VARIATION IN PHENOLOGY AND ITS INFLUENCE ON GROWTH, DEVELOPMENT AND YIELD OF DRYLAND WHEAT

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by

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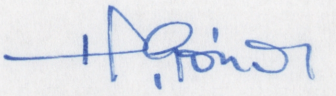
STATEMENT

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



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ABSTRACT

Yield of dryland wheat in south-eastern Australia is limited by low and erratic rainfall throughout the growing season, frosts at flowering time, and by high temperatures during the grain filling period. The timing of phenological events must be such that these environmental constraints are minimised for maximum adaptation and yield. In the field, the timing of the different phenological stages is mainly determined by genotypic responses to photoperiod and vernalization as influenced by the sowing date. The work presented here explored variation in phenology with sowing date to determine the optimal flowering time in relation to sowing that maximizes yield of rainfed wheat in the dry part of the south-eastern wheat belt. The experiments were carried out at three sites in New South Wales: Condobolin, Moombooldool and Wagga Wagga. Condobolin is representative of the drier environments within the region with an average rainfall from May to October of 230 mm. Extensive and detailed studies were done at this site. Moombooldool and Wagga Wagga are wetter environments with 270 and 360 mm average rainfall from May to October respectively and were used as contrasting sites. In this study, lines which differed in their flowering genes but which otherwise were similar genetically were sown at early, normal and late times. The lines used had a range in flowering time greater than is commonly found amongst commercial varieties grown in this region.

No penalty in grain yield was found with sowing wheat earlier than the usual time, which is late May in south-eastern Australia. This is consistent with the increasing practice of farmers of sowing wheat crops earlier. Water-use efficiency for above-ground dry weight was substantially higher in early sown crops but this did not translate into higher yields. Possible reasons for this lack of response of grain yield studied here were: greater incidence of barley yellow dwarf virus (BYDV), increased drought severity, frost damage, smaller sink size and competition for assimilates. Frost and BYDV were eliminated as being responsible for the low yields. It is suggested that the principal reason that greater yields were not obtained in the early sowings, particularly sowings in April, was because of greater competition for substrates between the growing spike and the elongating stem in early sown crops compared with conventional sowing times.

In most environments the intermediate flowering lines, which flower at a similar time to most commercial spring wheats, had the highest yields. Only in sowings earlier than mid-May did the late flowering lines yield similarly to the intermediate flowering lines. The very early flowering lines produced few shoots and accumulated little biomass, thus limiting yield.

Time to anthesis was reduced with later sowings. This was more pronounced for late flowering than for early flowering lines. Late flowering lines can be sown in April but still flower in the first week of October when there is no risk of frost.

Lines differed in the duration of the phenological phases up to anthesis both within and between sowings. Sowing date also affected the duration of phenological phases. In the early sowings, the presence of vernalization-sensitive and photoperiod-sensitive genes extended the vegetative period between sowing and double-ridge formation (DR) on the main shoot apex. This was probably because, firstly, temperatures were too high to fully vernilise plants, secondly, daylength was decreasing and thirdly, the photothermal quotient during April and May was low. May or later sowings did not affect the length of this vegetative period when time was expressed in degree days (with a base temperature of $0^{o}C$) for normal sowing times. The spikelet initiation period, between DR and terminal spikelet (TS) stage, was extended in lines having photoperiod sensitive genes whereas the time from TS to anthesis was largely unchanged. This last period was reduced with late sowing times.

Isolines with different flowering genes (vernalization, photoperiod and basic development rate) differed in the duration of the phenological phases for a given flowering time. These isolines were used in an attempt to clarify the complex relationship between growth and development. In the field, lines with a longer vegetative phase had higher maximum leaf and tiller numbers than earlier cultivars. However, more tillers died in the late line. In a similar way, late lines had more spikelets per ear but less kernels per ear at maturity. These relationships between plant organs reflects the complexity of attempting to increase yield by changing only one component. In most cases there is a tendency within the plant to compensate such variation. This compensation may arise from competition for assimilate between plant parts growing at the same time.

A breeding program which aims to produce late flowering lines of shorter height than commercially available varieties has started and will examine the hypothesis that reduction in stem height will favour ear development and result in higher harvest index and yield through increased grain number.

CONTENTS

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

1.1 INTRODUCTION

Wheat is cultivated in many environments around the world. In Australia, most wheat is grown under seasonal conditions, and thus, the first step to maximize yield is to match the life cycle of the crop to the seasonal window available. Once the main environmental constraints are avoided or minimised, breeding for traits that improve grain yield may then be possible.

In the drier part of the south-eastern Australian wheatbelt, the main environmental constraints are rainfall and temperature. The rainfall pattern in this area is characterised by an unpredictable break of the season and a low chance of an early break before May, by an unreliable rainfall during winter and spring and, most importantly, by a drought period at the end of the season. Water supply is therefore a limitation to the chioce of sowing dates and the growth of the crop and grain. Additionally, low temperatures during winter limit plant growth, frosts affect floret fertility, and high temperatures affect grain growth.

The common practice in this area is to sow spring wheats from the middle of May to early June. The varieties used are the same ones that are grown in most of the southern wheatbelt of New South Wales. Their vegetative period occurs during winter and they flower in early October when there is no risk of frost. In most years, this places grain filling during the late drought period. It is possible that the varieties commonly grown in this dry area are not the best for these environments. The primary aim of this thesis was to examine, using a range of isolines, the effects on yield of different combinations of developmental pattern and different sowing dates, and to establish the optimal combination of these factors for the area.

1.2 LITERATURE REVIEW

1.2.1 What are the main environmental constraints in the south-eastern Australian wheatbelt?

The wheatbelt in south-eastern Australia lies between the 255 and 635 mm annual rainfall isohyets (Nix, 1975). Most of this area is considered to have a Mediterranean climate and about 70 % of the rain falls during the May-October period. On the drier edge of this area, water supply is the main environmental constraint to crop growth and yield (French and Schultz, 1984). Water is particularly limiting at the end of the season when additional constraints are high temperature and

evaporative demand. Other environmental constraints identified in this area (Nix, 1975) are:

(i) the unreliable rainfall in autumn that determines the earliest possible sowing date. May and June are the two months when most sowings are done in this area. An April sowing is possible only in some years as the probability to have enough rain for sowing is low in this month. Sometimes, excessive or insufficient rain delays the sowing until July.

(ii) radiation and temperature are low during late autumn and winter. This limits plant growth during this period and may be important in development of leaf area and sink size development. Rawson (1993) found that in situations where there is a source limitation, eg high temperature and low radiation, there is a delay in wheat development. He suggests that source limitation could occur in the field during May-early June when photothermal quotient (solar radiation / mean temperature) is very low (see Chapter 2 in this thesis).

(iii) frost conditions determine the earliest flowering date. Frost can be a local phenomenon and the probabilities of occurrence should be determined in every location down to the level of the paddock. Nix (1975) defined 'the earliest safe ear emergence date' as the mean date of the last 0°C minimum screen temperature plus one standard deviation. In Wagga Wagga, Fischer (1979) using 2°C as critical temperature, estimated October 1 as the earliest safe date for flowering. In Western Australia, the Bureau of Meteorology provided a map of frosts risk also using 2°C (Loss, 1989).

Since early 1993, a computer program called MetAccess^{MT} has been available for farmers to analyse daily weather records of locations within the southern wheatbelt. The program has been developed at CSIRO (Division of Plant Industry) and it runs on any IBM-compatible personal computer. Because of its access to historical weather records, farmers can calculate with it the probability of frost or rain or other weather elements for any day and location.

(iv) during winter water stress is generally not a problem but excessive rain may induce leaching and waterlogging. Their negative effects on the crop can be largely overcome by the application of fertilizers.

(v) soil type and depth influence some of the constraints mentioned above. An example of this is given by Passioura (1992).

Of all these constraints, the main one in the drier part of the south-eastern wheatbelt is the period of drought and high temperature at the end of the season. To avoid it, flowering time should be advanced so that grain filling occurs under better conditions. Farmers have to choose the cultivar with the right combination of maturity type and sowing date so that flowering occurs within the window determined by the last frost and the period of water stress (Connor, 1975; Fischer, 1979).

1.2.2 Standard varieties and sowing time

A typical crop rotation in south-eastern Australia involves five year pasture, followed by wheat-wheat or wheat-barley. The field is usually fallowed in September and the wheat is sown in mid-May or June. The standard varieties sown are spring wheats that have a slow growth period during winter when temperature and radiation are low, and a rapid growth period during spring as temperatures start to rise and days are longer. These varieties flower in early October when there is no risk of frost. Another option that is becoming more common amongst farmers is the earlier sowing of later maturity varieties (winter wheats) that also flower in early October.

In New South Wales, every year the Department of Agriculture and Fisheries publishes the results of the variety trials with recommendations for farmers. Quality and maturity type and sowing time are recommended for every silo group. New South Wales is divided into six silo areas according to transport and marketing arrangments. Each group includes different environments and it may be that the recommendations are too general for the whole silo area.

1.2.3 What can be done in terms of adaptation to avoid the environmental constraints?

1.2.3.1 To advance flowering time

Studies comparing old and new cultivars show that most of the yield improvement achieved by new varieties has been made through an increase in harvest index (Austin *et al.*, 1980; Perry and D'Antuono, 1989) mainly because of the introduction of semidwarfs wheats and the changes in farming systems, eg the increased application of fertilizers. However, in the drier environments where wheat is grown, particularly in Mediterranean environments with a terminal drought period, yield improvement has been mainly achieved through increased earliness so that drought and high temperatures at the end of the season are avoided (Derera *et al.*, 1969; Fischer and Maurer, 1978; Kirby *et al.*, 1989; Richards, 1991).

In the traditional plantings of spring wheats sown in mid May to early June it is important to reassess whether the phenology of the standard varieties currently grown is the most appropriate. For example, the risk of frost may presently be overstated resulting in varieties which flower too late when the risk of frost is over, and this may result in a considerable sacrifice in yield as drought and high temperatures may then markedly limit yield. Furthermore, with a lag time of ten years in the breeding of new varieties, frost risk in spring may become less with the expected global warming and hence late frosts may be less of a constraint on crop

production in the future (Richards, 1991). Thus, varieties flowering earlier than those currently grown may have more potential now and in the future.

1.2.3.2 To advance sowing date

Since the mid-80s an increasing number of farmers have chosen to sow a winter wheat earlier in the season. Already in 1970, Kohn and Storrier underlined the need for research on late maturity lines that could be sown early in the season but still avoid frosts in spring. The winter wheats available at that time flowered too late and most of them were very tall and thus prone to lodging (Kohn and Storrier, 1970; Pugsley,1971). Since then other studies (Martin, 1981; Crofts *et al.*,1984; Batten and Khan, 1987; Connor *et al.*,1992) have looked at the potential of such an option in a diversity of Australian environments. In general, winter wheats yield better than spring wheats when sown in April or May.

In environments where water is limiting, yield will be increased if the harvest index, the water transpired or the water use efficiency (WUE) is increased (Passioura, 1977). One way to increase WUE is to grow the crops when the vapour pressure deficit is low such that transpiration is low and transpiration efficiency (carbon assimilated per unit of water transpired) high. In the field, this could be achieved by sowing early in the season (Tanner and Sinclair, 1983) as an important part of the growth would then take place during late autumn and winter. The increase in WUE with early plantings and the positive effect that has on yield has been shown in wheat (Richards *et al.*, 1993), chickpeas (Keatinge and Cooper, 1983) and sunflower (Gimeno *et al.*, 1989).

Longer season winter wheats that can be sown in April and early May are of interest not only because of the potential increase in WUE but also for other significant features that make them attractive to farmers. The following features are generally recognised. Firstly, they provide farmers with greater flexibility in planting time, particularly on heavy soils where machinery cannot be used if it is too wet in May, June and July. Regardless of planting time, they tend to flower at a similar calendar date (Stapper and Fischer, 1990). Secondly, they should result in a more sustainable cropping system as bare soil is exposed for less time and the risk of erosion is reduced. The earlier cover of the ground also results in less water lost by soil evaporation and more water available for transpiration (Richards *et al.*, 1993). Thirdly, a longer duration for growth could result in deeper rooting (Siddique *et al.*, 1990a) and hence less water and nitrogen may be leached from the root zone resulting in less soil acidification. Fourthly, these wheats can be grazed if stock feed is in short supply and they still produce significant yield (Davidson *et al.*, 1990). Fifthly, longer season wheats require less fertilizer (Fettell and Batten, unpublished data).

These features, as well as the release of more appropriate varieties, have resulted in an increase in the planting of winter wheats from 0% in 1984 to about

15% in southern New South Wales in 1991. Similar trends towards earlier planting have occurred in all other states in Australia. In Western Australia an advanced planting date in early May compared to a June sowing has recently been advocated (Perry *et al.*, 1989; Delane and Hamblin, 1989; Anderson and Smith, 1990; Kerr *et al.*, 1992). The advantages proposed by these authors are that seedling emergence is hastened and early growth increased, less water is lost by evaporation, water-use efficiency is improved so that more water is available for the grain filling period.

On the other hand, there is the concern that early sowings may deplete soil water prematurely (Martin, 1981; Marshall, 1987). Connor *et al.* (1992) have shown that this is not necessarily the case. Another major problem with earlier sowing is the increasing risk of frost damage (Kohn and Storrier, 1970) if the varieties used are not appropriate. For every maturity type there will be an earliest possible sowing date so that frost is avoided at flowering time. In Victoria, Crofts *et al.* (1984) found that the winter variety Osprey should be sown after April 28.

Other concerns with early sowings are low grain protein content, more effort required to control weeds and the increasing risk of damage by some disease or pest. Grain protein content generally decreases with early sowing (Kohn and Storrier, 1970) although Batten and Khan (1987) have shown the opposite trend. In the United Kingdom, Hill (1987) has shown higher yield losses due to barley yellow dwarf virus damage in early sown wheat than in spring sown wheat. In South Australia, French and Schultz (1984) and Marshall (1991) predicted an increase in cereal cyst nematode (CNN) damage with earlier planting.

1.2.3.3 To improve water use with later sowings

Water is stored in the soil and is either used by the crop or lost by evaporation from the soil surface. Anthesis time and the dry matter accumulated by anthesis determine the water used before and during grain filling within any specific environment. The importance of the balance between pre- and post-anthesis water use has been pointed out by Passioura (1977). A longer time to anthesis results in more biomass and leaf area and more water use before anthesis (Fischer, 1979). To avoid this, later sown crops may increase the soil water available at anthesis as the time from emergence to anthesis is shortened and the dry matter is reduced (Fawcett and Carter, 1973; McDonald *et al.*, 1983). However, the soil water reserve is not necessarily increased at anthesis with later sowings (Doyle and Fischer, 1979; O'Leary *et al.*, 1985). Also, it must be considered that as sowing is delayed the calendar day of anthesis is also delayed (Doyle and Fischer, 1979; McDonald *et al.*, 1983; French and Shultz, 1984; Batten and Khan, 1987; Stapper and Fischer, 1990a) and, if the delay is excessive, then the grain filling period will occur during the period of high temperature and evaporative demand. This will reduce yield (O'Leary *et al.*,

1985). Low yields from such combinations have also been shown in irrigated wheat (McDonald *et al.*, 1983; Stapper and Fischer, 1990b).

1.2.4. Can the relative durations of the phenological phases be manipulated to improve yield?

The foregoing discussion has pointed out the environmental constraints to growth in the south-eastern wheatbelt which determine the best flowering time in the year for producing yield. Once the time window has been determined, the next step is to examine whether the durations of different phases of the crop's development can be manipulated independently to increase yield within that window. The simplest subdivision of development is into the two phases of pre- and post anthesis, the first during which the numbers of grains per unit area are being largely determined, and the second during which the grains are being filled (Evans *et al.*, 1975). The grain filling period is flexible, but its flexibility is dominated by temperature and water stress (Wardlaw, 1971; Loss *et al.*, 1989; Asana and Williams, 1965), and is scarcely manipulable genetically. Consequently, once the window for the season is set, flowering date will be largely set also by back-dating from the close of the window. By contrast, the pre-anthesis phase, which can be further subdivided into a vegetative, spikelet initiation and ear development phases (Davidson *et al.*, 1984), is very manipulable genetically, and there appears to be scope for manipulating the durations of the three subphases independently. The question is whether there is any benefit to yield from altering the relative durations of these three phases within the fixed window. To build an hypothesis for changing the phases it is necessary first to understand what components of yield the plant is producing in the phases. The simplest model for examining this is to think of the plant as numbers of potential grain carrying structures (tillers, spikelets, florets) and structures that provide the resources for growth (leaves and roots). The plant has to apportion growth into these two. The related question is whether the transferring of grain sites between tillers, spikelets or florets will have any impact on yield or whether it is the total number of grains rather than their location which is the determinant of yield.

1.2.4.1 What is happening during the three phenological phases?

The vegetative phase is defined here as the time from seed germination to the start of spikelet initiation in the main apex. The embryo already has up to 3 leaf primordia (Lersten, 1987) and 3 to 6 seminal root primordia (Klepper at al., 1984). After germination and during the vegetative phase, the apex of the main shoot continues initiating leaf primordia until the reproductive phase starts with the initiation of spikelet primordia. In the base of most leaves a tiller bud is initiated (Williams *et*

al., 1975). So it is during this phase that the number of leaves, and the potential number of tillers is determined.

Varieties of different maturity differ in the length of the vegetative phase. In fact most variation in flowering time is due to the variation in this phase. In wheat, the length of the vegetative phase is mainly controlled by the degree of response to vernalization and/or photoperiod. Wheats with vernalization requirements need a period of chilling before spikelet initiation can commence whereas wheats with photoperiod requirements start the floral stage earlier with longer daylength. The genes that control the sensitivity to vernalization and photoperiod have been described by Pugsley (1971, 1972), Flood and Halloran (1986a) and Law (1987) among others.

Wheat varieties also differ in the 'basic development rate' (Flood and Halloran, 1984a). This is defined as the variation in the duration of the vegetative phase that remains when vernalization and photoperiod responses are removed. The basic development rate is also called 'intrinsic earliness' (Masle *et al.*, 1989a) or 'earliness *per se*' (Hoogendoorn, 1985) The genes that control the basic development rate have been studied by Flood and Halloran (1984a), Hoogendoorn (1985) and Law (1987).

The spikelet initiation period starts at the moment the apex in the main stem changes from producing leaf primordia to producing spikelet primordia and ends with the initiation of the terminal spikelet. After this, the ear continues to develop while the stem starts to elongate. During this last phase, most florets are initiated. The start of the spikelet initiation period is usually associated to the end of the tillering phase.

1.2.4.2 Leaves and roots

The source of assimilates and the proportion of water lost by transpiration and soil evaporation depends mainly on the leaf area per unit area of ground. Leaf area is determined by the rate of leaf primordia initiation, the rate of leaf emergence and the number and size of the leaves. During the vegetative phase the leaf primordia are initiated in the apex of the main stem and tillers. Varieties differ in the leaf appearance rate (or 'phyllochron interval', time between the appearance of two consecutive leaves) (Masle *et al.*, 1989b; Krenzer and Nipp, 1991). However these differences are not associated with vernalization requirements but more with the response of development to temperature. Late sowings generally decrease the phyllochron interval (Kirby and Perry, 1987) largely because phyllochron interval changes with photoperiod, so some of the apparent effects can be explained by using photothermal units (Masle *et al.*, 1989b). It has also been suggested that the differences in phyllochron interval due to sowing date are due to the rate of change in daylength (Baker *et al.*, 1980). Wheats with a longer vegetative phase have more leaves and tillers. The number of leaves and tillers largely determines maximum leaf area index (LAI) under non-stress conditions until full ground cover occurs.

Maximum LAI is lower in early flowering lines (Richards and Townley-Smith, 1987). However, Connor *et al.* (1992) found no differences in LAI at anthesis between a spring and a winter wheat.

Root appearance is coordinated with leaf and tiller appearance under non-stress conditions (Klepper *et al.*, 1984). Siddique *et al.* (1990a) have shown that a late maturity cultivar had higher root density in the top 35 cm soil compared to earlier maturing lines. On the other hand, Derera *et al.* (1969) found early maturing cultivars to have larger root systems.

1.2.4.3 Ear number per unit ground area

The number or ears is the result of tillers produced and tiller survival. The maximum number of emerged shoots (tillers plus the main shoot) per plant is usually reached in the field at the start of stem elongation (Simons, 1982; Hay, 1986). Tiller number depends on the length of the vegetative phase, temperature (Rawson, 1971), radiation (Evans *et al.*, 1975), soil water (Black, 1970) and nutrition (Bremner, 1969). Tillering can be strongly suppressed by the presence of low-tillering genes in both spring and winter wheats (Innes et al., 1981; Hucl and Baker, 1991). After the start of stem elongation the late formed tillers start to die. Tiller survival varies amongst cultivars (Simons, 1982) and is affected by nitrogen nutrition (Masle-Meynard, 1981; Thorne and Wood, 1988), plant population (Darwinkel, 1978), temperature (Rawson, 1971; Thorne and Wood, 1987) and water stress (Innes *et al.*, 1981). Masle-Meynard (1981) showed that under conditions of nitrogen limitation, only the tillers with three leaves and roots continued development until maturity. The association between the start of tiller senescence and the start of stem elongation has been related to competition for assimilates (Kirby and Appleyard, 1981; Simons, 1982; Hay, 1986).

A higher number of tillers can be produced with a longer vegetative period. However, in a winter line the tiller mortality might be higher and the final number of shoots with fertile ears similar to the number in a spring wheat (Watson *et al.*, 1963). Innes *et al.* (1981) found that yield was related to shoot survival rather than maximum shoot number. In late sowings the final ear number is generally reduced (Musick and Dusek, 1980; Simons, 1982).

1.2.4.4 Spikelet number per ear

The number of spikelets is mainly determined during the spikelet initiation period. A longer vegetative phase and longer spikelet initiation phase are associated with higher spikelet number (Rawson, 1970; Baker and Gallagher, 1983). Long daylengths (Rawson 1971; Rahman and Wilson, 1977), high temperatures (Rahman and Wilson 1978) and low light intensity (Friend, 1965) reduce the number of spikelets initiated.

The rate of spikelet primordia initiation is negatively related to the duration of the phase's duration when different vernalization or photoperiod treatments are compared (Rawson, 1970; Rahman and Wilson, 1977). This usually results in less variation in spikelet number than would be expected from considering the effects of duration alone.

1.2.4.5 Fertile florets per spikelet

The potential number of florets initiated per spikelet can be up to 12 (Hay and Kirby, 1990) but actual numbers depend on temperature, daylength and genotype. A large proportion of florets abort during stem elongation, mainly while the peduncle is growing (Langer and Hanif, 1973; Kirby, 1988; Siddique *et al.*, 1989). Water stress at this time reduces further the number of fertile florets (Ooesterhuis and Cartwright, 1983). The common explanation for this abortion is that there is competition for assimilates between the florets and the stem (Brooking and Kirby, 1981; Kirby, 1988) as the time of fast ear dry matter accumulation coincides with the end of stem elongation. This is supported by the strong effect of the pre-anthesis incident radiation on the final number of grains (Stockman et al., 1983; Jedel and Hunt, 1990).

1.3 OBJECTIVES

The main objective of this study is to determine the optimal flowering time in relation to sowing date to achieve maximum yield in the drier part of the wheatbelt in south-eastern Australia as well as to identify the principal determinants of yield in these different sowings. For this, it is necessary to study the relationships of the phenological stages and growth and their effect on yield as well as the variation in phenology, growth, water use and yield with sowing date. The use of isogenic material of different phenology is an important part in the achievement of these objectives.

CHAPTER 2

EFFECT OF SOWING DATE ON YIELD OF DRYLAND WHEAT

2.1 INTRODUCTION

Crop phenology must be matched to the prevailing environment as a first step to maximize grain yield and adaptation. In southern Australia, the optimum flowering time of dryland wheat is mainly determined by rainfall and temperature. Adapted wheat varieties should flower late enough to avoid frosts in spring but not so late that they run into drought and high temperatures which are common at the end of the season. Farmers have to choose the right combination of sowing time and genotype that will lead to the optimum flowering time and maximum yield for their particular environment. In the drier parts of the south-eastern Australian wheatbelt, the number of feasible options is not large as rainfall is unreliable and the chance of an early break to the season, and thus of an early autumn sowing, is small. Traditionally, spring varieties are sown from the middle of May to early June. These varieties will then flower in early mid-October when the risk of frost is minimised. It is important to reasses if this practice is the most appropriate.

In the last years, another option that is becoming popular amongst farmers is to sow late maturity lines early in the season. These lines will flower in similar dates than the traditional spring wheat. The main advantages recognised in this sowing are the more flexible sowing period, the soil is exposed for less time resulting in less erosion and soil water evaporation, the deeper rooting of the crop that may result in less water and nitrogen leached, the possibilities of grazing if stock feed is in short supply (Davidson *et al.*, 1990) and the lower requirement of fertilizers (Fettell and Batten, unpublished data).

The availability of isogenic populations that differ in vernalization and photoperiod requirements, and thus in flowering time, will facilitate enormously the assessment of optimal sowing time and genotype combinations available to farmers. In this study, lines differing in phenology but otherwise very similar genetically (isolines) were sown at three times at Condobolin (central New South Wales) in two consecutive years. This site is representative of drier environments within the wheatbelt. The isolines used in these experiments had a range in phenology greater than that of the current commercial varieties and therefore enabled the assessment of new crop opportunities. The range in flowering time was further increased with earlier or later sowings than are usual. Experiments were also conducted at two other locations with higher rainfall than at Condobolin; at Wagga Wagga on the wetter edge of the southern Australian wheat belt and at Moombooldool on a rainfall transect mid-way between Condobolin and Wagga Wagga.

The objective of this study is to determine the optimum sowing date to achieve maximum yield in the drier part of the wheatbelt in south-eastern Australia. The effect of sowing date on flowering time, yield and yield determining factors in the highest yielding lines is studied. Later chapters describe results in more detail of all lines sown in the field in relation to aspects of phenology, growth and development, yield and its components as well as water use and water use efficiency.

2.2 MATERIAL AND METHODS

2.2.1 Plant material

Five near-isogenic groups of lines or populations involving 23 genotypes as well as some commercial cultivars were grown in 1989. Isogenic populations referred to as M (6 lines) and B (7 lines) were derived from early and late flowering plants of the cross Arz/Cook//Sunset that were crossed to Millewa (M) twice and Banks (B) twice to form backcross-1 populations. Uniform BC_1F_4 lines homozygous for a single dwarfing gene in each population were formed into 6 groups for M and 7 for B depending on their flowering date. Millewa and Banks are high yielding spring wheat varieties whereas Sunset, released in Australia at the beginning of the century is very early flowering and was used as the principal source of earliness. The time to ear emergence of isolines in these two groups is strongly regulated by photoperiod (Appendix 1). The MQ (2 lines) and MWM (4 lines) groups were selected from F_2 populations; Millewa was the spring wheat parent in both groups, Quarrion and Winter Minflor were the winter wheat parents in the MQ and the MWM group respectively. These populations were formed by bulking true-breeding F_3 spring lines and F_3 winter lines from each cross. True breeding lines for winter or spring habit were identified by growing about 10 seeds of each line in a glasshouse at 24/15^{o}C day/night temperatures. Lines where all plants flowered in the glasshouse were classed as spring types whereas lines in which all plants remained vegetative were classified as winter lines. The MQ group are homozygous for Rht_1 whereas the MWM winter and spring populations were further split into tall and dwarf populations. The tall populations contain no major dwarfing gene whereas the dwarf populations contain Rht_1. The presence, absence or segregation for dwarfing genes was tested following the procedures outlined in Richards (1992). The lines in these groups are primarily vernalization sensitive (Appendix 1). The RAC isogenic populations were obtained from the Plant Breeding Unit at Roseworthy (South Australia). The four RAC lines used in these experiments were derived from a single F_3 plant of the cross Condor/Petit Rojo which segregated for vernalization genes. The RAC lines have also been selected for high yield.

In 1990, the number of isolines was reduced to the earliest, mid and latest lines within the M and B groups plus the four MWM lines. Commercial or advanced

breeding winter wheats (8 varieties), spring wheats (2 varieties) and barleys (4 varieties) were included to increase the range of better adapted genotypes to southern Australia.

All wheat lines used in these experiments are semi-dwarf and contain a single dwarfing gene except for the two tall lines in the MWM group (MWMwnt tall and MWMspr tall).

2.2.2 Sites and agronomy

There were a total of fourteen sowings in 1989 and 1990 at three locations in NSW: Condobolin (147°E, 33°S), Moombooldool (147°E, 34°S) and Wagga Wagga (147°E, 35°S). The monthly weather data from the three sites for both years is summarized in Table 2.1 along with the long term means. The long term average rainfall between April and October ranges from 230mm at Condobolin to 362mm at Wagga Wagga. The average rainfall at Moombooldool for the same period is 269mm.

Table 2.1a. 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
1989	24.0	19.8	14.9	13.9	15.0	20.5	24.7	29.1
1990	22.3	19.3	14.6	14.2	14.7	18.9	24.2	30.0
				Minimum temperature (°C)[a]				
Mean	9.5	6.0	2.9	2.1	3.4	5.2	9.0	12.4
1989	12.3	9.2	4.4	3.9	3.1	3.4	8.4	12.9
1990	13.4	7.1	4.3	5.0	5.2	5.3	8.3	11.8
				Solar radiation (MJ $m^{-2}d^{-1}$)[b]				
Mean	17.6	12.1	10.0	11.1	13.6	18.5	24.6	28.6
1989	15.5	10.6	9.8	8.8	13.6	20.3	23.6	26.2
1990	10.3	10.3	8.1	7.9	10.8	16.3	21.5	25.9
				Photothermal quotient (MJ $m^{-2}d^{-1}{}^{o}C^{-1}$)[b]				
Mean	1.0	1.0	1.0	1.3	1.4	1.4	1.4	1.4
1989	0.9	0.8	1.1	1.1	1.5	1.8	1.5	1.3
1990	0.9	0.8	0.9	0.9	1.2	1.4	1.4	1.3
				Rainfall (mm)[c]				
Mean	29.6	35.4	33.9	30.6	33.2	27.3	40.1	37.1
1989	53.2	56.6	49.0	42.5	21.8	8.6	20.6	32.8
1990	268.0	22.2	27.4	51.6	74.8	28.0	33.4	14.2
				Potential evapotranspiration (mm d^{-1})[d]				
1989	3.9	2.2	1.9	2.0	2.7	5.0	7.1	8.4
1990	3.0	2.0	1.3	1.3	2.0	3.0	4.6	8.1
				Frosts (days of minimum temperature $< 2^{o}C$)[d]				
1989	0	1	8	10	11	13	1	0
1990	0	2	6	7	5	8	0	0

[a] Long-term mean from 34 years
[b] Long-term mean from 3 years
[c] Long-term mean from 72 years
[d] Long-term mean not available

Table 2.1b. Monthly observed and derived weather statistics at Moombooldool

	April	May	June	July	Aug.	Sept.	Oct.	Nov.
				Maximum temperature (^oC)[a]				
Mean	23.2	18.1	14.5	13.7	15.4	18.4	22.1	26.3
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 (^oC)[a]				
Mean	9.2	6.6	3.4	2.6	3.6	5.4	8.3	11.2
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
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 $m^{-2}d^{-1}{}^oC^{-1}$)[b]				
Mean	0.9	0.5	0.8	1.0	1.1	1.2	1.2	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)[b]				
Mean	42.0	44.0	32.0	29.0	38.0	37.0	47.0	27.0
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
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

[a] Long-term mean from 29 years at Griffith and 17 years at Temora
[b] Long-term mean from 29 years at Griffith

Table 2.1c. Monthly observed and derived weather statistics at Wagga Wagga.

	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
				Maximum temperature (^oC)[a]					
Mean	22.1	16.9	13.6	12.4	14.3	17.3	21.1	25.3	29.2
1989	22.7	18.7	13.1	12.4	13.1	16.6	22.8	26.4	32.0
1990	23.5	18.8	13.5	12.9	13.3	17.5	22.7	28.4	32.6
				Minimum temperature (^oC)[a]					
Mean	9.1	5.9	3.5	2.5	3.6	5.1	7.8	10.5	13.6
1989	12.3	8.9	4.4	3.2	3.0	3.8	6.9	11.8	13.5
1990	12.8	6.5	4.0	5.0	5.2	6.5	8.3	11.9	14.7
				Rainfall(mm)[a]					
Mean	44	54	45	54	54	50	61	43	41
1989	113.1	86.8	45.5	31.2	71.2	21.3	53.3	58.6	20.9
1990	83.6	76.0	28.4	63.6	77.7	48.3	48.2	9.8	9.4
				Potential evapotranspiration (mm d^{-1})[b]					
1989		1.9	1.1	1.1	1.6	2.3	5.2	5.8	9.8
1990	3.8	2.0	1.2	1.2	1.8	3.4	4.7	8.8	10.8
				Frosts (days of minimum temperature $<2^oC$)[b]					
1989	0	1	7	9	7	3	1	0	0
1990	0	4	7	5	6	1	0	0	0

[a] Long term mean from 44 years [b] Long term mean not available

Sowing dates at every site and year are shown in Table 2.2 as well as seeding rate, length of fallow and soil type. Limitations on seed availability in 1989 resulted in slightly lower seeding rates in that year than in 1990. For the same reason, in 1989, the MWM isolines were not included in the last sowing at any site and, at Moombooldool, the MQ isolines were excluded in the last sowing. In 1990, heavy rain during April prevented an April sowing at all sites.

Phosphorus and nitrogen fertilizer was banded with the seed at a rate of 22 kg/ha P at Condobolin and of 20 kg/ha N and 14 kg/ha P at the other sites. A further 45 kg/ha N was applied as urea during tillering or beginning of stem elongation at all sites. Plot size was 15m by 2.2m (12 rows) at Condobolin in 1989. This length was increased to 20m in 1990. At Moombooldool and Wagga Wagga, plot size was 10m by 1.8m (10 rows) in both years. Nearest neighbour designs were used for all sowings and there were three replicates.

An insecticide (Le Mat^R) was applied to the experiment at Wagga Wagga in July 1989 to control lucerne flea. Herbicides (Bromoxynil MA, Buctril^R and Hoegrass^R) and a fungicide (Bayleton^R) were applied when required. After the earliest lines were at the beginning of stem elongation, weeds were removed by hand at Wagga Wagga during both seasons.

The presence of aphids in the experiments was monitored to estimate the risk of barley yellow dwarf virus (BYDV) infection. In 1990 rows of Coast Black oats, which are very sensitive to BYDV, were sown as indicator plots for the presence of the virus. Random plants samples were taken at Condobolin and Wagga Wagga for enzyme-linked immunosorbent assay (ELISA) tests when aphids were first detected in August. In October 1990, the flag leaf of twenty random plants were taken from every plot of 6M9 and from Rosella at Wagga Wagga. Every leaf was tested separately for the presence of BYDV using a double antibody sandwich ELISA test (Voller *et al.*, 1976). Plates for the test were first coated with an antibody specific for BYDV. Virus in the sap samples were then bound to the wells by the antibody. The sap was previously extracted from every leaf with stainless steel rollers and mixed with a buffer at a constant proportion (volume/weight) for every sample. After washing, the same antibody previously conjugated with alkaline phosphatase was added again to bind with the virus. When the substrate for the conjugated enzyme was added, a coloured product is produced that is proportional to the virus. The change in color was compared with the change in color of control sap extracted from infected wheat in the laboratory and from healthy plants. The proportion of infected plants per plot was estimated from the number of infected leaves.

Table 2.2. Experiments description

Experiment designation	Year	Site	Length of fallow	Sowing date	Sowing rate (kg ha^{-1})	Soil type
C1-89	1989	Condobolin	7 months	17/April	45	gradational
C2-89				26/May	45	red earth
C3-89				22/June	45	
M1-89	1989	Moombooldool	7 months	26/May	50	solonized,
M2-89				23/June	50	brown mallee
W1-89	1989	Wagga Wagga	5 months	20/May	50	grey silty
W2-89				23/June	50	clay loam
C1-90	1990	Condobolin	5 months	1/May	50	
C2-90				26/May	60	
C3-90				22/June	60	
W1-90	1990	Wagga Wagga	4 months	3/May	50	
W2-90				5/June	60	
W3-90				11/July	60	
M90	1990	Moombooldool	7 months	6/June	60	

2.2.3 Measurements

Anthesis was considered to have occurred at the time when 50% of the spikes in the plot had visible anthers. At maturity, samples of above-ground material were taken in every plot to determine harvest index (HI, the ratio of the grain divided by the total biomass of the sample). The fertile culms in the sample were counted in every experiment except in the first sowing at Moombooldool in 1989 and in the three sowings at Condobolin in 1990. Plant height was measured to the tip of the ear and the percent of lodging was estimated. Plots were machine harvested and the total above-ground dry weight was calculated from the grain yield (machine harvest) and HI (hand harvested sample). The number of culms m^{-2} was estimated from the number of fertile culms in the sample and the plot yield. One hundred kernels were weighed from the machine harvest sample and number of kernels/m^2 and kernels/spike calculated. Grain samples were ground and analysed for the total nitrogen (N%) by near infrared reflectance (NIR). Grain protein was estimated as N% x 5.9.

For comparative purposes water-use-efficiency (WUE) was calculated here as the total above ground biomass per unit of rainfall between April and October.

2.3 RESULTS AND DISCUSSION

Data on the ten highest yielding lines in every sowing and site are presented in this chapter. This is to show, for comparative purposes, the potential yields and the characteristics associated with achieving these yields in each sowing date at each site.

2.3.1 Meteorological data

In 1989, the accumulated rainfall during the growing season was similar to the average at each site but the distribution varied. Most of the rain fell during the first half of the season whereas the early spring period was relatively dry, especially at Condobolin in September. By contrast, the season in 1990 probably started with the soil at field capacity after heavy rains in April, especially at Condobolin where the rain during this month was equivalent to the long term mean for the whole growing season. April sowings were not possible because of this.

Minimum temperatures were low in September 1989 at Condobolin and Moombooldool (Table 2.1) and frost damage was considerable in the early flowering lines sown in April. In 1990, temperatures were milder and only the very early flowering line in the first sowing suffered frost damage.

2.3.2 Anthesis date

Table 2.3 shows the average time to anthesis of the 10 highest yielding lines in each sowing date and site. The time to anthesis decreased with later sowings at each

site. In 1989, at Condobolin, the time from sowing to anthesis was reduced by 32 and 54 days in the second and third sowing respectively when compared to the first sowing. Similar reductions were observed in other sites and years. These large differences were still maintained when time was expressed in heat units (thermal time). Figure 2.1 shows a general relationship between sowing date and the anthesis date to obtain maximum yield at any site and year. There was a reduction of 0.7 days (8.3 ^{o}Cd) per day delayed in sowing after April.

Table 2.3. Sowing, anthesis date and duration between sowing and anthesis, above-ground dry weight (AGDW), yield and harvest index of the ten highest yielding lines in every sowing and site. Mean and s.e.m.

	Sowing date (d.o.y.)[a]	Anthesis date (d.o.y.)[a]	(d.a.s.)[b]	(^{o}Cd)[c]	AGDW (g m^{-2})	Yield (g m^{-2})	Harvest Index
C1-89	**108**	**273**	**165**	**1884**	**908**	**194**	**0.21**
		1	1		39	9	0.01
C2-89	**147**	**279**	**132**	**1342**	**654**	**205**	**0.32**
		1	1		22	5	0.01
C3-89	**174**	**285**	**111**	**1128**	**326**	**119**	**0.37**
		1	1		13	3	0.08
C1-90	**122**	**278**	**156**	**1717**	**1334**	**434**	**0.33**
		2	2		43	11	0.01
C2-90	**147**	**282**	**135**	**1452**	**1237**	**406**	**0.33**
		1	1		29	10	0.01
C3-90	**174**	**288**	**114**	**1275**	**775**	**257**	**0.33**
		2	2		16	4	0.01
M1-89	**147**	**289**	**142**	**1401**	**706**	**286**	**0.41**
		2	2		15	5	0.01
M2-89	**175**	**298**	**123**	**1250**	**540**	**195**	**0.36**
		1	1		26	8	0.01
W1-89	**141**	**295**	**154**	**1590**	**885**	**353**	**0.40**
		1	1		21	7	0.01
W2-89	**175**	**302**	**127**	**1421**	**766**	**299**	**0.39**
		1	1		23	10	0.01
W1-90	**124**	**281**	**157**	**1655**	**1157**	**399**	**0.35**
		2	2		33	3	0.01
W2-90	**157**	**295**	**138**	**1535**	**902**	**327**	**0.36**
		1	1		16	5	0.01
W3-90	**193**	**305**	**112**	**1129**	**546**	**166**	**0.31**
		4	4		22	1	0.01

[a] Day of the year
[b] Days after sowing
[c] Thermal time using mean temperatures from Table 2.1

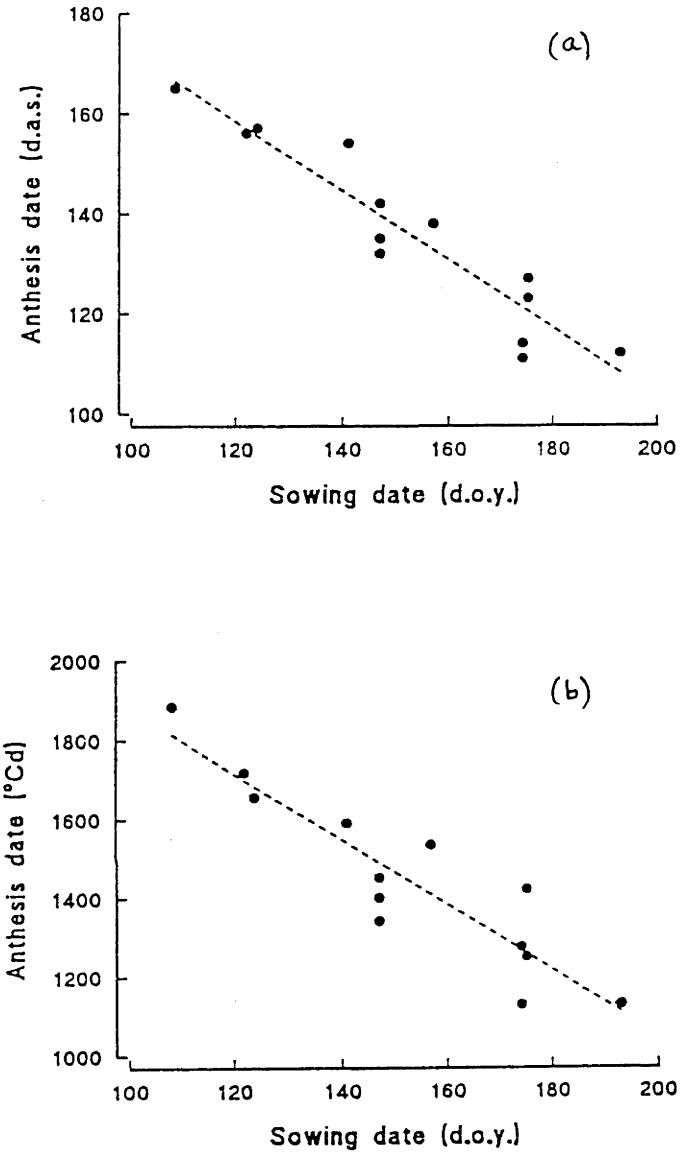


Figure 2.1. Average site-year anthesis date (a) in days after sowing (d.a.s.) and (b) in thermal time (^{o}Cd) of the ten highest yielding lines in all sowings, versus sowing date (day of the year).

2.3.3 Above-ground biomass and yield

The average grain yield, above-ground dry weight (AGDW) and harvest index (HI) of the ten highest yielding lines in each sowing is shown in Table 2.3. The AGDW was greatest in the early sowings at each site. Figure 2.2a shows the AGDW expressed as a percentage of the site-year mean for each sowing. AGDW declined by 1% for each day delay in sowing after mid-April. Surprisingly, this was not the same for grain yield. The highest yields were obtained in sowings that ranged from mid-April to late-May. After June grain yield declined by 1.3% for each day delay in

sowing (Fig. 2.2b). The wide optimum period for sowing was obtained using material that varied largely in flowering time. In Chapter 5, the optimum flowering time for every site is determined.

Harvest index was remarkably stable for sowings at each site (Fig. 2.2c). The exceptions were the very low HI in the earliest sowing at Condobolin 1989 and the high HI in the latest sowing at Condobolin 1989. Ignoring these values, there was a trend for a reduction in HI with late sowing (0.13% per day delay in sowing after early May).

The results at Condobolin 1989 are of particular interest as the range in sowing dates was greatest and it was the only site at which there was a very early planting. It is of interest because it had the greatest yield potential, ie it had the greatest AGDW, yet grain yield was low. If HI had been the same as in the conventional planting date in May then, grain yield would have been 40% higher than what was achieved. A low harvest index has been found before in early sowings in south-eastern Australia (Hollamby *et al.*, 1986; Batten and Khan, 1987).

The lower than expected grain yield and the low HI in the earliest sowing at Condobolin 1989 could be the result of a number of factors. It could be due to earlier flowering and frost damage. This is considered unlikely because early flowering lines with visual frost damage were eliminated from the data set in Table 2.3 and only the late flowering lines were included. It could be that the longer growth duration and biomass accumulation in early sown crops depletes soil water so that little remains after anthesis (Fischer, 1979; Marshall, 1987). This often results in shrivelled or smaller kernels. However, early sown crops in this study did not show visual signs of severe drought, and furthermore, kernels were in fact heavier in the earlier sowings (Table 2.4). The possibility of drought causing the lower harvest index in early sown crops therefore seems remote.

The explanation for the lower HI and yield of lines sown early that is favoured is to do with competition for assimilates between the growing spike and the elongating stem which is likely to be greater in early sown than in later sown crops. Early sowing results in earlier floral initiation and earlier flowering than crops sown later. Thus, in early sown crops, spike development would be occurring when radiation is low and this is likely to prevent crops from developing a large potential sink size (Fischer and Stockman, 1986). Furthermore, as will be evident in later chapters, early sown crops have a longer vegetative period which results in more leaves forming on the main stem which in turn resulted in more internodes and greater height. Table 2.4, for example, shows that stem height was greatest in the early sowings and declined with later sowing. This was most evident at C89 where differences in sowing date were greatest. Thus, it is suggested that the principal reason for low yields typically found in early sowings is the competition for carbohydrates between the growing spike and elongating stem when radiation levels are low. If this is the case

then HI and kernel number per m^2 would be lowest in the earliest sowing. Table 2.3 shows this to be true for HI in the earliest sowing at C89. Table 2.4 shows the lower kernel number per m^2 (KNO) at C1-89.

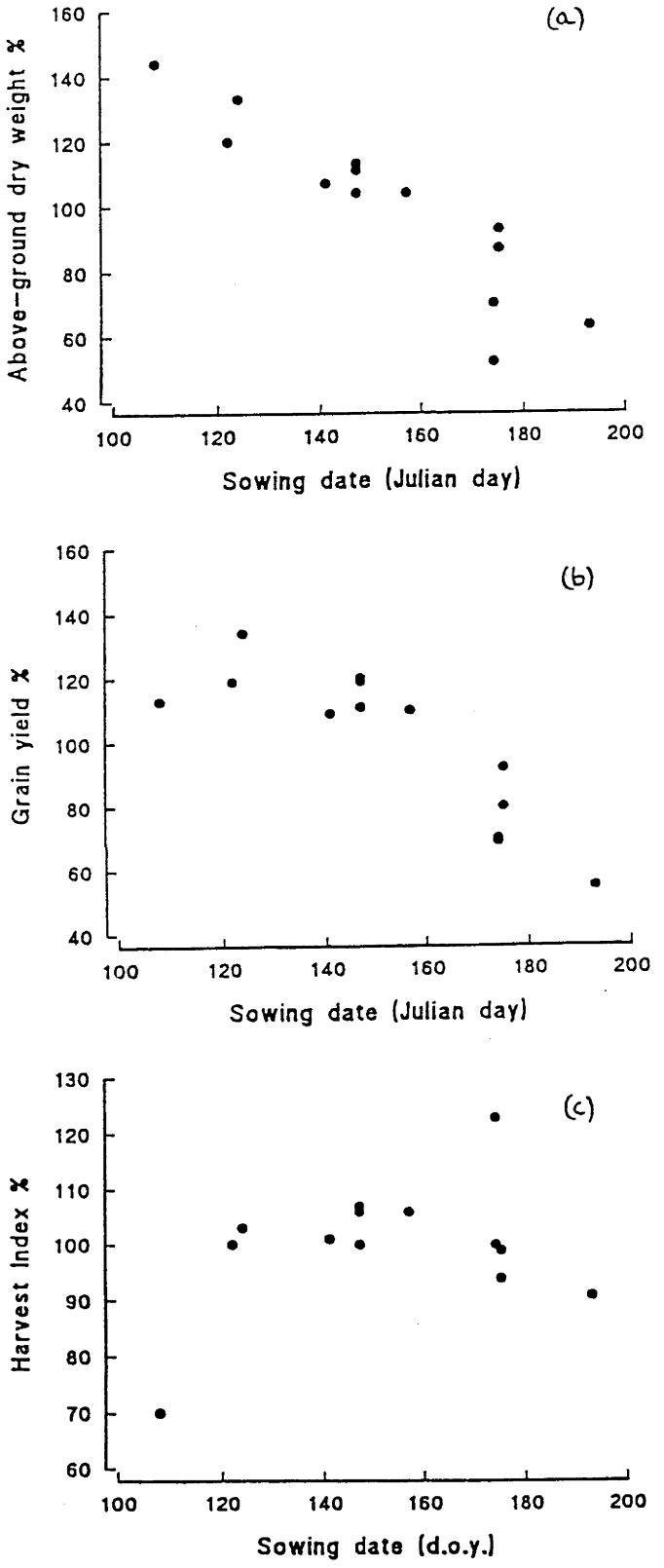


Figure 2.2. Percentage of the site-year mean for (a) above-ground dry weight (AGDW), (b) grain yield and (c) harvest index of the ten highest yielding lines in all sowings.

Table 2.4. Average kernel weight, kernels per unit area, percent of protein in grain, crop height and water-use efficiency of the ten highest yielding lines in every sowing. Mean and s.e.m.

	Kernel weight (mg)	Kernels per m^2	Seed protein %	Height (cm)	WUE (kg $ha^{-1}mm^{-1}$)
C1-89	**33.9**	**5735**	**15.2**	**98**	**36.0**
	1.1	271	0.4	2	1.6
C2-89	**30.8**	**6690**	**14.3**	**72**	**26.0**
	0.7	200	0.6	3	0.9
C3-89	**32.8**	**3648**	**13.2**	**58**	**12.9**
	0.1	182	0.2	1	0.5
C1-90	**37.6**	**10688**	**9.5**	**95**	**26.4**
	1.1	283	0.8	2	0.8
C2-90	**34.4**	**10354**	**9.1**	**97**	**24.5**
	0.5	346	0.6	2	0.6
C3-90	**31.7**	**7896**	*a*	**88**	**15.3**
	0.8	316		4	0.3
M1-89	**39.1**	**7334**	**9.1**	**78**	**26.1**
	0.8	181	0.5	2	0.6
M2-89	**38.4**	**5093**	**11.1**	**69**	**19.9**
	1.0	194	0.9	1	0.9
W1-89	**37.3**	**9480**	**9.6**	**96**	**21.0**
	1.2	245	0.5	3	0.5
W2-89	**37.0**	**8077**	**12.6**	**82**	**18.1**
	1.0	175	0.3	2	0.6
W1-90	**35.2**	**11312**	**9.5**	**97**	**26.5**
	0.7	239	0.4	2	0.7
W2-90	**31.0**	**10579**	**11.0**	**85**	**20.7**
	0.4	183	0.3	2	0.4
W3-90	**26.1**	**6234**	**13.0**	**81**	**12.4**
	0.8	199	0.6	4	0.5

a not available

The low KNO in the very early sowing is also evident when it is related to AGDW at maturity. This provides a measure of expected kernel number for a given sowing time. In all sowings and sites the KNO per unit AGDW was similar with little variation (10.2 $\pm$ 0.3 kernels per g AGDW) whereas in the early sowing at C89, this value was only 6.3 kernels per g AGDW. Thus kernel number which is determined in the 15 days before anthesis, is very much lower than expected in the early sowing and this is interpreted as an indication of greater competition for assimilates between the growing spike and the elongating stem. This hypothesis is further expanded in Chapter 6 and the consequences for winter wheat breeding are also discussed (Chapter 6).

The decline in grain yield and biomass with sowings in mid-June and early July have been reported before (Fischer and Kohn, 1966; Kohn and Storrier, 1970;

Fischer, 1979; McDonald *et al.*, 1983). Figure 2.3 shows that for sowings after June grain yield was mainly limited by the low number of kernels (1% per day delay in sowing after June) whereas kernel weight was less affected by sowing date (0.2% per day delay in sowing after mid April). The small variation in kernel weight with sowing date suggests that any significant increase in the number of kernels of early and late sown crops would result in an increased grain yield.

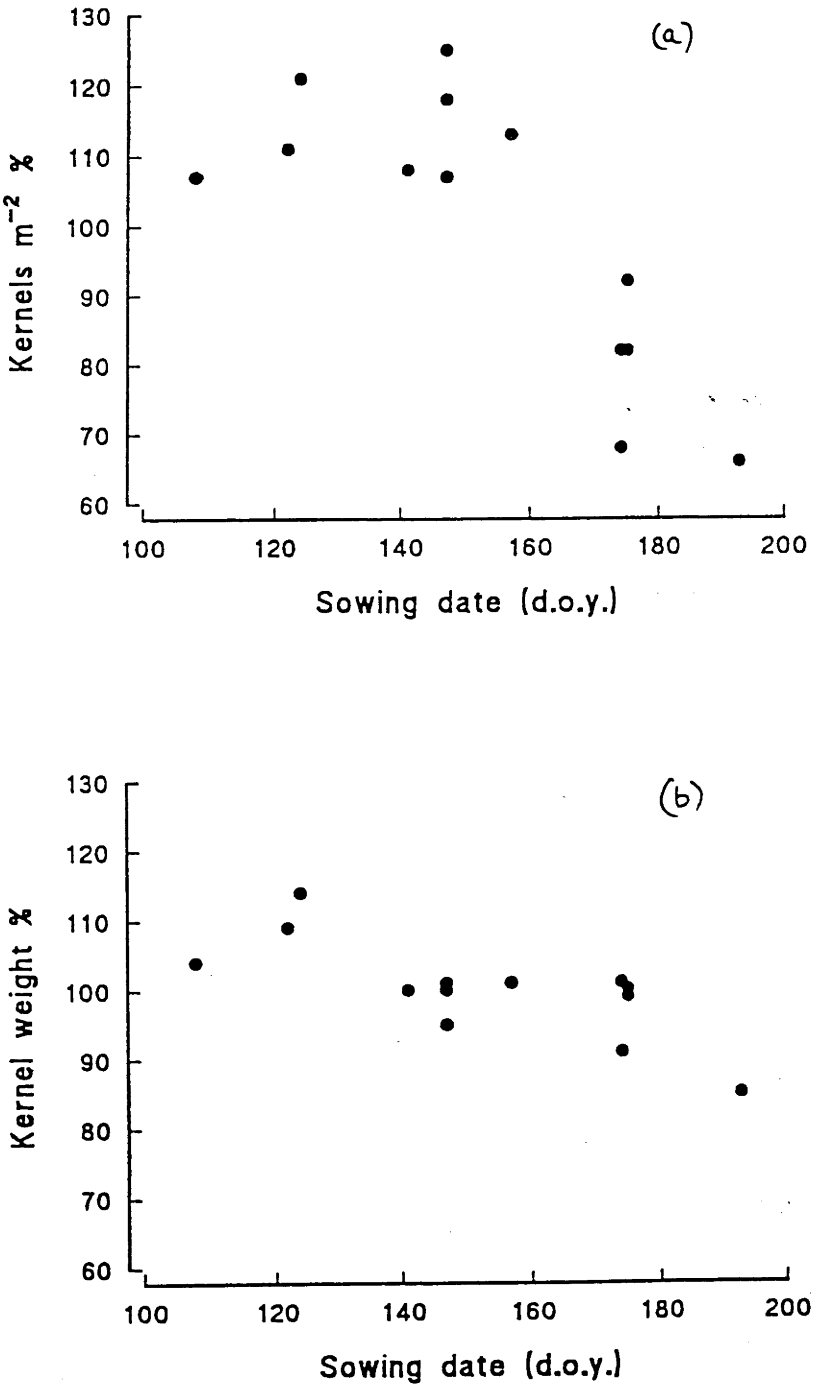


Figure 2.3 Percentage of the site-year mean for (a) the number of kernels and (b) kernel weight of the ten highest yielding lines in all sowings.

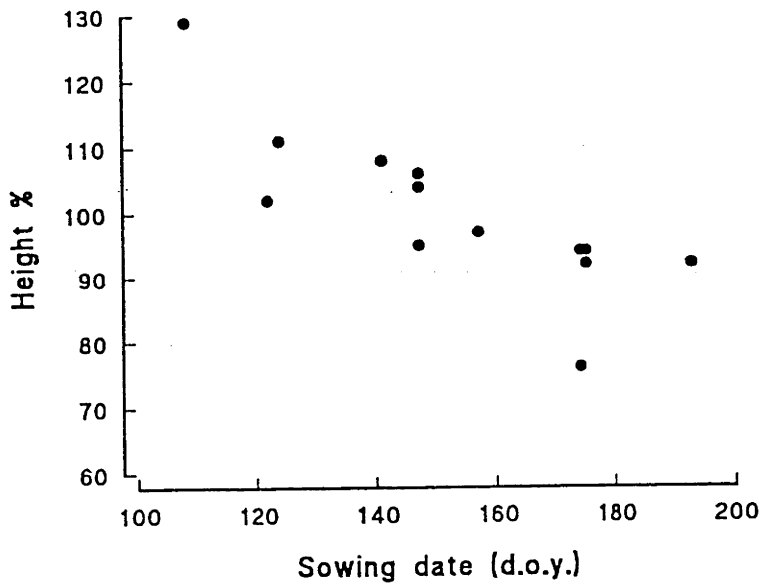


Figure 2.4. Percentage of the site-year mean for the crop height of the ten highest yielding lines in all sowings.

Plant height varied largely with sowing date (Table 2.4). The largest difference was found at Condobolin 1989 where differences in sowing days were greatest. When all sowings and sites were considered, the overall reduction in plant height was of 0.4% per day delay in sowing after April (Figure 2.4).

In southern Australia, low yields of late sown wheats have been attributed to high temperatures (irrigated wheat in the Namoi Valley; McDonald *et al.*, 1983) or greater water deficit around the time of anthesis and during grain filling and resulting in a lower photosynthetic area duration (Fischer and Kohn, 1966; Kohn and Storrier, 1970; Wagga Wagga). Fischer (Wagga Wagga, 1979) suggested that a lower kernel number per unit area and the lower efficiency in the use of the soil water limited yield in late sowings. This was aparent here (Table 2.4).

Water-use efficiency (WUE) expressed here as above-ground dry matter per mm of April-October rain (French and Shultz, 1984) is shown in Table 2.4 and Figure 2.5. Early sown crops had the highest WUE for AGDW (Fig. 2.3) This presumably occurred for two reasons. Firstly, early sown crops probably develop leaf area faster than later sown crops as soil and air temperatures are warmer in April and May than in June or July. The early sown crops would have a greater leaf area index (LAI) during the coolest part of the season when the evaporative demand is low and transpiration efficiency is high (Tanner and Sinclair, 1983). This would result in a more water use efficient crop because of the reduced exchange of H_2O for CO_2 at the leaf level. An improved WUE in early sowings would also result from their faster

early growth and the greater LAI for a longer duration that would result in less soil evaporation than in later sown crops. Chapter 4 will look in more detail at the differences in water use and water-use efficiency between early and late maturity lines sown at different times and the consequences to yield.

Protein percentage in the grain varied widely (Table 2.4). At Condobolin grain protein was greatest in the early sowings whereas at Moombooldool and Wagga Wagga the opposite trend occurred. Kohn and Storrier (1970) expressed concern with early sown crops as they found an increase in grain protein of 0.08% per day delay in sowing after April. This was not the case at Condobolin where early sown crops had higher grain protein than in later sowings and this is more in agreement with Batten and Khan (1987). At Condobolin, there was also a large difference in grain protein between crops in 1989 and in 1990 (Table 2.4). The main reason for this may be the greater fertility of the paddock in 1989 than in 1990. At the sowing in 1989, there had previously been a legume pasture for 2.5 years which was then fallowed for 7 months prior to sowing. The rainfall during the fallow period was well above average favouring the mineralization of soil nitrogen. Thus at sowing there was 52 ppm of soil nitrogen as NO_3^- and 3 ppm as NH_4^+ in the top 30 cm (Table 2.5). Whilst in the adjacent paddock used in 1990, an oat crop had previously been grown during 1989, then cut for hay and fallowed for 5 months until sowing in May 1990. During October 1989 to March 1990 rainfall was below average and there was presumably little mineralization. At sowing, the soil mineral nitrogen in the top 30 cm was 11.9 ppm as NO_3^- and 3.4 ppm as NH_4^+ (Table 2.5). The extreme low protein content in 1990 could mean that the crop was nitrogen deficient (Woodruff, 1992).

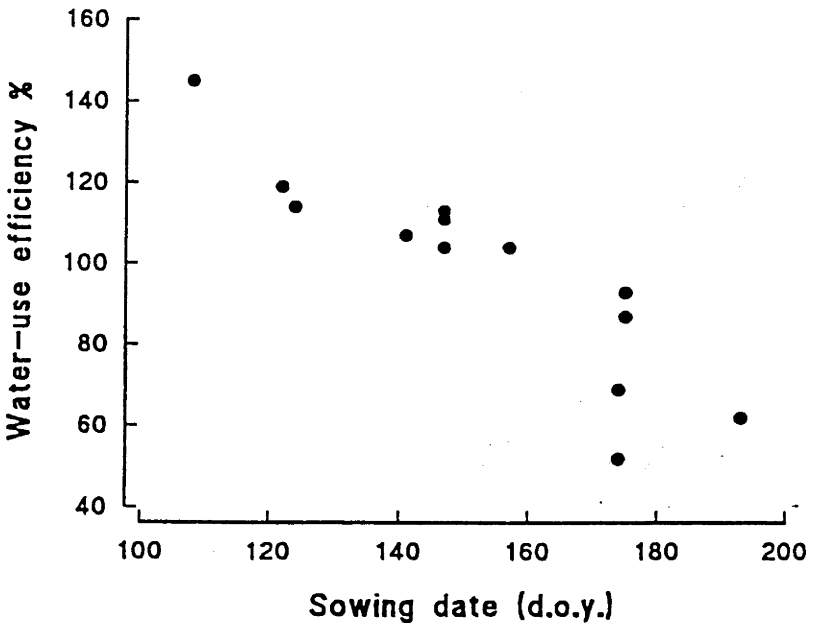


Figure 2.5. Percentage of the site-year mean for water-use efficiency of the ten highest yielding lines in all sowings.

Table 2.5 Soil nitrogen (ppm) in the top 30 cm at sowing time (Condobolin 1989 and 1990).

depth	1989 NO_3^-	1989 NH_4^+	1990 NO_3^-	1990 NH_4^+
0-10 cm	35	2.1	6.4	1.7
10-30 cm	17	1.8	5.5	1.7

2.3.4 Barley yellow dwarf virus (BYDV)

There is a general concern among farmers in New South Wales that earlier sowing increases the risk of BYDV infection. This was not the case in the experiments presented here. In 1989 no symptoms of BYDV infection were observed in any experiment. In 1990 aphids were observed in the crops in mid-August at Condobolin and in mid-September at Wagga Wagga. At Condobolin, ELISA tests did not detect the presence of the virus in either the crop or the Coast Black oat. On the other hand, at Wagga Wagga, the test showed BYDV infection of the wheat plants. In October, an extensive sampling in two of the winter lines showed 3, 12 and 21% of the plants were infected in the first, second and third sowing respectively (data not shown). These results may reflect the preference of aphids to feed on younger plants rather than older plants, and thus, the more developed plants may avoid late infections. At the time of the analysis the plants in the first sowing were in the grain filling phase, the plants in the second sowing were around anthesis and the plants in the third sowing around heading. Also, it has been suggested that winter wheats sown in autumn, that have a well developed root system, are better able to tolerate BYDV (Kainz and Hendrix, 1981).

In the UK, crops sown in early autumn had higher risk of damage by BYDV infection than spring sown crops as aphids that carried the virus had a second period of flight activity in early autumn (Hill, 1987). However, recent work in the ACT and NSW had shown that late infections during spring rather than early infections in autumn are the most damaging in the wheat crops (Dr. Phillip Banks pers. comm.). In Victoria, the overall loss in yield caused by BYDV infection has been estimated at 2% and only in the very wet environments the yield loss increased to a maximum of 20% (Sward and Lister, 1987). This suggests that in the drier environments within the wheatbelt the fear of yield losses due to BYDV may be overstated. However, because of the lack of information in aphid migrations in southern Australia and the enormous variability between locations and years, there is still a need for further research on BYDV infection and yield losses.

CHAPTER 3

VARIATION IN PHENOLOGY WITHIN AND BETWEEN SOWING TIMES

3.1 INTRODUCTION

The time from sowing to anthesis can vary substantially depending on the time of sowing and on genotype. In the previous Chapter it was shown that the highest yielding lines for a mid April sowing at Condobolin flowered after 165 days (about 1880 ^{o}Cd) whereas for an early July sowing the highest yielding lines flowered after 112 days (about 1130 ^{o}Cd). The aim of this Chapter is to understand the variation in development of different isogenic lines and populations sown at different times and sites.

Davidson and Christian (1984) recognised three simple phenological stages between seed germination and flowering time. These were vegetative, spikelet initiation period and ear development. Ear development occurs simultaneously with stem elongation. It is often condidered that the spikelet initiation period begins when the first spikelet primordium is visible on the apex (called the double ridge stage, DR) and it finishes when the terminal spikelet is initiated (called the terminal spikelet stage, TS). Although DR stage does not correspond exactly with the the start of the spikelet initiation phase (Dellecolle *et al.*, 1989), its use allows work with a large number of lines as it is less time consuming. During spikelet initiation the ear starts initiating florets in each spikelet. At the same time the stem elongates until the ear emerges from the flag leaf sheath and flowering takes place. Flowering time (anthesis) is obvious when the yellow anthers extrude out of the florets. After fertilization of the ovary in the floret a fourth developmental phase may be considered as the grain filling period. This period ends at maturity when the grains are hard and ready to harvest.

The duration of the developmental phases depends on the genotype and the environment. It is known that photoperiod (*Ppd*), vernalization (*Vrn*) and "basic development rate" (Flood and Halloran, 1984a) genes regulate the time from sowing to the beginning of reproductive development (DR) and hence the time from sowing to anthesis. However, little is known about the regulation of the duration of later developmental phases. Photoperiod genes regulate phenology because the beginning of the DR stage only occurs when the photoperiodic or daylength requirement is satisfied, whereas for the vernalization genes a period of low temperatures is required for the transition to DR. The basic development rate (also called intrinsic earliness or earliness *per se*, Masle et al., 1990 and Hoogendoorn, 1985) is defined as the time to reach floral initiation when vernalization and photoperiod do not constrain development. The genetic control of daylength and vernalization response have been

described elsewhere (Pugsley, 1971; Pugsley, 1972; Flood and Halloran, 1986a; Law, 1987). Two recessive genes have major effect on photoperiod response (Ppd_1 and Ppd_2) whereas five recessive genes have been described to control the vernalization response (Vrn_1, Vrn_2, Vrn_3, Vrn_4 and Vrn_5). Other minor genes modulate the response. Basic development rate is poorly understood genetically, though six genes have been described as controlling it (Flood and Halloran, 1984a; Hoogendoorn, 1985; Law, 1987).

Winter wheats are generally described as those which have strong requirements for either vernalization or photoperiod whereas spring wheats are relatively independent of vernalization and photoperiod. In Australia, most current wheat varieties are spring wheats with a slight response to vernalization and only since the mid-eighties have there been high yielding winter wheats available that require vernalization. The vernalization and photoperiod requirements for most of the Australian current varieties have been determined by Syme (1968), Halse and Weir (1970), Davidson *et al.*, (1985) and Penrose *et al.*, (1991).

This chapter describes the variation in phenology found in the genotypes studied in the field experiments described in Chapter 2, as well as the effect of sowing time on development.

3.2 MATERIAL AND METHODS

The origin of the various isogenic groups sown in these experiments and the field studies established were the same as described in Chapter 2. The time to ear emergence of the isogenic lines in the M and B groups is mainly controlled by photoperiod but the basic development rate also varied. In the other three groups (RAC, MQ and MWM) the isogenic lines had vernalization requirements and, to a lesser extent, photoperiod requirements (Appendix 1).

Anthesis date, when 50% of the ears in a plot had visible anthers, was recorded at all sites in all experiments. Physiological maturity was not recorded. More detailed measurements on the time of floral initiation and terminal spikelet were made at the experiments at Condobolin 1989 (C-89) and Condobolin 1990 (C-90). Emphasis was put on the Condobolin trials because of the greater range in sowing dates, and more extensive collection of growth and yield data. Previous studies have found a close relationship between phenology at Condobolin and Moombooldool (Lopez-Castaneda, 1992).

At Condobolin, ten plants of every line were regularly harvested for apex dissection around the time of floral initiation. The time of double ridge and terminal spikelet stages (Kirby and Appleyard, 1984) and the final number of initiated spikelets were determined in the main stem on all lines. Time to appearance of double ridge,

terminal spikelet and anthesis were determined in days and in thermal time. Thermal time was calculated as the accumulation of daily degree days (ΣT_i):

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

where T_{max} and T_{min} are the maximum and minimum daily air temperature on the *ith* day and T_b is the base temperature below which no growth occurs (0°C was used in this study). The experiments were located close to the meteorological station.

The results were also analysed using photothermal units as defined by Masle *et al.* (1989). However, as there were no significant differences with thermal units, it was decided to present the data in the more commonly used thermal units.

3.3 RESULTS

3.3.1 Variation in anthesis date

The time to anthesis of the different lines at the different sites was closely related. Figure 3.1 shows the relationship between genotypes sown at comparable times at the two most extreme sites, Wagga Wagga and Condobolin. The slopes of the lines for each sowing (May sowing: y (Wagga) = 1.04x (Condobolin) + 15 ; June sowing y (Wagga)= 0.89x (Condobolin) + 28) were close to unity indicating almost identical behaviour of lines at the two sites in each sowing date. The coefficient of variation (r^2) was also high, being 0.96 in the May sowing and 0.89 in the June sowing which also indicates the similar flowering behaviour at the two sites. However, the mean flowering time at Wagga Wagga, the cooler site, was 16 and 15 days later than at Condobolin for a similar sowing time in late May and June respectively. In thermal time, the difference in the mean flowering time with a similar sowing date (Wagga Wagga minus Condobolin) was 162 °Cd and 133 °Cd in the earlier and later sowing respectively (data not shown). The reason for the difference in thermal time to reach anthesis between the sites is not known. One cause may have been lower soil temperatures between sowing and terminal spikelet at Wagga Wagga as the apex up to double ridge is typically 1 or 2 cm below the soil surface. This is supported by the limited dissection data collected from plants grown at W-89. The data, although not complete, reveal a difference in time to DR or to TS between plants sown at similar dates at W-89 and C-89 of 300 °Cd, double the difference found at anthesis. A consistent error in the measurement of temperature equivalent to 1 °C at the two sites could also account for the difference in thermal time to reach anthesis.

A similar association between flowering time of different genotypes was evident with different sowing dates at the same site (Fig. 3.2). Surprisingly, there was less association between the genotypes at the diverse sowings at the same site than at different sites. Thus, the average coefficient of variation (r^2) between Wagga Wagga and Condobolin in 1989 in two comparable sowings was 0.90 whereas between

sowing dates at Condobolin 1990 the coefficient of variation averaged 0.82. This presumably reflects the greater diversity in environments generated by different sowing dates than by different sites. This was particularly evident in the early sowing (C1-89) when differences in vernalization and photoperiod responses were more fully expressed. Figure 3.2 shows the much greater range in time to reach anthesis in the early sowing compared to the later sowings although this clearly varied between early flowering and late flowering lines. The relationships between days to flowering in the different sowings were as follows:

$$SD2 = 0.42\ SD1 + 68\ ;\ r^2 = 0.81$$
$$SD3 = 0.35\ SD1 + 60\ ;\ r^2 = 0.83$$
$$SD3 = 0.76\ SD2 + 13\ ;\ r^2 = 0.93$$

These equations show the substantial deviations from unity (slope of 1.0) for the different lines, particularly in relation to the first sowing (SD1). A slope less than 1.0 indicates a larger range in flowering time between the lines in the earlier sowing (41 days) than in the second (SD2) and third (SD3) sowings (25 and 20 days respectively). It is also evident that the similarity between the lines was greater between SD2 and SD3 ($r^2 = 0.93$) than between the first and the subsequent sowings. Figure 3.2 also shows that there is a faster approach to flowering in the later flowering lines when sowing date is delayed.

When time is expressed in thermal time, rather than days, very similar results were found (Fig. 3.3) though SD2 and SD3 were more similar in thermal time. The following are the relationships between sowing dates when results are expressed in thermal time:

$$SD2 = 0.51\ SD1 + 457\ ;\ r^2 = 0.80$$
$$SD3 = 0.47\ SD1 + 355\ ;\ r^2 = 0.81$$
$$SD3 = 0.84\ SD2 + 35\ ;\ r^2 = 0.93$$

Thus whereas thermal time cannot account for differences in time to anthesis between lines in the first sowing and the later sowings, it largely accounts for the differences between SD2 and SD3. This is also shown by the difference in time to reach anthesis between SD1 and SD2 of 20 days and between SD1 and SD3 of 38 days but only 370 and 440 ^{o}Cd in thermal time respectively (Table 3.1). The explanation for the substantial differences between the first sowing and the later sowings at C-89 is the different vernalization and photoperiod responses of the genotypes in the different sowings.

Table 3.1 shows the variation in time to anthesis with sowing date at Condobolin 1989 and Table 3.2 summarises the range in flowering time in each isogenic group and the change with sowing date at C-89. The range declined with later sowings in all groups. The likely explanation for the differences noted in both tables is the different genetic control of flowering between the groups. It is likely that vernalization sensitive genes are responsible for the similar flowering times in the RAC, MQ and MWM in SD2 and SD3. Both of these sowings were made when

temperatures were very low and vernalization sensitive lines would be little different to vernalization insensitive lines (ie the former would be receiving their cold stimulus but growth would not advance greatly in any lines because of the low temperatures). On the other hand, for the M and B groups, although they may also possess vernalization sensitive genes, the likely controls of flowering in these lines are genes that are sensitive to photoperiod or to the basic development genes.

The flowering time of early and late lines tended to converge with later sowings in agreement with McDonald *et al.* (1983), Stapper and Fischer (1990) and Hay and Kirby (1991) for similar sowing dates. This was caused by the greater reduction in time to anthesis with sowing date in the late flowering lines than in the early flowering lines. Figure 3.4 shows that the flowering time of an isogenic late line in the predominantly photoperiod controlled group (M group; similar results observed in the B group) was reduced more with sowing date (0.71 days per day delay in sowing after April 17) than the earliest or intermediate flowering isogenic counterparts (0.31 and 0.45 days reduced per day delayed at sowing after April 17 respectively). The late flowering lines in the vernalization controlled groups (RAC and MWM) had a reduction in anthesis day of 0.69 or 0.61 days per day delayed at sowing after April 17 (Fig. 3.4b), a reduction slightly lower than for the late photoperiodic line although in all sowings they generally needed less days to flower. The convergence in anthesis time with sowing date is very evident in the MWM pair shown in Fig. 3.4b. The winter genotype took 10 more days to flower than the spring genotype at the earliest sowing but both genotypes flowered on the same day at the last sowing.

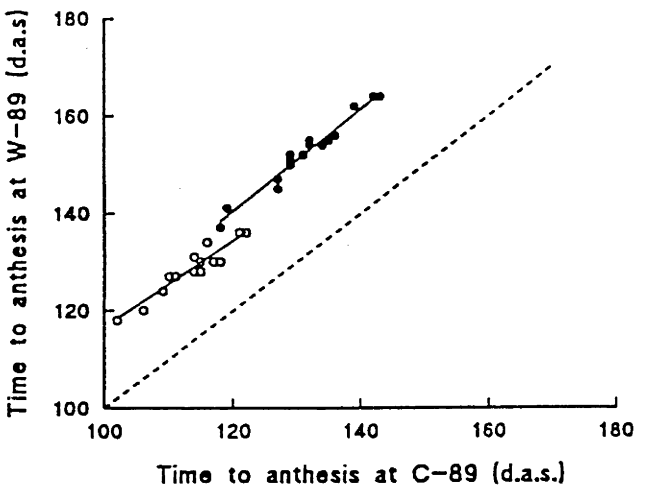


Figure 3.1 Relationship between days to anthesis of lines sown at similar dates at Condobolin and Wagga Wagga in 1989 (C2-89 *vs* W1-89 (●); C3-89 *vs* W2-89 (○).

Table 3.1 Time to anthesis of isogenic lines grown at Condobolin in 1989.

	C1-89		C2-89		C3-89	
	d.a.s.	°Cd	d.a.s.	°Cd	d.a.s.	°Cd
1M1S	127	1440	118	1142	102	996
1M5	141	1377	127	1260	109	1094
1M7	143	1596	129	1293	110	1107
1M10	143	1596	129	1293	110	1107
6M7	144	1609	132	1337	114	1173
6M9	168	1913	143	1504	122	1318
1B2	136	1527	119	1159	106	1054
1B5	142	1586	127	1260	109	1094
1B9	143	1596	129	1293	110	1107
6B1	145	1629	131	1322	111	1121
6B6	160	1802	135	1379	115	1190
1B10	168	1913	139	1439	116	1207
6B9	168	1913	142	1488	121	1303
RAC 416-1	156	1749	132	1337	114	1173
RAC 417-2	164	1853	134	1364	115	1190
RAC 417-3	167	1902	136	1392	117	1224
RAC 417-5	167	1902	136	1392	118	1249
MQs	144	1609	129	1293	111	1121
MQw	161	1820	131	1322	111	1121
MWMs short	144	1609	127	1260		
MWMw short	154	1725	130	1304	not sown	
MWMs tall	144	1609	130	1304		
MWMw tall	151	1691	129	1293		
mean	151	1694	131	1323	113	1155
s.e.	3	33	1	18	1	19

Table 3.2 Range in days and thermal time (°Cd) between the earliest and latest flowering lines in each isogenic group at each sowing at Condobolin, 1989.

Isogenic	C1-89		C2-89		C3-89	
group	d.a.s.	°Cd	d.a.s.	°Cd	d.a.s.	°Cd
M	41	473	25	362	20	322
B	32	386	23	329	15	249
RAC	11	153	4	55	4	66
MQ	17	211	2	29	0	0
MWM	7	116	3	44	*a*	

[a] Not sown at C3-89

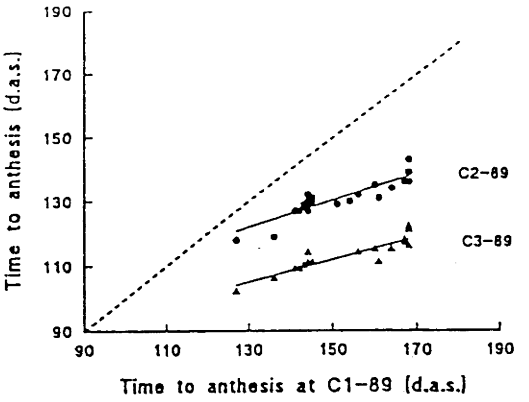


Figure 3.2 Relationship between time to anthesis (days after sowing) at C1-89 and at C2-89 (●) and between C1-89 and C3-89 (▲).

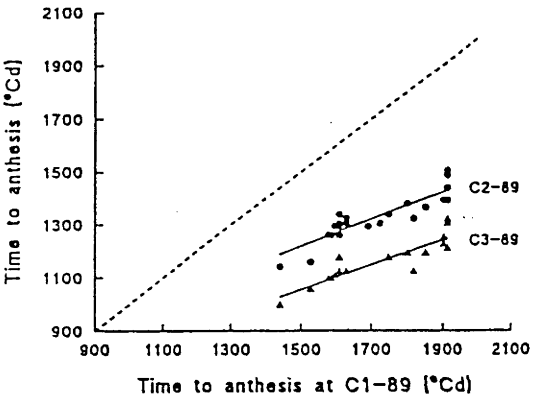


Figure 3.3 Relationship between time to anthesis (thermal time) at C1-89 and at C2-89 (●) and between C1-89 and C3-89 (▲).

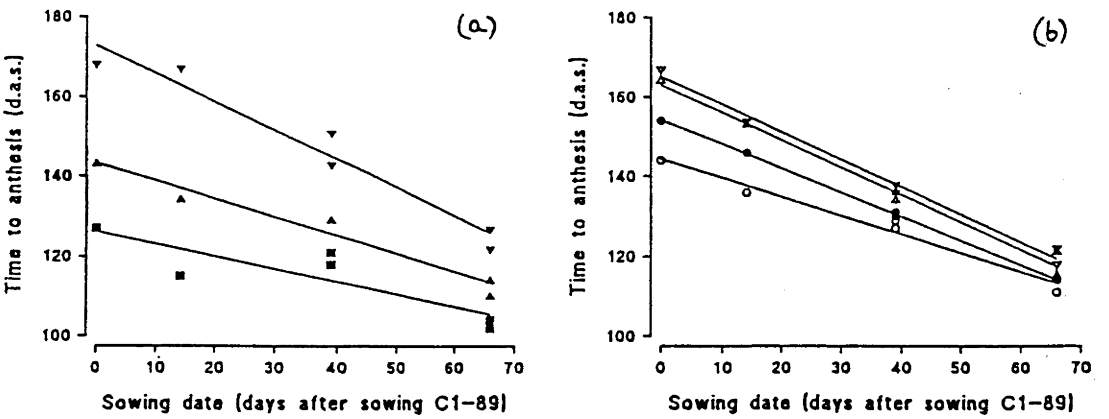


Figure 3.4 Relationship between sowing date and time to anthesis (days after sowing) of (a) an early (■), intermediate (▲) and late (▼) flowering lines within the M isogenic group and of (b) an intermediate (○) and late (●) flowering MWM lines and two late flowering (△▽) RAC lines at Condobolin (1989 and 1990).

3.3.2 Variation in the three phenological phases

Expressed in thermal time, the time to DR stage and the interval between TS and anthesis (TS-A) declined as sowing date was delayed at C-89 (Table 3.3). The time to DR stage and the interval TS-A declined substantially between the first and second sowings and there was a further reduction in the third sowing. This contrasts with the more constant interval between between DR and TS though there was some evidence that this interval was shorter in the earliest sowing (Table 3.3).

Table 3.3 Average time in days and thermal time to double ridge stage (DR), spikelet initiation period (DR-TS) and from TS to anthesis (TS-A) at each sowing at Condobolin, 1989. Mean values ± s.e.m.

	DR		DR-TS		TS-A	
	days	°Cd	days	°Cd	days	°Cd
C1-89	40 ± 3	616 ± 31	21 ± 3	226 ± 21	90 ± 1	862 ± 23
C2-89	51 ± 2	495 ± 17	29 ± 1	255 ± 10	51 ± 1	573 ± 8
C3-89	54 ± 1	455 ± 13	22 ± 1	239 ± 11	35 ± 1	461 ± 8

The time to reach the double ridge (DR) and terminal spikelet (TS) stage at Condobolin in 1989 varied both between sowing dates and within lines (Table 3.4) . At C1-89 the range in time to DR stage between lines was 44 days (535 °Cd) and the range in time to TS stage was 84 days (820 °Cd). As may be expected this variation was reduced at C2-89 to 34 days (295 °Cd) and 44 days (405 °Cd) in the time to DR and to TS stage respectively. At C3-89, the range further decreased to 21 days (295 °Cd) and 31 days (340 °Cd) for the same periods.

The range amongst lines in thermal time to DR and TS stage decreased with delayed sowing primarily because the interval between these stages became less in the late flowering lines. In the early flowering lines, the time to reach the DR or the TS stage was very similar in all sowings with the exception of time to DR stage at C1-89. Figure 3.5s shows the relationship between time to DR stage and the period of spikelet initiation (from DR to TS stage) at Condobolin 1989 for each of the isogenic groups. At C1-89 the spikelet initiation period increased as the vegetative period (time to DR) increased in lines of all groups except the MWM group (Fig. 3.5a). A similar increase in the spikelet initiation period was observed for the M and B groups at C2-89 and C3-89 and for the RAC group at C3-89 (Fig. 3.5b and 3.5c). There was very little variation for the other two groups, MQ and MWM, and in the case of MQ the relationship was negative at C2-89 and C3-89.

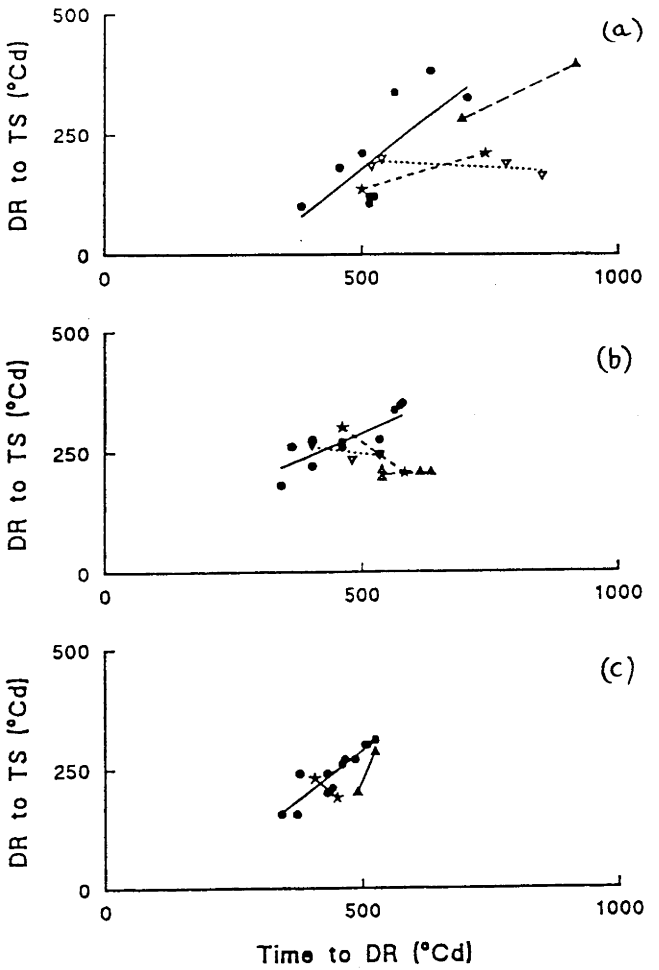


Figure 3.5 Relationship between thermal time to DR and thermal time from DR to TS of the M and B (●), RAC (▲),MQ (★) and MWM(▼) (a) at C1-89, (b) at C2-89 and (c) at C3-89.

The isogenic groups also differed in the relationship between the time to TS stage and the period from TS to anthesis (TS-A) (Fig. 3.6). In general, in the vernalization requiring groups, the period TS-A was shorter in lines that reached TS stage later. The exception was the MQ pair which did not show any difference in the period TS-A between the two lines (data not shown in Fig. 3.6a). The M and B groups had the largest range in the time to DR and between DR and TS but had the least variation in the TS-A period.

The variation in the time to any of the three phenological stages (DR, TS and anthesis) was largest at C1-89. It is in this sowing that the different types of phenological control in the isogenic groups were most apparent. Figure 3.7 shows the different relationships between thermal time to DR stage and anthesis for all isogenic groups sown at C1-89. The groups whose phenology is mainly controlled by vernalization (RAC, MQ and MWM groups) had a greater range in the time to DR stage than in time to anthesis showing an acceleration in development from the DR stage to anthesis for some of the lines. The slopes of the lines for the RAC, MQ and

MWM groups were 0.5, 0.9 and 0.3 ^{o}Cd respectively. These differences were mainly caused by the long vegetative period of the late lines in the RAC, MQ and MWM groups and by their shorter period between TS stage and anthesis in the late lines than in their earlier counterparts (Fig. 3.6). On the other hand, in the basic development and photoperiod controlled groups (M and B groups), the range in time to DR stage was smaller than the range in time to anthesis (Fig. 3.7: slope = 1.64 ^{o}Cd). In later sowings, all groups (photoperiod and vernalization controlled groups) tended to have similar relationship between time to DR stage and time to anthesis (Fig. 3.7). Thus, at C3-89 all groups fitted the relationship defined by: y (anthesis) = 1.35x (DR) + 540 (r^2=0.830, $p<0.001$).

In 1990 similar results were found in the smaller subset of lines. These results are presented as Appendix 2.

Table 3.4 Time to double ridge (DR) and terminal spikelet (TS) stage of isolines grown at Condobolin in 1989.

Sowing	C1-89				C2-89				C3-89			
Stage	DR		TS		DR		TS		DR		TS	
	d.a.s.	^{o}Cd	d.a.s.	^{o}Cd	d.a.s.	^{o}Cd	d.a.s.	^{o}Cd	d.a.s.	^{o}Cd	d.a.s.	^{o}Cd
1M1S	22	380	29	480	33	340	55	520	40	340	59	495
1M5	31	515	39	620	39	400	65	620	45	375	70	615
1M7	31	520	40	640	46	460	78	730	51	430	76	670
1M10	31	515	40	635	39	400	72	675	51	430	76	670
6M7	32	525	40	645	46	460	78	730	55	465	81	735
6M9	40	635	77	1015	60	565	96	900	60	510	88	810
1B2	27	455	40	635	35	360	65	620	44	370	61	525
1B5	30	500	47	710	39	400	71	670	51	430	72	630
1B9	30	500	47	710	46	460	77	720	52	440	74	650
6B1	30	500	47	710	57	535	84	780	55	460	80	720
6B6	35	565	64	900	57	535	87	810	57	485	83	755
1B10	46	705	79	1030	61	575	99	920	60	505	87	805
6B9	46	705	79	1030	62	580	99	930	61	525	90	835
RAC 416-1	44	695	74	975	58	540	79	735	58	490	78	690
RAC 417-2	44	695	74	975	58	540	81	750	58	490	78	690
RAC 417-3	66	915	113	1310	64	615	88	820	61	525	88	810
RAC 417-5	66	915	113	1310	67	635	90	840	61	525	88	810
MQs	30	500	40	635	46	460	82	760	48	405	72	635
MQw	49	740	71	950	63	585	85	790	54	450	73	640
MWMs short	32	520	46	705	39	400	70	665				
MWMw short	54	780	73	970	57	535	84	780		not	sown	
MWMs tall	33	540	49	740	48	480	76	715				
MWMw tall	60	850	77	1015	57	535	84	780				
mean	40	616	61	841	51	495	80	750	54	455	76	694
s.e.m.	3	31	5	47	2	17	2	21	1	13	2	22

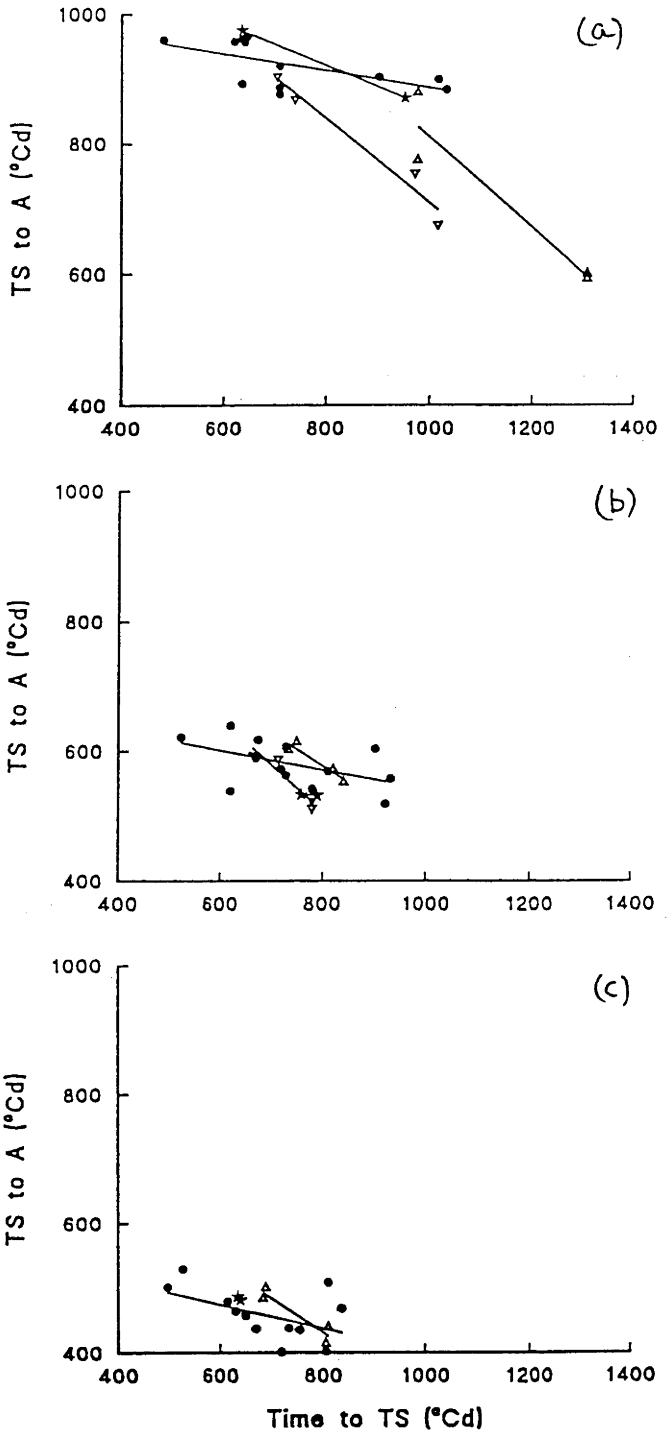


Figure 3.6 Relationship between thermal time to TS and thermal time from TS to anthesis of the M and B (●), RAC(▲), MQ (✱) and MWM (▲) (a) at C1-89, (b) at C2-89 and (c) at C3-89.

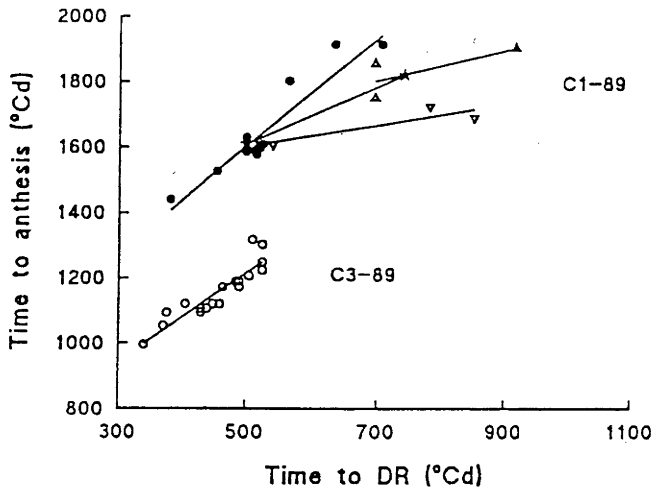


Figure 3.7 Relationship between thermal time to DR and thermal time to anthesis of lines at C1-89 (M and B (●), RAC (▲), MQ (✱) and MWM (▼)) and at C3-89 (all lines (○)).

3.3.3 Variation in spikelet number

Spikelet number was determined in the experiment at C-89. This was to determine whether the longer vegetative period and longer spikelet initiation period that was primarily associated with late flowering lines in all sowing dates resulted in more spikelets. Within most lines, spikelet number per main ear was reasonably constant with sowing date (Table 3.5). The lines with the longest time to DR and DR-TS duration also had the highest number of spikelets (Table 3.5). However, to some extent this was compensated by the longer thermal time required to produce *each* spikelet in the late flowering lines. Thus even though fewer spikelets were produced in the earliest lines because of the shorter duration between DR and TS, the initiation of each spikelet required less thermal time in the earliest lines (Table 3.5). Only in the late flowering lines sown late did the higher rates fail to compensate for the shorter duration and so the final number of spikelets was lower than in the earlier sowing.

In general, within an isogenic group, the late lines had a higher spikelet number (Table 3.5). These lines had a longer period of spikelet initiation but a slower rate of spikelet initiation. The M group at C1-89 showed the largest variation with a difference of 9 spikelets per ear between the earliest and latest lines.

Table 3.5 Final spikelet number per ear, inverse of the rate of spikelet initiation (°Cd/ spikelet), time to DR stage (°Cd) and period of spikelet initiation (°Cd) .

	spklt/spike			°Cd/spklt			Time to DR (°Cd)			Time from DR to TS stage (°Cd)		
	C1	C2	C3	C1	C2	C3	C1	C2	C3	C1	C2	C3
1M1S	17	17	17	5.9	10.6	9.1	380	340	340	100	180	155
1M7	21	22	21	5.7	12.3	11.4	520	460	430	120	270	240
6M1	26	26	23	14.6	12.9	13.0	635	565	510	380	335	300
1B2	21	19	20	8.6	13.7	7.8	455	360	370	180	260	155
6B1	21	20	20	10.0	12.1	13.0	500	535	460	210	242	260
1B10	26	25	22	12.5	13.8	13.6	705	575	505	325	345	300
MWMspr	19	20	*a*	9.7	13.3		520	400		185	265	
MWMwin	21	18		9.0	13.6		780	435		190	245	
RAC416-1	22	18	18	12.7	16.4	7.4	695	540	490	280	295	200
RAC417-5	24	20	18	16.5	10.3	15.8	915	635	525	395	205	285

a not sown

3.4 DISCUSSION

Flowering time in the lines grown in these experiments varied according to their response to vernalization and photoperiod. Lines were very similar at the different sites when sown at about the same time. The greatest variation between lines occurred in the earliest sowing date at C-89 when compared with later sowings. There are a number of possible reasons for the greater differences in development at C1-89. Firstly, the longer daylength during May may have coincided with the juvenile phase when the plant is insensitive to flowering inducing signals such as daylength and vernalization (Roberts and Summerfield, 1987). Secondly, temperatures in May and June might have been too mild to have a substantial vernalizing effect (Flood and Halloran, 1986a). The mean mimimum temperature in May was 9.2 °C compared to 4.4 °C in June (Table 2.1a in Chapter 2). Thirdly, there may have been a delay in initiation as a result of the low photothermal quotient. The photothermal quotient was lower in May than in any part of the year (Table 2.1a in Chapter 2) and the DR stage did not occur until the photothermal quotient became higher. In spite of these factors, lines insensitive to vernalization or photoperiod will initiate floral structures. Thus, the earlier flowering lines will be more similar in different sowings than later flowering lines. Indeed the thermal time to reach DR in the earliest flowering line, 1M1S, was 380 °Cd in the first sowing at C-89 and 340 °Cd in the subsequent sowings. The times to DR were also similar in all sowings (Table 3.4). However, the interval between TS and anthesis varied greatly. For 1M1S, this interval declined from 960 to 620 to 500 °Cd in the first, second and third sowing respectively and this

was common in all genotypes (Table 3.3). Thus, whereas the time to DR may be longer in early sowings, particularly in vernalization and photoperiod sensitive lines, the interval between TS and anthesis also contributes substantially to differences in thermal time to anthesis in different sowing dates. The reasons for this are unknown. There is clearly a lack of understanding of this period in the factors that regulate flowering.

The groups of isogenic lines differed in their response to vernalization and photoperiod. They also differed at different developmental stages. Lines and groups varied as expected in the period between sowing and DR in the different sowings (Table 3.2). However, the photoperiod and vernalization genes may also exert some influence over the duration of later developmental stages. There was evidence that photoperiod sensitive genes were important in the period between DR and TS as this period was longer in lines with higher photoperiodic requirements in both the M and B groups. On the other hand, in the vernalization controlled groups, the spikelet initiation period was unaffected or decreased with time to DR stage. These results are in agreement with other studies that have used isogenic lines. Thus, Law (1987) found that the presence of a photoperiod sensitive gene ppd_1 resulted in a longer spikelet initiation period when the end of the period was delayed, whereas, Flood and Halloran (1986b) found that the same period decreased in vernalization sensitive isogenic lines (Triple Dirk isogenic group) compared to insensitive lines. The variation in the time of spikelet initiation found among the groups with vernalization requirement in this experiment might reflect the level of photoperiod requirement in these groups. Manupeerapan *et al.* (1992) identified four types of winter wheat according to their requirement for vernalization and daylength. Surprisingly, Rosella, a common winter wheat in Australia, in addition to its vernalization requirement, also required long days after floral initiation to reach anthesis. Penrose *et al.* (1991) also showed the large variability among the Australian winter wheats in their response not only to vernalization but also to photoperiod and basic development rate.

The small variation in the period between TS and anthesis between lines in the M and B group suggests no effect of the photoperiod genes on this period and/or that all lines had the same gene whose requirements were satisfied. This is in agreement with the observations made by Halloran and Pennell (1982). The isogenic groups sensitive to vernalization were different to the M and B groups during this period as lines sensitive to vernalization had a much shorter period between TS and anthesis than the insensitive spring lines. The vernalization genes may confer less sensitivity to temperature once the vernalization requirements are satisfied such as that their base temperature (T_b) is lower than in the spring lines. This will mean that the period TS-A was overestimated in current studies. It is also possible that there was an interaction with daylength (independent of photoperiodic genes) as this period has been shown to decrease with long days under controlled environments (Rahman and Wilson, 1977).

In vernalization sensitive lines the number of spikelets is associated with the duration of the vegetative phase (Rawson, 1970; Halse and Weir, 1970). In these studies, no clear association was observed between time to DR or from DR to TS and spikelet number in the vernalization sensitive lines (RAC and MWM) (Table 3.5). However, the late photoperiod sensitive lines had a longer period from emergence to DR and from DR to TS than earlier lines and although the rate of spikelet initiation was lower it resulted in a higher number of spikelets. It is possible that both periods have an important effect on the number of spikelets. However, when time to DR or time from DR to TS varied with sowing date the rate of spikelet initiation changed in the opposite direction such that they compensated for each other resulting in similar number of spikelets.

In eastern Australia there has been increased emphasis on cultivars that can be sown both at the conventional time in late May as well as during April and early May if the opportunities are available. If flowering time is to be maintained in late September to early October then cultivars that are delayed in flowering when sown early are required. It has been suggested that this delay could be provided by cultivars having genes either sensitive to photoperiod or vernalization. Results here suggest that the vernalization sensitive genes would be the most appropriate to use as the photoperiod sensitive genes are likely to delay flowering too much in eastern Australia. The greater plasticity of winter wheats than spring wheats in terms of variation of flowering with sowing date results in a larger range of possible planting dates (from April until June) using winter lines whilst retaining an appropriate flowering time (Stapper and Fischer, 1990a).

CHAPTER 4

EFFECT OF SOWING DATE AND PHENOLOGY ON GROWTH AND WATER USE OF WHEAT

4.1 INTRODUCTION

The correct timing of different phenological events is generally considered the most important factor for adaptation and maximum yield in different environments (Syme, 1968; Fischer, 1979; Richards, 1991). The duration of the period before anthesis determines leaf and tiller number and these impact on potential leaf area and biomass production. Leaf area and its duration, in turn, largely determines water use and dry matter production. The timing of phenological events has also been implicated in changed growth rates (this is described in more detail in Chapters 7 and 8) (Kemp *et al.*, 1989; Green and Valdyanathan, 1986).

The aim of this Chapter is to study the effect of flowering genes and sowing dates on growth of wheat sown in the field. In the environments where the experiments were carried out, water is the main limitation to growth and thus the effect of these two factors on water use and WUE is also studied.

4.2 MATERIAL AND METHODS

In 1989, five groups of isogenic lines differing in flowering time were sown at three sites, Condobolin (C), Moombooldool (M) and Wagga Wagga (W), in New South Wales. A selection of lines from three of these isogenic groups was sown in 1990. The plant material, sites and agronomy of the experiments presented here have been described in Chapter 2. The Condobolin site was chosen for more detailed studies on crop growth and water use.

It was not possible to monitor leaf appearance, tiller number, leaf area and dry weight accumulation at the same site and year. Instead, above-ground dry weight was determined at periodic harvests in C-89 whereas leaf appearance and shoot number were determined at C-90. Regular harvests at both C-89 and C-90 were made to determine the time to double ridge (DR) and terminal spikelet (TS) (see Chapter 3).

In 1990, four random plants per plot of the isogenic lines were marked to record the leaf number on the main stem from plant emergence until flag leaf appearance at intervals of about 10 to 14 days. Shoot number (main stem and tillers) was recorded in the plants used for apex dissection. At Wagga Wagga, the numbers of emerged ears and fertile ears per unit ground area were counted at anthesis time and maturity respectively. Anthesis was considered as the time when 50% of the ears had visible anthers.

In 1989, dry matter harvests from approximately 0.5 m^2 were taken regularly (every 20 days aproximately) in the earliest (1M1S and 1B2), intermediate (1M7 and 6B1) and latest (6M9 and 1B10) flowering lines (according to Appendix 1) within the M and B isogenic groups, to determine above-ground dry matter (AGDW) accumulation before and after floral initiation and up to anthesis. Samples were oven dried at 70 ^oC and, occasionally, separated into leaves and shoots. The shoot dry matter included stems, sheath of leaves and ears. Samples were weighed and total AGDW per unit area was calculated. At anthesis, a harvest (0.5 m^2) was taken in all isogenic lines sown at the three sites and AGDW per unit area was determined.

At Condobolin, neutron moisture meters (CPN Model 503DR) were used to monitor changes in soil water content. One access tube was installed in each of three replicates of three pairs of contrasting isolines in 1989. The pairs were the earliest and latest flowering isoline of the M (1M1S and 6M9), B (1B2 and 1B10) and MQ (MQs and MQw) isogenic groups. In 1990, access tubes were installed again in the M and B pairs, and in the intermediate flowering isoline from the same groups (1M7 and 6B1). Regular readings of volumetric water content started on July 27 in 1989 and on June 8 in 1990. Readings were take approximately every 20 days until maturity. Analysis of variance (GENSTAT5 statistical package) was used to determine differences between treatments in volumetric water content at 10, 30, 50, 70, 90 and 110 cm depth as well as in the changes of the two consecutive readings. The cumulative values in depth were also analysed.

4.3 RESULTS

4.3.1 Leaf growth

Sowing date had a large effect on leaf appearance rate. Table 4.1 shows the phyllochron interval (the time in degree days above a base of 0^oC between the appearance of consecutive leaves) meaned for leaves 3 to the flag leaf in the M, B and MWM groups at Condobolin 1990. The phyllochron interval was reduced, and thus leaves appeared faster, with later sowings in all groups. The phyllochron interval was reduced on average by 14 % and 40 % at C2-90 and C3-90 respectively compared to C1-90. In general, lines within an isogenic group did not differ in leaf appearance rate and no relationship between leaf appearance rate and early, intermediate or late flowering was observed (data not shown).

Although later sowing consistently resulted in a shorter phyllochron interval there was no consistent effect of sowing date on final leaf number on the main stem (Table 4.2). The mean final leaf number averaged across genotypes was very similar at each sowing (Table 4.2) although there was an overall trend towards fewer leaves. Final leaf number of 1M1S, 6M9, 1B2, 6B1 and the two MWM spring lines remained constant in the three sowing dates whereas leaf number of 1M7, 1B10 and the MWM

winter lines declined. This would suggest that the latter lines are the most sensitive to vernalization or photoperiod, whereas the control of flowering time in the MWM spring lines and for 1M1S, 1M7, 1B2 and 6B1 may be more through variation in basic development rate. Within a sowing date, isogenic lines had different final leaf numbers according to their flowering time. The latest flowering lines had on average 4.7, 3.1 and 1.4 more leaves than the earliest flowering lines in the M, B and MWM groups respectively. Figure 4.1 shows the relationship between flowering time and final leaf number for the M and B lines in the three sowings at C-90. The relationship is represented by the following equation:

$$y\ (LN) = -9.88\ 10^{-6}\ A^2 + 0.0366\ A - 21.8$$

where LN is the final leaf number on the main stem and A is the thermal time to anthesis. The second degree of the equation is mainly due to the late lines at C1-90; lines at C2-90 and C3-90 are best described by a linear regression (not shown in Fig. 4.1):

$$\text{C2-90:}\quad y\ (LN) = 0.010\ A - 4.9\ ;\ r^2 = 0.89\ ;\ p = 0.005$$

$$\text{C3-90:}\quad y\ (LN) = 0.013\ A - 6.7\ ;\ r^2 = 0.91\ ;\ p = 0.003$$

Table 4.1. Phyllochron interval averaged for the three isogenic groups sown at Condobolin 1990 (^{o}Cd leaf^{-1}). Mean ± s.e.m.

Isogenic group	C1-90	C2-90	C3-90
M	114 ± 2	100 ± 2	74 ± 7
B	107 ± 4	93 ± 1	64 ± 2
MWM	115 ± 2	96 ± 2	63 ± 1
mean	112 ± 2	96 ± 2	67 ± 2

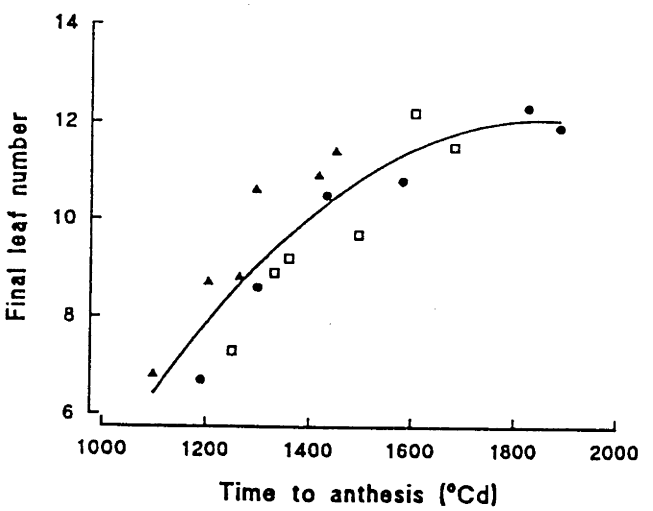


Figure 4.1 Relationship between thermal time to anthesis and final leaf number on the main stem at Condobolin, 1989. (● at C1-90, ❑ at C2-90 and ▲ at C3-90).

Table 4.2 Final leaf number in the main stem of the isogenic lines sown at Condobolin 1990 (mean ± s.e.m.).

Isogenic line	Flowering type[a]	C1-90	C2-90	C3-90	mean
1M1S	early	6.7 ± 0.1	7.3 ± 0.1	6.8 ± 0.2	6.9 ± 0.2
1M7	interm.	10.5 ± 0.2	9.2 ± 0.1	8.8 ± 0.2	9.5 ± 0.5
6M9	late	11.9 ± 0.1	11.5 ± 0.3	11.4 ± 0.2	11.6 ± 0.1
1B2	early	8.6 ± 0.2	8.9 ± 0.1	8.7 ± 0.3	8.7 ± 0.1
6B1	interm.	10.8 ± 0.2	9.7 ± 0.2	10.6 ± 0.2	10.4 ± 0.3
1B10	late	12.3 ± 0.3	12.2 ± 0.2	10.9 ± 0.3	11.8 ± 0.5
MWMspsh	interm.	8.8 ± 0.1	8.8 ± 0.2	8.8 ± 0.2	8.8 ± 0.0
MWMwnst	late	10.6 ± 0.2	9.5 ± 0.2	9.7 ± 0.2	9.9 ± 0.3
MWMsptl	interm.	8.7 ± 0.2	8.9 ± 0.1	9.1 ± 0.2	8.9 ± 0.1
MWMwntl	late	11.0 ± 0.3	9.9 ± 0.2	9.7 ± 0.2	10.2 ± 0.4
mean		10.0 ± 0.5	9.6 ± 0.4	9.5 ± 0.4	

[a] based on Appendix 1

The final leaf number is a function of the leaf primordia initiation rate and the duration of the vegetative period when primordia are initiated. No data are available on the plastochron interval (the time in degree days between the initiation of consecutive leaf primordia) but, as stated earlier, lines within a group did not differ in the phyllochron interval. This implies that the higher final leaf number on the main stem of late lines was the result of a longer vegetative period. Figure 4.2 shows the close relationship between thermal time to DR and final leaf number on the main stem for the M and B lines at C1-90 and C2-90. Results from C3-90 were not included because they were incomplete. Longer vegetative period (time to DR) resulted in a higher leaf number (y (LN) = 0.019 DR + 0.6 ; r^2 = 0.920 ; p = 0.001).

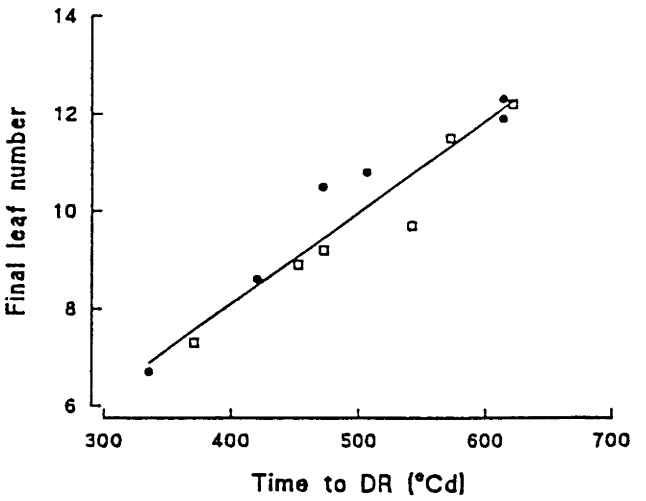


Figure 4.2 Relationship between thermal time to double ridge (DR) and final leaf number on the main stem at Condobolin, 1989. (● at C1-90 and ❑ at C2-90).

4.3.2 Shoot number

Sowing date had very little effect on maximum shoot number per plant at C-90 (Table 4.3). Average shoot number remained constant at about 4.2 per plant in all sowings and there was little variation across sowing dates for each genotype. The longer vegetative period in the late lines resulted not only in more leaves as seen above but also in more shoots. This was expected as the appearance of leaves and tillers is coordinated (Masle, 1985). Within the M and B group, the late lines had on average nearly double the number of shoots per plant than early lines (5.5 shoots compared to 2.9 shoots). The variation in shoot number in the MWM group was due to one extra tiller in the late lines. The shoot numbers per plant for the early, intermediate and late flowering lines of the B groups at C-90 are shown for the first two sowings in Figure 4.3. Maximum shoot number was achieved at about 600 ^{o}Cd after sowing in all lines in both sowing dates.

Table 4.3 Maximum shoot number per plant of the isogenic lines sown at Condobolin 1990 (mean $\pm$ s.e.m.).

Isogenic line	Flowering type[a]	C1-90	C2-90	C3-90	mean
1M1S	early	**2.9** $\pm$ 0.2	**2.8** $\pm$ 0.2	**2.9** $\pm$ 0.4	**2.9** $\pm$ 0.0
1M7	interm.	**3.3** $\pm$ 0.2	**3.8** $\pm$ 0.4	**3.6** $\pm$ 0.3	**3.6** $\pm$ 0.1
6M9	late	**5.5** $\pm$ 0.4	**5.1** $\pm$ 0.4	**5.8** $\pm$ 0.9	**5.5** $\pm$ 0.2
1B2	early	**3.3** $\pm$ 0.3	**3.2** $\pm$ 0.3	**2.6** $\pm$ 0.3	**2.9** $\pm$ 0.2
6B1	interm.	**3.9** $\pm$ 0.3	**4.4** $\pm$ 0.3	**3.8** $\pm$ 0.1	**4.0** $\pm$ 0.3
1B10	late	**5.3** $\pm$ 0.4	**5.2** $\pm$ 0.4	**5.9** $\pm$ 0.7	**5.5** $\pm$ 0.5
MWMspsh	interm.	**3.1** $\pm$ 0.1	**4.3** $\pm$ 0.3	**3.5** $\pm$ 0.3	**3.6** $\pm$ 0.2
MWMwnst	late	**4.8** $\pm$ 0.3	**5.2** $\pm$ 0.2	**4.0** $\pm$ 0.0	**4.7** $\pm$ 0.4
MWMsptl	interm.	**3.5** $\pm$ 0.2	**4.4** $\pm$ 0.4	**4.3** $\pm$ 0.3	**4.1** $\pm$ 0.3
MWMwntl	late	**4.7** $\pm$ 0.4	**5.1** $\pm$ 0.1	**4.8** $\pm$ 0.6	**4.9** $\pm$ 0.1
mean		**4.0** $\pm$ 0.3	**4.4** $\pm$ 0.3	**4.1** $\pm$ 0.4	

[a] based on Appendix 1

No data are available on shoots m^{-2} at anthesis or maturity at Condobolin, 1990. However, data were collected from Wagga Wagga in 1990 (W-90). At W-90 results at anthesis and maturity where ears m^{-2} was determined shows that the highest ear number occurred in the intermediate sowing date whereas the lowest ear number occurred in the last sowing (Table 4.4). There were no significant differences among genotypes although there was a tendency for the intermediate lines of the M and B group to have greater ear number in the last sowing at W-90. These differences between sowing dates were maintained until maturity although the number of ears m^{-2} had decreased on average by 36% compared to the shoots m^{-2} at anthesis (W-90). Similar results were found at maturity for the number of ears m^{-2} at Condobolin in

1989 where the highest number was obtained at C2-89 (265 ears m^{-2}) and the lowest number at C3-89 (152 ears m^{-2}). Assuming shoot number per plant in the different sowings was similar to the results in Table 4.3 for C-90 this means a higher tiller survival in the first and second sowing than in the third sowing as well as in the early flowering lines than in the late flowering lines as the number of established plants per unit area was not different for the three sowings.

Table 4.4 Number of shoots per m^2 at anthesis and ears at maturity in the isogenic lines at Wagga Wagga, 1990.

Sowing-Year		Anthesis			Maturity		
		W1-90	W2-90	W3-90	W1-90	W2-90	W3-90
Isoline	Flowering						
1M1S	early	411	462	388	253	297	219
1M7	inter.	330	471	343	277	270	271
6M9	late	427	375	298	243	271	226
1B2	early	270	310	366	197	267	188
6B1	inter.	370	348	370	223	254	237
1B10	late	370	490	375	236	304	198
MWMspsh	inter.	330	477	319	206	274	179
MWMwnsh	late	406	515	332	336	292	259
MWMsptl	inter.	439	437	245	196	293	189
MWMwntl	late	347	503	371	212	262	249
mean		**370**	**439**	**341**	**238**	**278**	**222**
s.e.m		16	22	14	14	5	10

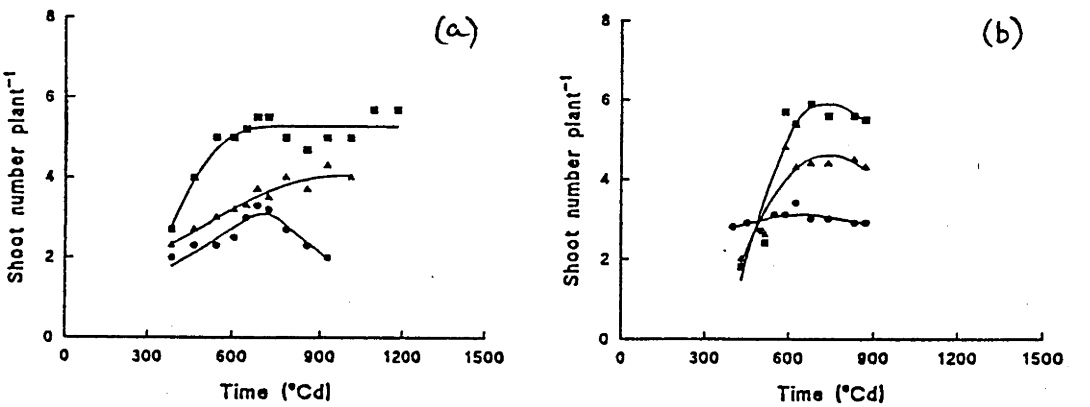


Figure 4.3 Shoot number per plant of the earliest (▲), intermediate (❑) and latest (■) flowering line in the B group (a) at C1-90 and (b) at C2-90. Data were smoothed.

4.3.3 Crop growth

Different sowing dates resulted in large differences in the timing of dry matter accumulation. Figure 4.4 shows dry matter accumulation from sowing to anthesis averaged for the six M and B lines common to the experiments at Condobolin in 1989 and 1990. The earliest sowing in both years resulted in a substantially greater above-ground dry matter up to anthesis than the subsequent sowings. The warmer temperatures in the first sowings at C-89 resulted in a faster time to the beginning of the linear growth period. Extrapolating the linear growth phase to the x-intercept for each sowing at C-89 indicates that the linear growth period began 25, 58 and 63 days after sowing in the first, second and third sowings respectively. Thus, by mid winter just after the third sowing date, the first sowing had accumulated as much dry weight as the third sowing had at anthesis and maturity.

The crop growth rate at C-90 in all sowings was very similar during the linear growth period (12.0 g $m^{-2}d^{-1}$). This was greater than at C-89 where the crop growth rate in the second and third sowing was 10.5 g $m^{-2}d^{-1}$ and this in turn was greater than the first sowing (8.9 g $m^{-2}d^{-1}$). When time was expressed in thermal time, and therefore the effect of variation on daily temperature removed, the crop growth rate was similar for all sowings in both years (0.9 g m^{-2} $^{o}Cd^{-1}$) except for slightly higher values at C1-90 and C2-90 (1.0 g m^{-2} $^{o}Cd^{-1}$).

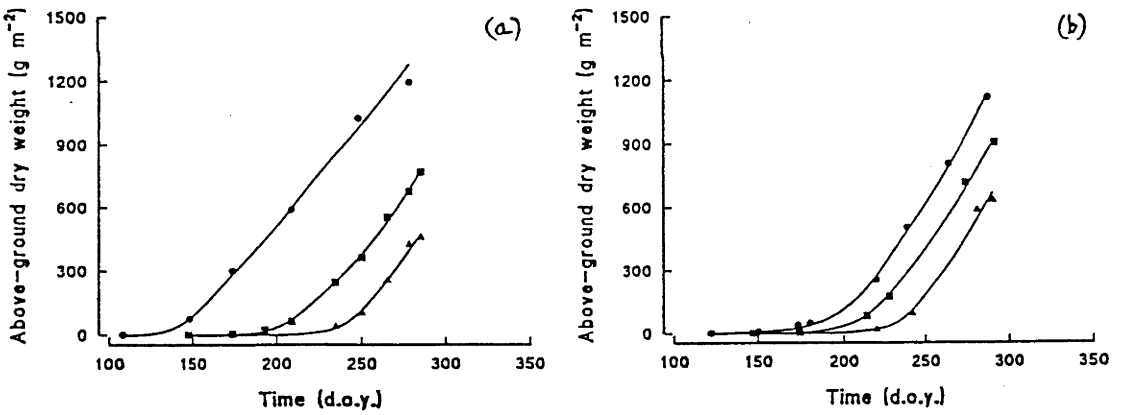


Figure 4.4 Accumulation of above-ground dry weight (a) at C-89 and (b) at C-90. (● first, ■ second and ▲ third sowing).

The mean leaf area index (LAI = leaf area per unit ground area) at anthesis was estimated at C-89, W-89 and W-90 where leaf dry weight per unit area was measured. LAI was calculated using an average value of specific leaf area of 200 cm^2 g^{-1} (Condon, 1988). The mean LAI at anthesis decreased with sowing date in the three environments (Table 4.5). The low values at the last sowing indicates that the ground was not fully covered at anthesis in this sowing.

Table 4.5 Average leaf area index (LAI) at anthesis for the M and B lines at C-89, W-89 and W-90.

Site-year	Sowing early	normal	late
C-89	4.5 ± 0.4	3.3 ± 0.4	1.9 ± 0.2
W-89	not sown	3.3 ± 0.3	3.2 ± 0.4
W-90	3.4 ± 0.4	2.8 ± 0.3	2.4 ± 0.2

At Condobolin, lines sown in mid-April differed in dry matter accumulation during the season. Figure 4.5a shows dry matter accumulation from sowing to anthesis of an early (1M1S), intermediate (1M7) and late (6M9) flowering line at C1-89. The early and intermediate flowering line accumulated biomass faster and earlier than the late-flowering line. Similar differences were observed in the B group (data not shown). At C2-89, the differences in biomass were smaller and not significant although the late line accumulated less dry matter than the earlier lines up to 1400 ^{o}Cd after sowing (Fig. 4.6a). The shoot dry weight (Fig. 4.5b and 4.6b) was greater in the early lines and this difference was maintained up to anthesis of the earliest line. However, this was compensated by the lower leaf weight in the early lines that began about 600 ^{o}Cd after sowing in both sowing dates (Fig. 4.5c and 4.6c). The specific leaf area (leaf area / leaf weight) was similar in each isogenic set and thus Figures 4.5c and 4.6c also show the substantial penalty in maximum leaf area associated with earlier flowering. Maximum LAI was 3, 4.6 and 5.7 in the early, intermediate and late flowering line respectively in the first sowing at C-89 and 2.2, 3.5 and 4.5 in the second sowing for the early, intermediate and late lines.

There was no apparent association between the time when biomass accumulation of early and late lines diverged and any phenological stage, although from the shoot dry weight data it is evident it is at about the time of terminal spikelet appearance and the beginning of stem elongation (Fig. 4.5b and 4.6b).

4.3.4 Water use and water-use efficiency

Water use was monitored at C-89 beginning from July 27. At this time the mean AGDW in the first, second and third sowings was 400, 60 and 15 g m^{-2} respectively. Despite differences in AGDW there were no significant differences in soil dryness at this first measurement (Fig. 4.7) and soil moisture content in the first sowing was identical to that in the third sowing. The same result was found at C-90, although water use measurements began earlier (data not shown). Figure 4.7 shows the soil moisture content for each sowing date over the growing season. At C-89, maximum water extraction occurred at the same time (October 20) and there were no differences between the different sowing dates in soil moisture content at this time. Figure 4.8 presents the soil water depletion from the beginning of measurements until

maturity. Water use was slowest in the last sowing (which also had the lowest leaf area) and was greater in the second sowing. The greater water use in the second sowing was presumably due to the wetter profile, 14 mm more water, at the beginning of the measurement period. At C-90, there were no differences in soil water extraction between sowing dates (Table 4.6). Water use for each of the isolines, measured from the first measurement to maturity, is given in Table 4.6. Differences between lines were not significant.

Water-use efficiency (WUE) during the period of measurement generally declined with later sowing in both years (Table 4.7). Differences between the first and second sowings were small but both were substantially greater than in the final sowing. Some differences between genotypes were evident. At C-90 the earliest flowering lines had the lowest WUE. This is likely to be due to frost damage in these lines. The late lines 6M9 and 1B10 had a significant lower WUE in the last sowing in both years.

Table 4.6 Water use (mm) from first reading of soil water content (0-120 cm depth) until maturity .

Year Sowing		C1-89	C2-89	C3-89			C1-90	C2-90	C3-90[a]
Isolines	Flowering				Isolines	Flowering			
1M1S	early	174	177	149	**1M1S**	early	333	342	337
6M9	late	169	174	176	**1M7**	mid	325	339	330
1B2	early	151	172	175	**6M9**	late	324	341	335
1B10	late	182	177	154	**1B2**	early	319	324	340
MQs	mid	163	175	159	**6B1**	mid	338	344	354
MQw	mid	165	176	153	**1B10**	late	337	340	334
mean		**167**	**175**	**161**			**329**	**338**	**338**
s.e.d.		5					5		

[a]Isolines at C3-90 were sown 14 days after the first reading of soil water content

Table 4.7 Water use efficiency (g $m^{-2}mm^{-1}$) for the interval from July 27 to maturity for lines at Condobolin 1989 and between June 8 and maturity in 1990.

Year Sowing		C1-89	C2-89	C3-89			C1-90	C2-90	C3-90
Isolines					Isolines				
1M1S	early	*a*	2.63	1.78	**1M1S**	early	2.76	3.58	2.81
6M9	late	3.46	3.08	0.99	**1M7**	inter.	4.76	4.84	3.37
1B2	early	*a*	2.38	1.57	**6M9**	late	4.50	4.16	2.41
1B10	late	3.81	2.99	1.64	**1B2**	early	2.77	4.99	3.05
MQs	early	*a*	3.11	2.04	**6B1**	inter.	3.30	3.97	2.75
MQw	late	2.32	3.22	2.19	**1B10**	late	4.55	3.87	2.65
mean		**3.20**	**2.90**	**1.70**			**3.77**	**4.24**	**2.84**
s.e.m		0.40	0.10	0.30			0.38	0.23	0.14

[a] not available due to frost damage

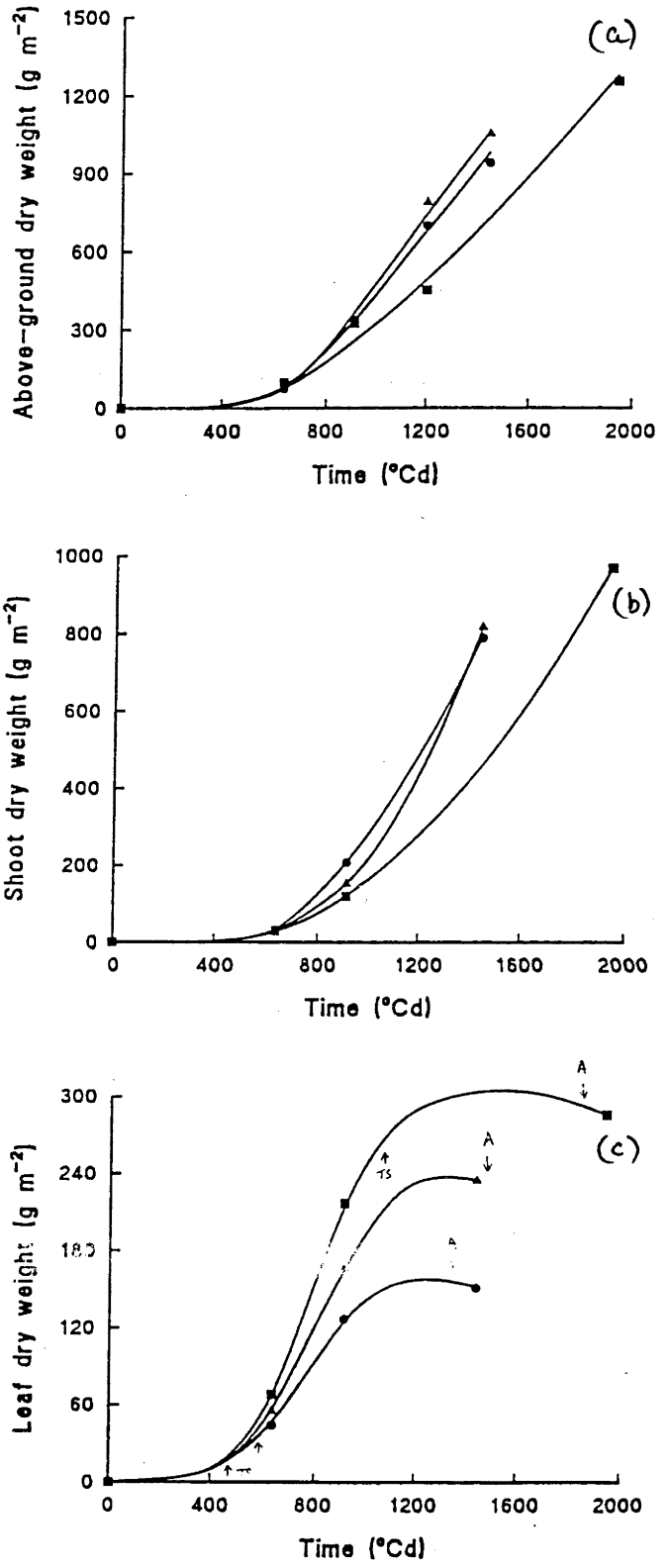


Figure 4.5 (a) Above-ground dry weight, (b) shoot dry weight and (c) leaf dry weight accumulation of an early (●), intermediate (▲) and late (■) flowering line in the M group at C1-89. TS is terminal spikelet stage and A anthesis time.

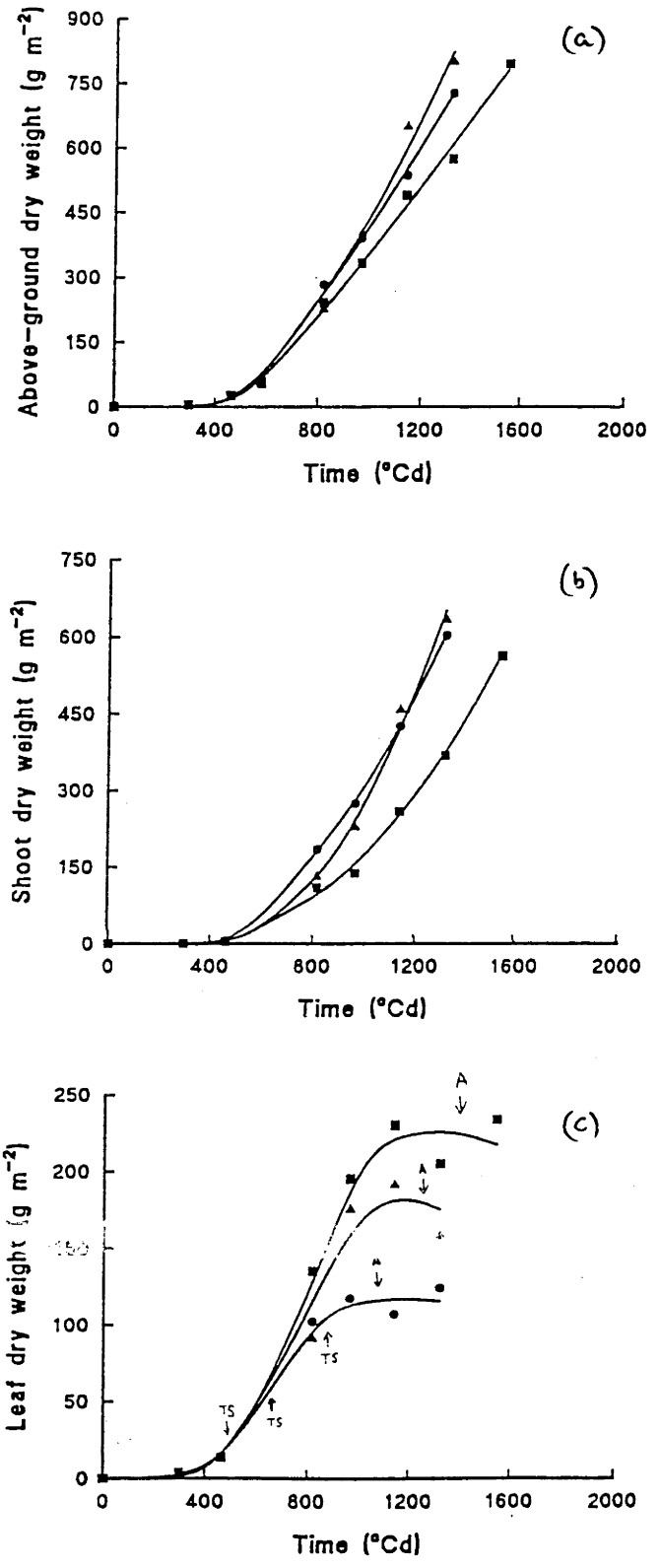


Figure 4.6 (a) Above-ground dry weight, (b) shoot dry weight and (c) leaf dry weight accumulation of an early (●), intermediate (▲) and late (■) flowering line in the M group at C2-89. TS is terminal spikelet stage and A anthesis time.

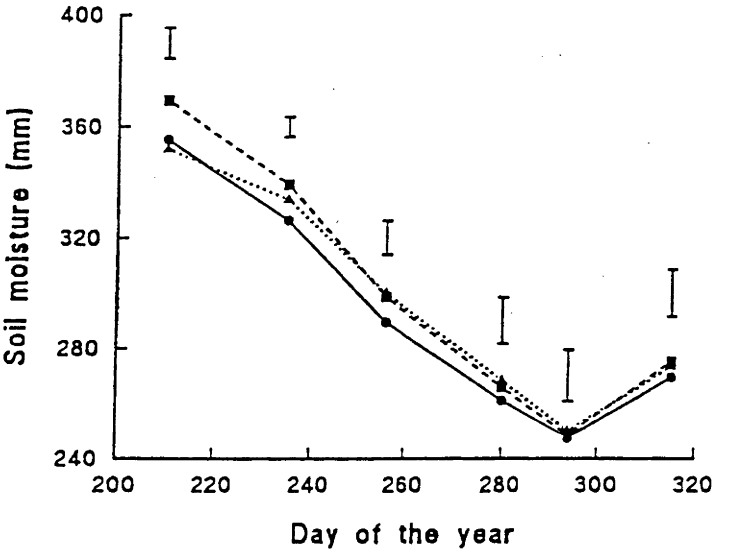


Figure 4.7 Soil moisture content (mm) down the profile to a depth of 120 cm at (●) C1-89, (■) C2-89 and (▲) C3-89. (bars are s.e.d.).

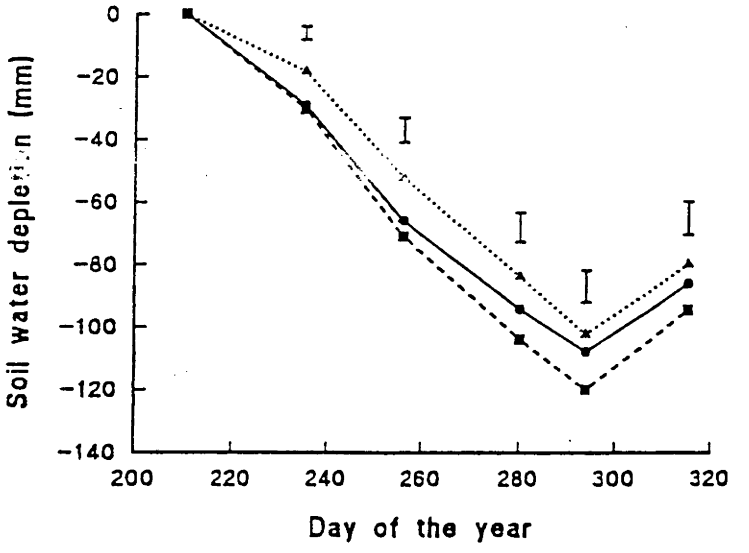


Figure 4.8 Soil water depletion (mm) down the profile to a depth of 120 cm at (●) C1-89, (■) C2-89 and (▲) C3-89. (bars are s.e.m.).

4.4 DISCUSSION

Monitoring of leaf appearance and final leaf number was only conducted at C-90 where sowing date varied from May 1 to June 22. Sowing date had a large effect on the phyllochron interval but very little effect on the final number of leaves on the main stem. Similar results have been found by Kirby and Perry (1987). However, in other studies where there was a larger range in sowing dates (in Canberra, 1991, in wheat, and Kirby *et al.*, 1982, in barley) than the present study, a difference of four leaves has been found between genotypes sown at different times.

At Condobolin 1990, there was little difference between sowings in the average length of the vegetative period (520 ^{o}Cd for the three sowing dates). Considering that the final leaf number was the same, this suggests that the total number of initiated leaf primordia and the rate of leaf primordia initiation was similar in all sowings. This is also supported by the relationship observed between time to DR and final leaf number (Fig. 4.2) that shows the appearance of an extra leaf for every 53 ^{o}Cd delay in time to DR. Similar values have been found by Kirby *et al.* (1987), Dellecole *et al.*, (1989) and Rawson (1993). This value gives then an estimate of the plastochron interval assuming this remained constant for all leaf primordia. It also indicates a similar plastochron interval for the two sowings (C1-90 and C2-90) used in Figure 4.2. The plastochron interval appears then to be less sensitive to sowing date than the phyllochron interval (Table 4.1). This result contrasts with the work presented by Hay and Kemp (1990) that showed a linear relationship between leaf number and the cumulative number of primordia initiated at the main stem apex. They implied that leaf appearance rate was then driven by leaf primordia initiation rate. However, most primordia used in the relationship presented in their work were spikelet primordia whose appearance rate might be more sensitive to sowing date.

The phyllochron intervals for genotypes within each isogenic group were very similar within each sowing date although the mean value of each group varied. This result shows that although temperature and photoperiod are considered to be responsible for variation in phyllochron interval the vernalization and photoperiod genes did not affect the leaf appearance rate. Variation in the phyllochron interval between genotypes has been reported by others (Masle *et al.*, 1989b; Krenzer and Nipp, 1991). Lines within a group had a similar phyllochron interval but late flowering lines had a greater number of leaves on the main stem (Fig. 4.1). The differences between genotypes were probably due to the longer vegetative period in the late flowering lines (Fig. 4.2) if all lines had a similar plastochron interval.

The longer vegetative period resulted in more shoots per plant in the late flowering lines than in the early flowering lines. However, shoot survival in the later lines was lower and thus at maturity there was no difference in the number of ears per m^2 between lines of different flowering type. Watson *et al.* (1963) also found very

little variation in ears per m^2 at maturity between winter and spring wheats sown at different times in spite of a large difference in the maximum shoot number. Shoot survival was also affected by sowing date as, in the late sowing, lines had fewer shoots per unit area at anthesis and maturity although the maximum shoot number was similar in all three sowings. This has also been observed by Simons (1982) and Musick and Dusek (1980). Thus, tiller survival in the last sowing was much lower than in early sowings. This effect is often attributed to drought. However, even under irrigation, shoot number can decline (eg 7 ears m^{-2} per day delay in sowing in the work by Musick and Dusek, 1980). The relatively constant number of shoots per m^2 at anthesis and maturity for early and intermediate sowings and early and late flowering lines probably reflects the environmental limitation on this trait such that the particular combination of temperature-radiation-water-nutrients in a season determines the number of spikes per unit area at maturity.

Crop growth up to anthesis can be divided in two phases, a period of slow dry matter accumulation followed by a much faster growth period (Green, 1989). At C-89, early and late flowering lines differed in their dry matter accumulation during the growing season as early flowering lines began the fast growth period earlier than the late flowering lines when sown at the same time. Differences in dry matter accumulation between spring and winter wheats sown at the same time in the field have been observed previously (Davidson *et al.*, 1990; Stapper and Fischer, 1990b). In rye-grass the change in growth has been attributed to the change in the apex from producing vegetative to reproductive structures (Kemp *et al.*, 1989), although this was not found in wheat (Rawson, 1991). Parsons and Robson (1981) explained the changes in growth of rye-grass by changes in the root-to-shoot ratio at the time of the reproductive phase. Results here show that shoot number differences between lines are not important in contributing to early growth as the early lines, with the fewest shoots, grew faster around the time of terminal spikelet stage than late lines with the most shoots. This contrast in growth between early and late flowering lines will be taken up in more detail in Chapters 7 and 8 that describe two experiments to investigate the effect of different vernalization and photoperiod genes on growth of wheat plants in controlled environments.

Although the early flowering lines accumulated dry matter faster than the late flowering lines they had a shorter growing period and this resulted in a lower biomass at anthesis and maturity. These differences between lines, associated with different times to anthesis, reversed in the later sowings as the variation in anthesis time was also reduced. At C3-89, the late flowering lines had lower dry matter at anthesis than early flowering lines (515 g m^{-2}, 455 g m^{-2} and 350 g m^{-2} on average for the early, intermediate and late flowering lines respectively). Similar results were observed when the average biomass at anthesis for each sowing date was compared as lines in the early sowing had a longer growing season and more biomass at anthesis than lines

in later sowings. Doyle and Fischer (1979) described the lower biomass at anthesis in late sowings as a general phenomenon caused by an acceleration in development due to higher temperatures, long days and higher radiation not matched by an increase in growth rate. They found a decrease in biomass at anthesis of 3.3 g m^{-2} per day's delay in sowing (Tamworth, New South Wales). This is a relative low value compared to the average 10 g m^{-2} per day delay in sowing found in this experiment at C-89 (r^2=0.994; p=0.05). If only the best yielding lines of every sowing at Condobolin in 1989 were considered then there was a decrease in biomass at anthesis of 12.5 g m^{-2} per day delay at sowing.

The absence of differences in soil water extraction between the different sowings was unexpected. Thus at C-89, on July 27 when the neutron access tubes were installed, AGDW varied from 400 to 15 g m^{-2} in the first and last sowing and yet there was no difference in soil water content between the sowing dates. Thus soil evaporation plus transpiration (evapotranspiration) during this period must have been the same in all sowings. Therefore, relative to the second and third sowings, the 400 g m^{-2} achieved by the first measurement in the first sowing was effectively free (in terms of the exchange of H_2O and CO_2). This has important implications for improving WUE in dry environments. It indicates that the additional growth obtained by sowing early is effectively at no cost in terms of water. Presumably in environments where the top soil is frequently wet, as it was in this environment, the evapotranspiration (ET) is the same whether the soil is cropped or uncropped.

WUE can be separated into a component due to transpiration efficiency (W_t = DM / transpiration) and a component due to the relative proportion of transpiration to soil evaporation (T /(E_s+T)) (Richards, 1991) such that:

$$WUE = W_t * T / (E_s + T)$$

Early sowing will result in both a greater W_t and a greater T / (E_s + T) than later sowings. The greater W_t in the first sowing in contrast with later sowings arises because a substantial proportion of growth in the first sowing occurs during the winter when vapour pressure deficit (vpd) is low. As W_t is inversely proportional to vpd then W_t in the early sowings should be high. The proportion of transpiration to E_s + T in early sowings will be greater than later sowings for the same reasons. That is, the earlier canopy growth in the early sowing will reduce evaporative water loss from the soil surface. Since there were no differences in soil water content at the beginning of the measurement period, WUE values in Table 4.7 for C-89 substantially underestimate the difference in seasonal WUE between the sowings. Assuming ET is 70% of pan evaporation (a value obtained by Condon *et al.* (1993) in a similar environment), between the first sowing and the begining of the soil moisture

measurement then the mean WUE for each sowing from April 17 to maturity was 2.55, 1.48 and 0.77 g m^{-2} mm^{-1} in the first, second and third sowings respectively.

These results agree with the data from one site in the work by French and Shultz (1984) and with the work by O'Leary *et al.* (1985). Seasonal WUE calculated for grain yield was also lower with late sowing dates in the work presented by Connor *et al.* (1992) though the transpiration efficiency increased as transpiration decreased relatively more than the biomass. The WUE was lower because of the lower dry matter accumulation in the later sowings.

CHAPTER 5

EFFECT OF ANTHESIS DATE ON YIELD, ABOVE-GROUND DRY MATTER AND HARVEST INDEX

5.1 INTRODUCTION

The time of flowering usually governs the success or failure of a crop in a given environment. If flowering is too early, frost can have a devastating effect on yield. If flowering is too late, drought and possibly high temperatures then limit yield. The optimum time for flowering therefore needs to be finely balanced to match the prevailing environment.

Flowering time can be regulated by sowing date, although as was shown earlier, sowing 66 days apart can result in only 12 days difference in flowering time (Chapter 2). Flowering time can also be regulated genetically and for the same sowing date there may be at least 20 to 40 days difference in flowering time of different genotypes (Chapter 3).

Maximum yield in Australia as well as in rainfed Mediterranean environments depends on the balance between adequate growth up to anthesis to set a reasonable potential yield and leaving sufficient water in the soil after anthesis for this yield to be achieved. The importance of the balance between pre and post-anthesis water supply in wheat has been clearly demonstrated (Passioura, 1983; Richards and Townley-Smith, 1987; Siddique *et al.*, 1990a).

The effect of sowing date on yield and seasonal water-use efficiency was presented in Chapter 2. It was shown that similar yields can be obtained with a range in sowing dates from mid-April to the end of May. These yields were obtained with different combinations of sowing and anthesis time. The aim of the work presented in this Chapter is to study the effect of anthesis date on yield of several series of isogenic wheats differing in flowering time, advanced breeding lines of wheat and commercial winter wheats and barleys sown at different times and to determine the optimum flowering period for maximum yield. The effect of anthesis date on above-ground biomass at maturity, harvest index and crop height at maturity is also presented.

5.2 MATERIAL AND METHODS

In 1989, 23 genotypes from five groups of isogenic lines or populations were sown. Within a group, lines differed in the vernalization and photoperiod requirements and thus in time to anthesis (Chapter 3). In 1990, a selection of these lines (10 genotypes from three of the groups) as well as some commercial or advanced breeding wheats (10 genotypes) and barleys (4 genotypes) were grown.

Lines were sown on different dates in 1989 and 1990 at three locations. The sites (Condobolin, Moombooldool and Wagga Wagga), sowing dates and agronomy are described in detail in Chapter 2.

Anthesis time was recorded for every line. At maturity, a hand harvest was taken in every plot to determine the harvest index (HI) calculated as the grain dry weight divided by the total biomass dry weight in the sample. The number of fertile spikes was counted in the samples of every experiment except at M1-89 and the three sowings at Condobolin in 1990. Plots were harvested by a small combine and the grain yield per unit area was determined. The above-ground dry weight was calculated dividing the grain yield by the harvest index ratio. The number of spikes/m^2 was estimated from the number of spikes in the hand sample and the plot yield. A sample of kernels were taken from the machine harvest and the weight of one hundred kernels was determined. The numbers of kernels/m^2 and kernels/spike were then calculated.

5.3 RESULTS

5.3.1 1989

5.3.1.1 Yield, above-ground dry matter and harvest index

The trial at Condobolin in 1989 was chosen for more detailed study as this trial had the widest spread in sowing dates. The results from this trial make up the bulk of this Chapter. The variation in anthesis date was greater than that found among commercial varieties grown in south-eastern Australia. Some lines flowered up to 10 days before the commercial spring wheats when sown in May. At C1-89, the range in anthesis date was 41 days (Table 5.1). This range decreased to 25 and 20 days in later sowings at C2-89 (Table 5.2) and C3-89 (Table 5.3) respectively and most of this variation was found in the M and B group. The variation in anthesis date within the RAC, MQ and MWM isogenic groups was rather small except at C1-89. This was because the variation in flowering time in these lines (RAC, MWM and MQ) was mainly determined by the response to vernalization. In April sowings, lines not requiring a vernalizing period that are also insensitive to photoperiod will flower, or at least initiate, before the onset of winter whereas floral initiation in lines requiring a vernalization period will be delayed. In later sowings, when temperatures are lower, both vernalization and thermal time requirements will be accumulated concomitantly in both winter and spring wheats and flowering time should be more similar. Flowering in the M and B lines was more variable in all sowings because of the predominant photoperiodic and basic vegetative period control of flowering in these lines. For this reason, the effect of anthesis date on yield is mainly presented for the M and B isogenic groups.

The data for grain yield, above-ground dry weight (AGDW), harvest index (HI) and plant height are given in Tables 5.1, 5.2 and 5.3 for the three sowing dates at Condobolin, 1989. Equivalent data for Wagga Wagga 1989 and Moombooldool 1989 are given in Appendix 3. In 1989, frost damage was only evident in the earliest sowing at Condobolin (C1-89) and Moombooldool (M1-89). Lines that flowered before September 20 (156 days after sowing) suffered frost damage and were low yielding. The latest flowering lines escaped frost and were the highest yielding in this sowing. Figure 5.1 shows the relationship between the number of days to anthesis and yield at C-89 for the M and B groups. At C1-89, the increase in yield with later flowering lines is a reflection of the decrease in frost damage. In this early sowing, low yields in the MWM tall lines (Table 5.1) were the result of lodging.

Table 5.1 Time to anthesis and above-ground dry weight (AGDW), yield, harvest index and crop height at maturity of isolines at C1-89.

	Anthesis (d.a.s)	AGDW ($g\ m^{-2}$)	Yield ($g\ m^{-2}$)	Harvest Index	Height (cm)
1M1S	127	156	0	0.00	92
1M5	141	573	28	0.05	102
1M7	143	638	47	0.08	108
1M10	143	654	37	0.05	105
6M7	144	744	84	0.12	107
6M9	168	1037	219	0.21	98
1B2	136	592	34	0.06	95
1B5	142	642	49	0.08	108
1B9	143	709	63	0.09	108
6B1	145	576	99	0.18	110
6B6	160	776	171	0.23	108
1B10	168	1060	209	0.20	95
6B9	168	972	170	0.18	97
RAC 416-1	156	892	219	0.25	97
RAC 417-2	164	772	151	0.20	100
RAC 417-3	167	1033	225	0.22	93
RAC 417-5	167	981	236	0.24	92
MQs	144	610	97	0.16	97
MQw	161	826	173	0.20	105
MWMspr sht	144	450	45	0.10	97
MWMwnt sht	154	439	90	0.21	112
MWMspr tall	144	839	94	0.11	122
MWMwnt tall	151	599	69	0.12	128
mean	151	720	113	0.15	103
s.e.d.	3	119	22	0.03	4

Table 5.2 Time to anthesis and above-ground dry weight, yield, harvest index and crop height at maturity of isolines at C2-89.

	Anthesis (d.a.s)	AGDW ($g\ m^{-2}$)	Yield ($g\ m^{-2}$)	Harvest Index	Height (cm)
1M1S	118	530	179	0.34	82
1M5	127	571	175	0.31	80
1M7	129	546	166	0.30	80
1M10	129	591	176	0.30	82
6M7	132	645	195	0.30	77
6M9	143	591	146	0.25	67
1B2	119	472	154	0.32	80
1B5	127	578	190	0.33	87
1B9	129	627	185	0.30	83
6B1	131	571	171	0.30	73
6B6	135	721	216	0.30	75
1B10	139	604	122	0.21	65
6B9	142	587	130	0.23	67
RAC 416-1	132	650	219	0.34	68
RAC 417-2	134	575	193	0.34	68
RAC 417-3	136	623	195	0.32	60
RAC 417-5	136	753	197	0.26	63
MQs	129	610	186	0.31	78
MQw	131	617	187	0.30	75
MWMspr sht	127	695	202	0.29	80
MWMwnt sht	130	482	139	0.29	75
MWMspr tall	130	615	180	0.29	93
MWMwnt tall	129	635	140	0.22	93
mean	131	604	176	0.29	76
s.e.d.	1	71	20	0.03	4

Table 5.3 Time to anthesis and above-ground dry weight, yield, harvest index and crop height at maturity of isolines in the C3-89 treatment.

	Anthesis (d.a.s)	AGDW ($g\ m^{-2}$)	Yield ($g\ m^{-2}$)	Harvest Index	Height (cm)
1M1S	102	280	111	0.39	58
1M5	109	330	120	0.36	59
1M7	110	307	108	0.35	59
1M10	110	366	128	0.35	63
6M7	114	272	96	0.35	56
6M9	122	190	51	0.27	54
1B2	106	289	110	0.38	55
1B5	109	309	113	0.36	57
1B9	110	361	116	0.32	64
6B1	111	400	143	0.35	63
6B6	115	271	89	0.33	55
1B10	116	268	92	0.34	50
6B9	121	176	54	0.31	48
RAC 416-1	114	276	107	0.39	51
RAC 417-2	115	288	116	0.40	55
RAC 417-3	117	287	112	0.39	49
RAC 417-5	118	278	99	0.36	53
MQs	111	339	119	0.35	60
MQw	111	350	103	0.30	59
mean	113	297	104	0.35	56
s.e.d.	1	40	14	0.02	4

For the sowing at the standard time near the end of May (C2-89) and for the late sowing (C3-89), the highest yielding lines had an intermediate time to flowering (Fig. 5.1a). Early flowering lines had lower yield in both sowings but there was less of a penalty with the latest sowing. Late flowering lines had the lowest yield at C2-89 and at C3-89 (25% and 37% lower than the mean of the sowing).

Above-ground biomass (AGDW) changed with flowering time similarly to yield (Fig. 5.1b). At C1-89, AGDW increased with later flowering mainly because frost damaged early flowering lines. For the second sowing (C2-89) there was very little variation in AGDW except for the lower values found in the early flowering lines (Fig. 5.1b). However, at C3-89 the early and intermediate flowering lines had similar AGDW whereas the late flowering lines had the lowest values (Fig. 5.1b). The highest AGDW occurred in late flowering lines of the first sowing. At C1-89, the early and late lines within the M and B group had shorter stature than the intermediate flowering lines (Table 5.1). The reduction in height of the late flowering lines compared to the rest was greater in later sowing dates probably because of an increase in drought (Tables 5.2 and 5.3).

Harvest index (HI) varied substantially between lines and sowings. Frost damage reduced HI in all early and intermediate flowering lines at C1-89 to zero in the worst case (Fig. 5.1c). For the sowings where frost damage was not present there was a decrease in HI with later sowings. In C2-89 and C3-89, the decrease in harvest index was 0.4 % and 0.5 % per day delay in sowing respectively.

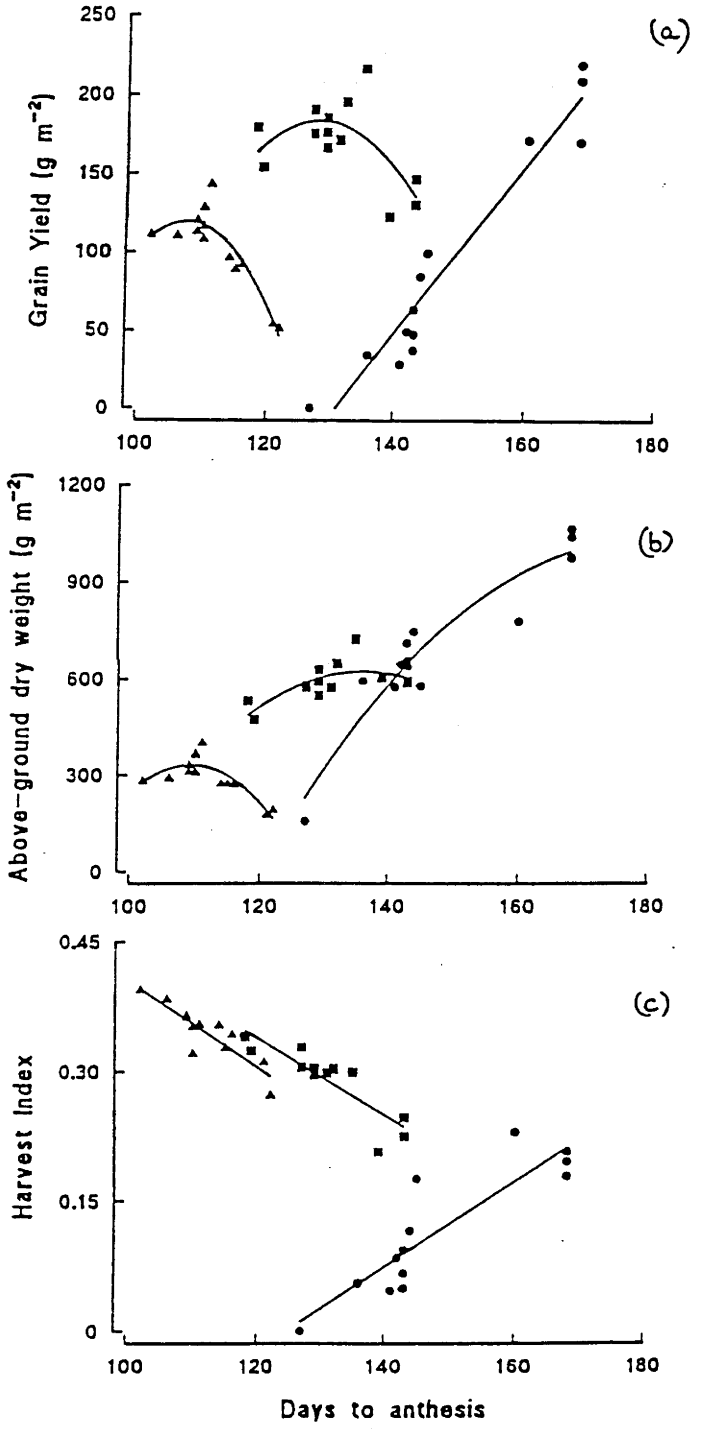


Figure 5.1 Relationships between days to anthesis and (a) grain yield, (b) above-ground dry weight and (c) harvest index for the M and B groups at C1-89 (●), C2-89 (■) and C3-89 (▲).

At the wetter sites, Moombooldool and Wagga Wagga, similar trends were found in the way grain yield, biomass and harvest index varied with anthesis date as that found in comparable sowings at Condobolin. For a May sowing (M1-89 and W1-89) the best yields were obtained by the intermediate flowering lines whereas there was a yield penalty for the late and early flowering lines (Fig. 5.2 and 3). Early flowering lines at M1-89 had low yields because of frost damage.

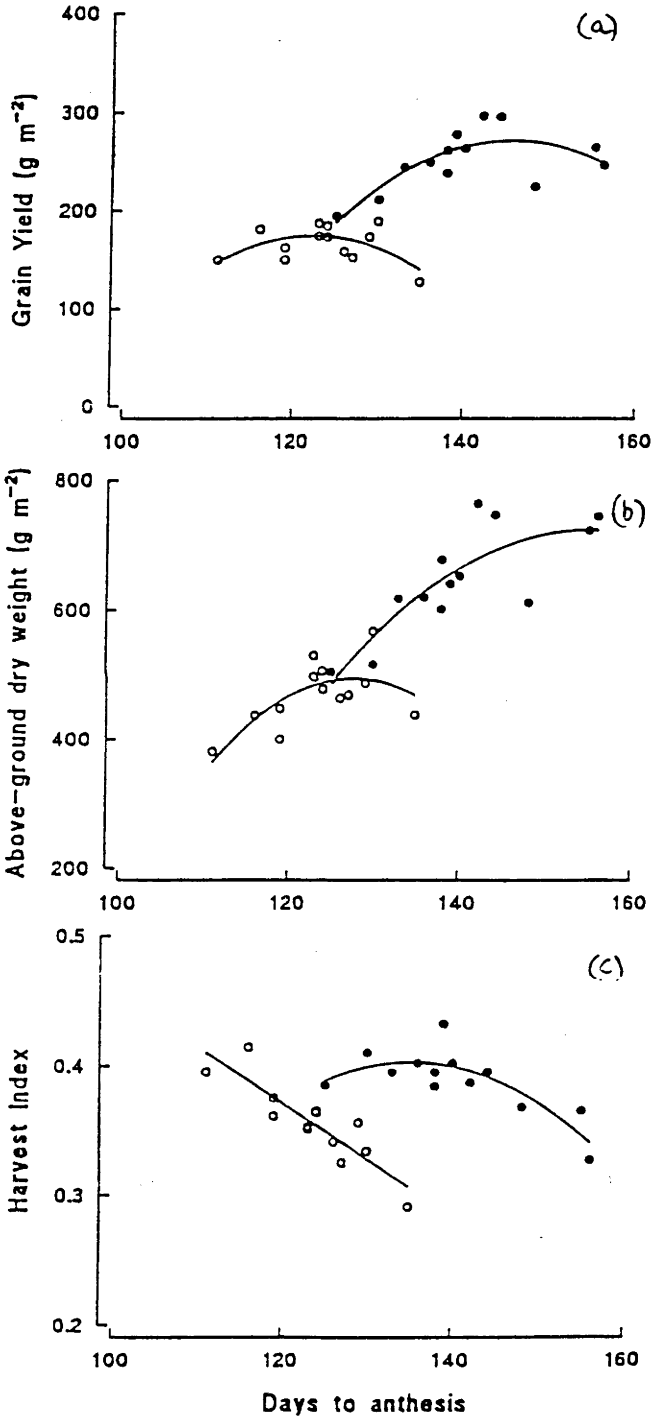


Figure 5.2 Relationships between days to anthesis and (a) grain yield, (b) above-ground dry weight and (c) harvest index for the M and B groups at M1-89 (●), M2-89 (○).

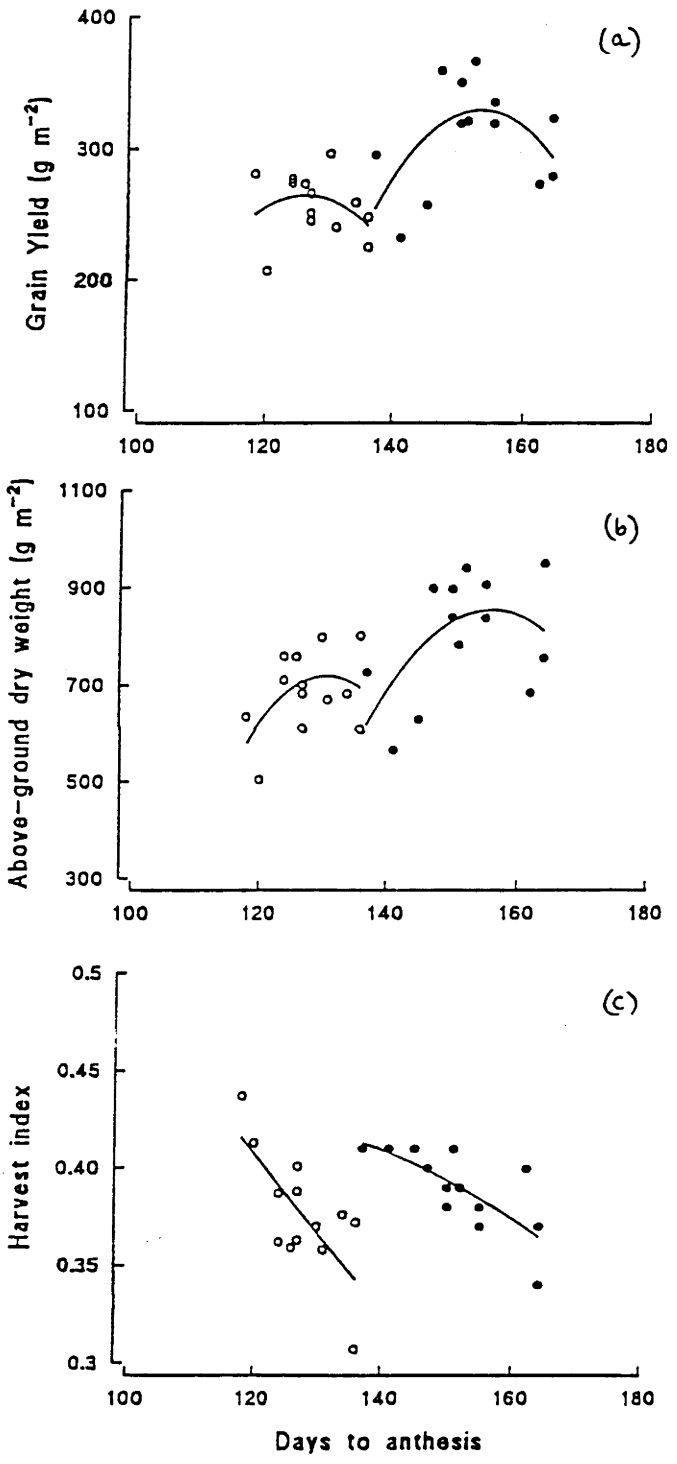


Figure 5.3 Relationships between days to anthesis and (a) grain yield, (b) above-ground dry weight and (c) harvest index for the M and B groups at W1-89 (●), W2-89 (○).

5.3.1.2 Yield components and plant height

Yield component data for the the sowings at Condobolin 1989 are presented in Table 5.4. There were consistent trends in some of the components of yield. In all sowings the number of kernels per unit area was closely related to grain yield (Fig. 5.4 and 5.5a). At C1-89 the number of fertile ears per unit area increased in the later flowering lines as less ears were killed by frost and the longer vegetative duration in the late lines as well as the favourable conditions presumably enabled more spikes to develop (Fig. 5.5b). Early and late flowering lines tended to have a lower number of spikes than the intermediate flowering lines at the later sowings. There was no relationship between number of spikes per unit area or kernel weight and grain yield except for spike number at C1-89. Kernel weight was not affected by either sowing or anthesis date (Fig. 5.5c) although some variation was found between the lines. This variation in kernel weight (27.5 and 35.0 mg) was not related to the changes in the number of kernels per unit area (relationship not significant for any of the three sowings).

At C1-89, plant height increased with time to anthesis except for flowering lines that were slightly shorter (Fig. 5.6). This pattern was reversed in later sowings where plant height decreased with flowering time.

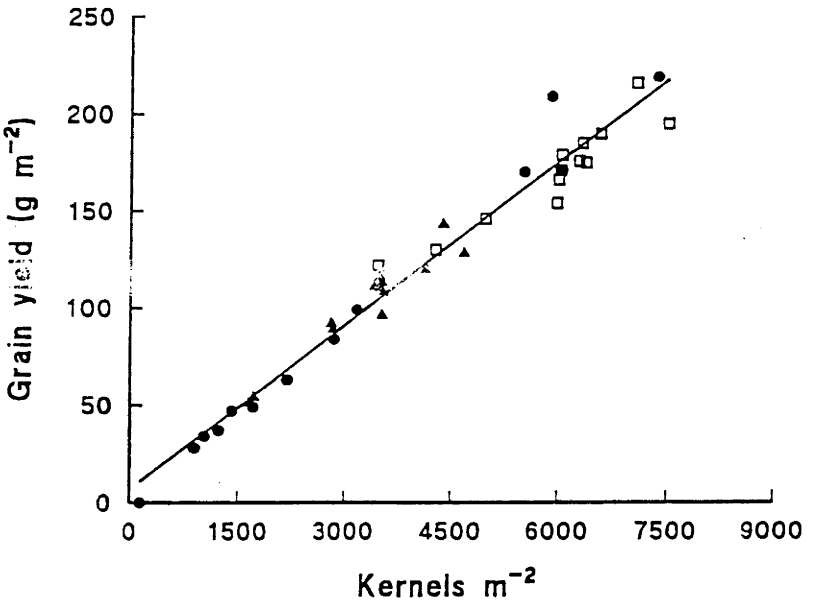


Figure 5.4 Average relationship between kernel number per m^{-2} and grain yield at for the M and B groups at C1-89 (●), C2-89 (□) and C3-89 (▲) ($y=0.028x+6.8$; $r^2=0.97$; $p<0.001$).

Table 5.4 Yield components of lines grown at C1-89, C2-89 and C3-89.

	C1-89				C2-89				C3-89			
	spikes m^{-2}	kn.wt. (mg)	kn m^{-2}	kn spk^{-1}	spikes m^{-2}	kn.wt. (mg)	kn m^{-2}	kn spk^{-1}	spikes m^{-2}	kn.wt. (mg)	kn m^{-2}	kn spk^{-1}
1M1S	106	33.3	147	4	234	29.2	6041	26	141	31.6	3424	25
1M5	195	32.0	894	5	233	27.8	6375	28	155	28.8	4150	26
1M7	165	30.9	1407	9	223	27.6	5999	27	156	30.8	3542	22
1M10	165	28.7	1227	7	246	28.2	6278	26	180	27.5	4674	26
6M7	173	29.4	2850	19	261	26.1	7506	28	151	27.4	3532	23
6M9	246	29.9	7357	31	231	30.5	4975	20	100	30.9	1641	17
1B2	190	31.4	1029	5	216	25.9	5971	29	125	31.2	3501	28
1B5	191	30.6	1705	10	261	28.4	6572	26	147	32.2	3525	24
1B9	221	29.5	2187	11	258	29.6	6322	24	146	33.2	3495	24
6B1	167	31.3	3172	20	255	28.8	6022	24	189	32.3	4380	23
6B6	216	27.7	6042	28	283	30.3	7070	25	150	31.9	2833	18
1B10	330	35.0	5892	18	301	33.8	3477	13	159	32.8	2813	17
6B9	282	30.1	5517	19	271	30.0	4282	16	103	31.5	1716	17
RAC416-1	231	36.1	6008	26	292	30.4	7247	25	133	33.1	3259	24
RAC417-2	220	37.2	4057	19	239	33.0	5959	23	145	37.4	2977	21
RAC417-3	338	37.4	6006	18	295	34.1	5765	20	162	37.5	2929	18
RAC417-5	305	38.2	6134	20	390	32.4	6055	16	166	36.8	2710	17
MQs	196	36.4	2618	18	245	30.3	6161	26	156	36.5	3332	21
MQw	312	34.5	5019	17	247	34.0	5587	22	165	38.8	2626	16
MWMs sht	307	35.2	1245	4	256	31.1	6513	25				
MWMw sht	128	32.6	2749	23	225	31.7	4379	20				
MWMs tll	165	34.3	2804	18	218	35.8	5077	24				
MWMw tll	135	33.9	1979	15	290	31.8	4304	15				
mean	223	32.9	3452	16	265	30.5	5931	23	152	32.8	3218	21
s.e.	47	1.4	507	4	37	1.2	607	3	17	0.1	417	2

5.3.2 1990

5.3.2.1 Isogenic groups

In 1990, the second year of testing, the rainfall during the growing season at Condobolin was 235 mm greater than during the relatively dry season in 1989 (Table 2.1 in Chapter 2) and consequently yields were also higher. However the trends in yield, AGDW and HI were similar to those in 1989 (Fig 5.7). In 1990 only a subset of each isogenic set were grown. At C1-90, frost was not a problem except in the earliest line. Grain yield was highest in the latest flowering lines at C1-90 whereas the lines with an intermediate time to anthesis had the highest yields at C2-90, W1-90 and W2-90. The earliest flowering lines were highest yielding in the last sowing at both sites. Above-ground dry weight generally mirrored grain yield whereas HI declined with later flowering. The main exception to the decline in HI was in the first sowing at both sites where HI tended to be independent of flowering time. This was not so

apparent at C1-90 where frost damage resulted in a reduction in HI in the earliest flowering lines.

Intermediate and late flowering lines were the tallest lines at C1-90, C2-90 and W1-90 whereas in the last sowing (C3-90) plant height decreased with later flowering at both sites (data not shown). At W2-90 early and late flowering lines were shorter than the intermediate ones.

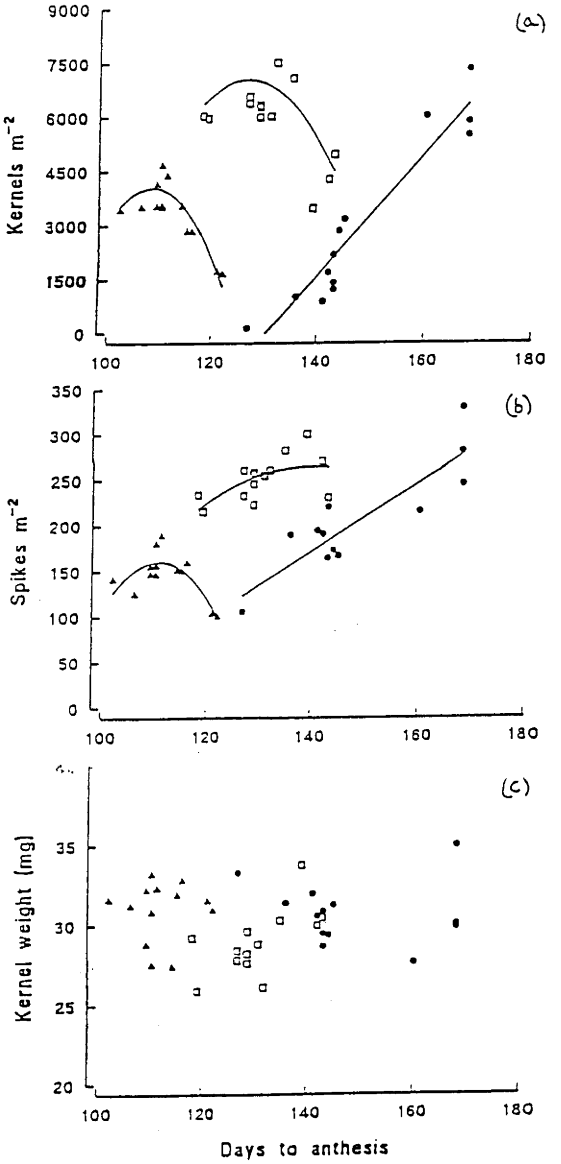


Figure 5.5 Relationships between days to anthesis and (a) kernel number per m^{-2}, (b) ear number per m^{-2} and (c) kernel weight for the M and B groups at C1-89 (●), C2-89 (□) and C3-89 (▲).

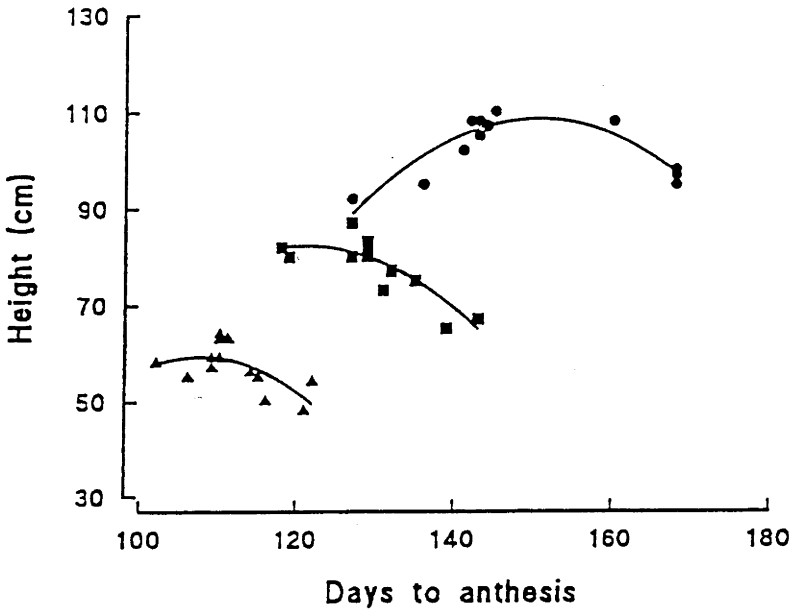


Figure 5.6 Relationships between days to anthesis and plant height at C1-89 (●), C2-89 (■) and C3-89 (▲).

5.3.2.2 Advanced breeding lines and commercial varieties

At Condobolin, 1990, the variation in anthesis time within the advanced breeding lines and commercial winter wheats was rather small whereas it was considerably greater within the barleys (Table 5.5). The effect of time to anthesis on yield was similar to that found in the 1989 experiments. The main exception was that at C1-90 there was no frost damage in the early flowering barleys. In this sowing yield and AGDW were very similar for all the varieties although late flowering lines tended to have lower yield. This contrasts with results at W1-90 where the spring genotypes had lower yield and biomass than late flowering varieties (Appendix 3). At later sowings (C2-90, C3-90 and W2-90), the early and late flowering varieties had the lowest grain yield, biomass and harvest index. The very early flowering in barley did not result in a yield advantage presumably because of the very wet season which favoured later flowering lines.

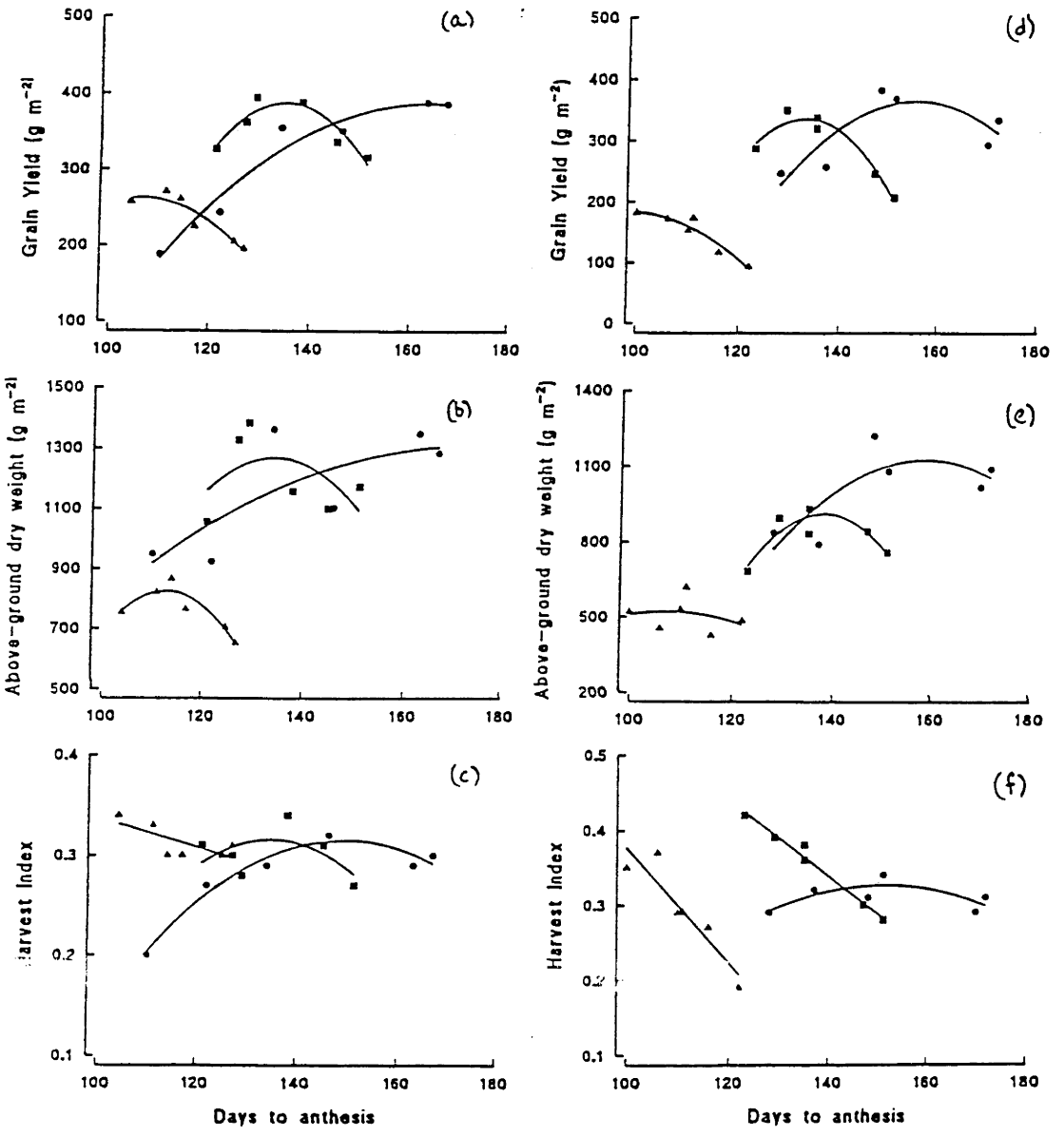


Figure 5.7 Relationships between days to anthesis and (a) grain yield, (b) above-ground dry weight and (c) harvest index for the M and B groups at C1-90 (●), C2-90 (■) and C3-90 (▲). Relationship between days to anthesis and (d) grain yield, (e) above-ground dry weight and (f) harvest index for the M and B groups at W1-90 (●), W2-90 (■) and W3-90 (▲).

5.4 DISCUSSION

The effect of anthesis date on yield in all environments is summarised in Figure 5.8. The grain yield of the early, intermediate and late flowering lines is plotted against the mean yield of the best ten lines in every sowing, site and year. Data for the M isogenic group is presented in Figure 5.8a and for the B isogenic group in the Figure 5.8b. Lines that suffered frost damage were excluded. Lines with an intermediate flowering date (similar to the spring commercial cultivars eg Banks) had the highest yield at all yield levels between a site mean of 200 g m^{-2} and 450 g m^{-2}. The earliest flowering lines had a yield advantage at the lowest yielding sites where yields were less than 200 g m^{-2} but a yield penalty at higher yielding sites. It is likely that water limitations determine this response in each of the flowering groups. Insufficient water in the lowest yielding environments favoured early flowering lines due to drought escape whereas in the more favourable environments the early lines were unable to develop sufficient leaf area and biomass to achieve a high yield. It is possible that sowing early flowering lines at higher density may extend their high yielding range beyond 200 gm^{-2}. Late flowering lines might have flowered too late resulting in an inbalance of pre to post anthesis growth and water used and this inbalance was probably greater with later sowings.

Frost damage was the major constraint to yield of early flowering isolines sown in April or early May. For these sowings only the late flowering lines avoided frost damage and had acceptable yields (Fig. 5.1). This included all commercial wheats recommended for early sowing. The surprising exception to this was the early flowering barley, Yagan, at C1-90 which did not show any frost damage yet it flowered in the middle of winter and just slightly earlier than wheats that experienced severe frost damage. Yagan flowered 5 days earlier than 1M1S wheat yet its grain yield was 490 g m^{-2} compared to only 190 g m^{-2} of 1M1S. In the development of these isogenic lines there was no selection pressure for frost resistance and it is possible that lines grown here were particularly susceptible. Some degree of frost resistance has been found among Australian wheat cultivars (Fletcher, 1983; Single, 1987). It is not known to what extent Yagan is more tolerant to frost than the best Australian spring wheats. As far as I am aware, there have not been any studies comparing frost tolerance of wheat and barley.

Plant height increased with flowering time in the best yielding environments where early sowings were generally superior. However, in later sowings plant height decreased with flowering time presumably because of more drought in these conditions.

The risk of lodging increased with early sowings as plant height increased. However, in these experiments lodging did not occur in the late flowering semidwarfs except for in the MWM winter lines. These tall lines do not have a major dwarfing

gene (*Rht* gene) and they lodged when sown in April or early May, or even later at Wagga Wagga. In later sowings plant height was less and no lodging was observed.

To summarise, these results confirm findings by other authors (McDonald *et al.*, 1983; Batten and Khan, 1987; Entz and Fowler, 1991; Connor *et al.* 1992) who have compared commercial varieties of different phenology sown at different times. The best yields in an April sowing were obtained with late flowering wheats as the spring wheats generally had frost damage. In the absence of frost, the best yields were obtained with intermediate flowering lines. Very early flowering lines had a yield advantage only in later sowings and drier environments.

The optimum flowering period for maximum yield was last week of September and first ten days of October at Condobolin. Lines that flowered during this time were either late flowering lines sown during mid-April or intermediate flowering lines sown in May. At Wagga Wagga, maximum yields were obtained by lines that flowered in early October when sown in early May.

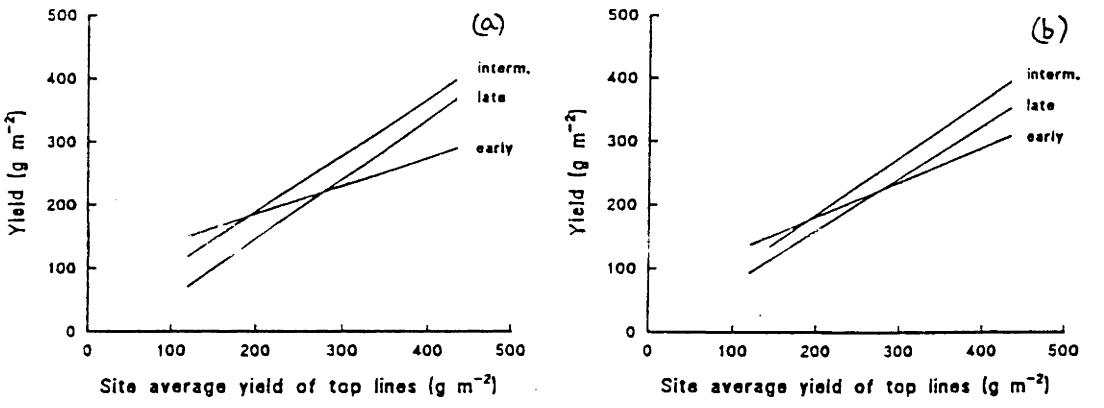


Figure 5.8 Relationships between the year-site average yield for the top ten yielding lines and the yield of the earliest, intermediate and latest flowering lines in the (a) M group (n=13; r^2=0.47, 0.94 and 0.89 respectively) and (b) B group (n=13; r^2=0.56, 0.94 and 0.91 respectively).

Table 5.5 Time to anthesis and above-ground dry weight, yield, harvest index and crop height at maturity of advanced breeding lines and commercial varieties at Condobolin, 1990.

	Anthesis (d.a.s.)	Yield ($g\ m^{-2}$)	AGDW ($g\ m^{-2}$)	HI	Height (cm)
C1-89					
Hartog[a]	147	460	1236	0.37	108
Banks[a]	147	383	1063	0.36	97
WW766[b]	155	433	1342	0.32	99
RAC417-2[b]	155	475	1330	0.36	95
RAC417-5[b]	155	480	1585	0.32	90
Osprey[b]	158	378	1091	0.35	98
M3087-222[b]	158	436	1302	0.34	93
M3856[b]	158	418	1332	0.32	94
M3508[b]	164	407	1343	0.31	88
Rosella[b]	164	460	1460	0.32	94
Yagan[c]	106	488	1280	0.38	87
Schooner[c]	133	487	1265	0.39	85
Franklin[c]	147	474	1239	0.39	92
Ulandra[c]	164	363	1112	0.33	80
C2-89					
Hartog[a]	132	480	1145	0.42	103
Banks[a]	132	400	1209	0.33	93
WW766[b]	137	388	1289	0.32	96
RAC417-2[b]	137	432	1312	0.33	96
RAC417-5[b]	139	402	1230	0.33	88
Osprey[b]	139	413	1326	0.31	99
M3087-222[b]	139	365	1269	0.31	92
M3856[b]	139	366	1290	0.30	93
M3508[b]	142	333	959	0.36	81
Rosella[b]	142	373	1081	0.35	93
Yagan[c]	110	401	1096	0.36	82
Schooner[c]	124	426	1108	0.39	81
Franklin[c]	139	427	1120	0.38	99
Ulandra[c]	142	269	902	0.31	72
C3-89					
Hartog[a]	115	272	787	0.35	90
Banks[a]	116	253	716	0.37	78
WW766[b]	116	213	631	0.34	77
M3856[b]	116	231	637	0.36	77
Osprey[b]	119	228	684	0.33	77
M3087-222[b]	119	220	756	0.30	75
RAC417-2[b]	123	261	812	0.32	79
RAC417-5[b]	123	255	745	0.34	73
M3508[b]	123	201	587	0.34	68
Rosella[b]	123	225	693	0.33	80
Yagan[c]	97	249	729	0.34	80
Schooner[c]	112	330	810	0.41	82
Franklin[c]	116	307	894	0.35	85
Ulandra[c]	123	131	582	0.25	60

[a] spring wheat
[b] winter wheat
[c] barley

CHAPTER 6

MANIPULATION OF PLANT HEIGHT GENETICALLY AND BY MANAGEMENT

6.1 INTRODUCTION

In Chapter 2 it was suggested that the height of winter wheat cultivars sown in eastern Australia in April is excessive and that this may be largely responsible for the reduced yields. It was suggested that it arises because of the long duration between sowing and flowering. As flowering must be delayed until September-October then vernalization genes must be used to delay floral initiation in lines sown in April. These genes extend the period between sowing and floral initiation and this results in more leaves produced on the main stem which in turn results in more and longer internodes and longer stems at maturity. Although the greater height in early sown wheats may result in lodging, in south-eastern Australia the more important effect may be on the reduction in yield that may arise from the competition for assimilates between the developing ear and elongating stem. This results in reduced harvest index (HI). The degree of competition is greatest in tall wheats and this results in a reduction in kernel number and yield (Brooking and Kirby, 1981; Gale and Youssefian, 1985; Fischer and Stockman, 1986; Siddique *et al.*, 1989; Youssefian *et al.*, 1992a).

There are two ways that plant height can be reduced in early sown wheats. Firstly, by managment with the use of plant growth regulators (PGRs), and secondly, by genetical manipulation. In this chapter, an experiment is described where PGRs were applied to a range of genotypes sown early at Condobolin to determine whether PGRs improve yields.

Plant growth regulators have been widely used to reduce lodging in cereal crops, and they are known for their effectiveness in shortening plant height (Hofner and Kuhn, 1982; Simmons *et al.*, 1988). The effect of PGRs on yield have been inconsistent as they have been found to increase yield by reducing lodging (Dahnous *et al.*, 1982; Wiersma *et al.*, 1986; Simmons *et al.*, 1988) or to increase yield in the absence of lodging (Korateng and Matthews, 1982) as well as to reduce yield (Green *et al.*, 1985; Nafziger *et al.*, 1986). Chlormequat (2-chloroethyl-N,N,N-trimethylammonium chloride, abreviated as CCC) and ethephon (2-chloroethyl phosphonic acid) are the most commonly used growth regulators in agriculture. CCC is an antigibberellin agent that when applied to wheat results in a reduction of endogenous gibberellin. Ethephon releases ethylene in the plant that inhibits auxin biosynthesis and thus inhibits the auxin promotion of stem elongation (Lurssen, 1982). Both CCC and ethephon were used in the experiment presented in this chapter.

The height of wheat can be reduced genetically and there are several major genes that have been important (Gale and Youssefian, 1985). The genes, Rht_1 and Rht_2, are present in many varieties grown in most wheat growing countries. These major dwarfing genes can reduce plant height by up to 50% if both genes are present or from 13 to 34 % if either one is present (Gale and Youssefian, 1985). The reduction in plant height by these genes depends also on whether a number of minor genes that also influence plant height are present (Allan, 1983). In New South Wales, most winter wheats are semidwarf and have the Rht_1 gene (Gale and King, 1988). In this chapter a breeding program is described that aims to introduce Rht_2 into current semidwarf winter wheats to obtain dwarf plants (Rht_1Rht_2) or to replace Rht_1 with the more potent Rht_3 dwarfing gene.

Plant height is one factor that is associated with reduced HI. Another may be the early depletion of soil water due to the larger biomass and leaf area in early sowings. In the field experiment presented next, there was an irrigation treatment to study the effect of water stress on yield and the interaction with sowing date. Leaf water potential was measured during the grain filling period of plants sown in both early and late May to determine any effect of sowing date on plant water stress.

6.2 MATERIAL AND METHODS

6.2.1 Plant growth regulators and irrigation experiment

An experiment with two sowing dates was planted on May 1 and May 26 at Condobolin, 1990. An earlier sowing in mid-April was not possible due to very wet conditions. Four genotypes Rosella, Osprey, Shrike and WW766 were sown. Those were chosen as the highest yielding and most suitable for early sowing in eastern Australia. Rosella, Osprey and Shrike are current commercial cultivars. A breeding line, WW766, was chosen for inclusion because of its superior performance in this region in 1989. A nested design was used with sowing dates as main plots followed by the nested hierarchy of irrigation, varieties and finally PGRs as sub,sub,sub plots. There were three replicate blocks. Plot size and agronomy were the same as the experiment described in Chapter 2 for Condobolin 1990. A third of every plot formed the irrigation treatment (6 m by 2 m).

Chlormequat and ethephon were applied according to procedure used with wheat at Griffith, NSW, that results in the most effective reduction in plant height (Dr. M. Stapper, personal comunication). Chlormequat was applied at a rate of 1000 g/ha using a knapsack spray just before stem elongation (Zadoks growth stage 30.5; Zadoks *et al.*, 1974). In the first sowing date, the dates of CCC application were August 10 in WW766 and August 14 in the other three varieties. In the second sowing CCC was given to all varieties on August 30. Ethephon was applied at a rate of 240 g/ha at Zadoks stage 39 (flag leaf fully expanded) on September 12 to WW766 and on

September 17 to the remaining varieties in the first sowing. In the second sowing ethephon was applied on September 18 to WW766 and Shrike, and on September 23 to Osprey and Rosella.

All plots were split into a rainfed and an irrigated treatment. Only one irrigation was applied because the crop was not visibly droughted until mid October. An irrigation of 46 mm of water was given on October 16 by drip irrigation. At this time all lines were in the grain filling period.

Three neutron meter access tubes were installed in every plot of Rosella and Osprey that were not treated with PGRs. A neutron probe (CPN Model 503DR) was used to monitor soil water content. Monitoring began on June 8 in both sowings. One of the access tubes was installed in the irrigated side of the plot, the other two in the dry control. Volumetric water content was measured at 10, 30, 50, 70, 90 and 110 cm depth. Analysis of variance (GENSTAT5 statistical package) was used to test the significance of differences between treatments.

On August 28 five plants per plot were harvested to measure stem height (from the base of the crown to the base of the apex) and to determine the number of tillers per plant. On October 4 a dry matter cut (0.85 m^2) was taken in all treatments, and green and dead leaves, shoot and ear dry weight were determined after oven drying at 70°C. The height of the main stem was measured from ground level to the base of the ear and the spike number per unit area was also determined.

Pre-dawn and midday leaf water potentials were measured on the flag leaf of untreated Osprey and Rosella plants in the field with a Scholander pressure bomb on October 18. Varieties were at the late milk stage (Zadoks stage 77) in the first sowing and water ripe (Zadoks stage 71) in the second sowing. On November 1, dawn and mid-morning leaf water potentials were measured in the flag leaf of Rosella plants. By November 1, the flag leaf of rainfed plants in the first sowing had fully senesced and leaf water potentials were not measured. Plants in the irrigated treatment were in late dough stage and 55% of the flag leaf was still green. Plants in the second sowing were in mid-dough stage and 15 and 70% of the flag leaf was still green in the rainfed and irrigated treatment respectively.

At maturity crop height was measured. A hand harvest and a mechanical harvest were taken to determine harvest index and yield as was described in Chapter 2. Total above-ground dry matter was estimated from the product of yield and harvest index. The number of spikes per unit area was estimated from the harvest index sample.

6.2.2 Breeding program

A backcrossing program to reduce the height of current winter wheat varieties or advanced breeding lines began in April 1990. The recurrent parents chosen were the best commercial cultivars available at the time Rosella, Osprey and Shrike, and

two breeding lines M3087-222 and M3508. The latter two lines were kindly supplied by Dr. L. Penrose, NSW Department of Agriculture, Temora. M3087-222 is a sib of Rosella and has superior septoria resistance whereas M3508 is somewhat shorter than the other lines. All lines contain Rht_1.

The donors of the additional dwarfing genes were from F_2 populations. These were used because the parent lines of these populations were either Condor, Banks or Phoenix which are closely related to the recurrent parent and would therefore lead more rapidly to genetic similarity to the recurrent parent. These lines were crossed to either Tordo (Rht_3 and spring donor), Yecora (Rht_1Rht_2 and spring donor) or AUS 20430 (Rht_2 and spring donor). Each F_2 population was screened for dwarfness and spring/winter habit and spring, dwarf plants were selected as donors to cross to the recurrent parent. Spring plants were chosen to hasten generation time in the breeding program. Dwarf plants containing both Rht_1 and Rht_2 or containing Rht_3 were selected by the length from the soil surface to the ligule of the second leaf when grown in 4 ppm gibberellic acid following the method described by Richards (1992a). Briefly, seeds from the crosses, parents and various known tall, semidwarf and dwarf lines were sown in plastic lined wooden flats containing small pots (3.5 cm diameter). The pots were filled with a perlite-vermiculite mix saturated with nutrient solution and containing 4 ppm gibberellic acid.

The success of the breeding program was evaluated on seed available in June 1992 (BC_2F_2). Plants were screened to identify dwarf winter wheats. Dwarf plants were identified using the GA test and the recurrent parents were used as controls. Winter plants were identified by growing them in the Lloyd Evans Phytotron, Canberra, in sunlit glasshouses maintained at 20/8°C (day/night). Aproximately 12 tall and 12 dwarf seedlings were selected from the GA treatment and transplanted into pots (8 cm diameter by 15 cm height) filled with 1:1 mixture of perlite and vermiculite. Similarly, ten seedlings of each recurrent parent were also transplanted. Water and nutrients were applied daily. Plants were grown under natural light and daylength was extended to 12 hours. Tall and short seedlings were separated in two blocks within the cabinet to avoid shading by tall plants. Plant height at anthesis and anthesis date was recorded to determine the number and height of dwarf and semidwarf plants and of winter and spring plants.

6.3 RESULTS AND DISCUSSION

6.3.1 Effect of plant growth regulators and irrigation

Yield and above-ground biomass were increased in the irrigation treatment by 6 and 5% respectively. In view of the small effect that the irrigation treatment had on yield and as there was no significant interaction with any of the other factors (except with variety for HI; $p=0.05$), most of the results are averaged for the rainfed and

irrigated treatments. Grain yield, AGDW, HI and height for the rainfed and irrigated treatment are given in Table 6.1.

Table 6.1 Effect of irrigation on yield, above-ground biomass (AGDW) , harvest index (HI) and plant height. Results are averaged over the two sowing dates.

	Yield (g m^{-2})	AGDW (g m^{-2})	HI	Height (cm)
Rainfed	374	892	0.419	84
Irrigated	399	940	0.424	84
s.e.d.	9	19	0.002	1

A reduction in stem height due to the CCC application was not observed at the harvest on August 28 in varieties in the first sowing date, except in WW766 in which there was a 2 cm reduction in stem length (data not shown). Plants then had two nodes (Zadoks stage 32). This application of CCC may not have been fully effective as differences in stem height can be detected quite soon after the treatment (Craufurd and Cartwright, 1989). Nevertheless by October 4 there was a significant effect of PGRs on stem length (Table 6.2). The reduction in length attributed to the PGRs averaged 16 cm in the first sowing and 9 cm in the second on October 4. This difference between sowing dates is likely to be due to lines in the second sowing not having completed stem elongation at the date of harvest. At this time it would appear that Rosella was the least sensitive to the applied PGRs although at this time stem elongation in Rosella had not finished. At maturity, Rosella showed the largest reduction in plant height of all varieties (14 cm).

There was some evidence that PGRs delayed anthesis in WW766 (2 days) and Shrike (1 day) in the early sowing (Table 6.3). This is less than in Keyes and Sorrells (1990) who found a 3.7 day delay in flowering time in semidwarfs wheats treated with ethephon before anthesis. On October 4, the PGR treatment had had no significant effect on above-ground dry weight or on leaf, shoot and ear dry weight (data not shown).

The reduction in plant height had a small though significant ($p < 0.001$) effect on plant dry matter partitioning (Appendix 3); the stem fraction decreased by only 2% and the leaf and spike fraction increased by 1%. Simmons *et al.* (1988) have shown that treated wheat plants had heavier stems per unit length than untreated plants resulting in similar above-ground dry weight per unit ground area. In this experiment also, there was little effect of PGRs on dry matter partitioning. However, the sheath of the leaves was not separated from the stem and it might be that, if sheath allocation increased as blades did, the reduction in stem allocation is underestimated.

At maturity the PGR treatment had reduced final plant height by 10 cm in both sowing dates but it did not significantly affect grain yield, AGDW or spike number (Table 6.4). There was a significant though small increase in HI approaching 2 % in the PGR treatment. In similar environments, an increase in plant height of 10 cm in spring wheats resulted in a 3.7 % decrease in HI (Richards, 1992a). This was not much lower than the 2 % increase in HI observed here.

Table 6.2 Stem height and spikes m^{-2} of varieties on October 4.

Sowing date	1/May		26/May		
	+PGRs	-PGRs	+PGRs	-PGRs	s.e.d.
Stem height (cm)					
WW766	64.3	81.7	49.3	56.3	
Shrike	54.7	73.3	43.7	57.7	
Osprey	58.7	79.0	48.0	58.3	
Rosella	53.0	61.3	41.0	46.7	1.7
mean	**57.7**	**73.8**	**45.5**	**54.8**	**0.8**
Spikes m^{-2}					
WW766	389	333	359	361	
Shrike	372	378	376	458	
Osprey	393	428	424	423	
Rosella	311	346	368	384	31
mean	**366**	**371**	**382**	**406**	**15**

Table 6.3 Anthesis date of varieties at the two sowings.

Sowing date	1/May		26/May	
	+PGRs	-PGRs	+PGRs	-PGRs
WW766	Oct 4	Oct 2	Oct 9	Oct 9
Shrike	Oct 5	Oct 4	Oct 10	Oct 10
Osprey	Oct 5	Oct 5	Oct 11	Oct 11
Rosella	Oct 11	Oct 11	Oct 15	Oct 15

Table 6.4 Plant height, yield, above-ground dry weight (AGDW), harvest index and spikes per unit area in the four treatments at maturity.

Sowing date	May 1		May 26		
	+PGRs	-PGRs	+PGRs	-PGRs	s.e.d.
Plant height (cm)	82	92	76	87	1
Yield (g m^{-2})	427	415	351	360	12
AGDW (g m^{-2})	968	975	847	876	27
Harvest Index	0.436	0.424	0.414	0.411	0.003
Spikes m^{-2}	299	305	320	312	12

Yield increases after PGR application have been attributed to a higher number of spikes per unit area or kernels per spike in the absence of lodging when PGRs were applied at a comparable time (Hofner and Kuhn, 1982; Waddington and Cartwright, 1986; Ma and Smith, 1992). However, neither on August 28 (data not shown) nor October 4 nor at maturity was there a significant effect of growth regulators on shoot number per plant or on spikes m^{-2} (Table 6.2 and 6.4). At maturity there were no differences in the number of spikelets per spike or the number of kernels per unit area nor kernels per spike as a result of the PGR treatment (data not shown).

There are several reasons why yield did not increase following the PGR treatment, despite the reduction in stem length. Firstly, ethephon has recently been shown to induce pollen sterility when applied prior to anthesis in wheat (Keyes and Sorrells, 1990) or barley (Ma and Smith, 1991). It is possible that this negative effect compensated for any positive effect from the reduced stem competion. Secondly, the reduction in stem dry weight may have been too small to have had any beneficial effect on ear growth. Finally, it is worth assessing the effect of a height reduction in this environment. Assuming that PGRs have no detrimental effects on growth, yield or fertility, what is the expected effect of a 10 cm reduction in height in this environment of low potential yield? From the data on spring wheat sown in May and June in a similar region (Richards, 1992a) there is little change in yield when height varies between 70 and 100 cm. This is because AGDW declines as height declines to the same extent as HI increases resulting in no net effect on grain yield. Assuming winter wheats are similar to spring wheats in this respect then it is not unexpected that PGR treatment should have little effect on grain yield.

Another objective of this experiment was to test whether early sowing may deplete soil water content to such an extent that plants become severely droughted after anthesis and unable to completely fill their grains resulting in a drought-induced, low HI. At the harvest on October 4 there were significant although small differences

in AGDW between the two sowing dates. AGDW averaged 847 g m^{-2} in the first sowing and 787 g m^{-2} in the second sowing. Despite this 8 % range the soil water contents on October 3 were identical in both sowings (305 mm in 120 cm soil depth). This result was also found in the experiments on the early and late isogenic lines in 1989 and 1990 (see Chapter 4). There was, however, a greater volumetric soil water content in the top 40 cm in the irrigated treatment. The leaf water potential measurements made on October 18 and November 1 were consistent with these findings. The leaf water potentials in the irrigated treatment were always higher (less negative) than the control (rainfed) plants (Table 6.5) whereas the pre-dawn and midday leaf water potentials were the same in both sowing dates. Two weeks later, when pre-dawn values were substantially more negative, values for the two sowing dates were again similar although the early sowing had a significantly higher (albeit small) and hence more favourable leaf water potential than the later sowing.

6.3.2 Breeding dwarf winter wheats

Figure 6.1 summarises the backcross breeding program carried out from April 1990 until the end of 1992 with the production of BC_4F_1 seed.

Eight BC_2F_2 populations involving several different recurrent parents were screened for GA insensitivity and compared with their parents to determine whether winter wheats had been selected. BC_2F_2 seedlings in each population varied substantially in the distance from the soil surface to the ligule of the second leaf (data not shown). The length of the tallest seedlings was similar to that of the parents confirming the presence of at least one dwarfing gene. This was also confirmed with the height of the selected plants at anthesis. Table 6.6 shows the height at anthesis of the selected tall and short plants within the spring (97 days to anthesis on average) and winter (124 days to anthesis on average) genotypes. In every population the short plants were significantly smaller than the tall plants by between 30 and 50 %, and this range was greater in the winter wheats. This large range in height reduction with an extra dwarfing gene contrasts with the relatively constant value of 30% found by Richards (1992a) in spring wheats. It may be that *Rht* genes have a stronger effect on plant height when in a winter wheat background.

Table 6.6 also confirms the presence of winter dwarf wheats in every population tested and that all were significantly shorter than the recurrent parents. The dwarf winter and the tall winter plants were consistently taller than their corresponding spring counterparts in every population for which this comparison is possible. This result supports the rationale behind the breeding program. That is, longer duration wheats will be taller than short duration wheats even when they are similar genetically, and this may result in them having a lower yield. The incorporation of another dwarfing gene into winter wheats may then result in a similar

height to their spring counterparts that have only one major dwarfing gene. This result was confirmed in this preliminary experiment.

A reduction in height in winter wheats with the incorporation of an additional dwarfing gene may result in plants with a similar height and harvest index to that found in spring wheats. In spring wheats there is an optimum height between 70 and 100 cm where there is little change in grain yield as any change in HI is counterbalanced by changes in biomass (Richards, 1992a). Thus a reduction of 30% in height within this optimum would mean a 12% increase in HI and a 13% decrease in biomass. In the case of winter wheats sown in April, plant height was around 100 cm having a maximum in a semidwarf wheat of 110 cm (Chapter 5). A decrease in this height by 30% due to an extra dwarfing gene would result in a yield increase only if the corresponding increment in HI is not balanced exactly by a decrease in biomass.

Table 6.5 Flag leaf water potential (MPa) on October 18 and November 1

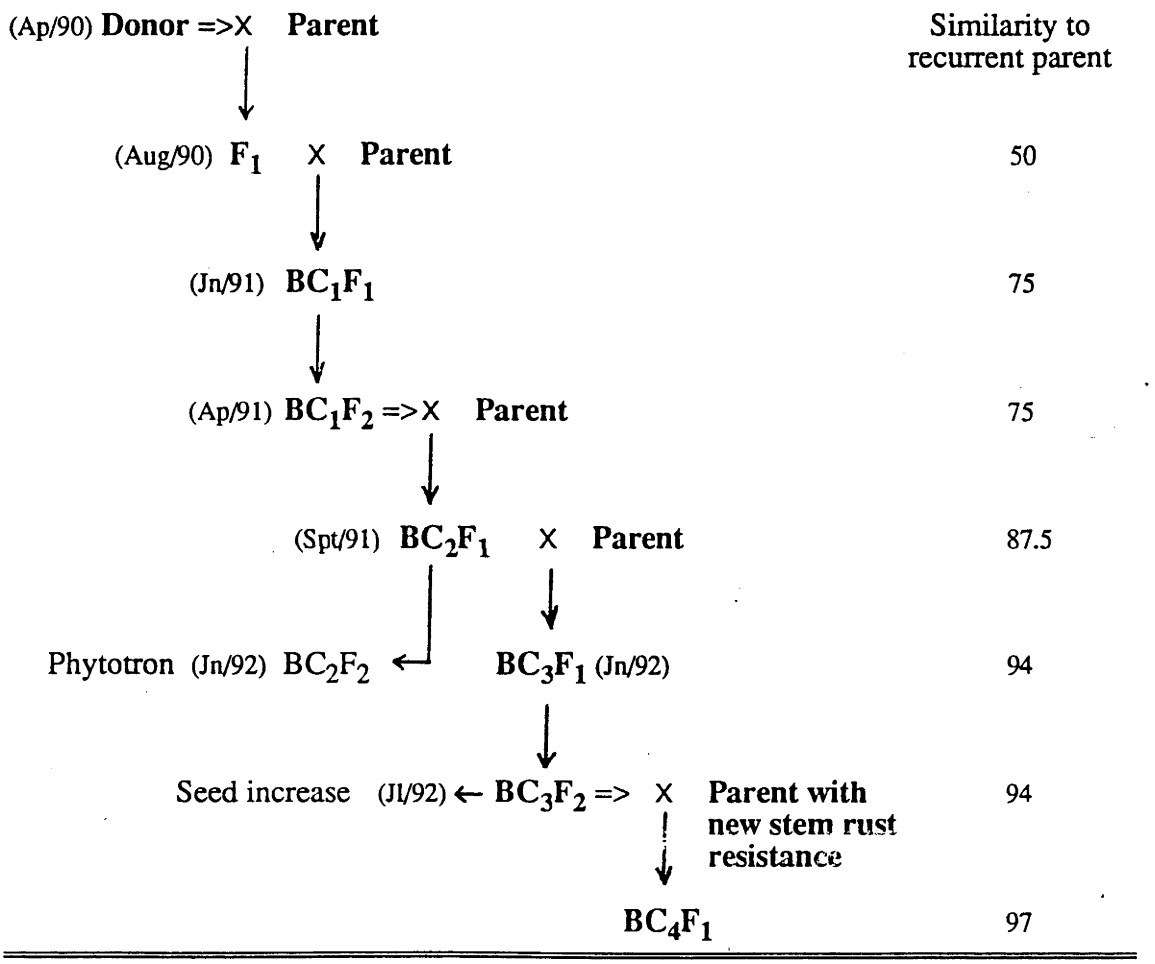
Sowing	May 1		May 26	
	Rainfed	Irrigated	Rainfed	Irrigated
October 18				
Pre-dawn	**-0.20** ±0.06	**-0.11** ± 0.02	**-0.21** ± 0.07	**-0.10** ± 0.02
Midday	**-2.48** ± 0.12	**-1.76** ± 0.11	**-2.41** ± 0.10	**-1.64** ± 0.10
November 1				
Pre-dawn	**-0.73** ± 0.01		**-0.86** ± 0.07	
midday	**-1.90** ± 0.03		**-2.11** ± 0.09	

Table 6.6 Plant height (cm) at anthesis (Zadoks growth stage between 65 and 70) of BC_2F_2 populations (mean ± s.e.). Average plant height for the parents was 75.5 cm.

Flowering type	spring lines			winter lines			
	tall	short	%reduction[a]	tall	short	%redt.[a]	%redt.[b]
Population							
1	**52** ± 2	**36** ± 1	**31**	**80** ± 2	**53** ± 2	**34**	**30**
2	**58** ± 2	**35** ± 1	**40**	**90** ± 2	**44** ± 2	**51**	**42**
3	**52** ± 2	**37** ± 1	**29**	**62**[c]	**54**[c]		
4	**58** ± 1	**38** ± 2	**34**		**44**[c]		
5	**48** ± 1	**30** ± 2	**38**	**61** ± 5	**38**[c]		
6	**46** ± 2	**28** ± 2	**39**		**45**[c]		
7				**72** ± 2	**43** ± 1	**40**	**43**
8				**77** ± 3	**48** ± 2	**38**	**36**

[a]short lines with respect to the tall lines [c]based on one plant
[b]short lines with respect to the recurrent parent

Figure 6.1 Breeding program (sowing time in brackets; => indicates that plants crossed were previously screened with GA).



CHAPTER 7

EFFECT OF VERNALIZATION AND PHOTOPERIOD GENES ON PLANT GROWTH OF SPACED PLANTS IN CONTROLLED ENVIRONMENT

7.1 INTRODUCTION

Field studies in Chapter 4 suggest a relationship between dry matter production and plant development, as later flowering winter wheats had slower growth up until anthesis than earlier flowering spring wheats. A link between growth rate and development has previously been suggested in wheat and other graminaceous species (Hodges and Kanemasu, 1977; Kemp *et al.*, 1989; Green and Valdyanathan, 1986; Green, 1989; Davidson *et al.*, 1990). Kemp *et al.* (1989) showed that an increase in leaf expansion rate coincided with the beginning of floral initiation in perennial ryegrass. Hodges and Kanemasu (1977), Green and Valdyanathan (1986), and Green (1989) suggest an internal control related to phenology that accelerates crop growth during the time of stem elongation.

However, some recent studies have reported contrasting results. Rawson (1991), working with plant canopies, found no direct relationship between leaf expansion and apex development in wheat isolines differing in vernalization response. He found that it was long days *per se* that affected leaf expansion and not plant development. The results of the work of Flood and Halloran (1986a) showed that the relative growth rates of isolines with different phenologies were the same.

As winter genotypes may be distinguished from spring types by the presence or absence of a single gene (*Vrn*) it suggests that this gene may have a significant influence over growth as well as over the switch in development of the apex from producing leaf primordia to producing spikelet primordia. It may also have important implications in the adoption of winter wheats by farmers in Mediterranean-type regions where maximizing growth during winter is important for maximizing grain yield (Richards, 1991).

The objectives of the work presented in this Chapter is to study the relationship between plant development and plant growth and to determine if the switch from vegetative apex to reproductive apex induces a change in plant growth. The timing of plant development was varied by the use of different photoperiods and different genotypes, isogenic for vernalization or photoperiod genes. In this Chapter, results are presented for spaced plants to amplify any variation between phenotypes in growth rates. In the next Chapter results are reported for plants grown in canopies.

7.2 MATERIAL AND METHODS

Plants of five near-isogenic lines differing in their vernalization and photoperiod requirements (Table 7.1) were grown. These near-isogenic lines were selected from two backgrounds. The first set of lines (TDs, TDt and TDc) are related to the Triple Dirk group developed by Pugsley (1968). TDs is a fourth back-cross derivative of TD which contains genes for insensitivity to photoperiod from Sunset whereas TDt, although similar, contains genes for sensitivity to photoperiod from Thatcher. TDc is the same winter wheat described by Pugsley (1968). None of these lines has an *Rht* dwarfing gene. The second set of lines (MQw and MQs) were selected from the second back-cross of a spring wheat, Millewa, by a winter wheat, Quarrion. Their vernalization and photoperiod requirements were determined as in Appendix 1. Both MQ lines are semi-dwarf wheats and have the Rht_1 dwarfing gene.

Table 7.1 Expected vernalization and photoperiod responses of near-isogenic lines.

Isoline	Vernalization Response	Photoperiod Response
TDs	-	-
TDt	-	++
TDc	++	+
MQs	-	+
MQw	+	+

- no response; + medium response; ++ strong response

Seeds sown had the same weight (43mg). They were sown in pots 50cm high by 9cm diameter filled with a standard, highly fertile, potting mix. Two seeds were sown in each pot and they were thinned at emergence to one plant. Pots were widely spaced.

The experiment was conducted in a walk-in Conviron growth cabinet (PGW36) maintained at day/night temperatures of 18.4/14°C (15.4°Cd). A double bank of cool white fluorescent tubes and incandescent light globes provided 700Omol $m^{-2}s^{-1}$ of photosynthetically active radiation, measured with a Sunfleck Ceptometer (Delta-T) at pot height, for 10 hours. The cabinet was partitioned into two; one compartment had the standard 10 hour day and in the other compartment daylength was extended by 5 hours with two incandescent globes.

Regular harvests were taken in each treatment and each line until the first line of each isogenic set reached ear emergence. Harvests consisted of three plants from each line. These plants were washed and their stems dissected to record the phenological stage of the apex. Double ridge and terminal spikelet stages were

determined according to Kirby and Appleyard (1981). Leaves were removed and the leaf area measured using a video operated planimeter (Delta-T). In some harvests, length and width of main stem leaves were also determined. The weight of roots, crown, leaves and shoots were determined after drying in a forced draught oven at 70°C. Root-to-shoot ratios were calculated as root dry weight divided by the weight of the rest of the plant.

Relative growth rate, RGR, and net assimilation rate, NAR, were determined following the procedure used by Poorter (1991) in order to avoid autocorrelation between harvests. However, in this experiment, the first and the last values of these rates have not been considered. These values were not good estimates of RGR and NAR as a double harvest was not taken at the beginning and end of the experiment. Leaf area ratio, LAR, was calculated as total plant leaf area divided by total plant dry weight.

Relative growth rate differences among isolines within treatments were tested as recommended by Poorter and Lewis (1986). Relative growth rate differences were considered significant if the isoline*time interaction was significant in the analysis of variance of total plant dry weight, after natural logarithmic transformation. The analysis of variance was calculated with the GENSTAT 5 statistical package.

7.3 RESULTS

7.3.1 Phenology

Considerable variation in phenology both between and within the isogenic sets was found when lines were grown in the two photoperiod treatments (Table 7.2). Lines within each isogenic group behaved in the expected way. The vernalization requiring lines, MQw and TDc, reached double ridge later than their isogenic counterparts which lacked the major vernalization genes, or not at all in the case of TDc. All lines were sensitive to photoperiod and reached double ridge and terminal spikelet earlier in the 15 hour photoperiod treatment than in the 10 hour treatment.

Table 7.2 shows time in days to reach the double ridge and terminal spikelet stage in all lines and treatments. The first line to reach floral initiation was TDs; it took 11 days to reach double ridge in the 15 hour light treatment and 13 days in the 10 hour treatment. Similar results were obtained by Rawson (1970) in the variety Sunset which is the donor of earliness in TDs. The interval between double ridge and terminal spikelet was more sensitive to daylength than the period to double ridge in TDs as it needed 10 extra days when grown in short day conditions. The time to both double ridge and terminal spikelet in TDt, MQw and MQs, was also affected by daylength. The time to reach terminal spikelet in MQw was delayed by a further 21 days compared to MQs when grown in the 10 hour treatment and this occurred when the main stem already had one node. The winter line TDc remained vegetative during

the entire time, as was expected because of its strong vernalization requirement (it has genes vrn1, vrn2, vrn3 and vrn4, Flood and Halloran, 1986b). The use of phothermal time (Masle *et al.*, 1989) reduced the differences in development between the two daylength treatment (data not shown).

Table 7.2 Time (days after emergence) to double ridge stage (DR) and to terminal spikelet stage (TS) and period between both.

	Daylength					
	10 hour			15 hour		
Lines	DR	TS	TS-DR	DR	TS	DR-TS
TDs	13	29	16	11	17	6
TDt	21	37	16	13	22	9
TDc	-	-	-	-	-	-
MQs	22	40	18	13	26	13
MQw	33	60	27	28	39	11

7.3.2 Leaf appearance and tillering

There was a significant effect of daylength on leaf appearance rate as well as on phenological development. There was no evidence that rate of leaf appearance for these lines changed at the time of double ridge or terminal spikelet stage. Figure 7.1a shows leaf number in relation to time to double ridge and terminal spikelet for the TD lines. For TDc, which did not reach double ridge or terminal spikelet stage, leaf numbers at 15 and 30 days after emergence are shown. The line is fitted to TDs and TDt in the 15 hour treatment ($y=0.55+0.18x$; $r^2=0.998$; $p<0.001$). Leaf number was less in each line in the 10 hour treatment at an equivalent time after emergence. It was also evident that the rate of leaf appearance declined with later leaves in those lines that did not initiate (TDc), or that reached terminal spikelet late (TDt in the 10 hour treatment). Similar results were found for the MQ lines (Fig. 7.1b).

The later formed leaves on the main stem of TD isolines not only differed in their appearance rate but also in their blade length and width (Fig. 7.2). Leaf dimensions of lines within each isogenic set before double ridge stage were similar, but subsequently there were differences in leaf size among the TD lines. Later formed leaves in the winter line, TDc, had longer and narrower blades (and a larger area) than later leaves of TDt or TDs lines. Blade length in TDc increased linearly, 75mm and 78mm per leaf in the 10 and in the 15 hour treatment respectively, whereas blade length in TDt and TDs decreased after reaching the double ridge stage (Fig. 7.2). The extremely long blades of later formed leaves in TDc may account for their slower rate of emergence as they would need more time for full expansion. Blade length in the

MQ lines followed a similar trend as the TD lines but did not show such extreme differences (data not shown).

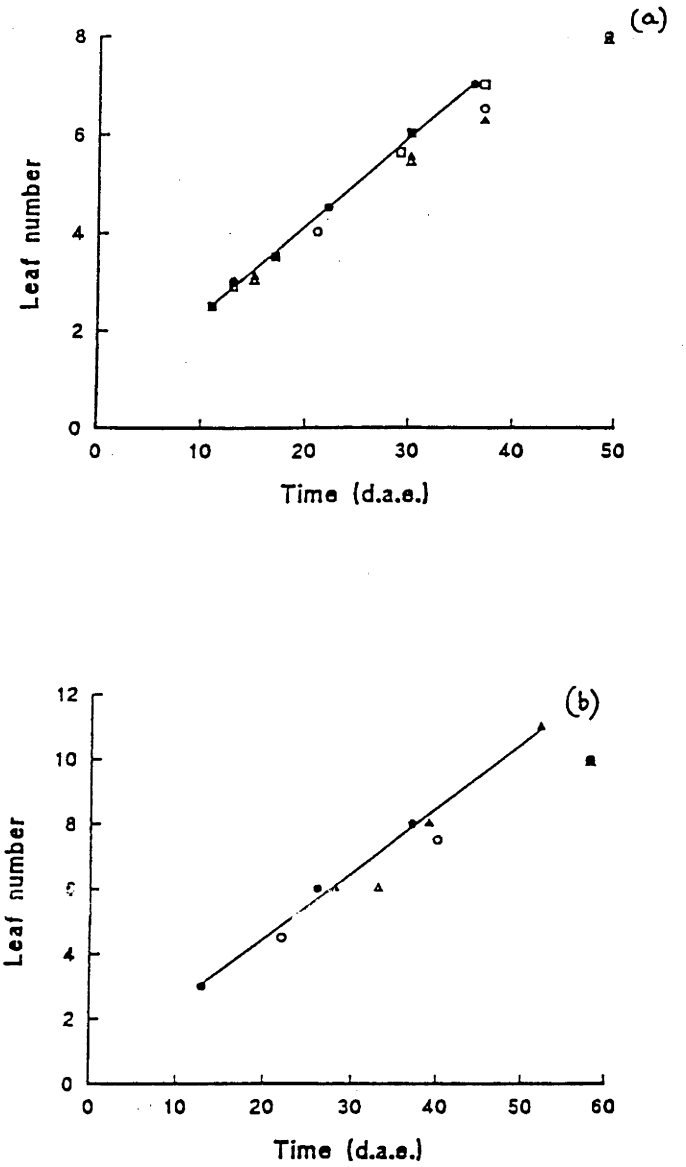


Figure 7.1 Relationship between leaf number and time for (a) TD lines (TDs - ■,□; TDt - ●,○; TDc - ▲,△) and (b) MQ lines (MQs - ●,○; MQw - ▲,△). Open symbols are for the 10 hour treatment, closed symbols for the 15 hour treatment. Data points shown correspond to day 15 and 30 in TDc and to DR and TS for all other lines.

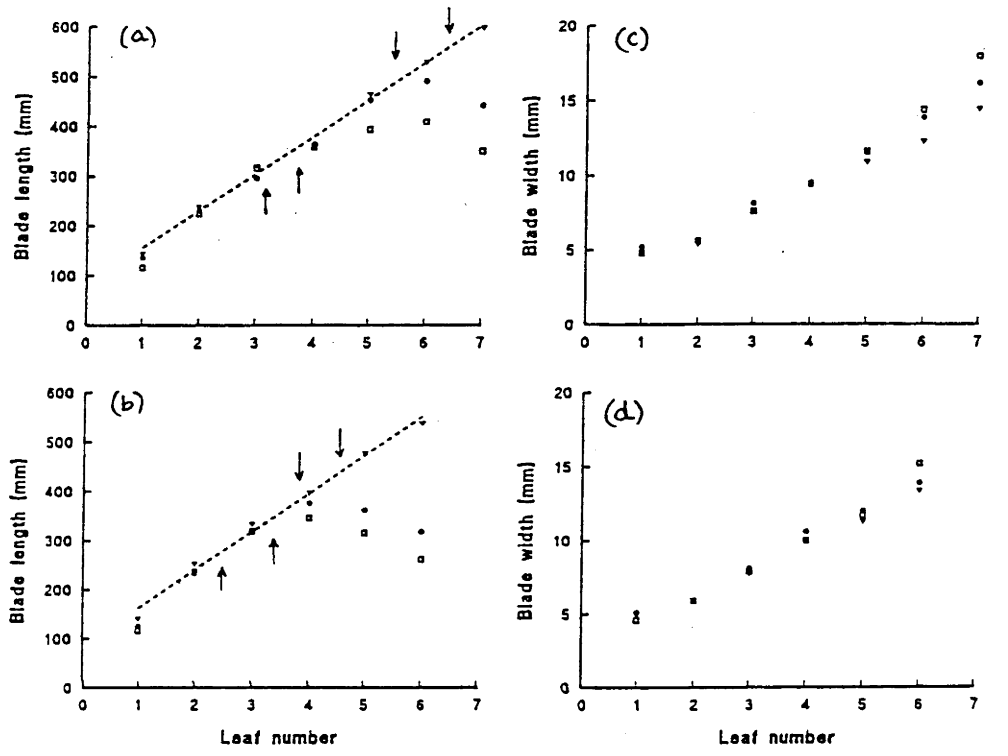


Figure 7.2 Relationship between leaf number and leaf length and width for main stem leaves under the 10 hour treatment (a and b) and under the 15 hour treatment (c and d) for the TD lines. Arrows indicate DR (↑) and TS (↓) for TDs and TDt lines. Symbols as in Figure 7.1

Phenology also had an effect on tillering. The rates of tillering of lines in each isogenic set were similar up to the time of double ridge stage but declined thereafter. Figure 7.3a presents the shoot number (main stem and tillers) of each TD line at the time of double ridge and terminal spikelet stage. A line has been fitted to TDc, which did not initiate ($y=-6.7+0.64x$; $r^2=0.999$; $p<0.001$). Values below the lines are shoot number at the time of terminal spikelet stage. Thus, it is evident that tiller number increased after double ridge stage but at a slower rate. An exception to this trend was TDt in the 10 hour treatment.

Daylength did not affect tiller appearance in TDc as plants had the same number of tillers in both treatments at the time the 15 hour treatment was terminated. Similar results were found for the MQ set. Figures 7.3b and c shows the shoot numbers at each harvest. Shoot number at the time of terminal spikelet in MQs was below the shoot number at MQw indicating a reduced tiller appearance rate after floral initiation.

7.3.3 Total plant biomass and partitioning

Results of all harvests indicated that there were no differences in total plant dry weight between lines within treatments. Figure 7.4 shows that the main difference between the lines was not the total biomass per plant but the way it was partitioned. Winter lines partitioned most of their biomass to leaves, which formed about 50% of the total plant dry weight during the entire experiment. On the other hand, spring lines, once they reached floral initiation, stopped producing leaf primordia for spikelet primordia. After terminal spikelet stage, the stem and the ear growth of the spring lines increased at the expense of leaves and roots whereas the winter line, TDc, had a constant proportion of leaf dry matter throughout the experiment. As a result, leaf dry matter increased at a lower rate than in the winter lines whereas shoot dry matter, and then ear weight, increased sharply (Fig. 7.4). By the end of the experiment leaf area was significantly higher in the winter lines (Fig. 7.5). At the last harvest of the TD set of lines grown in the 15 hour treatment (37 d.a.e.), TDs had a leaf area of $428cm^2$ compared with $669cm^2$ in TDt and $950cm^2$ in TDc.

Root-to-shoot ratio decreased with time in all lines (Fig. 7.6). There was some evidence that winter lines had lower root-to-shoot ratios than spring lines at the beginning of the measurement period but that these differences disappeared later. Additionally, root-to-shoot ratio tended to be higher in MQw than in MQs at the end of the experiment.

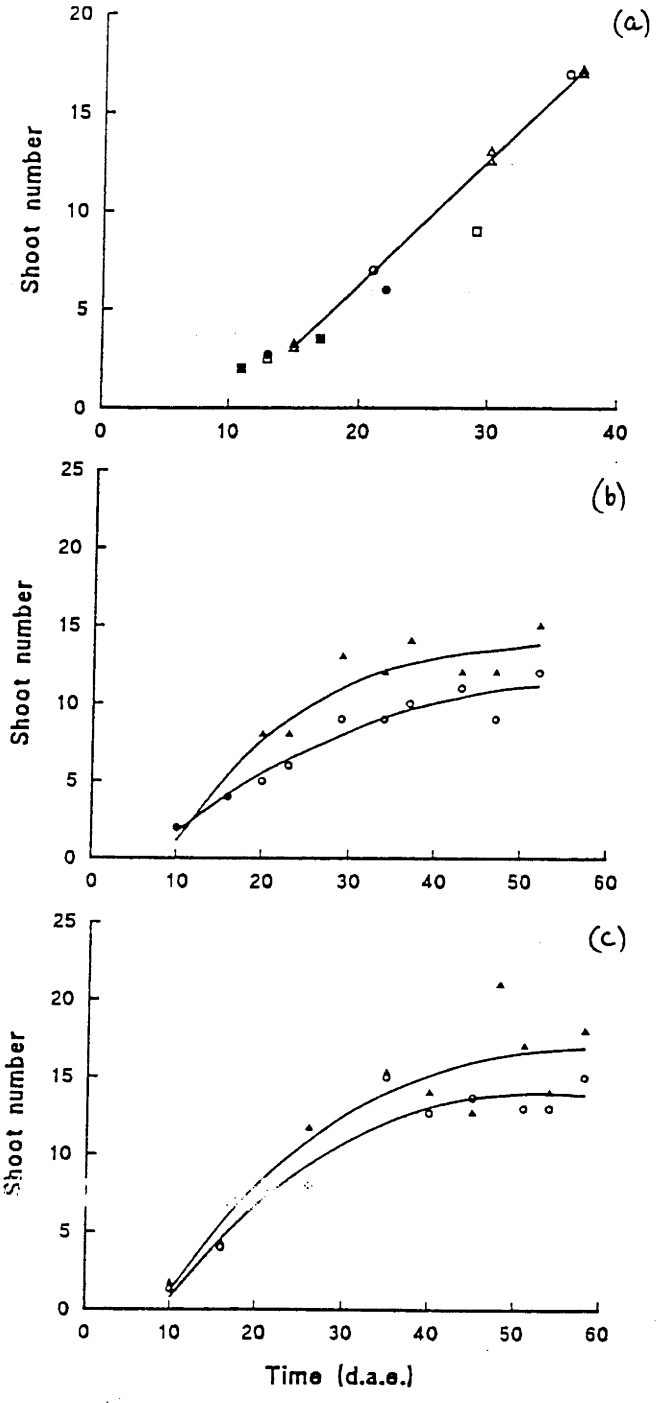


Fig 7.3 Relationship between shoot number and time for
(a) the TD lines under both the 10 hour and 15 hour daylengths (data points at DR and TS; symbols as in Fig 7.1a),
(b) the MQ lines under 10 hour daylength (MQs - o; MQw - ▲), and
(c) the MQ lines under 15 hour daylength (MQs - o; MQw - ▲).
Data points in (b) and (c) are from all harvests.

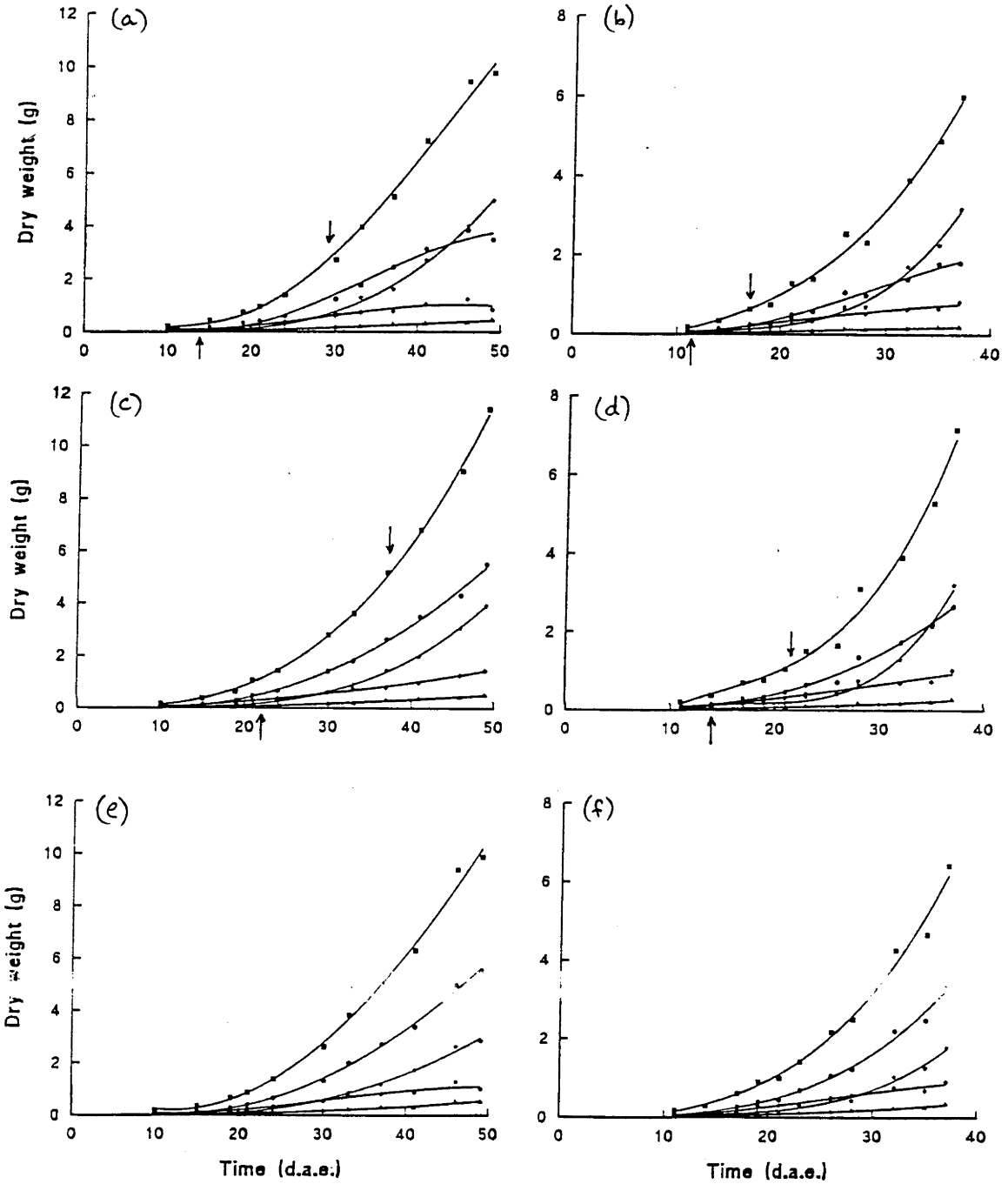


Fig. 7.4 (i) Relationship between dry matter accumulation and time for the TD lines.
(a) TDs under 10 hour and (b) TDs under 15 hour daylengths.
(c) TDt under 10 hour and (d) TDt under 15 hour daylengths.
(e) TDc under 10 hour and (f) TDc under 15 hour daylengths.
Symbols: ■ - total plant; ● - leaf; ★ - shoot; ✦ - root; ▲ - crown.
Arrows indicate DR (↑) and TS (↓).

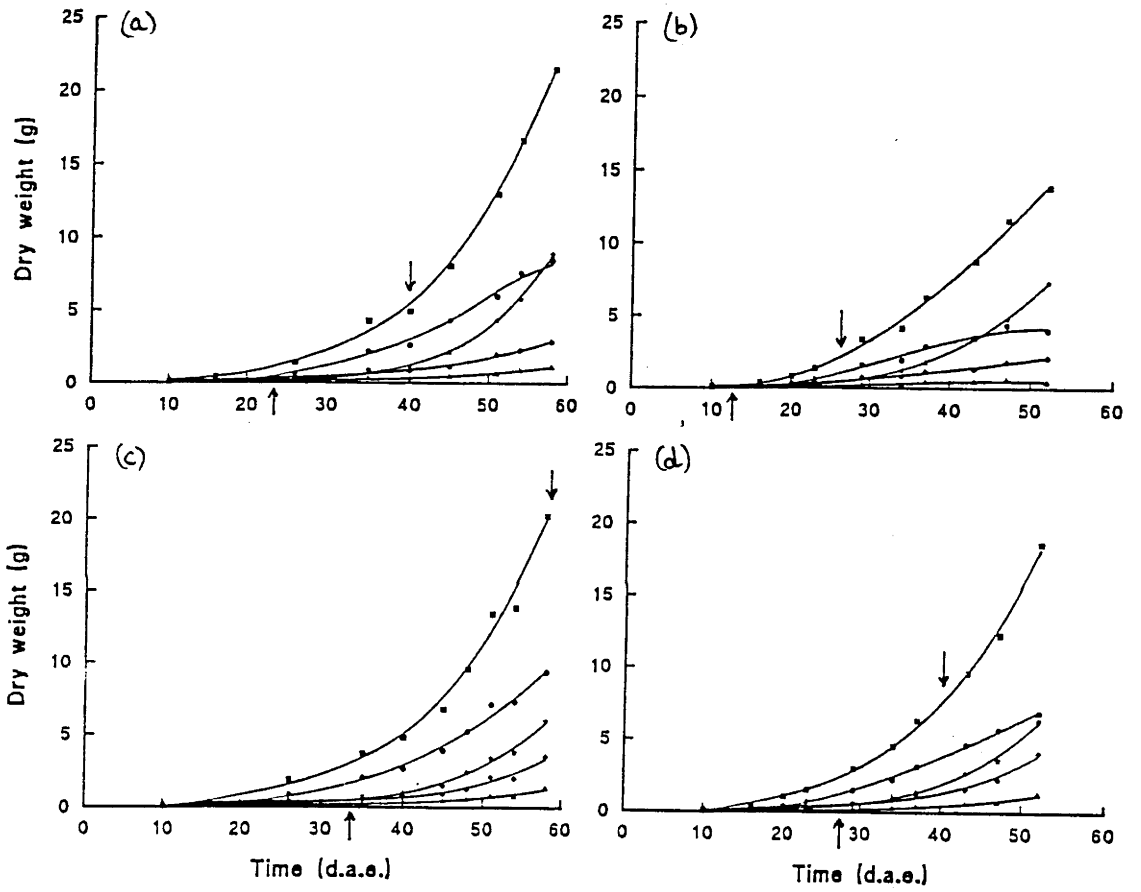


Fig. 7.4 (ii) Relationship between dry matter accumulation and time for the MQ lines.
(a) MQs under 10 hour and (b) MQs under 15 hour daylengths.
(c) MQw under 10 hour and (d) MQw under 15 hour daylengths.
Symbols: ■ - total plant; ● - leaf; ✯ - shoot; ✦ - root; ▲ - crown.
Arrows indicate DR (↑) and TS (↓).

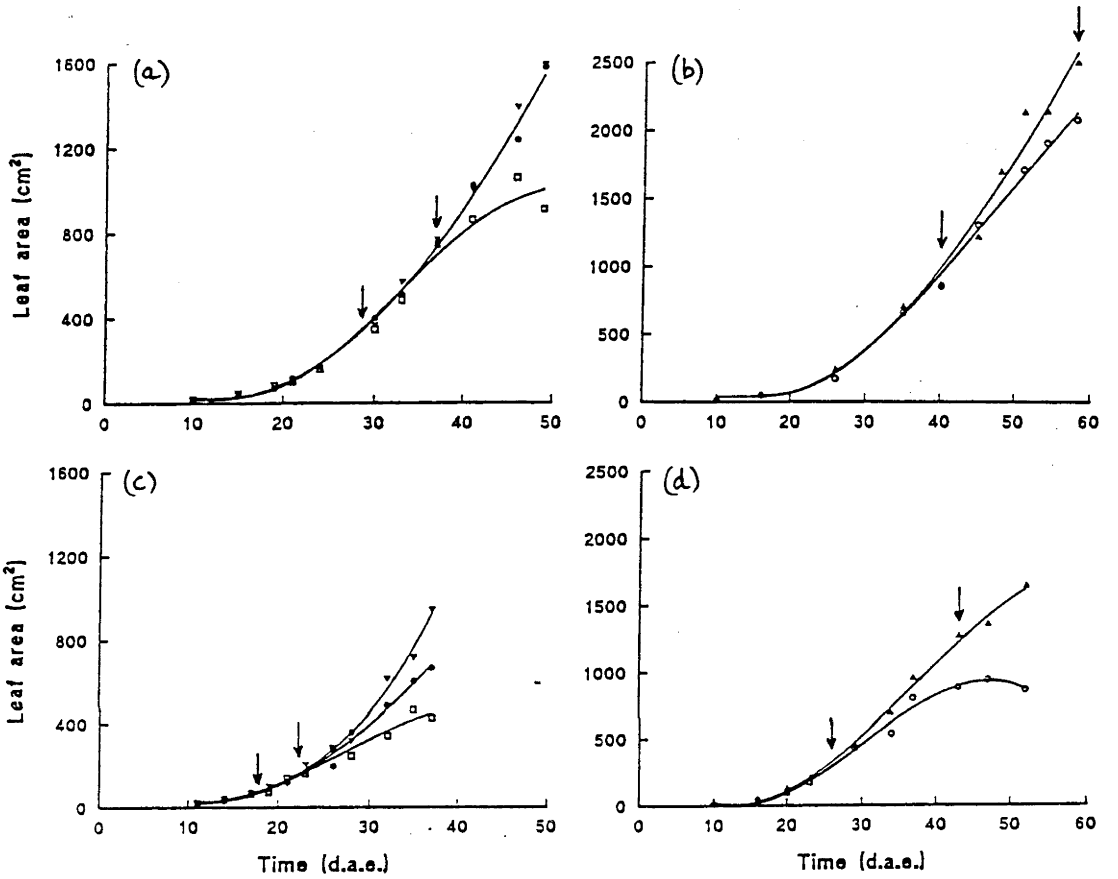


Fig. 7.5 Relationship between leaf area and time for (a) TD - 10 hour, (b) MQ - 10 hour (c) TD - 15 hour and (d) MQ - 15 hour daylength.

Symbols: ❑ - TDs; ● - TDt; ▼ - TDc; ○ - MQs; ▲ - MQw.

Arrows indicate DR (↑) and TS (↓).

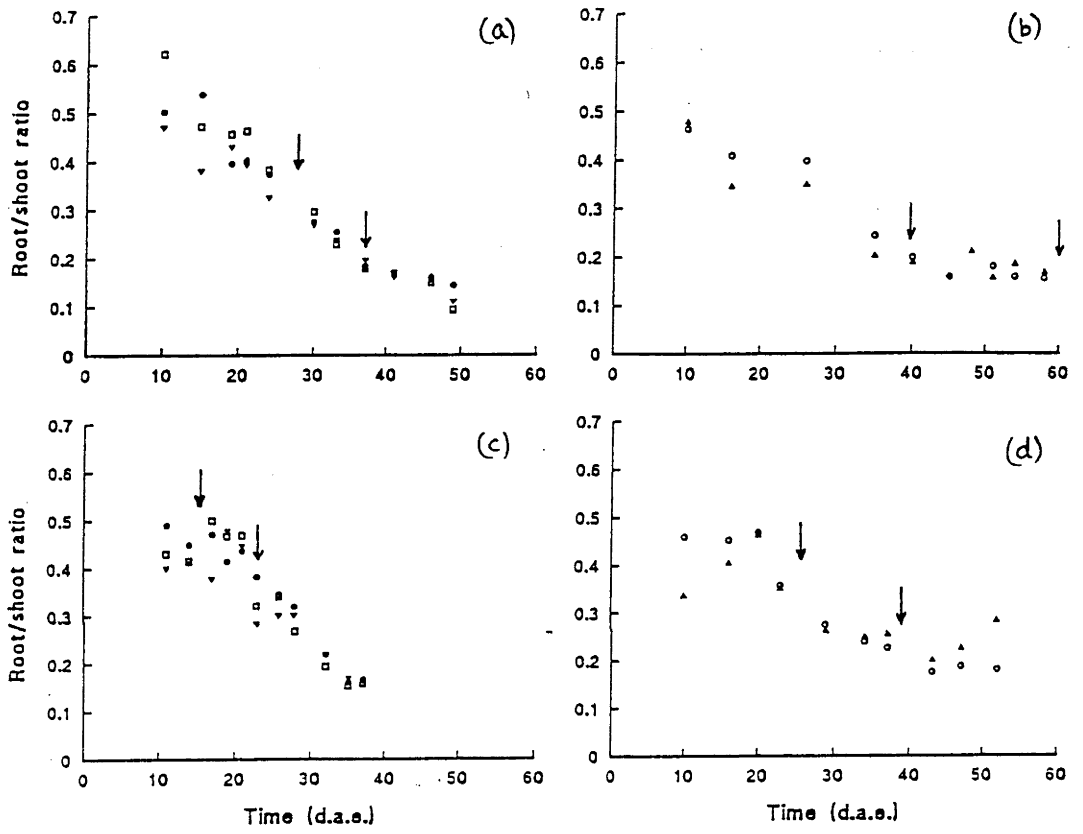


Fig. 7.6 Relationship between root/shoot ratio and time for (a) TD - 10 hour, (b) MQ - 10 hour, (c) TD - 15 hour and (d) MQ - 15 hour daylength.
Symbols: ❑ - TDs; ● - TDt; ▼ - TDc; ○ - MQs; ▲ - MQw.
Arrows indicate DR (↑) and TS (↓).

7.3.4 Growth analysis

There was no clear evidence that lines within treatments differed in their relative growth rate, RGR, when considered over the duration of the experiment. Analysis of variance using total plant dry weight (after natural logarithmic transformation) as the dependent variable showed no significant isoline*time interaction except for the TD set grown in the 15 hour day (Table 7.3). In this treatment the decline in RGR with time was greater in TDc than in TDt. The vernalization sensitive lines TDc and MQw generally had a higher RGR at the beginning of the measurement period (Table 7.4). Although these lines also tended to have a lower weight after emergence. Of more significance is the finding that at about the time of terminal spikelet, RGR increased in every treatment (Table 7.4). However, this increase was often not sustained and in time reverted back to a lower level than the control values.

Relative growth rate declined with time in all lines but its components, net assimilation rate, NAR, and leaf area ratio, LAR, varied in different ways (Fig. 7.7 and 7.8). NAR also declined with time and, except for the beginning of each experiment, spring lines had higher values than winter lines (Fig. 7.7). The higher values for NAR in the spring lines were consistently associated with the timing of terminal spikelet or just before. LAR varied considerably depending on treatment and isoline (Fig. 7.8). In general LAR values were more similar at the beginning of the experiment than at the end. This was associated with the continued production of leaves in the winter lines compared to the growth of stems rather than leaves in the line that reached floral initiation. This resulted in the LAR of winter lines deviating markedly from that of spring lines with time.

Variation in relative growth rate was mainly explained by changes in NAR (Fig. 7.9). Only the extreme winter line, TDc, showed a significant relationship between RGR and LAR but this association was probably due to the strong correlation between NAR and LAR ($r^2=0.95$ in the 10 hour treatment and $r^2=0.87$ in the 15 hour treatment; $n=9$; $p<0.01$). Nevertheless, low RGR values in TDs and MQ lines in the 15 hour treatment appeared to be better explained by LAR than NAR as leaf area production ceased and leaves were aging.

Table 7.3 Analysis of variance of total plant dry weight after natural logarithmic transformation.

Source of variation	df	MS	P
TD 15 hour treatment:			
Isoline	2	0.016	NS
Time	10	11.419	***
Isoline.Time	20	0.041	*
Isoline.Linear	2	0.007	NS
Isoline.Quadratic	2	0.071	NS
Deviations	16	0.041	*
Residual	66	0.023	
Total	98		
TD 10 hour treatment:			
Isoline	2	0.045	NS
Time	10	16.233	***
Isoline.Time	20	0.013	NS
Isoline.Linear	2	0.035	NS
Isoline.Quadratic	2	0.005	NS
Deviations	16	0.011	NS
Residual	66	0.024	
Total	98		
MQ 15 hour treatment:			
Isoline	1	0.098	*
Time	9	14.621	***
Isoline.Time	9	0.025	NS
Isoline.Linear	1	0.041	NS
Isoline.Quadratic	1	0.006	NS
Deviations	7	0.026	NS
Residual	40	0.019	
Total	59		
MQ 10 hour treatment:			
Isoline	1	0.054	NS
Time	8	17.580	***
Isoline.Time	8	0.034	NS
Isoline.Linear	1	0.002	NS
Isoline.Quadratic	1	0.012	NS
Deviations	6	0.042	NS
Residual	36	0.276	
Total	53		

Table 7.4 Relative growth rate (RGR mg $g^{-1}d^{-1}$) on whole dry plant basis of every isoline and treatment. Values in bold are higher or equal to the value in the winter isoline for the same day and treatment.

TD 10 hour treatment:

Time	15	19	21	24	30	33	37	41	46
TDc RGR	149	150	143	126	107	90	77	64	63
TDs RGR	133	132	127	122	**108**	**94**	**78**	60	54
TDt RGR	**157**	**158**	**145**	124	100	**91**	**77**	**69**	**63**

TD 15 hour treatment:

Time	14	17	19	21	23	26	28	32	35
TDc RGR	217	187	157	129	124	127	105	95	84
TDs RGR	180	178	**159**	**154**	**135**	107	96	87	**92**
TDt RGR	170	148	139	124	**138**	**127**	**122**	**114**	**99**

MQ 10 hour treatment

Time	16	26	35	40	45	51	54
MQs RGR	130	116	**91**	**81**	**78**	**81**	**77**
MQw RGR	**143**	**118**	83	74	**78**	77	70

MQ 15 hour treatment:

Time	16	20	23	29	34	37	43	47
MQs RGR	170	166	**142**	**113**	88	75	66	57
MQw RGR	**200**	**172**	136	102	**91**	**82**	**76**	**72**

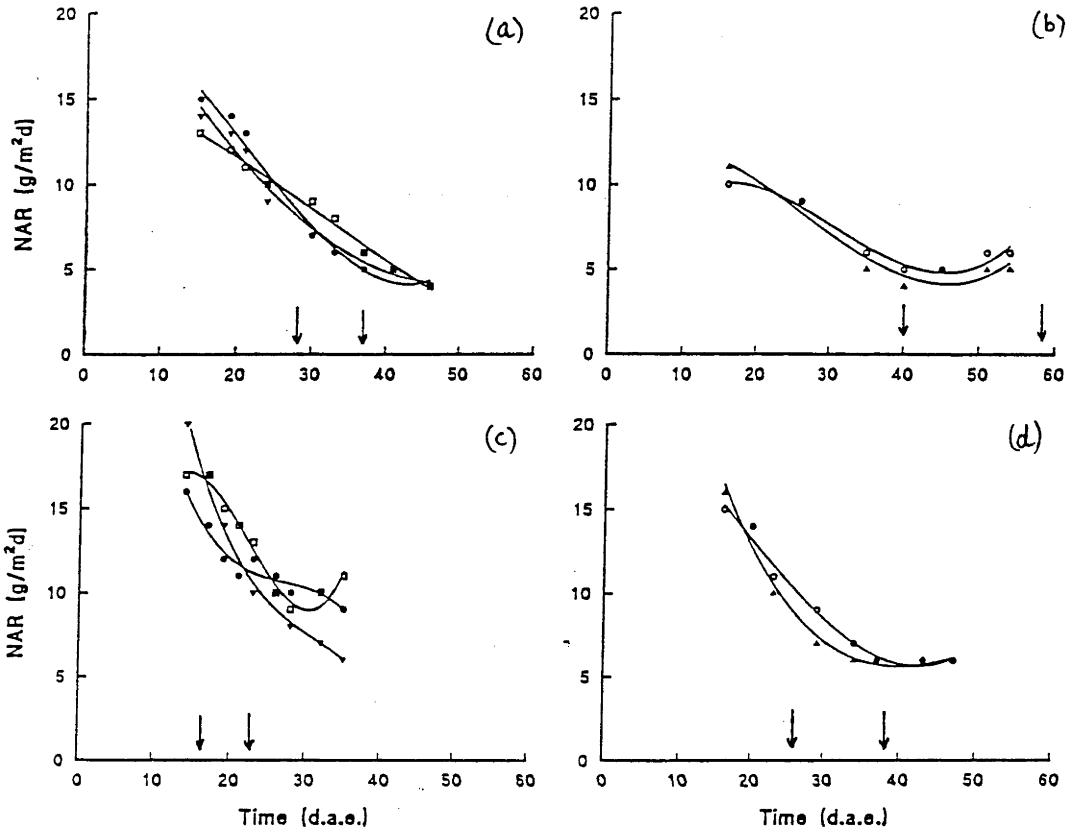


Fig. 7.7 Relationship between net assimilation rate and time for (a) TD - 10 hour, (b) MQ - 10 hour, (c) TD - 15 hour and (d) MQ - 15 hour daylength.
Symbols: ❑ - TDs; ● - TDt; ▼ - TDc; o - MQs; ▲ - MQw.
Arrows indicate DR (↑) and TS (↓).

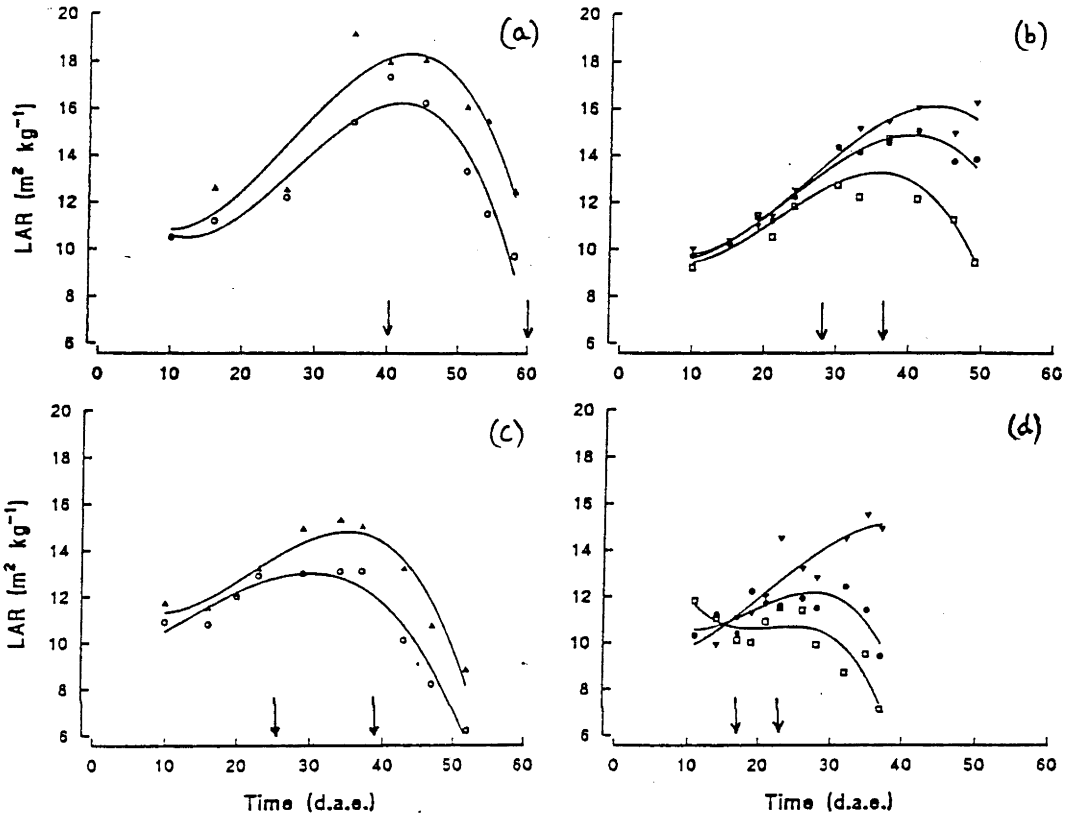


Fig. 7.8 Relationship between leaf area ratio and time for (a) TD - 10 hour, (b) MQ - 10 hour, (c) TD - 15 hour and (d) MQ - 15 hour daylength. Symbols: ❑ - TDs; ● - TDt; ▼ - TDc, ○ - MQs; ▲ - MQw. Arrows indicate DR (↑) and TS (↓).

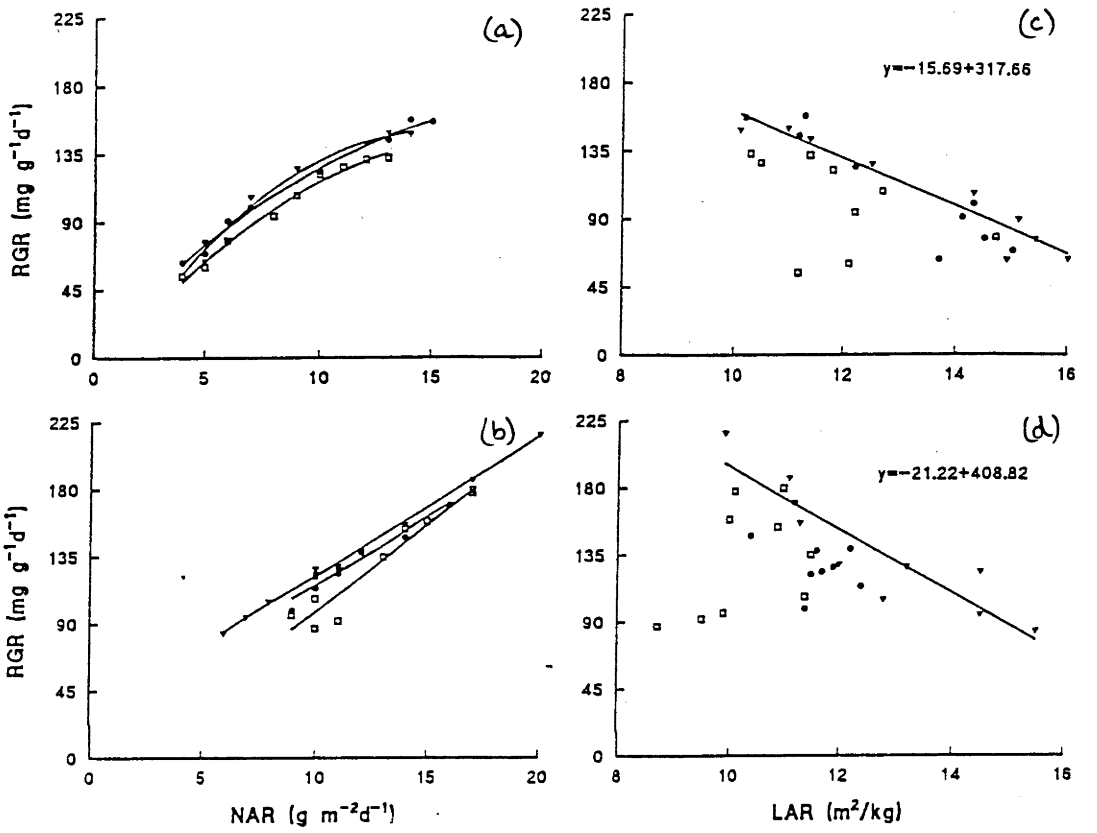


Fig 7.9 (i) Relationship for TD lines between relative growth rate and net assimilation rate under (a) 10 hour and (b) 15 hour daylength, and relationship for TD lines between relative growth rate and leaf area ratio under (c) 10 hour and (d) 15 hour daylength. Symbols as in Figure 7.8.

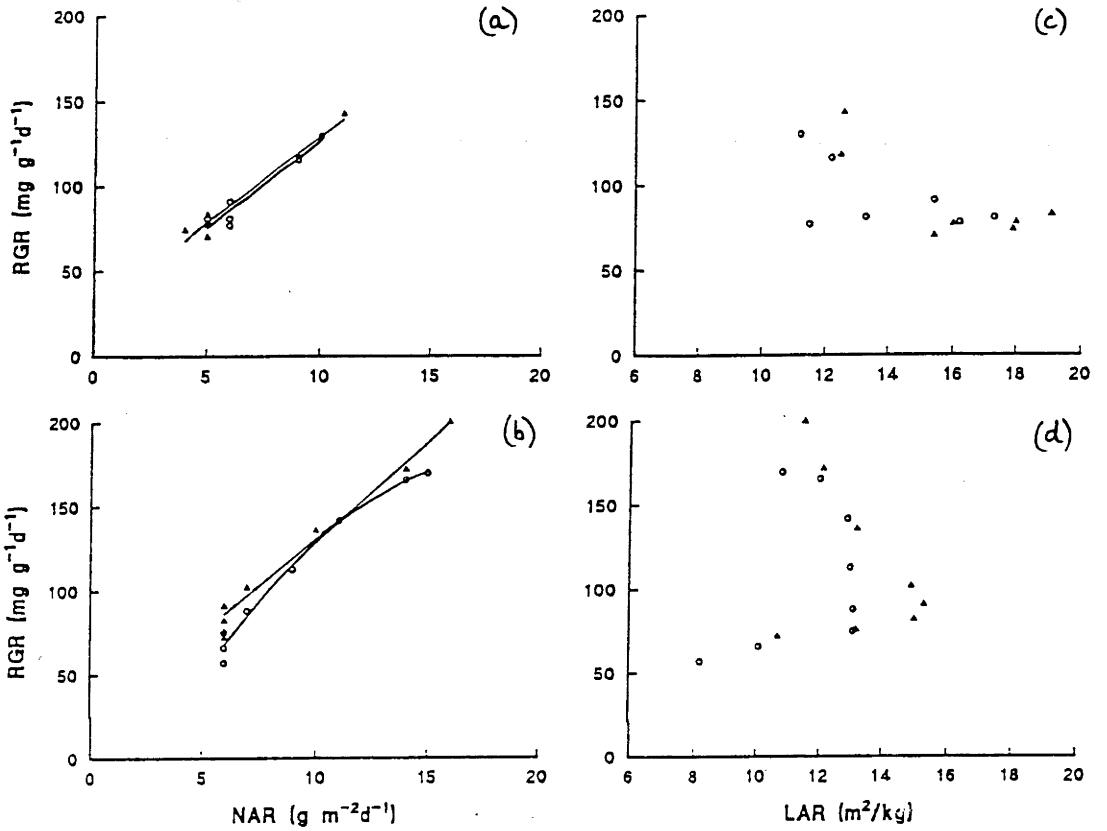


Fig 7.9 (ii) Relationship for MQ lines between relative growth rate and net assimilation rate under (a) 10 hour and (b) 15 hour daylength, and relationship for MQ lines between relative growth rate and leaf area ratio under (c) 10 hour and (d) 15 hour daylength. Symbols as in Figure 7.8.

7.4 DISCUSSION

In this experiment phenology was varied by photoperiod and by the use of near-isogenic lines with and without genes for photoperiod and vernalization sensitivity. A longer time to reach floral initiation and terminal spikelet was associated with the production of more and larger leaves as well as more tillers. This resulted in substantial differences in leaf area but no differences in final dry weight at the termination of the experiment (Fig. 7.10). Thus the major effect of the different phenological developments of the lines was in the partitioning of dry weight to leaves, leaf sheaths and roots in the winter lines compared to the growth of stems and heads in the spring lines.

The larger leaf area and hence leaf area ratio was expected to result in a greater relative growth rate in the lines that took longer to reach the double ridge and terminal spikelet stages. Surprisingly, this was not found, and the greater LAR in later lines was compensated for by the greater NAR in the shorter duration lines. RGR over the duration of the experiment was more closely related to NAR than to LAR. The RGR of lines for the duration of the experiment was similar and this is in accord with Flood and Halloran (1986a). It is also consistent with the absence of any differences in final dry weight. However, there was evidence in all lines in each treatment that at the time of terminal spikelet appearance RGR declined less than their isogenic counterparts that remained vegetative. This relative improvement in RGR was short lived and it soon reverted back to or just below the base level.

Associated with this relative improvement in RGR was a higher NAR in lines after reaching terminal spikelet stage than in lines that remained vegetative. Furthermore, the same higher RGR of earlier initiating lines was achieved throughout the experiment despite their leaf area becoming substantially less than their winter counterparts that remained vegetative. The higher NAR could arise from the better light penetration to lower leaves of lines that began stem elongation. It could also arise from an increased rate of photosynthesis due to the presence of an actively growing stem and ear (Hodges and Kanemasu, 1977; Herold, 1980)

These results for spaced plants may account for the differences between the better growth of spring wheats compared to winter wheats in field canopies. In canopies, winter wheats would be unable to maintain a high rate of tillering, as they were able to do it in this experiment, because of competition for light and space (Masle-Meynard, 1981). Thus their leaf area index may be little different to spring wheats. Thus, in canopies, differences in LAR between spring and winter wheats would be less than in this experiment and, if the differences in NAR are maintained, then this should result in higher RGR of spring wheats and hence in greater dry matter accumulation at a given time after double ridge stage in spring wheats. Furthermore, when the RGR of above-ground weight is considered in this experiment, the

differences between early and late developing lines is greater than when RGR is calculated on a whole plant basis. This must be due to the greater reduction in root-to-shoot ratio of the earlier developing lines. The appearance of new roots is coordinated with the appearance of tillers (Klepper *et al*, 1984) and growth of new roots must proceed for longer in the later developing lines.

Other findings in this Chapter that are noteworthy are: a) the reduction in the maximum rate of tillering beginning at the double ridge stage; b) the reduced rate of leaf appearance of last leaves in the lines with the longest delay in floral initiation; and c) the apparent lower root-to-shoot ratio of lines with the longest delay in floral initiation at the start of the experiment. Each of these findings will be described further in the next Chapter where a similar experiment is described using TDt and TDc grown in a canopy.

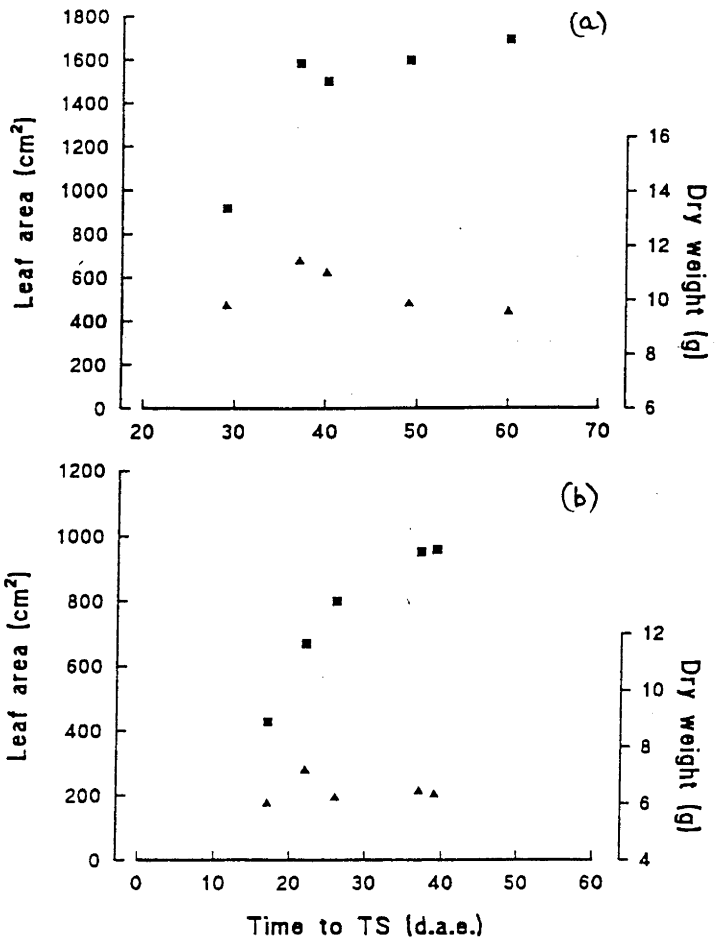


Fig 7.10 Leaf area (■) and dry weight (▲) at TS for all five lines grown under (a) the 10 hour treatment and (b) the 15 hour treatment. Data for TDc, which did not reach TS, are given for the last harvest date, i.e. day 49 in (a) and day 37 in (b).

CHAPTER 8

EFFECT OF VERNALIZATION AND PHOTOPERIOD GENES ON PLANT GROWTH IN A CANOPY

8.1 INTRODUCTION

The experiment described in the previous chapter was conducted primarily to determine whether differences in the growth of plants differing in photoperiod and vernalization genes, when grown as spaced plants, were associated with the timing of reproductive development. In this chapter growth in a simulated canopy of a subset of the lines is described

8.2 MATERIAL AND METHODS

Plant material consisted of two isogenic lines, TDt and TDc, described in Chapter 7. TDt is a photoperiod sensitive line and TDc remains vegetative unless its vernalization requirement is satisfied.

The methodology used was the same as that used for the experiment in Chapter 7 except for the following. Seeds weighing 36mg were sown in pots which were kept together to establish a canopy of plants with a density of 140plants/m^2. Pots of each line were arranged in four rows of 20 pots in a Conviron cabinet (PGW36). The two center rows were divided into three blocks and harvests consisted of three plants, each from a different block. As plants were harvested pots were rearranged to keep the same plant density. Four plants in the central rows were marked and leaf and tiller appearance was recorded on most days. Plots with TDc plants were lifted to match the increase in height with time of TDt plants.

Day/night temperature were maintained at 18/15^oC (16.2^oCd) with 705 $\mu mol\ m^{-2}s^{-1}$ of radiation for 10 hours during the day. These conditions remained until 21 days after emergence (d.a.e.). A light fault occurred and from 21 d.a.e. to the completion of the experiment radiation during the night period was 210 $\mu mol\ m^{-2}s^{-1}$.

8.3 RESULTS

8.3.1 Phenology

Floral development of the two lines in this experiment was in accordance with that in Chapter 7. The winter line, TDc remained vegetative for the entire experiment. The photoperiod sensitive line, TDt, reached the double ridge stage twenty days after emergence which was equivalent to the 10 hour day treatment in

Chapter 7. When double ridge occurred, daylength was increased to 24 hour. This caused an acceleration in TDt development that resulted in the same period, from double ridge to terminal spikelet stage as in the 15 hour day treatment in Chapter 7 (10 days). The main stem of TDt plants reached terminal spikelet stage 30 d.a.e.. At this time, all of the remaining shoots were in the floral initiation phase despite their different ages and sizes.

8.3.2 Leaf appearance and tillering

The first five leaves on the main stem appeared at the same rate in both isolines (Fig. 8.1a). However, the last leaves in the main stem of TDc (leaves six to eight) appeared at a slower rate than the earlier leaves. By contrast, the last leaves in the main stem of TDt appeared at a faster rate than the earlier leaves. The phyllochron interval for leaves one to five in both isolines was 5.5 days (89°Cd). This interval increased to 9.5 days (154°Cd) for the later formed leaves of TDc whereas for TDt the interval decreased to 4.4 days (71°Cd).

There were no differences in tiller appearance rate between the isolines until 30 d.a.e. (Fig. 8.1b). Tillering started 10 d.a.e. and ceased 30 d.a.e. in TDt and 45 d.a.e. in TDc. This tillering in TDt stopped on the same day the terminal spikelet appeared on the main stem. Ten days after terminal spikelet stage, the younger tillers in TDt started to look lighter in colour than the older tillers and than the tillers of TDc. At the end of the experiment (51 d.a.e.), 28% of TDt tillers were still very small and were dying, even though all had reached the terminal spikelet stage of apex development, 32% were small, thin, of pale colour, and also with initiated apices, whereas the remaining 40% had three to four nodes, looked healthy, and were already at ear emergence. TDc did not show any of these effects.

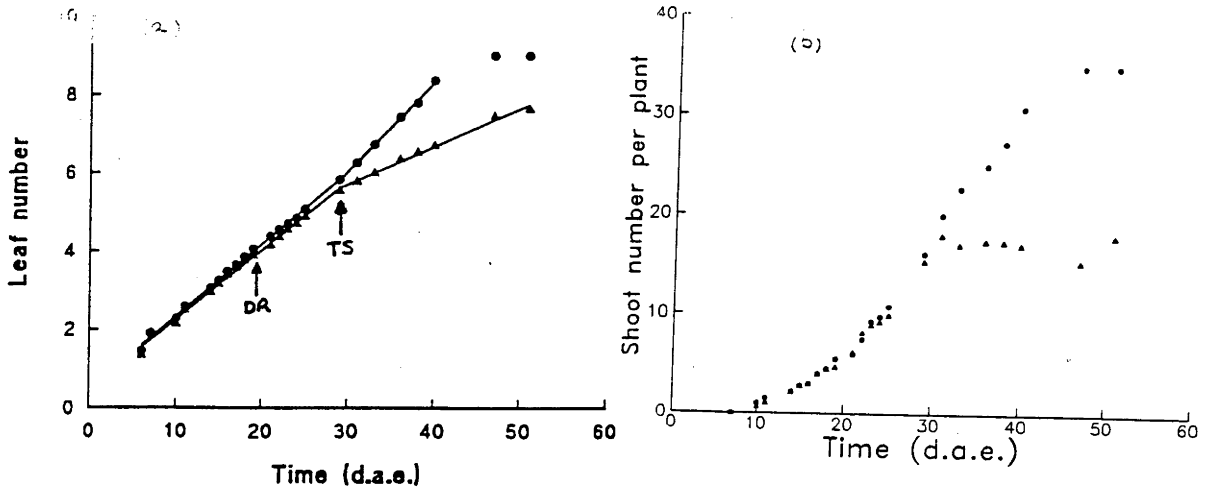


Figure 8.1 Relationship between time (days after emergence) and (a) leaf number on the main stem and (b)shoot number per plant for TDt (●) and TDc (▲).

8.3.3 Total plant biomass and partitioning

Total plant dry weight and leaf area accumulation is shown in Fig. 8.2. Total dry weights of TDc and TDt were very similar at each harvest; the final dry weight of both lines was the same (Fig. 8.2a). Above-ground dry weight of both lines, on the other hand, was the same until just after the terminal spikelet stage and after ten days TDt was 13% heavier than TDc (Fig. 8.2b). Leaf area was also the same at each harvest in both lines up to 30 d.a.e. (the time of terminal spikelet appearance in TDt), but deviated thereafter (Fig. 8.3). The time of terminal spikelet appearance in TDt also marked the time when leaf, shoot, root and crown weight of the two lines began to differ. Leaf, crown and root weight all became less in TDt than in TDc whereas shoot weight in TDt became greater (Fig. 8.4). Root-to-shoot ratio was initially greater in TDt than TDc but this reversed after terminal spikelet stage (Fig. 8.5). The root-to-shoot ratio declined until day 30 in both lines. After terminal spikelet stage, this ratio continued to decline in TDt whereas, in TDc, it remained constant.

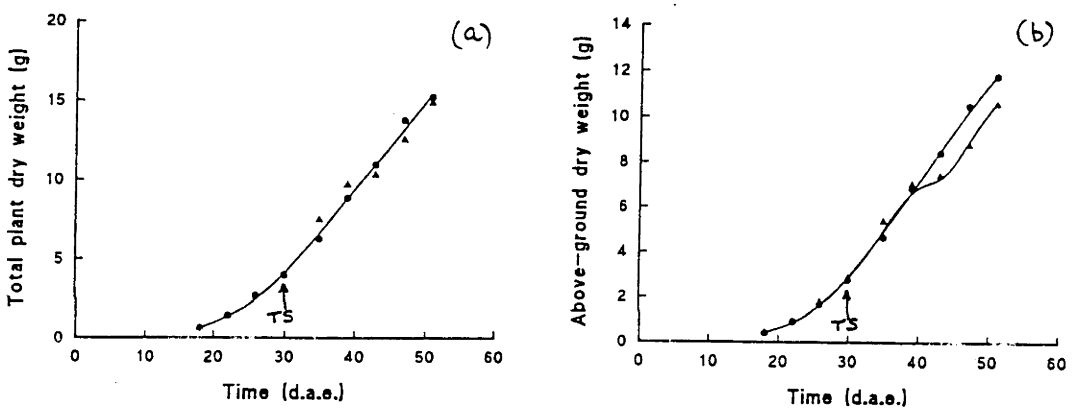


Figure 8.2 (a) Relationship between total plant dry weight (g) and time (days after emergence) for TDt (●) and TDc (▲); (b) relationship between total plant dry weight (g) and time (days after sowing) for TDt (●) and TDc (▲).

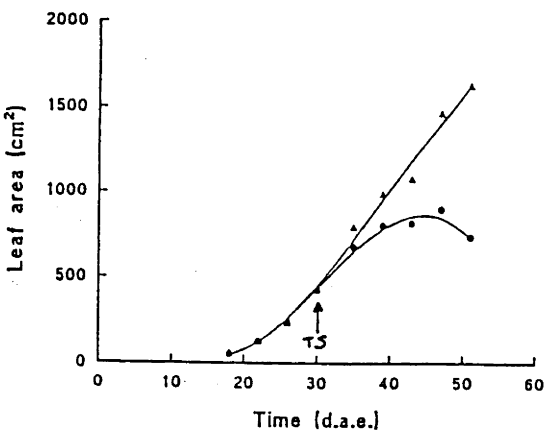


Figure 8.3 Relationship between leaf area (cm^2) and time (days after emergence) for TDt (●) and TDc (▲).

Relative growth rate (RGR) between double ridge and terminal spikelet stage was slightly higher in TDc than in TDt. However, this reversed after terminal spikelet stage and TDt had the greater RGR (Fig. 8.6a and 8.6b). Furthermore, after terminal spikelet stage the net assimilation rate (NAR) values were substantially higher for TDt than for TDc (Fig. 8.7a). At this time, leaf area ratio (LAR) also declined in TDt but continued to increase in TDc (Fig. 8.7b). The components of LAR, i.e. specific leaf area (SLA) and leaf weight ratio (LWR), also varied between the isolines (Fig. 8.8). The LWR in TDt declined after double ridge stage and declined at a faster rate after terminal spikelet stage as stems began to grow, whereas in TDc the LWR remained constant for most of the experiment. SLA, although highly variable, increased in both isolines during the experiment. SLA was initially highest in TDt but it became lowest in the final ten days of the experiment.

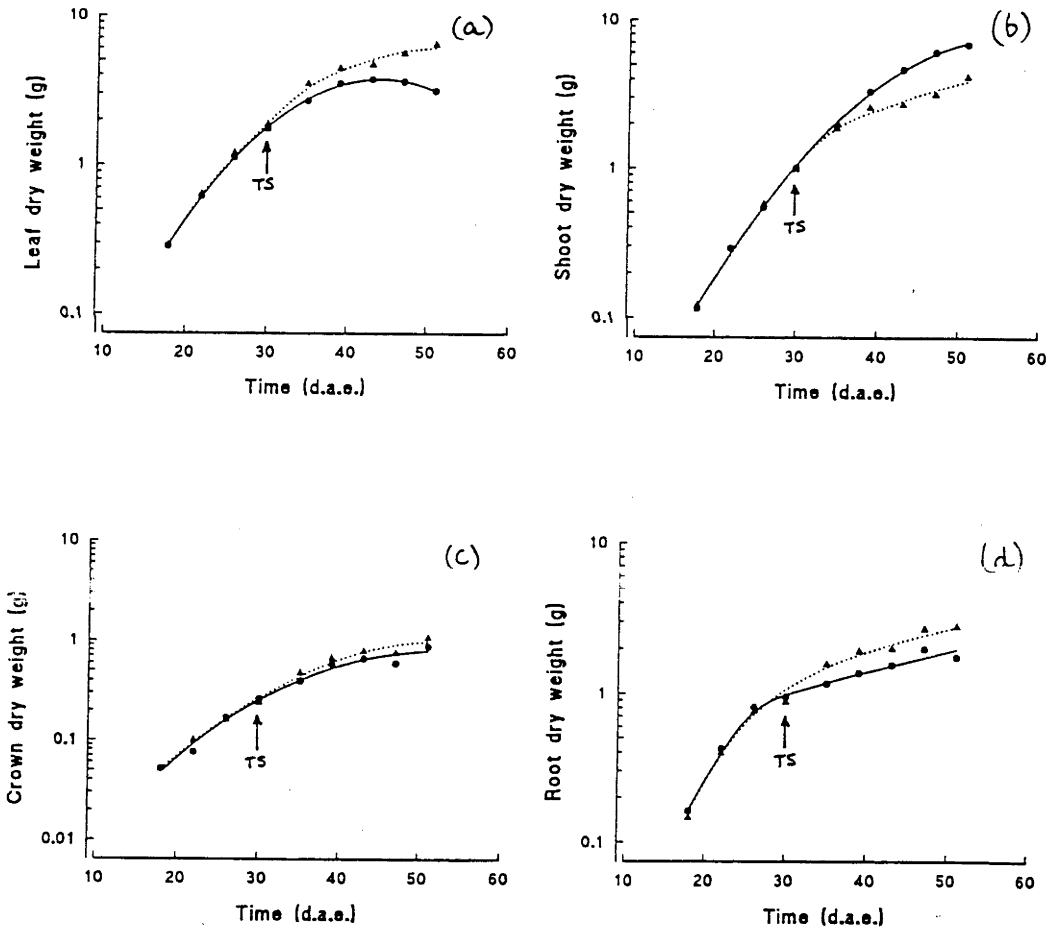


Figure 8.4 Relationship between (a) leaf dry weight, (b) shoot dry weight, (c) crown dry weight, (d) root dry weight and time (days after emergence) for TDt (●) and TDc (▲).

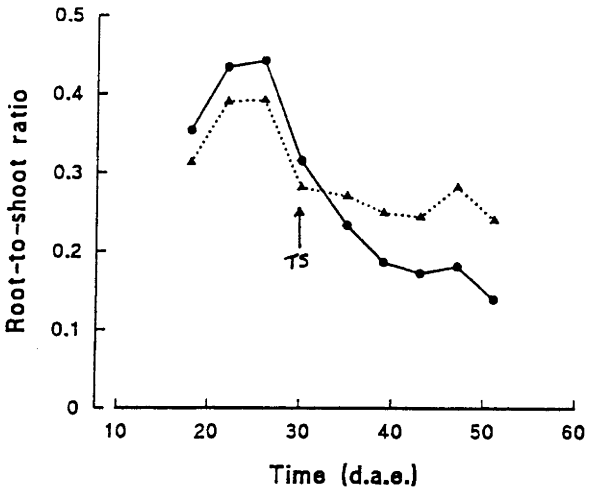


Figure 8.5 Relationship between root to shoot ratio and time (days after emergence) for TDt (●) and TDc (▲).

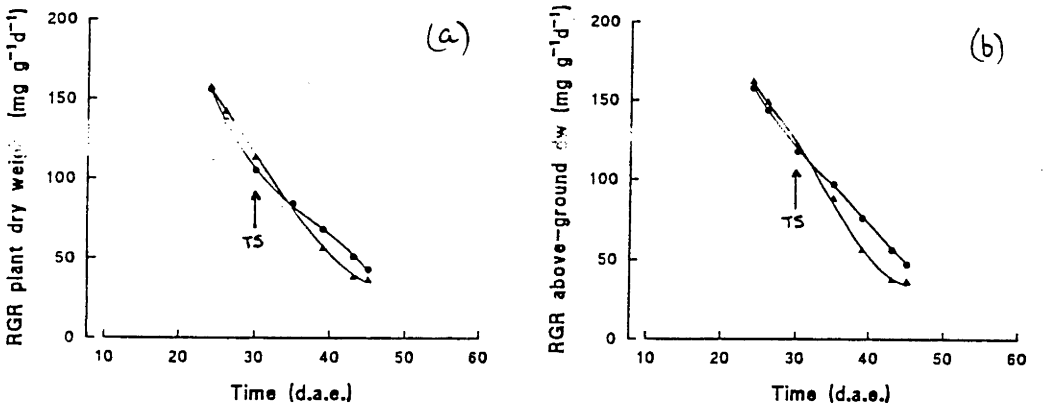


Figure 8.6 (a) Relationship between RGR based on total plant dry weight (mg g^{-1} d^{-1}) and time (days after emergence) for TDt (●) and TDc (▲); (b) Relationship between RGR based on above-ground dry weight (mg g^{-1} d^{-1}) and time (days after emergence) for TDt (●) and TDc (▲).

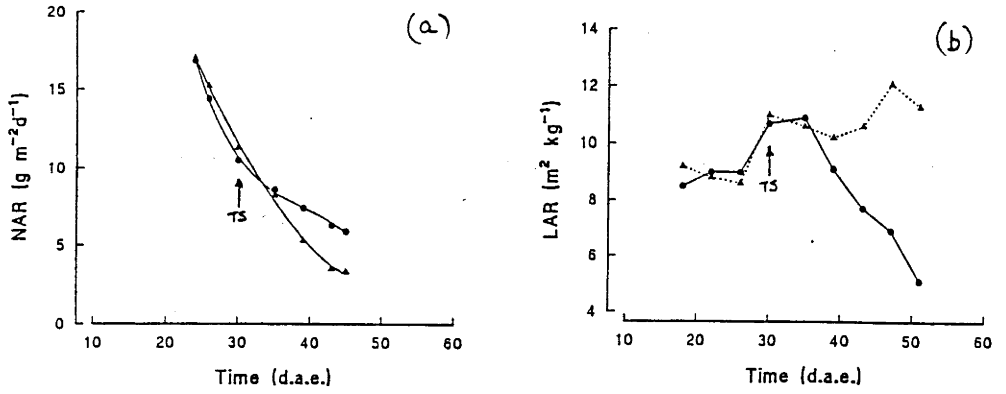


Figure 8.7 (a) Relationship between NAR (g $m^{-2}d^{-1}$) and time (days after emergence) for TDt (●) and TDc (▲); (b) Relationship between LAR (m^2 kg^{-1}) and time (days after emergence) for TDt (●) and TDc (▲).

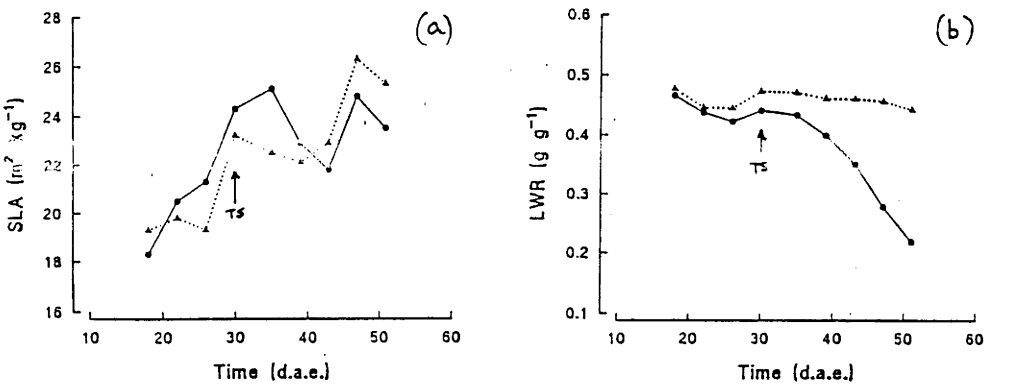


Figure 8.8 (a) Relationship between SLA (m^2kg^{-1}) and time (days after emergence) for TDt (●) and TDc (▲); (b) Relationship between LWR (g g^{-1}) and time (days after emergence) for TDt (●) and TDc (▲).

8.4 DISCUSSION

The results in this chapter showing the higher above-ground dry weight of the early-developing compared to the late-developing line confirm the results found in the field. In the field, lines that initiated floral development first started the fast accumulation of above-ground biomass earlier than lines with later floral development (Chapter 4). These differences were not found in this experiment when total plant dry weight is considered. The reason for the difference between lines occurs because of greater below-ground growth of roots and crowns in the winter line whereas the spring line had greater above-ground (stem) growth. The root-to-shoot ratio in TDt declined from 0.32 at terminal spikelet to 0.14 at the termination of the experiment whereas the values at the same time after emergence in TDc were 0.28 and 0.24 (Fig. 8.5). The differences described above arose just after the time of terminal spikelet appearance on the main stem when the growth of stems begins. Also coinciding with this time was a change in ranking in RGR. Up to terminal spikelet stage TDc had a marginally higher RGR for total weight than TDt; this reversed after terminal spikelet stage (Fig. 8.6a). The greater RGR in TDt after the terminal spikelet stage was more apparent when above-ground weight only is considered (Fig. 8.6b). The increase in RGR in TDt was due to the greater NAR rather than to LAR. This result also matches those found in the previous chapter. The presumed reasons for the higher NAR and RGR in TDt starting from the beginning of stem elongation are eventually the better light distribution within the canopy and the presence of an actively growing stem and ear.

The differences in above-ground dry weight and RGR between TDt and TDc arose despite the substantially higher leaf area and LAR in TDc after terminal spikelet - a result also found in the previous chapter. This difference in leaf area was not expected in the simulated canopy and it contrasts with results in the field where LAI values of winter and spring wheats were not significantly different. The likely reasons for the differences in leaf area are that in the field water and nutrients were limiting whereas in the pot experiments both water and nutrients were optimal. The very low nutrient levels and sub-optimal water supply would have inhibited tillering (Masle, 1985; Thorne and Wood, 1988; Krenzer *et al.*, 1991) and the potentially large leaf area in the winter lines. Assuming spring lines also have a greater NAR after terminal spikelet than winter lines, and that differences in LAR are considerably less between lines in the field, then the RGR of early initiating lines should be greater in field grown plants and this may accentuate the difference in total dry weight.

The additional light received by plants at night in this experiment in contrast to the previous one cannot be discounted for having an effect on growth and partitioning. This extra light may have contributed to the higher root to shoot ratio in

TDc and to the greater shoot growth in TDt than what was found in Chapter 7. The extra availability of assimilates seems, therefore, to reinforce the differences in growth between lines of different phenology showing that in TDt the elongating stem and the developing ear were stronger sinks than leaves and roots.

Main stem leaf appearance rate is considered to be fixed at the time of emergence and to vary according to genotype, temperature and, to a lesser extent, to photoperiod (Baker *et al.*, 1980; Kirby *et al.*, 1982; Masle *et al.*, 1989b; Cao and Moss, 1989ab). Nevertheless, in this experiment, main stem leaves had a different appearance rate (Fig. 8.1a) and it was shown that the stage of apex development also influences rate of leaf appearance. The later leaves of TDt needed one day ($16^{o}Cd^{-1}$) less to appear than leaves one to five, whereas the later leaves of TDc needed four days ($64^{o}Cd^{-1}$) more than was required for earlier leaves. Later leaves of TDt were located in the nodes of the main stem, which expanded as the plant increased in height. The gradient in temperature from the base of the stem to the flag leaf was $2^{o}C$ which might partly explain the faster appearance rate of later formed leaves. However, TDc plants were raised in height to match the height of TDt and, despite this, the rate of leaf appearance of later formed leaves of TDc declined. Presumably this was because of the longer blades in TDc and the longer duration to reach full expansion (see Fig. 8.2 in previous chapter).

Tiller and leaf appearance are coordinated (Friend, 1965; Masle, 1985). Tiller buds are located in the base of the leaves (Baker and Gallaher, 1983) and they elongate and appear in a Fibonacci series generally until the main stem reaches terminal spikelet stage (Baker and Gallagher, 1983; Thorne and Wood, 1988; Craufurd and Cartwright, 1989). After that, the later formed tillers begin to die in the reverse sequence (Rawson, 1971; Thorne and Wood, 1988). In this experiment, tiller appearance ceased (Fig. 8.1b) in spite of the presence of tiller buds in the axils of every leaf. Tiller buds were observed in the axil of all main stem leaves (except the flag leaf) as early as the time when the next leaf primordium took its place as the cap leaf. Just before TDt reached double ridge (18 d.a.e.), leaf 2 already had one emerged tiller while leaves 3, 4 and 5 had tiller buds in their bases (length of tiller buds was 14mm, 1mm and 0.1mm respectively). Twelve days later, when TDt plants reached terminal spikelet, leaves 3 and 4 had a visible tiller, and leaves 5 to 8 had tiller buds in their base. The tiller bud of leaf 5 was then 5mm long; by the end of the experiment (51 d.a.e.) it had reached 24mm in length (Fig. 8.9), still concealed by the sheath and its apex already passed terminal spikelet stage. In TDc, tiller buds corresponding to main stem leaves 1 to 4 had the same length as in TDt. However, the tiller bud of leaf 5 was two times longer by day 30 and had already emerged by day 51. Similar differences were observed for tiller bud in leaf 6 (Fig. 8.9). This suppression of buds shows that, although TDt plants had the potential to continue with the same rate of tiller appearance as in TDc, there was a suppression of visible

tillering. Buds were presumably inhibited by a limited carbohydrate supply due to the strength of other sinks (stems and ears) as rapid growth of these organs was beginning. In TDt, the tiller bud of leaf 5 was located in the base of the elongating stem while the tiller bud of leaf 6 was in the first node. A hormonal control should also be considered. There is some evidence that hormones inhibit tiller buds possibly through auxin-directed nutrient transport (Cline, 1991).

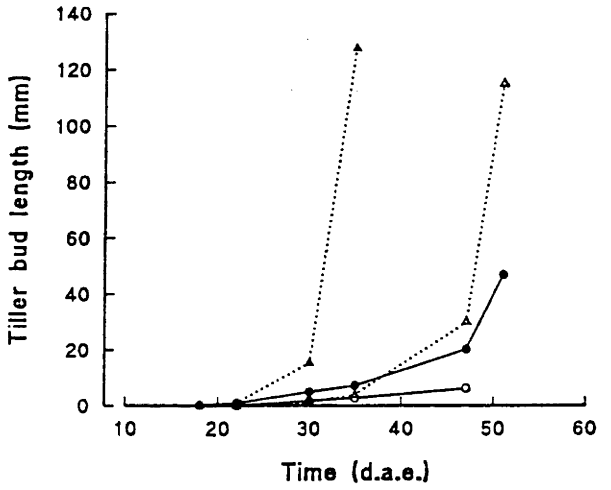


Figure 8.9 Relationship between tiller bud length (mm) and time. Tiller on the fith position of TDt (●) and TDc (▲); tiller on the sixth position TDt (○) and TDc (△).

In addition to the suppression of tiller buds at terminal spikelet stage in TDt, stem development in the later formed tillers was also suppressed and they began to die. No such tiller death was noted in TDc. When the main stem of TDt plants reached terminal spikelet, 31 d.a.e., the apices of all emerged tillers were beyond the double ridge stage. At this time TDt also reached its maximum stem number of 17-18 per plant (Fig. 8.1b). By day 47 the apices of all tillers had passed terminal spikelet stage and the last expanding leaves of at least 50% of them was dying. These tillers were the last to emerge and in terms of dry matter they only represented 10% of the shoot biomass. It has been proposed that these later formed tillers fail to develop because of insufficient surplus assimilate from developing tillers or from insufficient water and nutrients because of a poorly developed root system (Klepper *et al.*, 1984). The former seems the most likely explanation here as both water and nutrients were plentiful and because tillers in TDc continued to develop under the same conditions. There are several other possibilities. The sink strength of the larger tillers may be such that late tillers become a source rather than a sink, although it is noted that the contribution of assimilates or nitrogen from dying tillers to the rest of the plant is negligible (Bremner, 1969; Rawson and Donald, 1969; Thorne and Wood, 1987). Another explanation could be an hormonal response.

CHAPTER 9

GENERAL DISCUSSION

The main environmental limitation to wheat production in southern-Australia is the amount of rainfall during the growing season. Most of the wheat belt is classified as a Mediterranean environment with about 70% of the annual rainfall received during the winter between May and October. This rainfall can be as low as 200 mm in the drier parts of the wheat belt. Most of the work presented here was carried out in the drier margin environments within the south-eastern wheat belt. Temperature is another environmental factor that affects wheat yield greatly. Frosts during flowering time can reduce yield drastically and so can high temperatures during the grain filling period at the end of the season. Thus wheat varieties should flower late enough to avoid frosts during flowering but early enough to escape drought and high temperatures during the grain filling period.

In the field, flowering time is mainly determined by the genotype and the sowing date. Commercial wheat varieties are generally classified as either winter or spring wheats. Winter wheats have vernalization and/or photoperiod sensitive genes and they normally take longer to flower than spring wheats as they have to fulfil their vernalization or photoperiodic requirements. These requirements are less in spring wheats. In southern-Australia spring wheats are commonly sown between mid-May and late June and they flower in late September to mid October when there is little risk of frost. Since the mid-eighties farmers have started to grow winter wheats that can be sown between April and early June and still flower by mid October. Another option for farmers is to sow cultivars during the conventional sowing period that flower earlier. Although this would increase the risk of frost damage, yields may be increased because drought would limit yields less.

The main objective of the work presented here was to explore the different options (genotype and sowing date) available to farmers so as to determine the optimal flowering time of wheat grown in the low rainfall areas within the south-eastern Australian wheat belt to achieve maximum yield. For this it was necessary first to understand the variation in crop phenology with sowing date in the field and the effect of this variation on growth, water-use and water use efficiency of the wheat crop. Detailed discussion of the results was given in the previous Chapters whereas the main findings and overall view is presented in this Chapter. The type of material used in these experiments played an important role in this work. It consisted of populations that were very similar genetically apart from their genes associated with flowering. These genes conferred different degrees of sensitivity to photoperiod and vernalization and this led to different patterns of phenology and, in particular, different times of flowering. These populations were an ideal tool for studying the

effects of flowering time on yield. Five groups of near-isogenic populations were used in this study. They were derived from several genotypes with different vernalization and photoperiod requirements, and had a range in flowering time greater than currently recommended varieties. The lines were sown at three different times at Condobolin in both 1989 and 1990. This site is in central New South Wales and, with an average rainfall during the growing season of 230mm, it is representative of the drier environments within the wheat belt. At this site, detailed measurements were taken on apex development, crop growth and water use in early, intermediate and late flowering lines within the isogenic groups. The same material was sown in both years at two wetter locations, Moombooldool and Wagga Wagga (270 and 360 mm average rainfall during the growing season, respectively). There was at least one very early sowing between mid-April and early May as well as a sowing at the normal time of mid-May to early June and a late sowing between late June and early July.

Phenological phases studied

Determination of the optimal time for flowering was a primary aim of this study. However, the time from sowing to flowering is dependent on the cumulative durations of three phenological phases, the vegetative, spikelet initiation and from terminal spikelet to anthesis periods as described by Davidson and Christian (1984). If the durations of these three phases varied independently, then one time to anthesis may be comprised of many combinations of earlier phases. If, in turn, the three phases contribute differently to yield, their relative durations may have to be balanced within the time available between sowing and anthesis.

The components of the plant developing during the three phases have been well described in the literature. During the vegetative period leaf primordia are initiated in the apex of the main stem and tillers. The interplay between the duration of this phase and the rate at which leaf primordia are initiated determines the final leaf number on the main stem and tillers. At the same time leaf and tiller appearance are generally coordinated (Masle, 1985). Thus, it is during this phase that the potential number of shoots and leaf area are determined. In the work presented here, the vegetative period was estimated as the time from sowing to visible double ridge (DR) on the main shoot. Although DR stage does not correspond exactly with the end of the vegetative period (Delecolle *et al.*, 1989) it still gives sufficient approximation for comparative purposes. The use of DR stage, being relatively easy to observe, was also convenient due to the large number of lines involved in the experiments.

It is during the second phase, the period of spikelet initiation, that the number of spikelets in the ear is largely determined. Spikelet number is dependent upon the duration of the phase, the rate of spikelet initiation and the number of leaf primordia accumulated on the apex at the time of double ridges (Rahman and Wilson, 1977; Rawson, 1970). The number of spikelets is one of the grain yield components and it

has been suggested that an increase in this component is an important way to improve grain yield (Rawson, 1970; Halloran, 1977). However, in field comparisons of wheats, new cultivars have been found to have similar numbers of spikelets per ear to old cultivars (Kirby *et al.*, 1989).

Appearance of the terminal spikelet (TS) marks the end of the second phase and the start of the third. It generally coincides with the start of fast stem elongation and change in patterns of dry matter partitioning and also in the field with the start of the death of tillers (Rawson, 1971; Hay, 1986). The TS stage is sometimes difficult to observe under the microscope.Thus, in these experiments, the stage was checked retrospectively and compared with the time when the final number of spikelets primordia was reached. At the time of TS, some spikelets had already initiated florets as also observed by Kirby and Appleyard (1984). The development of florets continues up to ear emergence (Kirby 1988) but during the peduncle elongation and fast ear growth most florets die (Kirby, 1988; Siddique *et al.*, 1989). Thus the third phase is one of considerable reallocation and reorganization.

By anthesis time the potential number of kernels is set and, as seen above, this potential number is the result of different events prior to anthesis. The potential number of shoots per plant and leaf area, the number of spikelets and the number of fertile florets are, to a degree, determined by the durations of the three phenological phases and by the surrounding environment when they occurred. Thus, there is a need to understand how these phases can be changed genetically and by the environment and otherwise how they can be manipulated to improve yield.

Another important aspect that was studied was the relationship of the phenological phases and plant growth or leaf area as the last two are directly associated with water use and water-use efficiency.

Phenology and sowing date: the vegetative and spikelet initiation phases

The time to anthesis varied within and between sowing dates. The three phenological phases also changed in different ways according to the groups. These differences between groups could be caused by the presence of different minor vernalization or photoperiod genes in the various backgrounds.

The vegetative period was extended with the presence of vernalization or photoperiod sensitive genes. By contrast, the duration of the period of spikelet initiation was only influenced by photoperiod sensitive genes. In spring lines there was little variation in the duration of these periods in the different sowings. However, there was substantially greater variation in the later flowering lines.

(a) the photoperiod ppd sensitive genes

The photoperiod sensitive lines remained vegetative for the greatest period in the April sowing, when daylength was longest immediately after emergence. This was presumably because

(i) daylength was insufficient to induce floral initiation
(ii) plants may have a long juvenile phase during which they would be unresponsive to photoperiod
(iii) plants may possibly respond to an increasing daylength and not to a decreasing daylength
(iv) the low photothermal quotient in May could have delayed floral initiation

The spikelet initiation period became longer and the rate of initiation of spikelets was lower with increasing sensitivity to photoperiod in those isogenic groups where phenology is mainly controlled by photoperiod genes. The result was more spikelets in late maturity lines in agreement with Law (1987) although he did not find variation in the rate of the spikelet initiation, only longer duration of the period. The negative interaction between duration and rate is clear when different sowing dates are compared as the number of spikelets remained relatively constant for the range of sowings although both components changed. Stern and Kirby (1979) also found no effect of sowing date on spikelet number. Only in the more photoperiod sensitive lines sown later in the season was the number of spikelets changed, and then it was reduced. This reduction was mainly associated with a shorter vegetative period and probably with low number of primordia at the DR stage rather than to the duration or rate of spikelet initiation.

(b) the vernalization vrn sensitive genes

The extended vegetative period in the vernalization sensitive lines sown in April was probably due to the warmer soil temperatures in April and May compared to later, and hence the longer period required to satisfy their vernalization requirements.

In the vernalization sensitive lines, the number of spikelets has been associated with the duration of the vegetative phase (Halse and Weir, 1970; Rawson, 1970; Flood and Halloran, 1986b). In these studies no general association was observed between spikelet number and either time to DR or time from DR to TS. Only in the extreme winter line of the present study (RAC 417-5) was such an association apparent. There appeared to be no effect of vernalization genes on the duration of the phase between DR and TS in agreement with Halse and Weir (1970) and Flood and Halloran (1984) but in disagreement with Halloran and Pennell (1982). Most variation of this phase in the vernalization sensitive groups could be explained by the different photoperiod requirements of these lines. Appendix 1 shows that nearly all lines used in the field experiments show photoperiod responses between 9 and 13 hour per day and that often the spring lines are more sensitive to photoperiod than their winter counterparts. This could explain why the vernalization sensitive lines generally had a shorter time between DR and TS which sometimes resulted in a lower number of spikelets. It may be desirable then that the late lines with vernalization requirements also have a photoperiod requirement that assures a longer period of spikelet initiation.

This would not affect the time to anthesis if the time from TS to anthesis were reduced but may improve their yield when planted later than early May.

The phase from terminal spikelet to anthesis

This study identified the third phase, the time between terminal spikelet and anthesis, as the least understood in terms of genetic and environmental effects. The duration of this period varied from 860 ^{o}Cd to 460 ^{o}Cd in the first and last sowing at Condobolin in 1989. Reasons for this variation in duration are not clear and the use of different isogenic sets did not elucidate the causes for the different durations. 1M1S (early flowering line) contrasted with 6M9 (late flowering line) in that it was relatively insensitive to photoperiod in its time to flower in the growth cabinet and in the time to double ridge in the field. However, both varied in the same way in response to sowing date for the interval between terminal spikelet and anthesis. The time from TS to anthesis decreases with long days (Rahman and Wilson, 1977) and this could explain the differences between sowings as days were longer in later sowings for this period. However, it does not explain why there were no differences in the duration of this phase between early and late photoperiod sensitive lines sown at the same time although their phase occurred under different daylengths.

Genetic control in the phase between terminal spikelet and anthesis has not been studied in detail and the results from this work suggest it is not simple. The difficulties in interpreting the changes in this period with genotypes and sowing date were apparent in Chapter 3. The results in the field were not as clear as those from controlled environments where only one factor was changed at a time. In the field, daylength and temperature change daily and independently, and the plant seems to respond to both factors in a complex way. However, this study does indicate that the major genes for photoperiod and vernalization sensitivity are probably not important in the control of the time between terminal spikelet and anthesis. The response to long days after TS shown by Rahman and Wilson (1977) may be controlled by other genes than the major photoperiod genes.

It is possible that the analysis of the results was complicated by the use of thermal units to measure time calculated with a single base temperature of 0^{o}C. Although this is a common practice in plant development studies, it has been shown that the base temperature increases as the plant develops (Angus *et al*, 1981; del Pozzo *et al.*, 1987; Slafer and Savin, 1991). This means that the durations of later phases would be overestimated. Also, plants increase their sensitivity to daylength with later stage (Angus *et al.*, 1981) indicating again that the phenological phases after floral initiation could be overestimated in the early flowering lines when daylength is shorter. There is a need to determine the base temperature, critical photoperiod and interaction of both with temperature for every phenological stage.

On some occasions differences in development due to sowing date are minimized with the use of photothermal time (Masle *et al.*, 1989b) rather than thermal time. In the work presented here, such an analysis was done though not presented. However, as found by Stapper and Fischer (1990a) with their early sowings, there was no significant improvement over thermal time to explain differences in development of early sown wheats. As most published studies use thermal time, it was decided to express time in this unit for comparative purposes.

Within each isogenic group the time to reach DR, TS and anthesis of each line were strongly related in different sowings. In the photoperiod sensitive groups the rankings to reach the three stages were maintained so that the earliest line to reach DR also reached TS and anthesis first whereas the late lines reached the same three stages last. This was the case because the vegetative and the spikelet initiation period increased with late lines while the ear development period remained constant. However, in the vernalization sensitive groups, the relationships between the phenological periods changed in different ways, particularly when the April sowing was considered. Generally, late lines had a shorter time from DR to TS and from TS to anthesis than their spring counterparts although their vegetative phase was longer. Similar results were found by Flood and Halloran (1986b) using isogenic material differing in vernalization requirements. Occasionally, isolines sown at normal or late dates would have similar flowering time but different durations of their phenological phases. This indicates that there is an opportunity to manipulate the duration of these phases without changing anthesis time.

The rankings in the time to DR, TS or anthesis changed when all lines in the sowing were compared due to the various relationships between phenological phases found in the groups. The different relationships between the phenological periods for every group and sowing was probably due to different alleles of the vernalization or photoperiod genes and to other minor genes. Hunt (1979) and Stapper and Fischer (1990a) also found no relationship between floral initiation time and flowering time when comparisons were made between unrelated varieties.

Time to anthesis was reduced with later sowings and differently so for spring and winter wheats. The winter wheats showed greater plasticity than the spring wheats in time to flower with sowing date. This indicates that the winter wheats can be planted over a wider range of sowing dates, particularly in earlier sowings than mid-May, and still flower when there is no risk of frost. Similar results have been shown for commercial winter and spring varieties (Stapper and Fischer, 1990a). The late photoperiod sensitive lines always flowered later than the vernalization sensitive lines, making them inappropriate for May or later sowings as they flowered too late in the season.

Phenology and growth rate

Vernalization and photoperiod genes affect the dry matter partitioning into the plant organs as they control the length of the vegetative phase and the start of the reproductive phase and stem elongation. A relationship between growth and development has been suggested by several authors (Hodges and Kanemasu, 1977; Kemp *et al.*, 1989; Green and Valdyanathan, 1986; Green, 1989). Differences in above-ground dry matter accumulation between spring and winter wheat varieties have been observed in field studies (Davidson *et al.*, 1990; Stapper and Fischer, 1990b). These studies raise the interesting possibility that there is some stimulus to plant growth at around the time of floral initiation or stem elongation. However, Rawson (1991) did not find any change in relative leaf expansion rate among near isogenic lines of wheat differing in vernalization or photoperiod genes at the time of floral initiation. The difference in growth between winter and spring wheats may have particular relevance to dry environments as any penalty in growth during the winter may result in a reduced water-use efficiency.

In the field experiments, early and late flowering lines differed in the rate of dry matter accumulation up to anthesis suggesting a relationship between growth and plant development. Early lines started to accumulate dry matter faster than late flowering lines. This difference in growth was associated with a faster stem dry matter accumulation. Leaf dry matter accumulation was similar for all lines until the early flowering line started stem elongation at which time further leaf growth stopped but stem growth began. Isogenic lines within a group had similar leaf appearance rates on the main stem but the final leaf number as well as the maximum shoot number differed according to the length of the vegetative phase. Thus, later lines had more leaves on the main stem and higher maximum shoot number. Leaf appearance was monitored at Condobolin in 1990 where the range in sowing date was from May 1 to July 7. That year the duration of the vegetative period was similar for all sowing dates and thus the final leaf number was the same. In 1989, the vegetative period was extended in lines sown in April and it most probably resulted in more leaves on the main stem.

Two experiments were carried out in controlled environments to further investigate a relationship between growth rate and floral initiation or stem elongation. In the first experiment, isogenic lines differing in vernalization and photoperiod requirements were grown at different daylengths; plants were spaced to determine whether there were intrinsic differences between genotypes that may be masked when plants were grown as a canopy. The results of this experiment showed no effect of the flowering genes on total dry matter accumulation (from plant emergence to ear emergence of the earliest line) and there were no differences in relative growth rates for total plant dry weight between the different lines. Similar results were obtained by Flood and Halloran (1986b) using related material (Triple Dirk isogenic lines) to the

ones used here. In this first experiment, lines varied in the partitioning to the different organs: leaves, shoots and roots. Later developing lines had more and larger leaves, more tillers and a greater leaf area. On the other hand, spring wheats compensated for their reduced leaf area and leaf area ratio by having a higher net assimilation rate (NAR) and were thereby able to maintain the same relative growth rate as their winter counterparts. Higher NAR could be explained by the better light penetration as the stem elongated and, it may also be that the rate of photosynthesis was promoted by the strong demand of assimilates for the developing stem and ear as suggested by Green and Valdyanathan (1986). Plants grown under longer daylength developed faster, but the differences were reduced when expressed in photothermal time as suggested by Masle *et al.* (1990).

Canopy effect

The main reason for the different results in the field and in the spaced pot experiment was probably that winter lines in the field did not maintain a similar rate of tillering to that of in pots because of competition for light and space. The second experiment was then designed to study the effect of flowering genes on growth in a canopy. Although there were no differences in total plant dry matter at the end of the experiment when the earliest lines approached ear emergence, lines differed in above-ground dry weight (AGDW) and in RGR of the above-ground parts. The root and leaf dry matter proportion decreased and the stem dry matter increased in the early flowering line compared to the late flowering line when stem elongation began. The different partitioning of biomass into the plant organs resulted in lower root-to-shoot ratio after stem elongation.

The fast stem and ear growth started in the early flowering line after TS stage at the expense of root and leaf growth. Consequently, the root to shoot ratio was lower and the AGDW higher. This difference could explain the differences in dry matter accumulation between early and late maturity lines found in the field. However, it is also possible that the difference in AGDW, shown only in the second experiment, was mainly due to the extended 24 hour day rather than a canopy effect. This is supported by the higher biomass accumulated for a similar period of time in the second experiment than in the first experiment instead of the expected lower dry matter accumulation because of the shading effect in the canopy. The second experiment should be repeated but using daylengths similar to the ones reached in the field to further study the canopy effect on plant growth.

Anthesis time and yield

The effect of anthesis date on yield was presented in Chapter 5. In the environments where the site-average yield for the top yielding lines was more than 200 g m^{-2}, the intermediate flowering lines had the highest yields. These lines had

flowering dates similar to commercial spring wheats eg Banks. The superiority of cultivars of similar maturity over late maturity ones, and for similar range of sowings, have been shown in other Australian environments (Stapper and Fischer, 1990b; Connor *et al.*, 1992).

Earlier flowering wheats performed better than intermediate flowering lines only in the late sowings probably because late drought and high temperatures during the grain filling period were the main limitation to yield production. Early flowering wheats had a short growing season and so did not have sufficient time to accumulate enough biomass to produce high yields. Their numbers of ears and kernels per unit area were less than in the intermediate flowering lines. The better growth conditions during grain filling because of the early anthesis and the resulting high HI could not compensate for the low biomass. Studies on plant density of very early varieties would be desirable. Although in these experiments it was shown that not all emerged tillers in these plants survived, it might be that increased plant density is not counterbalanced by higher tiller mortality.

The late maturity lines generally yielded less than the intermediate lines and only in the very early sowing did the late lines yield as much as the other lines. The higher yield of late lines sown early was associated with a higher water-use efficiency (WUE) than lines in later sowings. Early sown crops had greater WUE partly due to a greater leaf area index (LAI) during winter when the evaporative demand is low and transpiration efficiency is high (Tanner and Sinclair, 1983). Photosynthesis at this time is less costly in terms of water transpired. Early sown crops also had a greater LAI earlier than later sown crops and this resulted in lower soil water evaporation. In Western Australia similar advantages have been shown for early sown crops and it is a management practice that is now recommended to increase yield (Perry *et al.*, 1989; Anderson and Smith, 1990; Kerr *et al.*, 1992). The environment is different from that in central New South Wales as there is less spring rainfall, lower risk of frost and later break of the season in Western Australia. It is recommend sowing the local spring wheats in early May rather than late May-June and indicated the need for more studies particularly on the use of later maturity cultivars.

Optimum flowering period

The earliest flowering date that can be planned for is determined by the probability of frost damage. In the early sowings most spring wheats suffered frost damage and yield was low. However the early flowering barley was not affected by frost and it yielded 50% more than the equivalent wheat that flowered at the same time. It is not known how barley achieves this but it would be an important line of investigation.

The critical range in temperature immediately after ear emergence is between -3 and -5 ^{o}C (Single, 1991). A temperature of -3 ^{o}C at the spike would be similar to a

screen temperature of -1 °C. Probabilities of having air temperatures below 2°C are also considered as it is the temperature which is commonly used by the Bureau of Meteorology to define likely frost damage (Loss, 1989). The probability (%) of 1, 3 and 5 days with minimum air temperature below 2°C and of 1 day below -1 °C for September at Condobolin (25 year weather data) is as follows:

Period	1 day < 2°C	3 days < 2°C	5 days < 2°C	1 day < -1 °C
1/9-7/9	29	17	8	4
8/9-14/9	22	15	8	4
15/9-21/9	22	7	6	4
22/9-28/9	13	7	4	2
29/9-5/10	5	0	0	1

In these experiments it was not possible to associate any critical temperature or number of cold days to damage in the field as a daily check was not possible. From the probabilities shown above, the risk of frost damage is negligible after September 29. For the week September 22 to 28, the probability of frost increases to 2-7 % (1 in 20 years), or 13 % (1 in 10 years) if only one day with less than 2 °C of minimum temperature is considered as damaging. There are similar probabilities of frost for the week September 15 to 21 except when 1 day of temperatures below 2°C is considered (22% or 1 in 5 years chance of frost). The lack of an advantage in yield with early sown wheats or early flowering wheats may not make it worthwhile to take the risk of flowering earlier than the last week of September. If those flowering dates are to be achieved with late flowering lines then an early planting is necessary. In only 1 out of 5 years is there a break of the season (15 mm of rain in two consecutive days) before April 22. Therefore, in most years farmers will have to sow a spring wheat in May that would flower in the last week of September or early October. At Wagga Wagga, the earliest time with low probabilities of frost is early October.

The end of the optimum flowering period was determined by the time yield started to decrease with flowering time. At Condobolin and Wagga Wagga, the optimum flowering period was estimated between end of September and October 9 and around October 8 respectively. Delaying flowering resulted in yield decreased of 37% and 14% per week at Condobolin and Wagga Wagga respectively. The reductions at Condobolin are higher than reductions found at other sites in New South Wales (Table 9.1). The main reason for this could be the lower rainfall and higher temperatures at Condobolin. Results from irrigated experiments in Table 9.1 showed yield reductions between 9and 16% which have been explained as caused by high temperature (McDonald *et al.*, 1983). The value obtained at Wagga Wagga lies within the range found by Fischer and Kohn (1966) at the same location and it is similar to what was found at a wetter and cooler location (Tamworth; Doyle and

Marcellos, 1974) or under irrigation (Namoy Valley, McDonald *et al.*, 1983; Griffith, Stapper and Fischer, 1990). Cooper (1992) obtained lower values (9.1% per week flowering was delayed after mid-September) at Trangie where frost did not occur before September 7.

Table 9.1 Optimum flowering period and yield decrease when flowering occurs after the optimum in experiments carried out at different locations in New South Wales.

Experiment Location	sowing range	Optimum flowering period	Yield decrease per week delayed
Fischer and Kohn (1966) Wagga Wagga. Rainfed.	Apr 28 - Jl 18	early October	24 % (dry year) 8 % (wet year)
Doyle and Marcellos (1974) Tamworth. Rainfed.	May 19 - Oct 5	early October	9-13 %
McDonald *et al.* (1983) Namoi Valley. Irrigated.	Apr 17 - Aug 13	late September	16 %
Stapper and Fischer (1990) Griffith. Irrigated.	Apr 14 - Aug 27	Spt 22 - Oct 10	11 %
Cooper (1992) Trangie. Irrigated.	Apr 18 - Aug 27	mid-Sept	9.1 %
This Thesis			
Condobolin. Rainfed.	(Apr 17 - Jn 22)	end Sept - Oct 9	37 %
Wagga Wagga. Rainfed.	(May 3 - Jl 11)	aprox. Oct 8	14 %

Relationships between biomass production and yield

The maximum biomass increased with earlier sowing date. This is because of the improved WUE associated with earlier sowing. Surprisingly, this increase in biomass was not matched by an increase in yield. In fact, there was very little variation in yield between early and normal sowings in spite of the large differences in biomass. Similar results were found by Watson *et al.* (1963). The harvest index of early sown crops was consequently very low compared to later sowings as in Hollamby *et al.* (1986) and Batten and Khan (1987). The possible reasons for the low HI of early sown crops were discussed in Chapter 2. Frost damage and barley yellow dwarf virus (BYDV) were eliminated as being responsible for this decline in HI. The

greater biomass and leaf area that developed early may well have used all of the soil water during the pre-anthesis period leaving little behind for grain filling. However, there was no evidence for this. There were no visual differences in drought stress between plants sown very early or at a standard time. This was supported by similar soil water contents between anthesis and maturity and similar leaf water potentials measured during grain filling.

Long stems and competition for assimilates with the developing ear

It was suggested in Chapter 2 that the most likely reason for the low yield and HI of early sown crops was the greater allocation of biomass to the longer stem in the early sowings and hence greater competition for assimilates between the growing ear and the elongating stem. This is because the ear in early sowings develops when radiation is low and thus potential sink size is reduced relatively (Fischer and Stockman, 1986). For example, in 1989, a late maturity cultivar (Osprey) sown in mid-April will reach terminal spikelet stage on June 22 when daylength is shortest and radiation is low whereas a spring cultivar (Banks) sown at the end of May will reach terminal spikelet on August 18 when daylength and radiation are increasing. Also, terminal spikelet stage was reached by the winter isolines sown in April when their apex size was similar or slightly greater than their spring counterparts when they reached the same stage. However, the stem was nearly twice as long in the winter lines. Thus the ratio of apex length to stem height was 67 % lower in the winter lines sown in April than in the early lines sown in May. It is not known if this ratio affects the balance between both sinks, apex and stem, or if it can be taken as an indication of their strength as sinks. But other works have shown the relevance of the ear/stem ratio on yield (Fischer and Stockman, 1986; Siddique *et al.*, 1990b). In this experiment the ratio of the ear to the stem dry matter per unit area at anthesis in the winter lines sown in April was half that of the spring lines sown in May (0.15 vs 0.31).

The source/sink contention presented here is supported by the low number of kernels and the taller plants found in early sown crops. Plants in the April sowing had a longer vegetative period that resulted in more leaves and internodes and in taller plants. Thus, part of the decline in HI must be associated with the additional leaves (and internodes) produced in the early sowing. This would result in an inevitable decline of say 1-2% in HI. The contention that early sowing increased height of winter wheats was further supported by the finding that within a sowing date height was positively related to flowering date up until the time drought reduced height in the latest flowering lines. The increase in height with later flowering was also associated with more leaves on the main stem and more internodes. Plate 9.1 shows two genetically related wheats sown on the same day at Condobolin. Plant A flowered about 7 days before plant B and was 15 cm shorter. The nodes, marked in red, which

reflect main stem leaf number, were one less in plant A than in plant B. The increase in height of plant B was also due to a longer peduncle.

Plate 9.1 Two related wheat cultivars which differ in maturity and in plant height (A, M3087 and B, its sib, Rosella).

Longer stems implies greater competition between the growing ear and the elongating stem (Brooking and Kirby, 1981; Gale and Youssefian, 1985; Fischer and Stockman, 1986; Kirby, 1988; Siddique *et al.*, 1989; Youssefian *et al.*, 1992b) and may be the main reason for low HI of early sown crops. Brooking and Kirby (1981) have shown that tall isogenic wheats partitioned less dry matter to the developing ear than the related isogenic semidwarfs. In their work, the semidwarf lines had greater ear weight at anthesis and more kernels per spike resulting in higher HI and grain yield. Consequently, it was hypothesized that a reduction in height may decrease the competition between ear and stem, thus favouring the number of fertile spikelets and florets and increasing kernel number and yield of early sown wheats. A reduction in height should increase the supply of assimilates to the ear and therefore increase its growth. To test this hypothesis an experiment using plant growth regulators in four high yielding winter genotypes was carried out at Condobolin, 1990. Plant growth regulators reduced crop height by 12% but there was no difference in yield between treated and untreated plants. It is possible that one of the PGRs, ethephon, induced pollen sterility (Keyes and Sorrells, 1990) and this was responsible for the absence of an effect on yield. Unfortunately, this was not checked in the field. However, the main reason may be that although PGRs increased HI, this was counterbalanced by a corresponding decline in biomass with no net effect on yield. In spring wheats growing in a similar region there is little change in the grain yield of crops whose height varies between 70 and 100 cm because of the trade off between HI and biomass (Richards, 1992a).

Reducing plant height by genetics

Plant height can also be reduced genetically. There are several major genes that control plant height (Gale and Youssefian, 1985) and of these, Rht_1 and Rht_2 have been extensively studied. The effect of these major genes is modulated by other minor genes. Thus, Rht_1 and Rht_2 can reduce plant height by up to 50% if both genes are present or from 13 to 34% if only one gene is present (Gale and Youssefian, 1985) and depending on the genetic background (Allan, 1983). In Australia, most winter wheats have one major dwarfing gene, Rht_1. In Chapter 6, it was proposed that the introduction of another dwarfing gene, Rht_2, into the current commercial winter wheats or the replacement of Rht_1 by the more potent Rht_3 dwarfing gene would result in winter wheats with a greater HI and yield when sown early. With this aim, a breeding program was described in Chapter 6 and seed of BC_4F_1 in a number of commercially acceptable lines is now available. After selection for dwarf winter wheats and seed increase, the hypothesis can be tested.

There is an optimum crop height for rainfed spring wheats from 70 to 100 cm below or above which the crop does not perform optimally, and this height is independent of the *Rht* genes (Richards, 1992a). Under irrigation this optimum is

reduced to 70 cm (Fischer and Quail, 1990). No such studies have been done in winter wheats but it is possible that when plants are sown early, and thus grow in more favorable conditions, their height exceeds the optimum height. The combination of two different *Rht* genes may reduce plant height and result in an increased yield. The difference in the optimum height of wheats under favorable irrigation conditions and the unfavorable rainfed conditions is the poorer WUE of dwarf spring wheats in rainfed conditions. Dwarf wheats sown in late May - early June have a slower early growth than taller wheats and this accounts for the differences in biomass with height (Richards, 1992b). A semidwarf winter wheat may reach a height of 100-110 cm when sown at Condobolin in mid-April and presumably would be even taller in a wetter environment such as Wagga Wagga. Thus any reduction in this height may increase yield. Furthermore, the penalty in WUE for mid-April sowing for a dwarf wheat may not be the same as a sowing in late May to June because of the substantial growth possible before the onset of winter (Fig. 4.4) and the associated high WUE.

Although there are several studies comparing the yield of semidwarf winter wheats with tall ones (eg Gale and Youssefian, 1985), there are only a few which provide information about dwarf wheats. Furthermore, results from previous works that compare isogenic lines differing in their *Rht* genes are contradictory. Thus, it has been shown that dwarf wheats can have higher yield than semidwarf or tall isogenic counterparts (Fischer *et al.*, 1981; Allan, 1983; Fischer and Quail, 1990), higher than tall lines but lower or similar to semidwarf lines (Allan and Pritchett, 1980; Allan, 1983; Allan, 1989) or lower than both tall and semidwarf lines (Allan, 1986; Kiyomoto and Gent, 1989). Often dwarf wheats have a very low biomass that increased harvest index can not compensate for so that yields are low relative to the semidwarfs. In the present study, the height of the low performance dwarf lines was always low (below 60 cm) whereas the best dwarf lines were taller than 70 cm. When the isogenic set was derived from crosses that used high yielding tall lines, the dwarfs were extremely short, probably because the tall parents were well adapted and thus most likely of short stature. On the other hand, the best dwarf lines were originated from crosses between high yielding semidwarfs that were taller than in the previous case. In the breeding program described in Chapter 6 the recurrent parents were either high yielding cultivar or advanced breeding lines, all semidwarf winter wheats.

Pleiotropic effects

Some *Rht* pleiotropic effects deserve discussion. *Rht* genes have been associated with low protein grains (Gale and Youssefian, 1985). However, Fischer and Quail (1990) showed that the characters are not linked. *Rht* genes have also been associated with poor emergence (Bush and Evans, 1988; Richards, 1992b). This could be detrimental in rainfed conditions where water limits production and where an early cover of the ground is desirable. It will be necessary to determine if the same penalty

applies to dwarf winter wheats sown in autumn. Another concern in these environments is the possibility of limited root growth in *Rht* genotypes and thus an increased sensitivity to water stress. However, it has been shown that semidwarfs varieties had more roots below 50 cm than taller varieties (Lupton and Oliver, 1974) and that there are very small differences between semidwarf and tall isolines in water use or water extraction from the soil (Innes and Blackwell, 1984). Additionally, there are likely to be advantages to root growth of earlier sowing. Root growth is related to the length of the vegetative period (Klepper at al., 1984; Siddique *et al.*, 1990). Thus, wheat sown in south-eastern Australia in April should have substantially more root growth than the same lines sown in late May. This may also account for the absence of any detrimental effect of drought in the mid April sowing. Such plants may have had deeper roots and access to water deeper in the profile (providing water was available). In Western Australia, Anderson and Smith (1990) have found that semidwarf cultivars were more sensitive to water stress than tall cultivars but no information was available on root growth.

The success of dwarf winter wheats might be limited by their extreme short stature, low biomass and poor emergence. However, the large variation in plant height within the backcross populations should lead to dwarfs winter wheats within an optimum height range.

Conclusion

In the drier part of the south-eastern Australian wheatbelt, the optimum flowering period for best grain yield is between end of September and early October. Maximum grain yields are possible for a relatively large range in sowing date in combination with different maturity lines, from winter wheats sown in mid-April to spring wheats sown in May. The expected yield advantage of early sown winter wheats was not found in this work because of the low harvest index. However, it is suggested that the winter wheats available may be improved with the introduction of an extra dwarfing gene. New lines obtained in a breeding program based on this hypothesis will soon be ready to be tested in the field.

Studies for the future

Topics for further research that arose from the work presented here include:

(i) effect of sowing date on nitrogen utilization and grain quality.

(ii) the assessment of the base temperature and the critical photoperiod of the three phenological phases.

(iii) the canopy effect on crop growth of lines differing in phenology. Studies to determine if tillering of late flowering cultivars is limited in a canopy situation or if differences in root-to-shoot ratio after floral initiation can explain the differences in above-ground dry weight found in the field.

(iv) the mechanisms that confer greater frost tolerance to barley than to wheat with respect to grain setting.

(v) the effect of increasing sowing density on biomass and yield of very early flowering lines sown in May or June.

(vi) the evaluation in the field of dwarf winter wheat selections from the breeding program. Studies are also needed of the effect of an extra dwarfing gene on grain protein, plant emergence, root growth and water uptake compared to the semidwarf parents.

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APPENDIX 1

Thermal time (^{o}Cd calculated using 0^{o}C as base temperature) from seedling emergence (non-vernalized seed) or transplanting day (vernalized seed for six weeks at 2^{o}C) to ear emergence of populations grown at 9, 11, 13 and 15 hours daylength.

	non-vernalized				vernalized			
	9	11	13	15	9	11	13	15
1M1S	1049	937	848	826	1115	937	847	803
1M5	1539	1182	982	893	1427	1137	937	892
1M7	1695	1227	1026	915	1628	1160	1004	914
1M10	1851	1294	1026	915	1583	1204	1026	937
6M7	*a*	1495	1138	1004	1676	1227	1204	1070
6M9	*a*	*a*	1450	1138	*a*	*a*	1450	1182
1B2	1495	1205	937	870	1271	1004	847	803
1B5	*a*	1294	982	893	1583	1070	959	870
1B9	*a*	1272	1049	870	1561	1182	981	937
6B1	*a*	1383	1093	937	1673	1204	959	892
6B6	*a*	1539	1138	982	1717	1293	1070	981
1B10	*a*	*a*	1227	959	*a*	*a*	1182	981
6B9	*a*	*a*	1383	1026	*a*	*a*	1449	1182
RAC 416-1	*a*	1851	1517	1272	1717	1227	1115	1026
RAC 417-2	*a*	*a*	*a*	*a*	1717	1427	1249	959
RAC 417-3	*a*	*a*	*a*	*a*	1784	1360	1115	1026
RAC 417-5	*a*	*a*	*a*	*a*	1695	1316	1070	959
MQs	1985	1294	1026	937	1606	1204	1004	937
MQw	*a*	1829	1495	1383	1360	1115	1004	914
MWMspr sht	*a*	1272	982	915	1717	1271	1026	981
MWMwnt sht	*a*	1985	1584	1450	1450	1182	1026	892
MWMspr tall	*a*	1584	1093	1026	*a*	*a*	1293	1093
MWMwnt tall	*a*	1918	1562	1428	1561	1316	1070	1026
Osprey	*a*	*a*	*a*	*a*	1673	1227	981	937
Banks	*a*	1339	959	870	1583	1204	914	870

[a] main apex died before ear emergence

APPENDIX 2

Table A2.- Time (°Cd) to double ridge stage (DR), to terminal spikelet stage (TS) and to anthesis (A) and periods from DR to TS (DR-TS) stage and from terminal spikelet stage to anthesis (TS-A) of isogenic lines grown at Condobolin in 1990.

	DR	TS	A	DR to TS	TS to A
C1-90					
1M1S	335	536	1190	201	654
1M7	471	737	1432	266	695
6M9	614	1052	1888	438	836
1B2	420	687	1300	267	613
6B1	506	832	1582	326	750
1B10	614	1142	1826	528	684
MWMs short	420	666	1454	246	788
MWMw short	657	867	1582	210	715
MWMs tall	471	742	1582	271	840
MWMw tall	680	867	1582	187	715
mean	519	813	1542	294	729
s.e.	37	57	67	35	24
C2-90					
1M1S	372	547	1252	175	705
1M7	472	707	1360	235	653
6M9	572	1012	1681	440	669
1B2	452	642	1333	190	691
6B1	542	762	1496	220	734
1B10	622	1017	1605	395	588
MWMs short	452	662	1360	210	698
MWMw short	602	732	1389	130	657
MWMs tall	527	717	1389	190	672
MWMw tall	586	737	1389	151	652
mean	520	754	1425	234	672
s.e.	25	48	43	32	17
C3-90					
1M1S	-	520	1096	-	576
1M7	-	625	1265	-	640
6M9	627	845	1449	218	604
1B2	-	610	1203	-	593
6B1	575	770	1296	195	526
1B10	640	845	1416	205	571
MWMs short	500	630	1203	130	573
MWMw short	560	750	1265	190	515
MWMs tall	520	700	1265	180	565
MWMw tall	550	730	1265	180	535
mean	567	703	1272	185	570
s.e.	20	34	32	11	12

APPENDIX 3

Summaries of variation in time to anthesis, grain yield, above-ground dry weight (AGDW), harvest index and crop height at maturity among lines in every sowing at Moombooldool and Wagga Wagga in 1989 and at Condobolin and Wagga Wagga in 1990.

Table A3.1 Time to anthesis and above-ground dry weight (AGDW), yield, harvest index and crop height at maturity of isolines at Moombooldool, 1989.

	Anthesis (d.a.s)	AGDW ($g\ m^{-2}$)	Yield ($g\ m^{-2}$)	Harvest Index	Height (cm)
M1-89					
1M1S	125	504	194	0.39	77
1M5	133	618	244	0.40	82
1M7	138	678	261	0.38	80
1M10	138	602	238	0.40	80
6M7	142	764	296	0.39	82
6M9	156	745	246	0.33	79
1B2	130	516	211	0.41	73
1B5	136	620	249	0.40	81
1B9	139	641	277	0.43	85
6B1	140	653	263	0.40	80
6B6	144	747	295	0.40	82
1B10	148	612	224	0.37	74
6B9	155	723	264	0.37	78
RAC 416-1	143	690	296	0.43	72
RAC 417-2	144	761	309	0.41	72
RAC 417-3	145	728	304	0.42	71
RAC 417-5	145	651	262	0.40	72
MQs	141	641	267	0.42	77
MQw	141	666	234	0.36	75
MWMspr sht	136	715	289	0.41	77
MWMwnt sht	138	585	225	0.39	79
MWMspr tall	137	717	253	0.35	104
MWMwnt tall	137	700	235	0.34	100
M2-89					
1M1S	111	381	150	0.40	68
1M5	119	400	150	0.38	70
1M7	123	530	187	0.35	73
1M10	124	478	173	0.36	72
6M7	127	469	152	0.32	74
6M9	135	438	127	0.29	70
1B2	116	437	181	0.41	67
1B5	119	448	162	0.36	73
1B9	123	497	174	0.35	75
6B1	124	506	184	0.37	71
6B6	126	464	158	0.34	74
1B10	129	487	173	0.36	65
6B9	130	568	189	0.33	73
RAC 416-1	123	419	167	0.40	63
RAC 417-2	124	513	189	0.37	68
RAC 417-3	126	705	253	0.36	65
RAC 417-5	126	650	223	0.34	62
MQs	122	516	199	0.39	65
MQw	124	481	169	0.35	71

Table A3.2 Time to anthesis and above-ground dry weight (AGDW), yield, harvest index and crop height at maturity of isolines at Wagga Wagga, 1989.

	Anthesis (d.a.s)	AGDW ($g\ m^{-2}$)	Yield ($g\ m^{-2}$)	Harvest Index	Height (cm)
W1-89					
1M1S	138	725	297	0.41	92
1M5	148	898	359	0.40	107
1M7	151	839	319	0.38	104
1M10	151	897	350	0.39	101
6M7	156	906	335	0.37	104
6M9	165	950	323	0.34	104
1B2	142	565	232	0.41	89
1B5	146	628	257	0.41	99
1B9	153	782	321	0.41	100
6B1	153	940	366	0.39	101
6B6	156	838	319	0.38	98
1B10	163	684	273	0.40	87
6B9	165	755	279	0.37	90
RAC 416-1	155	854	350	0.41	83
RAC 417-2	155	919	386	0.42	91
RAC 417-3	157	757	348	0.46	83
RAC 417-5	157	949	389	0.41	87
MQs	152	764	313	0.41	92
MQw	153	783	305	0.39	94
W2-89					
1M1S	119	634	281	0.44	86
1M5	125	759	274	0.36	87
1M7	128	682	266	0.39	90
1M10	128	758	273	0.36	88
6M7	132	669	240	0.36	90
6M9	137	801	248	0.31	93
1B2	121	504	207	0.41	81
1B5	125	710	277	0.39	83
1B9	128	610	245	0.40	88
6B1	128	700	251	0.36	87
6B6	131	798	296	0.37	88
1B10	135	682	259	0.38	81
6B9	137	608	225	0.37	87
RAC 416-1	129	831	357	0.43	72
RAC 417-2	129	774	310	0.40	78
RAC 417-3	131	866	312	0.36	75
RAC 417-5	131	847	340	0.40	72

Table A3.3 Time to anthesis and above-ground dry weight (AGDW), yield, harvest index and crop height at maturity of isolines at Condobolin, 1990.

	Anthesis (d.a.s)	AGDW ($g\ m^{-2}$)	Yield ($g\ m^{-2}$)	Harvest Index	Height (cm)
C1-90					
1M1S	110	949	188	0.20	94
1M7	134	1361	354	0.29	104
6M9	167	1284	386	0.30	108
1B2	122	924	243	0.27	93
6B1	146	1103	350	0.32	105
1B10	163	1348	388	0.29	95
MWMspr sht	136	1083	339	0.31	96
MWMwnt sht	146	1051	331	0.32	112
MWMspr tall	146	1121	305	0.27	129
MWMwnt tall	146	894	245	0.28	138
C2-90					
1M1S	121	1056	326	0.31	95
1M7	129	1383	393	0.28	105
6M9	151	1173	316	0.27	105
1B2	127	1326	361	0.30	95
6B1	138	1157	387	0.34	103
1B10	145	1100	336	0.31	90
MWMspr sht	129	1240	394	0.32	97
MWMwnt sht	131	1170	359	0.31	108
MWMspr tall	131	1179	339	0.29	128
MWMwnt tall	131	981	254	0.27	130
C3-90					
1M1S	104	754	257	0.34	85
1M7	114	867	260	0.30	90
6M9	127	653	195	0.31	84
1B2	111	823	270	0.33	84
6B1	117	765	224	0.30	85
1B10	125	705	205	0.30	77
MWMspr sht	111	770	270	0.35	88
MWMwnt sht	114	783	236	0.30	92
MWMspr tall	114	693	236	0.34	118
MWMwnt tall	114	568	171	0.28	119

Table A3.4 Time to anthesis and above-ground dry weight (AGDW), yield, harvest index and crop height at maturity of isolines at Wagga Wagga, 1990.

	Anthesis (d.a.s)	AGDW ($g\ m^{-2}$)	Yield ($g\ m^{-2}$)	Harvest Index	Height (cm)
W1-90					
1M1S	128	836	246	0.29	81
1M7	148	1222	383	0.31	98
6M9	172	1091	335	0.31	108
1B2	137	792	257	0.32	92
6B1	151	1082	369	0.34	99
1B10	170	1019	294	0.29	97
MWMspr sht	147	939	323	0.35	92
MWMwnt sht	148	1385	396	0.29	112
MWMspr tall	149	1025	296	0.29	128
MWMwnt tall	149	998	256	0.26	136
W2-90					
1M1S	124	683	287	0.42	76
1M7	136	933	338	0.36	93
6M9	152	758	207	0.28	87
1B2	130	895	349	0.39	82
6B1	136	833	321	0.38	91
1B10	148	842	246	0.30	82
MWMspr sht	135	819	292	0.35	82
MWMwnt sht	136	775	277	0.36	89
MWMspr tall	136	915	259	0.29	115
MWMwnt tall	136	721	249	0.35	124
W3-90					
1M1S	100	522	182	0.35	75
1M7	112	620	173	0.26	82
6M9	123	486	93	0.19	67
1B2	107	464	170	0.36	78
6B1	111	531	152	0.29	79
1B10	117	428	117	0.27	57
MWMspr sht	146	454	151	0.33	74
MWMwnt sht	147	588	173	0.29	81
MWMspr tall	147	555	168	0.30	100
MWMwnt tall	147	681	154	0.23	106