sci., 26: 698-703.

Waddington, S.R., Osmanzai, M., Yoshida, M. and Ransom, J.K., 1987. The yield of durum wheats released in Mexico between 1960 and 1984. J. Agric. Sci. Camb., 108: 469-477.

Walpole, P.R. and Morgan, D.G., 1971. A quantitative study of grain filling in three cultivars of *Hordeum vulgare L.* Ann.Bot., 35: 301-310.

Warren Wilson J., 1981. Analysis of growth, photosynthesis and light interception for single plants and stands. Ann. Bot., 48: 507-512.

Whan, B.R., Carlton, G.P. and Anderson, W.K., 1991. Potential for increasing early vigour in spring wheat. I. Identification of genetic improvements. Aust. J. Agric. Res., 42: 347-361.

Wright, G.C., Hubick, K.T. and Farquhar, G.D., 1988. Discrimination in carbon isotopes of leaves correlates with water-use efficiency of field-grown peanut cultivars. Aust. J. Plant Physiol., 15: 815-825.

Wych, R.D. and Rasmusson, D.C., 1983. Genetic improvement in malting barley cultivars since 1920. Crop Sci., 23: 1037-1040.

Wych, R.D. and Stuthman, D.D., 1983 Genetic improvement in Minnesota-adapted oat cultivars released since 1923. Crop Sci., 23: 879-881.

Yasuda, S., 1989. Differences in mechanism of early maturity between cultivated common wheat and barley. Japan J. Breed., 39: 327-335.

APPENDIX 1

1.1 Calculating daily vapour pressure deficit (VPD) and potential evapotranspiration (E_p)

1.1 Calculation of VPD

The vapour pressure deficit (VPD) was calculated as:

$$VPD = e^*(T) - e_a \qquad (A1.1)$$

where $e^*(T)$ (kPa) is the saturated vapour pressure at the temperature, T, and e_a (kPa) is the actual vapour pressure of the air. Values of $e^*(T)$ were calculated using standard psychrometric equations as:

$$e^*(T) = 0.6108 \exp (17.27T/(T+237.3)) \qquad (A1.2)$$

where T is the mean dry bulb temperature (°C). The actual vapour pressure (e) was calculated as:

$$e = e^*(Tw) - 0.000660 (1+0.00115 Tw)(T-Tw)P, \qquad (A1.3)$$

where $e_{w(}T_{w)}$ is the saturation vapour pressure at the wet bulb temperature in the afternoon calculated from equation 2, the second term in the equation is the psychrometric constant (kPa $°C^{-1}$) expressed as a function of wet bulb temperature, Tw (°C), and P is the atmospheric pressure.

1.2 Calculation of E_p

E_p at Condobolin was calculated using Penman's method. Before calculations of E_p were made, uncertainty due to extrapolation of solar radiation from Griffith to Condobolin was assessed. Uncertainty was 11% (1988) and 13% (1989) for differences in solar radiation between sites but these differences were not systematic through the season. The regression of % differences against solar radiation from Condobolin (1989) and from Griffith (1989) gave low and insignicant coefficients of correlation (r=0.16 and r=0.20, respectively). These analyses indicated Griffith solar radiation could be applied to a wide range of sites over the region.

A second test, involved a comparison of available radiant energy between Griffith and Wagga Wagga. This test showed that there was a good relation between sites. The equation describing that relation is the following:

$$y = 0.513 + 0.955x, \qquad (A1.4)$$

where y is the available radiant energy (MJ m^{-2} d^{-1}) at Griffith and x is the available radiant energy (MJ m^{-2} d^{-1}) at Wagga Wagga (r=0.94). In conclusion these analyses suggested that extrapolation of solar radiation from Griffith to calculate E_p at Condobolin was effective for determining E_p for a wide range of seasons extending beyond the existing record at Condobolin. The extrapolation procedure was also confirmed from the comparison of available radiant energy between Wagga and Griffith. The relationship between Condobolin and Wagga is:

$$y = 0.777 + 1.135x, \qquad \text{(A1.5)}$$

where y is the E_p from Condobolin and x is the available radiant energy at Wagga (r=0.81).

Finally, E_p (mm d^{-1}) was calculted (Dunin and Reyenga,1976) as:

$$E_p = (s/s+\gamma)\,(Rn-G) + (0.26(\gamma/s+\gamma)\,(1+u/161)\,(e^*-e)), \qquad \text{(A1.6)}$$

where s is the slope of saturation vapour pressure curve (Pa $°C^{-1}$); γ is the psychrometric constant (Pa $°C^{-1}$); Rn is the net long-wave and short-wave radiation water equivalent (mm) ; G is the ground heat flux into the soil (mm) water equivalent; u is the wind speed (km d^{-1}) at 2 m height and e_o and e are the saturation and actual vapour pressure (Pa) of the atmosphere respectively.

Values of $s/s+\gamma$ were calculated as a function of dry bulb temperature as:

$$s/s+\gamma = -0.000139T_d^2 + 0.0169T_d + 0.395 \qquad \text{A1.7)}$$

where T_d is the mean dry bulb temperature, and 0.000139, 0.0169, and 0.395 are the coefficients of the second order polynomial for dry bulb temperature.

Values of $\gamma/s+\gamma$ were calculated as:

$$\gamma/s+\gamma = 1-\gamma/s+\gamma \qquad \text{(A1.8)}$$

APPENDIX 2

Yield, yield components, and agronomic characteristics of genotypes grown in each field experiment

Table A2.1 Grain yield (GY), above-ground dry weight (AGDW), harvest index (HI), anthesis (A), crop eight (Ht), kernels m^{-2}, and kernel weight for experiment C88.

Genotype	GY	AGDW	HI	A	Ht	Kernels	Kernel
	($g\ m^{-2}$)			(Days)	(cm)	m^{-2}	weight (mg)
Barley							
Galleon	345	795	0.43	116	77	8669	40
O'Connor	363	843	0.43	117	84	10288	35
Ulandra	284	966	0.29	131	66	10084	28
Malebo	301	869	0.35	120	101	9317	33
Bread wheat							
Kulin	290	775	0.37	119	88	9053	32
Meteor	283	807	0.35	122	96	9210	31
Rosella	265	810	0.33	129	82	11418	24
M 3344	262	793	0.33	130	82	9531	27
Triticale							
Dua	264	720	0.37	119	92	7602	35
Currency	312	729	0.33	120	105	8471	37
Oats							
Echidna	342	832	0.41	121	66	12990	26
Hakea	229	824	0.28	130	83	12606	19
Overall mean	**295**	**830**	**0.36**	**123**	**85**	**9936**	**31**
Lsd (P=0.05)	65	171	0.02	2	5	2951	3

Table A2.2 Grain yield (GY), above-ground dry weight (AGDW), harvest index (HI), anthesis (A), crop height (Ht), kernels m^{-2}, and kernel weight (mg) for experiment C89.

Genotype	GY	AGDW	HI	A	Ht	Kernels	Kernel
	($g\ m^{-2}$)			(Days)	(cm)	m^{-2}	weight (mg)
Barley							
Galleon	370	908	0.41	114	72	10762	34
O'Connor	373	934	0.40	117	74	10824	34
Ulandra	177	670	0.26	137	50	5191	34
Malebo	329	932	0.35	127	79	9278	35
Bread wheat							
Kulin	254	693	0.37	127	73	7803	32
Meteor	223	649	0.34	137	70	6674	33
Rosella	216	636	0.34	135	72	6087	36
M 3344	161	592	0.27	137	60	4173	39
Durum wheat							
Altar 84	210	603	0.35	136	73	6056	35
Carcomun	223	635	0.35	133	64	6442	35
Triticale							
Dua	265	869	0.30	126	80	7705	34
Currency	276	913	0.30	129	89	6793	41
Oats							
Echidna	288	669	0.43	127	52	10354	28
Hakea	135	642	0.22	134	64	5251	26
Overall mean	**250**	**739**	**0.33**	**130**	**69**	**7385**	**34**
Lsd (P=0.05)	44	74	0.03	1	8	1343	1

Table A2.3 Grain yield (GY), above-ground dry weight (AGDW), harvest index (HI), anthesis (A), crop height (Ht), kernels m^{-2}, and kernel weight for experiment M88.

Genotype	GY	AGDW	HI	A	Ht	Kernels	Kernel
	($g\ m^{-2}$)			(Days)	(cm)	m^{-2}	weight (mg)
Barley							
Galleon	376	850	0.44	115	84	7511	50
O'Connor	454	966	0.47	115	92	8683	52
Ulandra	270	739	0.37	129	70	7426	36
Malebo	247	832	0.42	116	116	6610	53
Bread wheat							
Kulin	320	787	0.41	114	89	8812	36
Meteor	292	850	0.34	122	100	9124	32
Hahn/Parula	319	823	0.39	119	84	10152	31
Rosella	272	791	0.34	128	81	9754	28
M 3344	267	801	0.33	128	80	9676	28
Durum wheat							
Altar 84	307	808	0.38	118	88	8713	35
Carcomun	301	860	0.35	119	86	8189	37
Triticale							
Dua	344	950	0.36	115	96	9248	37
Currency	309	858	0.36	121	115	7190	43
Overall mean	**321**	**840**	**0.38**	**120**	**91**	**8545**	**38**
Lsd (P=0.05)	65	145	0.04	2	4	1536	3

Table A2.4 Grain yield (GY), above-ground dry weight (AGDW), harvest index (HI), anthesis (A), crop height (Ht), kernels m^{-2}, and kernel weight (mg) for experiment M89.

Genotype	GY	AGDW	HI	A	Ht	Kernels	Kernel
	($g\ m^{-2}$)			Days)	(cm)	m^{-2}	weight (mg)
Barley							
Galleon	514	1087	0.47	121	68	11867	43
O'Connor	539	1138	0.47	123	75	11112	48
Ulandra	361	909	0.39	142	58	8235	44
Malebo	505	1124	0.45	129	92	10214	49
Bread wheat							
Kulin	400	969	0.41	131	75	9790	41
Meteor	426	1057	0.40	139	83	11298	38
Rosella	389	992	0.39	141	75	9405	41
M 3344	349	899	0.39	142	69	8471	41
Durum wheat							
Altar 84	363	839	0.43	137	83	8266	44
Carcomun	366	891	0.41	138	77	8502	43
Triticale							
Dua	357	983	0.36	129	88	8185	44
Currency	393	1108	0.35	137	105	8634	46
Oats							
Echidna	453	967	0.47	129	56	13399	34
Hakea	307	803	0.38	138	78	10548	29
Overall mean	**409**	**983**	**0.41**	**134**	**77**	**9852**	**42**
Lsd (P=0.05)	61	146	0.02	2	6	1889	2

Table A2.5 Grain yield (GY), above-ground dry weight (AGDW), harvest index (HI), anthesis (A), crop height (Ht), kernels m^{-2}, and kernel weight (mg) for experiment M90.

Genotype	GY	AGDW	HI	A	Ht	Kernels	Kernel
	($g\ m^{-2}$)			(Days)	(cm)	m^{-2}	weight (mg)
Barley							
Galleon	421	1052	0.40	116	79	8552	49
O'Connor	512	1349	0.38	114	95	9596	53
Ulandra	280	907	0.31	136	73	7803	36
Malebo	404	1128	0.36	123	104	7387	55
Bread wheat							
Kulin	332	892	0.37	120	83	7754	43
Meteor	385	1199	0.32	127	98	11180	36
Rosella	302	973	0.31	130	84	7662	39
M 3344	307	950	0.32	132	80	8132	38
Durum wheat							
Altar 84	293	825	0.35	126	87	7308	40
Carcomun	304	927	0.33	127	84	7286	42
Triticale							
Dua	322	913	0.35	122	93	7006	46
Currency	333	1105	0.30	127	112	7234	46
Oats							
Echidna	431	1086	0.40	126	67	13735	31
Hakea	263	947	0.28	131	97	7983	33
Overall	**349**	**1018**	**0.34**	**125**	**88**	**8472**	**42**
Lsd(P=0.05)	47	168	0.04	2	6	1813	4

APPENDIX 3

Degree and calendar days to different phenological stages of field grown plants.

Table A3.1 Degree and calendar days (in parentheses) to double ridge (DR), terminal spikelet (TS), anthesis (A) and physiological maturity (PM) in C89.

	DR	TS	A	PM
Genotype	(°Cd)			
Barley				
Galleon	437(43)	718(76)	1105(114)	1622(149)
O'Connor	422(41)	653(68)	1140(117)	1665(151)
Ulandra	578(61)	882(94)	1415(137)	1889(163)
Malebo	454(45)	828(88)	1276(127)	1698(152)
Bread wheat				
Kulin	455(45)	818(87)	1276(127)	1914(165)
Meteor	653(68)	854(91)	1415(137)	1952(167)
Rosella	653(68)	905(96)	1389(135)	2018(171)
M-3344	669(70)	927(98)	1415(137)	1996(169)
Durum wheat				
Altar 84	557(59)	819(87)	1402(136)	1914(165)
Carcomun	577(61)	819(87)	1361(133)	1907(164)
Triticale				
Dua	520(54)	718(76)	1260(126)	1886(163)
Currency	577(61)	819(87)	1304(129)	1924(165)
Oats				
Echidna	514(53)	828(88)	1276(127)	1789(158)
Hakea	636(66)	863(92)	1376(134)	1918(165)
Lsd(P=0.05)	20(2)	15(2)	13(1)	60(3)

Table A3.2 Degree and calendar days (in parentheses) to double ridge (DR), terminal spikelet (TS), anthesis (A) and physiological maturity (PM) in M89.

	DR	TS	A	PM
Genotype	(°Cd)			
Barley				
Galleon	446(46)	798(90)	1115(121)	1668(160)
O'Connor	472(50)	689(77)	1140(123)	1817(169)
Ulandra	620(68)	889(100)	1386(142)	1962(176)
Malebo	500(54)	851(96)	1216(129)	1845(170)
Bread wheat				
Kulin	478(51)	851(96)	1238(131)	1926(174)
Meteor	620(68)	870(98)	1336(139)	1975(177)
Rosella	620(68)	931(104)	1366(141)	2082(182)
M-3344	688(77)	955(106)	1382(142)	2051(180)
Durum wheat				
Altar84	500(54)	851(96)	1312(137)	1912(174)
Carcomun	620(68)	851(96)	1332(138)	1950(175)
Triticale				
Dua	467(49)	672(75)	1216(129)	1938(175)
Currency	479(51)	689(77)	1309(137)	1992(178)
Oats				
Echidna	481(51)	851(96)	1216(129)	1897(173)
Hakea	656(73)	899(101)	1330(138)	1903(173)
Lsd(P=0.05)	18(3)	27(3)	22(2)	53(3)

Table A3.3 Degree and calendar days (in parentheses) to anthesis (A), and physiological maturity (PM) and the interval between anthesis and physiological maturity (A-PM) in M90.

	A	PM	A-PM
Genotype	(°Cd)		
Barley			
Galleon	1166(116)	1759(153)	593(37)
O'Connor	1142(114)	1760(153)	618(39)
Ulandra	1438(136)	1854(158)	416(22)
Malebo	1258(123)	1804(155)	546(32)
Bread wheat			
Kulin	1219(120)	1889(160)	670(40)
Meteor	1314(127)	1969(164)	656(37)
Rosella	1356(130)	2040(168)	684(38)
M-3344	1386(132)	2002(166)	615(34)
Durum wheat			
Altar84	1299(126)	1933(162)	634(36)
Carcomun	1314(127)	2002(166)	688(39)
Triticale			
Dua	1246(122)	1969(164)	724(42)
Currency	1314(127)	2040(168)	716(41)
Oats			
Echidna	1299(131)	1804(155)	518(29)
Hakea	1371(126)	1889(160)	518(29)
Lsd(P=0.05)	24(2)	34(2)	43(2)

APPENDIX 4

Calculation of transpiration and soil evaporation from evapotranspiration.

The procedure to separate evapotranspiration into its components evaporation from the soil under the crop, E_{SC}, and crop transpiration, T, in this study was similar to that used by Cooper *et al.* (1983). This procedure is based on the estimation of the proportion of incident radiation intercepted by the crop canopy.

It is widely recognized (Black *et al.* 1970; Ritchie, 1972; Tanner and Jury, 1976; Cooper *et al.* 1983; Boesten and Strossnijder, 1986; Allen, 1990) that evaporation from a bare soil surface (E_S) is a two stage process. Stage one is the constant rate stage during which the soil is wet enough for water to be transported to the surface at a rate equal to the evaporative demand; in this stage evaporation is limited by the supply of radiant energy to the soil surface. In stage two, the falling rate stage, the soil surface water content has decreased to a level such that the rate of evaporation becomes more dependent on soil hydraulic properties, and is much less dependant on the evaporative demand.

Cooper *et al.* (1983) argue that in rainfed systems of Mediterranean environments such as northern Syria or southern Australia, where potential evapotranspiration is low during the growing season and the soil surface is frequently rewetted, E_S is largely determined by conditions in which stage one of soil drying is dominant and conditions favouring stage two of evaporation would only dominate during the ultimate phases of crop maturation. They suggest that the ratio of of E_{SC}/E_S, g.e. the ratio of soil evaporation beneath the crop, E_{SC}, to that from a bare soil, E_S, will depend on the proportion of radiant energy intercepted by the crop canopy. E_{SC} can be computed from the following equation:

$$E_{SC}=E_S(1-\alpha) \qquad \text{(A4.1)}$$

where α is the proportion of incident radiant energy intercepted by the crop canopy. Cooper *et al.* (1983) estimated cummulative and daily values for E_{SC} by fitting curves of E_S vs time and green leaf area index (G) vs time. They calculated the extinction coefficient, K, to be 0.37 for crops in different sites and sowing times from measurements of a and G from the following relationship:

$$\alpha=1-e^{-KG} \qquad \text{(A4.2)}$$

Combining E_S and α according to equation A4.1 gives daily values of E_{SC}. Daily values of T are obtained from the expression:

$$T=E_T-E_{SC} \qquad \text{(A3.3)}$$

In this study E_T was partitioned into E_{SC} and T according to the procedure described in this appendix for experiments C89 and M89.

The most frequent measurements of leaf area index (LAI) in this study were made in experiments C88 and M88. These values of LAI were used to compute values of a to calculate E_{SC} for experiments C89 and M89.

Values for K of 0.44 have also been reported for temperate cereals (Gallagher and Biscoe, 1978). As there is little difference on α in using o.44 or 0.37, the value of 0.37 (Cooper *et al.* 1983) has been used for all calculations of α.

E_S for the period between sowing and the first soil moisture measurement were equated to E_T during this period. During this early growth period when leaf area is very small and a is negligible, E_S has been found to be little different to E_T for a variety of crops and locations in regions with a winter rainfall distribution (Cooper *et al.* 1983).

APPENDIX 5

Plant growth techniques

Plant growth analysis has been used to compare plant growth attributes of different genotypes. It integrates genetic and physiological effects and partitions growth into components that can result in a better understanding of the variation among and within species.

Analysis of plant growth was first attempted early this century by Blackman (1919). He proposed that plant growth follows the compound interest law and that dry weight (W) depends on (i) the initial capital, (ii) the rate of interest on growth and (iii) time. Blackman (1919) proposed that final dry weight (W_1) was a function of the initial weight (W_0), the rate of sry weight increase (r) and time (t) such that:

$$W_1 = W_0 e^{rt} \qquad \text{(A5.1)}$$

where W_1 is the final plant dry weight, W_0 is the initial weight, r the rate of interest or the rate of dry weight increase, t is time and e is the base of natural logarithms. This expression was simplified by Fisher (1920) as:

$$RGR = (\log_e W_2 - \log_e W_1)/(t_2 - t_1) \qquad \text{(A5.2)}$$

where RGR is the relative growth rate, W_1 and W_2 and t_1 and t_2 indicate the first and second values for dry weight and time respectively. Further partitioning of RGR into its physiological component, net assimilation rate (NAR) and its morphological component, leaf area ratio (LAR) are given by:

$$NAR = (1/L_A)(dW/dT) \qquad \text{(A5.3)}$$

where L_A is the total leaf area present on the plant and,

$$LAR = L_A/W \qquad \text{(A5.4)}$$

where L_A is the total leaf area and W is the plant dry weight.

Since NAR and LAR evolve simultaneously as subdivisions of RGR it is by definition that:

$$RGR = NAR \times LAR \qquad \text{(A5.5)}$$

Simply expressed the growth rate of the plant depends simultaneously on the efficiency of its leaves as producers of new material and on the leafiness of the plant.

The LAR can be further partitioned into specific leaf area, the ratio of leaf area to leaf weight (L_A/W_L, SLA) and leaf weight ratio, the ratio of leaf weight to total plant weight (W_L/W, LWR) such that:

$$RGR = NAR \times SLA \times LWR \qquad (A5.6)$$

RGR and its components can also be expressed as the gain of carbon by the plant in terms of relative growth rate, r (10^{-6} s^{-1}), assimilation rate, A (mmol CO_2 m^{-2} s^{-1}), the rate of CO_2 assimilation by the shoot in the light, such as would be measured in a gas exchange chamber and r (mol C m^{-2}), the ratio of total plant carbon to leaf area, s (Masle and Farquhar, 1988). Then the rate of increase of carbon mass in the plant, M, (mol C), is

$$dM/dt=((sA-R_r^L)L-(R^N_r+R^N_s)N)/(L+N) \qquad (A5.7)$$

where s (m^2) is the area of the photosythetic tissue, R^L_r and R^N_r (mol CO_2 s^{-1}) are the respiration rates of the roots during the light period (duration Ls) and during the night (duration Ns), respectively; R^N_s (mol CO_2 s^{-1}) is the shoot respiration rate at night.

The proportion of losses by respiration during the daytime shoot fixation is given by,

$$\phi=(R^L_r \cdot L+(R^N_r+R^N_s)N)/sAL \qquad (A5.8)$$

so that equation 5.7 can be expressed conveniently in terms of carbon as:

$$dM/dt=s \cdot A \cdot (L/L+N)(1-\phi)=s \cdot Al(1-\phi) \qquad (A5.9)$$

where l is the light period as a proportion of the day. The relative growth rate, r(s^{-1}), is then,

$$r=(1/M \cdot dM/dt)=(Al(1-\phi))/\rho \qquad (A5.10)$$

where r (mol C m^{-2})is the ratio of total plant carbon, M, to photosynthetic area, s.