THE EFFECT OF DAYLENGTH ON APICAL DEVELOPMENT AND GRAIN PRODUCTION IN BARLEY CULTIVARS

W. JAMES THOMSON, B.Sc. HONS

Thesis submitted for the degree of

Doctor of Philosophy

Department of Biology
University of Stirling

July 1979

Awarded Feb. 1980

ACKNOWLEDGEMENTS

I would like to express my sincere thanks to my principal supervisor, Dr S Matthews, for his guidance and encouragement throughout the course of this study. My thanks are also due to my external supervisor, Mr R N H Whitehouse and his staff at the Scottish Plant Breeding Station, Pentlandfield, Edinburgh, for their advice and help in arranging the sowing date field trials.

I am also grateful to Professor H Meidner for the use of his infra-red gas analyser and the other facilities in the Department, and to Dr R E Gaunt (Lincoln College, New Zealand) for his guidance in setting-up the radio-isotope labelling study.

I wish further to thank Mr H Milne and his garden staff for their help during the past three years and to Mrs P Brown for typing this thesis.

Finally, the financial support of the Science Research Council is gratefully acknowledged.

ABSTRACT

Differences in the magnitude of the response to daylength (8h S.D. and 16h L.D.) of a large number of two-row spring barley genotypes were found in both final spikelet number (100 cultivars, glasshouse) and in apical development (five cultivars, growth rooms). Apical growth and development of all genotypes was accelerated in L.D. compared with S.D. treatment and two physiological groups could be distinguished on the basis of the magnitude of this response. Group one cultivars (Clipper and Spartan) showed a more marked acceleration of apical development in long days compared with group two cultivars (Domen, Golden Promise and Ymer) and this was reflected in rapid spikelet primordium production resulting in a reduced maximum spikelet primordium number. A high spikelet primordium maximum was reflected in a high spikelet number.

Apical growth and development, and spikelet primordium production were similarly accelerated by late sowing treatment in the field, both in 1976 (14 cultivars) and in 1977 (five cultivars), and cultivars differed in the magnitude of this response. Two physiological groups could again be distinguished and these corresponded to the two groups distinguished on the basis of their apical response to daylength. Because of the similarities in the apical response to daylength (growth room) and to sowing date (field) it is suggested that daylength is an important environmental factor influencing apical development in the field. A high spikelet primordium maximum was again reflected in high spikelet and grain numbers. Grain yield per plant was decreased by late sowing and this

reduction was associated with grain number per plant (both ear number per plant and grain number per ear) rather than 1000 grain weight. This indicated the importance of the sink capacity of the plant in determining final grain yield.

Photoperiod studies (using both Night interruption and Day extension treatments) indicated that cultivars which were very sensitive to long days (e.g. Clipper) responded to both the photoperiodic and radiation components of daylength whereas cultivars which were less responsive to daylength treatment (e.g. Golden Promise) were only responsive to the light energy available for photosynthesis. Movement of ^{14}C-labelled assimilates to the main shoot apex was increased in both L.D. and D.E. treatments compared with short days for Clipper but, in contrast, was increased only in L.D. compared with D.E. and S.D. conditions for Golden Promise. This indicated that daylength, through the light energy available for photosynthesis, may control the absolute amount of assimilate available for transport to the apex, while superimposed on this, is the effect of photoperiod on apical development which, in turn, may alter the distribution pattern of assimilate movement to the apex.

The implications of these physiological studies to plant breeding, with particular reference to Scottish growing conditions, is discussed.

C O N T E N T S

GENERAL INTRODUCTION

Cereal crops are one of the major sources of carbohydrate in the world and are grown in both temperate and tropical climates. In Britain, the cereal species are represented by Hordeum vulgare (barley), Triticum aestivum (wheat) and Avena sativa (oats). These occupy more than 75% of the cultivated land area in both Britain as a whole and in Scotland (Table 1). Nearly 50% of the total tillage in Britain is sown with barley and the percentage is even higher in Scotland where it has increased from 53 to 63% between 1971 and 1975 (Table 1). Thus, in terms of the area on which it is grown, barley is the most important cereal crop in both Britain as a whole and in Scotland in particular. This thesis will be primarily concerned with barley although some of the work discussed in this review has been drawn from investigations into wheat and oats.

Cereal yield is defined as the grain weight per unit area and, in order to suggest methods by which grain yield potential may be increased, it is important to understand how the parameters contributing to yield are genetically and environmentally determined. Early attempts to study these parameters were based on the yield component analysis of Engledow and Wadham (1923) on field crops of wheat. Although these studies recognise that grain yield was determined by three components: ear number per unit area, grain number per ear and grain weight, they provided little information of the physiological determinants of grain yield.

Growth analysis studies of field crops by Watson (1952) suggested that crop productivity was controlled by the total dry matter accumulation and by the partition to the

TABLE 1. Area (000's hectares) of total tillage, barley, wheat and oats sown in Great Britain and Scotland. The percentage for these cereal species of the total tillage is presented in parenthesis.

	1971		1973		1975	
	Britain Area %	Scotland Area %	Britain Area %	Scotland Area %	Britain Area %	Scotland Area %
Total tillage	4812	597	4736	578	4741	582
Barley	2232 (46)	314 (53)	2219 (47)	346 (60)	2295 (48)	369 (63)
Wheat	1096 (23)	36 (6)	1145 (24)	31 (5)	1034 (22)	28 (5)
Oats	347 (7)	112 (19)	271 (6)	78 (13)	223 (5)	66 (11)

Table compiled from Department of Agriculture and Fisheries for Scotland (Agricultural Statistics) 1978.

economically useful part of the plant. However, this work is of somewhat limited physiological value because the period of grain filling is less for cereals than the corresponding period of dry matter accumulation for other crops such as potato and sugar beet (Watson 1971).

More recent genetic and physiological work has therefore been focussed on the parameters determining grain yield rather than dry weight accumulation. These parameters may be divided into 1) factors affecting the ability of the crop to photosynthesise carbohydrate for grain filling i.e. photosynthetic capacity and 2) the ability of the ear to accumulate the photosynthates, i.e. ear capacity.

Photosynthetic capacity

Studies on barley by Archbold (1942) and Porter et al (1950) demonstrated that carbohydrate movement to the grain was mainly derived from current photosynthesis. This has been confirmed by many other reports including studies by Buttrose and May (1959), Quinlan and Sagar (1962), Stoy (1963, 1965) and Lupton (1966) using ^{14}C-labelled assimilate distribution assays on wheat and by Thorne (1965) and Carr & Wardlaw (1965) with gas analysis studies on barley and wheat respectively. These authors have shown that the majority of the assimilates from the flag leaf are transported to the ear and relatively little is translocated down to the stem. Most of the ear photosynthate is retained within the ear and though the lower leaves contribute some assimilate to the developing grain this is relatively unimportant.

Few estimates of all the sources of carbohydrate for grain filling have been made in the same study. Lupton (1968) has attempted to estimate the contributions to the wheat grain

of photosynthesis of a) ear, b) flag leaf and sheath and c) second leaf and sheath by measuring leaf photosynthesis using an infra-red gas analyser at several times during grain filling and calculating the fraction of fed $^{14}CO_2$ in the grain. He computed the values of 10%, 58% and 32% for the contributions of ear, flag leaf and second leaf photosynthate to grain filling, respectively. In two further experiments in 1969 and 1972 in which he combined the gas analysis/^{14}C-assimilate movement techniques with models he derived the following values: 12%, 62% and 26%, and 23%, 74% and 3% for ear, flag leaf and second leaf, respectively (Lupton 1969, 1972). The percentage contribution to grain filling of the ear of barley has been shown to be greater than wheat (Thorne 1963, 1965 and Birecka et al 1964, Bireka and Dakic-Wlodkowska 1966) and this has been attributed to the presence of awns.

In the above studies the contribution of stem stored assimilate to grain filling was found to be small, generally in the region of 15-20% (Thorne 1966, 1974; Rawson & Evans 1971 and Bidinger et al 1977). Until recently, the contribution from the stem has not usually been regarded as important although it was known that if assimilate movement from the flag leaf is decreased then compensation from stem carbohydrate can occur (Wardlaw et al 1965 and Wardlaw 1968). However, Yoshida (1969) reported that translocation of stored assimilate of 40% was possible and Gallagher et al (1975) has suggested that in conditions of extreme drought compensation could be as high as 70%.

However, because of the assumption that grain yield was determined by photosynthetic capacity of the crop and the

of photosynthesis of a) ear, b) flag leaf and sheath and c) second leaf and sheath by measuring leaf photosynthesis using an infra-red gas analyser at several times during grain filling and calculating the fraction of fed $^{14}CO_2$ in the grain. He computed the values of 10%, 58% and 32% for the contributions of ear, flag leaf and second leaf photosynthate to grain filling, respectively. In two further experiments in 1969 and 1972 in which he combined the gas analysis/^{14}C-assimilate movement techniques with models he derived the following values: 12%, 62% and 26%, and 23%, 74% and 3% for ear, flag leaf and second leaf, respectively (Lupton 1969, 1972). The percentage contribution to grain filling of the ear of barley has been shown to be greater than wheat (Thorne 1963, 1965 and Birecka et al 1964, Bireka and Dakic-Wlodkowska 1966) and this has been attributed to the presence of awns.

In the above studies the contribution of stem stored assimilate to grain filling was found to be small, generally in the region of 15-20% (Thorne 1966, 1974; Rawson & Evans 1971 and Bidinger et al 1977). Until recently, the contribution from the stem has not usually been regarded as important although it was known that if assimilate movement from the flag leaf is decreased then compensation from stem carbohydrate can occur (Wardlaw et al 1965 and Wardlaw 1968). However, Yoshida (1969) reported that translocation of stored assimilate of 40% was possible and Gallagher et al (1975) has suggested that in conditions of extreme drought compensation could be as high as 70%.

However, because of the assumption that grain yield was determined by photosynthetic capacity of the crop and the

carbohydrate required for grain filling was supplied by current photosynthesis, many workers tried to correlate grain yield with the leaf area duration (LAD) at anthesis (i.e. the potential photosynthetic capacity of the crop before total leaf senescense). Early studies reported good correlations between grain yield and LAD (Thorne and Watson 1965 and Watson et al 1958, 1963). Welbank et al (1966) found that the correlation of yield with LAD was improved when LAD was measured from anthesis onwards instead of at ear emergence and was improved still further when only the flag leaf duration was considered. However, Thorne (1974) has indicated that recent studies at Rothamsted did not show such a close relationship and Fischer and Kohn (1966) with wheat and Yap and Harvey (1972) with barley, have found strong correlations between grain yield and both LAD and grain number per m^2.

This observation suggests that grain yield may be determined by both the photosynthetic capacity of the crop and the ear capacity per m^2. Evidence accumulated during the past decade increasingly suggests that the sink capacity of the crop, defined here as the potential grain weight per unit area has an important influence on grain yield.

Evidence for the importance of sink capacity

Evidence for the influence of sink capacity in determining grain yield can be derived from a wide range of studies (Willey and Dent 1969; Bingham 1969, 1971 and Thorne 1974). These can be divided into those experiments in which ear capacity has been shown to regulate assimilate movement to the grain, and secondly, studies of field populations in which grain yield was dependent on grain number per m^2.

Wardlaw (1965) found that if the ear size was decreased (e.g. by spikelet removal) the velocity of assimilate movement

from the flag leaf node was decreased with a corresponding increase in assimilate movement down the stem to the young tillers and roots thus suggesting that the demand for assimilates was regulated by sink size. This has been confirmed by King et al (1967) who inhibited ear photosynthesis using DCMU (3-(3,4-dichlorophenyl)-1,1-dimethyl urea) and found a corresponding increase in flag leaf photosynthesis to compensate for the reduction in ear assimilate. Later work by Evans and Rawson (1970) and Rawson and Evans (1971) suggested that the measured photosynthesis by the flag leaf and ear of wheat alone were sufficient to meet the growth requirements of the grain even during the most rapid period of grain growth.

Bingham (1966) drew attention to the importance of genotype in determining final grain size in an experiment in which he emasculated hybrid ears of a Cappelle x Holdfast cross and pollinated one row of spikelets with the larger grain cultivar, Cappelle and the other row with the smaller grain cultivar, Holdfast. He found that the larger grains on the FI ear were derived from the Cappelle parent thus suggesting that, because the potential assimilate supply for each row was identical, there was a sink effect which was dependent on the genotype of the grain. In a similar study on a field crop of wheat, Cappelle-Desprez (Bingham 1967) reduction of grain number by hand-pollinating a limited number of florets caused an increase in the size of the restricted number of grains thereby indicating control by the photosynthetic capacity but the final grain yield was decreased thus suggesting control by grain capacity.

Studies on field populations on both wheat and barley have revealed that grain yield is often correlated with grain number per m^2 (Fischer and Kohn 1966 and Yap and Harvey 1972). This relationship has also been suggested by Willey and Holliday (1971 a,b) in a series of shading studies on barley and wheat. Shading of barley during the pre-anthesis period decreased yield by reducing grain number per m^2 but post-anthesis shading had no effect on grain yield. They attributed this to compensation by stored pre-anthesis assimilate indicating that there was an excess of assimilate available and the sink capacity of the grain was limiting final yield. Pre-anthesis shading of wheat again reduced grain yield by decreasing grain number per m^2 but, in contrast to the barley study, post-anthesis shading did reduce yield thus suggesting control by source factors.

Clearly the sink capacity of the cereal crop is a more important determinant of grain yield than was once thought. It is unlikely, however, that grain yield is controlled solely by either the photosynthetic or ear capacity but by the interaction of the two parameters (Willey and Dent 1969; Thorne 1974 and Gifford 1974). Several authors have suggested that grain yield may be increased by increasing the sink capacity of the crop (Donald 1968; Langer 1967, and Bingham 1969, 1971) and the components contributing to sink capacity of the crop are described in the following sub-section.

Components of sink capacity

The sink capacity of the cereal crop is determined by three components: ear number per m^2, grain number per ear and potential mean grain weight. These three components are

interdependent such that a reduction say, in ear number per m^2 may be compensated by increased grain number per ear and/or grain weight. The influence of these components on grain yield will be discussed in turn in the following pages.

1. Ear number per unit area

Following the studies of Engledow and Wadham (1923), tiller development has been recognised as one of the major components of grain yield. Tiller buds are formed in the axils of the early leaves of the main stem (Bergal and Clemenset 1962 and Jarviss 1972) and thus the final number of primary tillers is limited, e.g. five to six in the barley cultivar, Proctor (Fletcher and Dale 1974). Secondary, tertiary and quaternary tiller buds may also be formed from the primary tillers.

Initially, tillers are dependent on photosynthate produced by the main stem (Quinlan and Sagar 1962 and Lupton 1966) and, in particular, from the leaf immediately above it on the main stem (Fletcher and Dale 1974). Some re-translocation of assimilate may occur between the main shoot and tiller but this is generally small (Clifford et al 1973). Adventitious roots are formed and the tillers become autonomous after emergence from the subtending leaf sheath (Aspinall 1961 and Lupton 1966).

Tillering reaches a peak during the early growth of the plant then declines to a constant level before ear emergence (Cannell 1969). The duration and rate of tiller production may be increased by increased light intensity (Aspinall and Paleg 1964) or increased nutrient supply

(Aspinall 1961).

The earliest formed tillers ear earlier than later formed tillers and have a higher grain number and grain weight (Aspinall 1961 and Cannell 1969). In the study by Cannell (1969), 91% of the final yield was accounted for by the main shoot, coleoptile tiller and the first two primary tillers. Some of the last formed primary tillers and most of the second and third order tillers fail to ear and therefore contribute little to grain yield (Thorne 1962 and Kirby and Jones 1977). These tillers will, therefore, be in direct competition with the main shoot and primary tillers for assimilates during the period of early growth and development of the plant and may therefore reduce the potential size and final grain yield of these shoots (Thorne 1962 and Aspinall 1963). Kirby and Jones (1977) and Jones and Kirby (1977) in a series of de-tillering experiments found that grain yield of the main shoot and primary tillers could be increased with a resultant overall increase in yield by excising all second and third order tillers. Failure of these late-formed tillers to produce ears constitutes a loss of assimilated dry matter and although some remobilization of assimilate and other nutrients such as nitrogen occurs, this will not be complete (Donald 1968 and Puckridge and Donald 1967).

The increased yields of some modern barley cultivars (e.g. of Proctor compared with Plumage Archer) has been attributed to better dry matter partition between the ears and the rest of the plant (Watson et al 1958 and Thorne 1962). These cultivars tend to exhibit a low tiller number combined with high tiller survival with correspondingly larger ears.

Although Donald (1968) has suggested that the 'ideal' wheat should be uniculm, the potential for tillering can be valuable in order to compensate for poor seedling establishment. Boyd (1952); Kirby (1967) and Kirby and Faris (1972) have suggested that the principal reason for the comparatively narrow range of grain yield over a wide range of sowing densities can be attributable to the crop's capacity for tillering. However, if the sowing density is too low, the compensation may not be sufficient; and if the density is too high, tillering may result in a reduction of both grain number per ear and grain weight with a subsequent decrease in yield (Kirby 1967, 1969, and Puckridge and Donald 1967).

2. Grain number per ear.

The importance of an ear containing a large number of grains as a means of increasing the sink capacity of a crop has been stressed by many authors including Donald (1968), Bingham (1969, 1971), Thorne (1974), Langer and Dougherty (1976) and Williams and Hayes (1978). This thesis is primarily concerned with this component of grain yield.

In the dry barley or wheat grain the coleoptile, coleoptile tiller bud and three or four leaf initials have already been formed (Bonnett 1966; Felippe and Dale 1973 and Kirby 1977). The first three to ten primordia to be initiated on the apex will form leaves and these appear as alternate, lateral, simple ridges formed acropetally from below the apical meristem dome. The leaf primordium then grows to envelop the dome but within the preceding leaf (Barnard 1955 and Williams 1966, 1974). These primoria are formed at a constant but slow

rate (Nicholls and May 1963; Kirby 1973, 1974 and 1977, and Lucas 1972).

Axillary buds develop in the axils of these primordia and the buds will either form tiller buds or spikelet initials depending on the stage of formation (Barnard 1955) and, as the spikelet initial develops, the leaf initial is suppressed. The axillary primordium differentiates to form a single many-flowered spikelet in wheat or three single-flowered spikelets in barley (Bonnett 1966, Nicholls 1974 and Kirby 1973a, 1974, 1977). In barley, the central spikelets develop faster than the side-spikelets and, in the case of two-row cultivars, the side-spikelets do not set grain. The rate of spikelet primordium production is faster than that of the leaf primordium (Kirby 1973a, 1974, 1977; Lucas 1972 and Allison and Daynard 1976).

Kirby (1977) in a detailed study on the barley apex noted that the primordium size at initiation and the rate of its subsequent growth was affected by position on the apex. Although the relative volume growth rate exhibited an acropetal increase from the collar primordium, the complex gradients of primordial development resulted in the most morphologically advanced primordia occurring in the lower-mid region of the ear. Other workers have also noted that the spikelet primordia in this region are more advanced than those basipetal and acropetal to this area (Nicholls and May 1963; Bonnett 1966; Rawson and Evans 1970; Kirby 1973, 1977; Bremner and Rawson 1978 and Pinthus and Millett 1978). These early differences in initiation and growth rates persist through to maturity such that final grain weight is greatest in this region.

Maximum spikelet primordium number is generally high in barley and approximately 40 spikelet primodia may be set down on the main shoot apex (Aspinall 1966; Kirby and Faris 1970 and Kirby 1977). Degeneration of the last-formed distal primordia occurs, however, after this maximum has been reached with the subsequent loss of potential spikelets and, therefore, of final grain number.

Grain number in wheat is determined by both the spikelet number per ear and the number of fertile florets per spikelet (Kirby 1974). The maximum spikelet number is generally about 25 (Rawson 1970, 1971 and Wall and Cartwright 1974), and up to nine florets may be formed per spikelet but usually only between two and four will develop to form grains (Kirby 1974 and Langer and Dougherty 1976). Floret initiation occurs first in the morphologically most advanced spikelets (in the mid-region of the ear) and development within each spikelet begins at the base and proceeds acropetally (Kirby 1974). These differences in the pattern of floret development in the ear is again reflected in the final grain number and grain weight (Kirby 1974; Bremner and Rawson 1978, and Pinthus and Millett 1978).

It has been shown that the longer the period of spikelet primordium set down the greater the final spikelet number determined (Aspinall 1966 and Kirby and Faris 1970 for barley, and Rawson 1970, 1971; Wall and Cartwright 1974 and Allison and Daynard 1976 for wheat). However, it is not known what causes the death of the distal spikelet primordia in barley or floret number per spikelet in wheat. Several workers (Kirby and Faris 1970 and Kirby 1977 for barley, and Bremner 1972 and Kirby 1974 for wheat) have suggested that death of

the distal florets may be due to a shortage of assimilate caused by competition from the morphologically better developed middle and basal spikelet primordia (floret primordia in wheat).

Control over final spikelet and grain numbers may also be exerted through a hormonal system of correlative inhibition (Kirby and Faris 1970 and Nicholls 1974 for barley, and Langer and Dougherty 1976 and Pinthus and Millett 1978 for wheat) either through a direct effect on the apex or by influencing assimilate movement. This aspect will be examined in greater detail in page 82.

3. Potential grain weight

It has generally been considered that grain weight is determined by the photosynthetic capacity of the crop during the post-anthesis period of growth (Watson 1952 and Thorne 1966 among others - see page 2). However, Willey and Holliday (1971a,b) have shown that grain weight may be influenced by environmental factors before anthesis. The idea that assimilate supply to the grain may be less important than at first thought and factors operating within the grain may be equally as important in determining final grain weight has gained strength during the past decade.

Following fertilization of the ovary, the endosperm is coenocytic for several days (i.e. nuclear division occurs without cell wall division) during which time 5000 free nuclei may be formed (Brocklehurst 1979). Cell walls then form and cell division occurs normally, with the production of 100,000 to 150,000 endosperm cells. Brocklehurst (1977) suggested that the final number of endosperm cells may be regulated by

supply of assimilate available to the grain but cell number may also be regulated by internal resistance to the transport of assimilates (Bremner and Rawson 1972) or by some form of hormonal control (Wheeler 1972, 1976).

There then follows a period of cell expansion during which the final endosperm cell weight is dependent on the potential cell size, and the rate and duration of starch deposition before the onset of grain maturation. Jenner and Rathjan (1972a,b) and Sofield et al (1977) have suggested that dry matter accumulation in the grain may cease even if there is sufficient carbohydrate available for starch synthesis. Jenner and Rathjan (1975) further suggested that the onset of this phase may be caused by the reduced capacity of the grains to synthesise starch.

Final grain size is, therefore, dependent on the number of endosperm cells formed during the period of active cell division and by the rate and duration of starch synthesis. An increase in the duration of either or both of these phases may result in increased yield (Brocklehurst 1977, 1979).

The sink capacity of the barley crop is clearly a more important determinant of grain yield than was once thought. This thesis is primarily concerned with the apical development and spikelet primordium production on the main shoot apex and the subsequent spikelet and grain number per ear. Spikelet primordium production occurs during the early growth and development of the plant (page 9) and it is to be expected that any environmental factor which affects the early growth of the plant may also influence spikelet primordium set down and thus potential grain number. The literature on the influence of environmental factors including daylength, light

intensity and temperature on apical growth and development is reviewed in Section 1.

The underlying objective of much of the physiological work on cereals has been to gain a better understanding of the factors limiting yield as an aid to defining useful physiological features which may be incorporated by plant breeders into new genotypes. Much of this work has, however, been carried out on a limited number of cultivars but it is of more relevance to plant breeding to examine the effect of environemntal factors such as daylength on a wide range of cultivars. In this way, physiological responses that influence yield in a large number of cultivars can be revealed. Further, by examining a large number of cultivars, it is possible to determine the extent of the physiological variation between cultivars from which new genotypes may be derived.

In this thesis, the influence of one environmental factor, daylength was examined on one hundred barley cultivars and from the range of response exhibited by these cultivars (Section 1), more detailed physiological studies were carried out on genotypes which contrasted in their response to daylength. The effect of daylength on apical growth and development of these cultivars was examined both in controlled environment conditions and in the field using different sowing dates (Section 1). Many other studies have examined the effect of environmental factors on barley cultivars either in the field or in controlled environments. In the field, such results are often difficult to interpret physiologically because several environmental factors may be changed by changes in one agronomic factor and this is the case when the

effects of different sowing dates are compared. Experiments carried out in controlled environment conditions also have their limitations because these often involve extremes of conditions not usually found in the field and it is therefore difficult to extrapolate results of such experiments directly to the field situation. Thus, in this thesis, the apical response to daylength was examined both in growth rooms and in the field in an attempt to investigate physiological responses relevant to growth in the field. Other environmental factors such as temperature will be altered with different sowing dates and the influence of temperature on the apical development of two cultivars which contrasted in their response to sowing date is examined in Section 2. The nature of the daylength response was clarified in Section 3 using cultivars which contrasted in their response to daylength determined in Section 1. In the final section (Section 4) the movement of ^{14}C-labelled assimilates to the apex was investigated for two cultivars with contrasting responses to daylength.

SECTION 1. The influence of daylength and sowing date on the ear development of selected genotypes.

INTRODUCTION

Grain yield per unit area is the result of the interaction between the environment and the genotype of the plant. Many environmental factors during growth and development in the field may influence cereal yield including: daylength, light intensity, temperature, and nutrient and water availability. This thesis will consider only the first three factors. Physiological analyses of the interaction of these factors on the development of barley and wheat cultivars are of assistance to plant breeders in that such analyses may suggest the selection criteria that can be used to match genotype with environment so as to achieve improvements in yield (Lupton and Whitehouse 1961; Bell and Kirby 1966; Lupton and Kirby 1968; Bingham 1972, and Thorne 1974).

Comparisons of the responses of cultivars to different sowing dates is one approach to the investigation of the interaction between genotype and the environmental factors of daylength, light intensity and temperature. Late sowing conditions may arise in normal agricultural practice due to adverse weather conditions but such field comparisons are complicated by the fact that, in the sowing date treatments, all three factors are confused. Early sowings are characterised by shorter daylength, lower light intensity and lower temperature during the early stages of plant growth and development compared with later sowings. The situation is further complicated because these factors have manifold effects on plant growth and development influencing vegetative growth,

apical development and grain filling.

Previous work under controlled environmental conditions has shown that daylength, light intensity, temperature, and nutrient and water availability can have an important influence on grain yield per unit area of cereals (Thorne 1966, 1974). Since this thesis is primarily concerned with the environmental factors that differ between different sowing dates (daylength , light intensity and temperature) and their effects on apical development and final spikelet and grain number per ear, consideration of previous work will emphasise the effects of these factors on ear development. Firstly, studies in which these environmental factors have been examined under controlled environmental conditions will be reviewed, followed by a resume of the work concerned with the effect of sowing date on cereal growth and development in the field.

Barley and wheat are generally regarded as quantitative long day plants, although a wide range of response between different cultivars of both barley and wheat have been found (Takahashi and Yasuda 1960; Ormrod 1963; Aspinall 1966; Kirby 1969, and Allison and Daynard 1976). Long days are not essential for ear emergence but the physiological development of the plant is accelerated and, as a consequence of this more rapid development, both leaf number and spikelet number per ear are reduced. Although plants in short day conditions have a slower rate of spikelet primordium production, the period of set down is prolonged resulting in a larger spikelet number (Aspinall and Paleg 1963 and Paleg and Aspinall 1964 for barley, and Rawson 1971 and Lucas 1972 for wheat).

The developmental stage at which daylength is varied

determines which of the yield components are most affected. In a series of comparisons on barley (Guitard 1960 and Thorne et al 1967) and wheat (Thorne et al 1968), short days during the period of sowing to the onset of spikelet primordium production were found to increase yield by increased grain number per ear in both cereal species. Grain yield of both barley and wheat was considerably decreased when short day treatment was provided in the period up to anthesis because of reduced grain number per unit area caused by a low ear number per unit area and a reduction in floret fertility. Later stages of growth can also be affected by daylength and both sets of workers found that grain yield was reduced by short day treatment during the post-anthesis period due to decreased grain weight.

Many of the daylength investigations have involved only a limited number of cultivars and thus some of the conclusions derived from these studies may not be generally applicable to all barley and wheat genotypes. The initial objective of this project was, therefore, to examine the effect of daylength in the glasshouse on the spikelet and grain number per ear of a large number of barley cultivars originating from different regions of the world and to compare the magnitude of the response between cultivars. On the basis of these comparisons, further experiments were designed to investigate in more detail the response of apical development and final grain yield to different sowing date conditions in the field using cultivars which exhibited a contrasted response to daylength in the glasshouse. A further daylength experiment was designed to examine the influence of daylength on the apical development of selected genotypes again showing a contrasted

response to daylength.

At this stage, no attempt was made to distinguish between the photoperiods and radiation components which are confounded in daylength. This aspect will be discussed more fully in Section 3. However, since daylength does contain a radiation component it is appropriate to consider at this point, studies examining the effect of light intensity on apical growth and development. Under low light intensities, the rate of apical morphogenesis and spikelet primordium production is slow with a subsequent reduction in the maximum number of spikelet primordia (Aspinall and Paleg 1963 on barley, and Friend et al 1963 and Friend 1965 on wheat). The lower spikelet primordium number can be attributed to the reduction in the light energy available for photosynthesis. All three components of yield:ear number per unit area, grain number per ear and grain weight are increased with increased light intensity both when given throughout the life-cycle and at specific growth stages (Friend et al 1963 and Friend 1965).

Similar effects on yield can also be obtained by shade treatments. The shading studies of Willey and Holliday (1971a, b) on barley and wheat, again indicated that the effect of shade treatment on grain yield depended on the time of treatment. Early and late shading during the pre-anthesis development of barley reduced yield either by decreasing ear number per unit area or by a reduction in grain number per ear respectively. Post-anthesis shading did not affect grain yield. In wheat, pre-anthesis shading again reduced grain yield; earlier shading reduced ear number per unit area accompanied by a small decrease in spikelet number per ear and

later shading reduced yield by decreasing grain number per spikelet. Post-anthesis shading did, however, decrease yield because of reduced grain weight.

Temperature is the third environmental factor which is altered with change in sowing date. Increased temperature hastens the rate of development of all phases of growth: vegetative, spikelet production, ear emergence and maturity (Guitard 1960 and Thorne et al 1967 on barley, and Friend et al 1963; Friend 1965 and Thorne et al 1968 for wheat). This rapid development leads to reduced tiller number, grain number per ear and grain weight. Several workers (Friend 1966; Aspinall 1969 and Wall and Cartwright 1974) have suggested an optimal temperature for grain number per ear for both barley and wheat in the range 10-15%. The interaction between daylength and temperature will clearly be important in influencing grain number per ear and Guitard (1960) and Thorne et al (1968) working with barley and wheat respectively have suggested that optimal grain number per ear occurs with low temperature (15^{o}C) and short days during the spikelet production phase followed by cool long days after anthesis.

The effect of temperature on apical development and grain number per ear is complicated by the vernalization response (Hasle and Weir 1970; Rawson 1970 and Wall and Cartwright 1974). Vernalization treatment hastens spikelet production with a subsequent reduction in grain number per ear. The cold requirement appears to be quantitative rather than qualitative in nature and Chujo (1961) and Gott (1961) have found that temperatures of around 10^{o}C may be sufficient to vernalize several cultivars of barley and wheat respectively.

The environmental factors of daylength, light intensity

and temperature are clearly important influences on ear development and final grain yield of barley. The interaction between genotype and these factors may be examined in the field using a range of different sowing dates although, as indicated earlier, all three factors will be confounded in the response to sowing date treatment.

Late-sown crops of barley and wheat exhibit a reduced time to anthesis and maturity (Last 1957; Kirby 1969 and Nass et al 1974). Generally there is a marked decrease in yield with delay in sowing but, because of the variability in environmental factors during the growing season, the results may be inconsistent (Jessop and Ivins 1970). All three yield components (ear number per unit area, grain number per ear and grain weight) may be reduced but, again, there are variations as to which component contributes most to the reduced yield. This is partly due to the compensation which occurs between these components. For example, if ear number per unit area is reduced, this may be compensated for by an increased grain number per ear. Generally, cereal yield of crops sown at different dates is determined by the grain number per unit area (Thorne 1966, 1974 and Cannell 1969) but grain weight may also be reduced by late sowing (Kirby 1969).

All these studies have examined the effect of sowing date on external morphological characters. Little work has been done on the effect of environmental factors on apical development in the field and no work has been published on the apical response to sowing date. However, other aspects of apical development in the field have been investigated. Paleg and Aspinall (1966) subjected field plots of barley to a two-hour light break of varying intensities of incandescent light given in the middle of the night, and found that the

light break treatment accelerated apical development and spikelet primordium production. However, as with long day treatment, both leaf and spikelet number were reduced with this treatment. This study will be discussed further in Section 3. Kirby and Faris (1970) showed that the rate of apical development increased as plant density increased and this was reflected in a lower spikelet primordium maximum due to the reduced period of set down.

Evidence presented earlier suggests that factors which affect apical development and spikelet primordium production also influence final grain number per ear. In the sowing date field trials described in this section of the thesis, the effect of sowing date on both apical development and final grain yeild is examined in order to gain a clearer picture of the effect of late sowing on ear development.

Kirby and Eisenberg (1966) have suggested that one of the major environmental factors influencing the effect of sowing date on cereal yields in Britain is daylength. The daylength impinging on the crop is dependent on the time of sowing and on the latitude and will, therefore, be different under Scottish and English growing conditions. Much of the spring barley sown in England (e.g. in the Cambridge area) is carried out during late February and early March although some crops on sandy soil may be sown much earlier in January (F. R. Hubbard, pers. comm. 1979). These crops will be sown in relatively short daylength conditions of 9 to 12h daylight (Fig. 1). Sowing dates are later in Scotland, generally from March until mid-April and are, therefore, sown under longer daylength conditions (between 10.5 and 14h) and in North Scotland sowing may be delayed until early May (daylength of

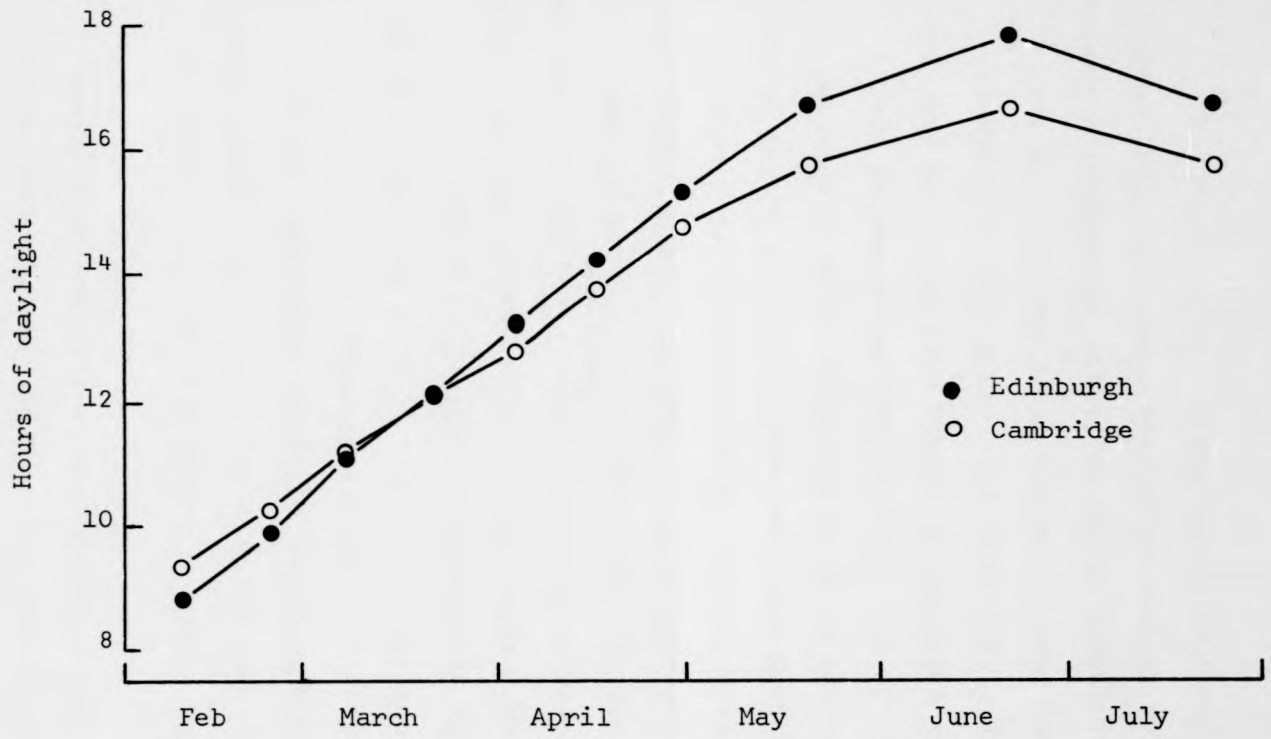


Fig. 1. Hours of daylight during early growth of Spring barley in Edinburgh area (●) and Cambridge area (○). Figure compiled from daylight data - Smithsonian Tables.

15h) (M. Richardson, pers. comm. 1979). Thus the daylengths under which many Scottish barley crops undergo their early development is rather longer than is the case in Southern England.

Although the effect of sowing date on grain number and grain yield in barley has been investigated in England (Kirby 1969, at the Plant Breeding Institute, Cambridge), little information is available for the somewhat different Scottish growing conditions (Davies 1973). One of the objectives of this thesis is to investigate the effect of sowing date on apical development, spikelet primordium number and final grain number in the field under Scottish conditions (at the Scottish Plant Breeding Station, Edinburgh). Twenty-nine and fifteen cultivars were examined in two sowing date field trials in 1976 and 1979 respectively; these cultivars being selected from the one hundred cultivars examined in the initial glasshouse daylength experiment so as to include a range of cultivar responses. It was also thought that comparison of the responses of the cultivars in sowing date trials in the field with the daylength responses under controlled environment conditions (glasshouse and growth room) may indicate the extent of the influence of the daylength differences associated with sowing dates on the apical development and final grain number per ear observed in the field.

MATERIALS AND METHODS

Glasshouse daylength experiment

The effect of daylength on spikelet and grain number per main ear was examined in the glasshouse on one hundred two-row spring barley cultivars obtained from the genotype collection at the Scottish Plant Breeding Station, Pentlandfield, Edinburgh. The cultivars were selected so as to include representatives from as wide a range of growing conditions as possible including cultivars from both North temperate and Mediterranean climates as well as accessions from the Southern hemisphere. The cultivars selected and their area of accession are presented in Table 2. The cultivars chosen were thought to have little vernalization requirement (Giles, 1975 pers. comm.).

The experiment was designed as a split plot in four replicate blocks with the two daylength treatments (8h short day and 16h long day light periods) as the main plot treatment. Within each main plot, each subplot consisted of one pot representing one cultivar and these were completely randomised within each daylength treatment. To minimize the effects of variation of temperature or light intensity within the glasshouse, the main treatments and the subplots were re-randomised at weekly intervals.

Long day and short day treatments were obtained by using supplemental high intensity light of 16h and 8h duration respectively. The supplemental light which consisted of a combination of mercury vapour, fluorescent and incandescent light to provide a balanced spectral composition (c. 20,000 lux, 150 Wm^{-2}), was used in addition to the natural daylight at the time of the experiment (autumn-winter 1975). Each replicate

TABLE 2. One hundred two row spring barley cultivars and country of accession sown in glasshouse daylength experiment

No	Cultivar	Country of Accession
1	Abacus	Great Britain
2	Ackermanns MGZ	Germany
3	Afghan R668	Afghanistan
4	Akka	Sweden
5	Alfor	Holland
6	Alpha	France
7	Archer	Great Britain
8	Ariel	France
9	Ark Royal	Great Britain
10	Arla	Sweden
11	Autotele	Poland
12	Banba	Eire
13	Betina	France
14	Bohmerwald	Austria
15	Camion	Great Britain
16	Charlotte Town 80	Canada
17	Chevallier	Great Britain
18	CI 5791	Canada
19	Chipper	Australia
20	Cossack	France
21	Danpro	Denmark
22	Domen	Norway
23	Dr Sauli (0192)	Finland
24	Drusp	W Pakistan
25	Early 12A Bonus	Sweden
26	Ethiopian (ST 473)	Ethiopia
27	Ethiopian (ST 1746)	Ethiopia
28	Freyman	Iran
29	Georgie	Great Britain
30	German (MR2)	W Germany
31	Golden ARcher	Great Britain
32	Golden Promise	Great Britain
33	Gold (Morayshire)	Great Britain
34	Gull (Selection)	Sweden
35	Gunilla	Sweden

contd.

Table 2 (contd.)

No	Cultivar	Country of accession
36	Hannchen	Canada
37	Heils Franken	W Germany
38	Hemma	Austria
39	Hen Gymro A	Great Britain
40	Hillmarsh	Holland
41	Hiproly	Sweden
42	Ingrid	Sweden
43	Jet	Ethiopia
44	Julia	Holland
45	Kenia	Denmark
46	Klages	United States
47	Klintso	Denmark
48	Larni	Denmark
49	La Prevision 19	Argentina
50	Lara	Australia
51	Long-eared Nottingham	Great Britain
52	Malta	Denmark
53	Mari	Sweden
54	Maris Badger	Great Britain
55	Maris Baldric	Great Britain
56	Maris Mink	Great Britain
57	Maythorpe	Great Britain
58	Mazurka	Holland
59	Midas	Great Britain
60	Mimi	Great Britain
61	Minn 84.7	United States
62	Minn 90.5	United States
63	Margennot	W Germany
64	Mosane	Belgium
65	Mayjor	Norway
66	Naked 2-row	Great Britain
67	Nepal 1	Nepal
68	Prior	Great Britain
69	Proctor	Great Britain
70	Rene Guillemart	France
71	Riff	Great Britain
72	Rogue A	Great Britain

contd.

Table 2 (contd.)

No	Cultivar	Country of accession
78	Ruby	Great Britain
74	Russian (Kaluga)	Russia
75	Russian (Mosdoksky)	Russie
76	Scotch Common	Great Britain
77	Short-awned mutant	Sweden
78	Smyrnakorn	Austria
79	Spartan	United States
80	Spratt	Great Britain
81	Spratt Archer	Eire
82	Sultan	Holland
83	Turkish 1106	Turkey
84	Turkish 1823	Turkey
85	Tyra	Denmark
86	Union	W Germany
87	Urais 062	Finland
88	Uzu	Sweden
89	Voila	W Germany
90	W5414	Sweden
91	Wieselburger	Austria
92	Wisa	Denmark
93	Ymer	Sweden
94	Yugoslavian I	Yugoslavia
95	Yugoslavian J	Yugoslavia
96	Yugoslavian J895	Yugoslavia
97	Yugoslavian (Maksimir)	Yugoslavia
98	Zarina	Great Britain
99	Zephyr	Holland
100	Zoe	Holland

block consisted of four trolleys (two per daylength treatment) and these trolleys were positioned directly below one of the light cradles.

The long day supplemental light period was controlled by automatic time-clocks from 6.00 to 22.00h. The short day treatment remained under the light cradle from 8.00 to 16.00h before being transferred to adjacent brick garages and the blackout screens drawn. At the end of the 16h dark period, the short day treatment was removed from the garages and positioned directly below the light cradles.

Temperature was maintained at approximately 20°C during the day but fell to around 10°C during the dark period in both glasshouse and garages.

Sowing was carried out on 27 October 1975 and completed within the day. For each of the one hundred cultivars, four seeds were sown per 10.2 cm diameter plastic pot containing John Innes No 2 compost, at a depth of 2.5 cm. Once the seedlings were established they were thinned to give a final number of two plants per pot.

Seeds of cultivars which failed to emerge within 14 days of sowing were given a short period of thermal stratification. Fifty seeds of these genotypes were placed on moist germination paper in petri dishes and stored at -4°C for four days. The germination dishes were then transferred to a controlled environment room at 20°C for a further two days. The germinated seeds were then transplanted into pots as described above. In all instances, seedlings were successfully transplanted after only one period of stratification.

Plants were staked and tied at several stages during growth. This served as support for the stems and was particularly

necessary for the short day plants which were especially prone to injury during the manual transfer of trolleys to the garages because of the weaker stems often associated with short day treatment. The plants were watered in the morning and afternoon when required.

Several of the plants showed signs of attack by mushroom fly (Lycoriella auripila) after 14 days, and all pots were treated with the commercial pesticide 'Diazitol' (containing diazinon; supplied by Ciba-Geigy, Agrochemical division) at a rate of 2.0 $cm^3 l^{-1}$. A slight infection of mildew (Erysiphe graminis f.sp. hordei) was noticed on a few plants after 70 days and this was immediately treated with the commercial systematic fungicide, 'Calixin' (75% w/v tridemorph) at a rate of 2.0 cm^3 l^{-1}. This proved to be completely effective and only one spray was required.

When it was estimated that spikelet primordium production was complete on the main shoot apex for all cultivars in both daylength treatments (90 days after sowing), all short day plants were transferred to long day conditions. All plants then remained in long days until maturity. At the time of transfer, all plants were fed with the commerical liquid nutrient feed 'Vitafeed 101' (nitrogen N_2 26%, phos. acid P_2O_5-, potash K_2O 26%, plus trace elements: boron, copper, iron, magnesium, manganese, molybdenum and zinc) at a rate of 5g per 10 litres.

The grain was defined as mature and ready for harvest when the kernel was hard and could not be scratched by finger-nail. The long day treatment was harvested between 8-12 March 1976 but, because of the slower development of short day plants, harvest did not commence until 5 April. Spikelet

number and grain number both per main ear and per tiller were counted separately for the one hundred cultivars. Grain set was not determined because of the low grain set found in many of the cultivars.

Growth room daylength experiment.

(i) Plant culture

The influence of daylengths on the apical development of five two-row spring barley cultivars was examined in growth rooms. The five cultivars were selected from the one hundred cultivars examined in the initial glasshouse experiment which showed contrasted response to daylength in spikelet number per main ear. The cultivars, country of accession, and the daylength response in the glasshouse are presented in Table 3.

The two daylength treatments used in this study were short day (S.D., 8h light period) and long day (L.D., 16h light period). The required daylength was obtained by automatic time-clocks. Artificial lighting consisted of a combination of fluorescent tubes and incandescent strip lights to obtain a balanced spectral light composition. The lights were separated from the main growth room by glass plate. The total light intensity measured at pot level was c. 15,000 lux, (c. 120 Wm^{-2}).

The temperature in both growth rooms was maintained at $20^{o}C \pm 1^{o}C$. Air was introduced from one side of the growth room, circulated around the room then vented through the opposite side. No control of atmosphere humidity was attempted.

Each growth room measured 2.04 x 1.66 x 1.94m and thus only four trolleys each containing 20 plastic pots (diameter 12.5cm) could be positioned in each room. This allowed for

number and grain number both per main ear and per tiller were counted separately for the one hundred cultivars. Grain set was not determined because of the low grain set found in many of the cultivars.

Growth room daylength experiment.

(i) Plant culture

The influence of daylengths on the apical development of five two-row spring barley cultivars was examined in growth rooms. The five cultivars were selected from the one hundred cultivars examined in the initial glasshouse experiment which showed contrasted response to daylength in spikelet number per main ear. The cultivars, country of accession, and the daylength response in the glasshouse are presented in Table 3.

The two daylength treatments used in this study were short day (S.D., 8h light period) and long day (L.D., 16h light period). The required daylength was obtained by automatic time-clocks. Artificial lighting consisted of a combination of fluorescent tubes and incandescent strip lights to obtain a balanced spectral light composition. The lights were separated from the main growth room by glass plate. The total light intensity measured at pot level was c. 15,000 lux, (c. 120 Wm^{-2}).

The temperature in both growth rooms was maintained at $20^{o}C \pm 1^{o}C$. Air was introduced from one side of the growth room, circulated around the room then vented through the opposite side. No control of atmosphere humidity was attempted.

Each growth room measured 2.04 x 1.66 x 1.94m and thus only four trolleys each containing 20 plastic pots (diameter 12.5cm) could be positioned in each room. This allowed for

TABLE 3. Name, country of accession and daylength response of five two-row barley cultivars examined in growth room daylength experiment. Daylength response based on means of 6 to 8 plants in each daylength treatment. A negative value denotes an increase in spikelet number in L.D. treatment.

Cultivar	Country of accession	Main ear % spikelet reduction in L.D.
Clipper	Australia	46.5
Spartan	United States	30.5
Domen	Norway	2.4
Golden Promise	Great Britain	-3.7
Ymer	Sweden	-27.9

eight sampling occassions (two pots per sample) for each of the five cultivars examined.

Two days prior to sowing, all pots were treated with the commercial pesticide 'Diazitol' (containing diazinon; supplied by Ciba-Geigy, Agrochemical division) at a rate of 2.0 $cm^3 \ell^{-1}$ to prevent attack by mushroom fly (Lycoriella auripila).

Six seeds were sown per 12.5cm diameter plastic pot containing John Innes No 2 compost at a depth of 2.5cm and the sowing was completed within the day. Once the seedlings were established they were thinned to give four seedlings per pot.

In order to reduce the effects of light intensity and temperature variations within each growth room, all pots were completely randomised at the beginning of the experiment and then re-randomised on alternate days. The pots were watered morning and afternoon when required. The plants were staked and tied at several stages during growth. No infection of mildew (Erysiphe graminis f.sp. hordei), was noticed in the growth room plants.

(ii) Samples for apical dissection

For each cultivar, each sample consisted of two randomly selected replicate pots per daylength treatment. All four plants per pot were carefully and individually removed for apical dissection thus giving a final total of eight plants per sampling time for each daylength treatment for each of the five cultivars.

Sampling commenced seven days after sowing for both daylength treatments and continued at seven-day intervals in the long day treatment until the maximum spikelet primordium number had been reached for all cultivars (week 7). Because of the slower apical development in short days, it occasionally

proved necessary to sample on alternate weeks to enable a value for spikelet primordium maximum to be obtained within the experimental period.

(iii) Technique of apical dissection

In all studies of apical development in this thesis only the main shoot apex was examined.

The "shoot apex" is defined so as to include both the shoot apical meristem and the undifferentiated primordia basal to it (Kirby 1974). The "shoot apical meristem" refers to the hemispherical dome of tissue at the tip of the apex acropetal to the last-formed primordi (Fig. 2). A "primordium" was defined as being initiated when a clear discontinuity could be seen at the upper and lower limit of the primordium (Fig. 2).

The total number of primordia produced was taken to include both the differentiated leaves on the main stem and the undifferentiated lateral structures on the shoot apex. During the early stages of apical development it cannot be determined whether a primordium will differentiate into a leaf or spikelet primordium. At this stage, the total primordium number was counted and the spikelet primordium number was determined by subtracting the final leaf number per main shoot, determined from later sample occasions, plus the collar from the total primordium number.

When the leaf and spikelet primordia could be distinguished, these were counted separately. At this stage, the collar (the vestigeal leaf-like structure on the lowermost node of the ear) was designated c (Bonnett 1966 and Kirby 1974) and given the number, 0. Counting of the spikelet primordia then proceeded in an acropetal sequence.

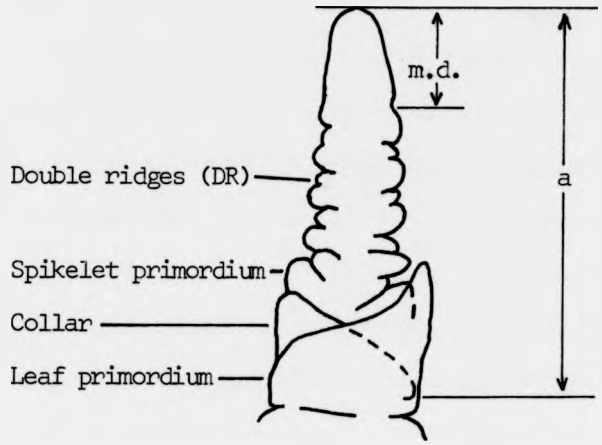


Fig. 2. Diagram of shoot apex, showing leaf collar and spikelet primordia, at double ridge stage of development.

a = apex length

m.d. = meristem dome length

Death of some of the last-formed distal spikelet primordia occurs after the maximum spikelet number has been produced. After this stage, living and degenerated spikelet primordia were counted separately.

A ten-stage scoring scale was used to assess the developmental stage of the shoot apex (Table 7). In the vegetative phase (i.e. before the onset of spikelet primordium production, the assessment was based on the shape of the apical meristem dome. During reproductive development the assessment was based on the developmental stage of the most advanced spikelet primordium usually found in the lower-middle region of the shoot apex. The scoring technique is a slight modification of that used by Nicholls and May (1968), Bonnett (1966) and Kirby and Faris (1970).

Several of these developmental stages are illustrated in Plates 1-4 for cv. Golden Promise grown in 16h light period at 20^{o}C in the growth room.

It should be noted that the assessment scores are qualitative in nature and not quantitative. The time interval between any two stages will vary depending on the developmental stages involved.

Apical dissections were performed using a binocular dissecting microscope on freshly harvested plant material. Each differentiated leaf on the main shoot was carefully removed in sequence with sharpened dissecting needles until the main shoot apex was visible. Before the collar could be distinguished, the dissection was continued by removing all undifferentiated structures on the shoot apex which overlapped the primordium initial immediately acropetal to it on the same side of the apex. Once the collar could be distinguished, all leaves and differentiated leaf primordia were removed from

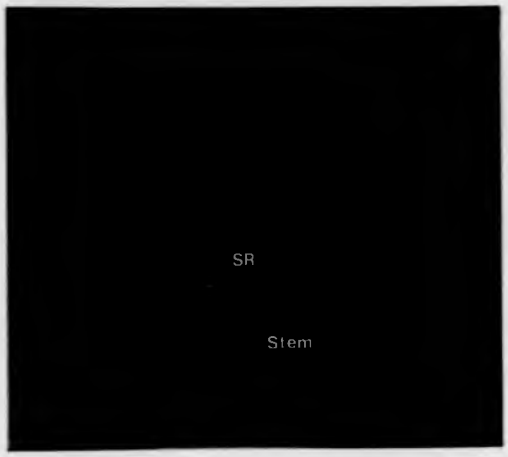


Plate 1. Main shoot apex of Golden Promise at Simple ridge (late, LS) stage of development.

12 day old, primordia on apex = 5, apex length = 0.39mm

SR = simple ridge.

Plate 2. Main shoot apex of Golden Promise at Double ridge (DR) stage of development.

21 day old, primordia on apex = 22, apex length = 1.11mm

SR = simple ridge

DR = double ridge

LP = leaf primordium

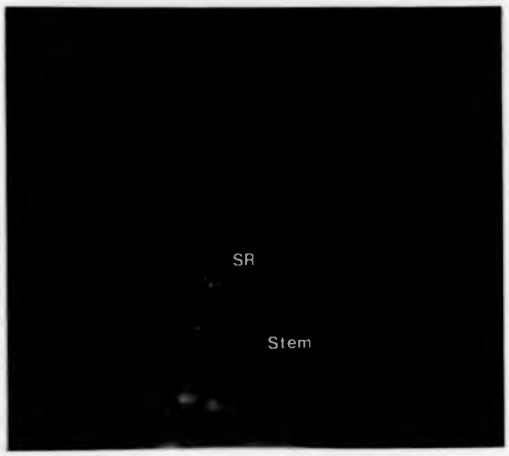


Plate 1. Main shoot apex of Golden Promise at Simple ridge (late, LS) stage of development.
12 day old, primordia on apex = 5, apex length = 039mm
SR = simple ridge.

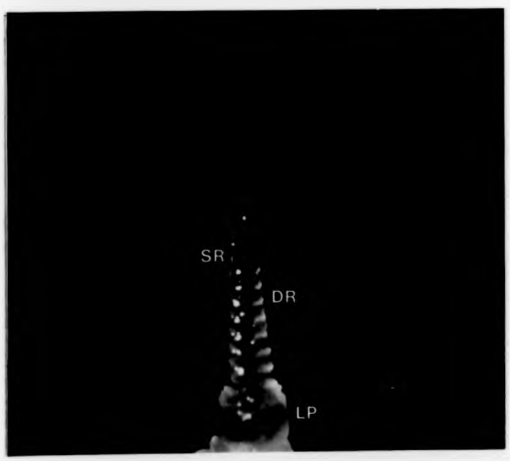


Plate 2. Main shoot apex of Golden Promise at Double ridge (DR) stage of development.
21 day old, primordia on apex = 22, apex length = 1.11mm
SR = simple ridge
DR = double ridge
LP = leaf primordium

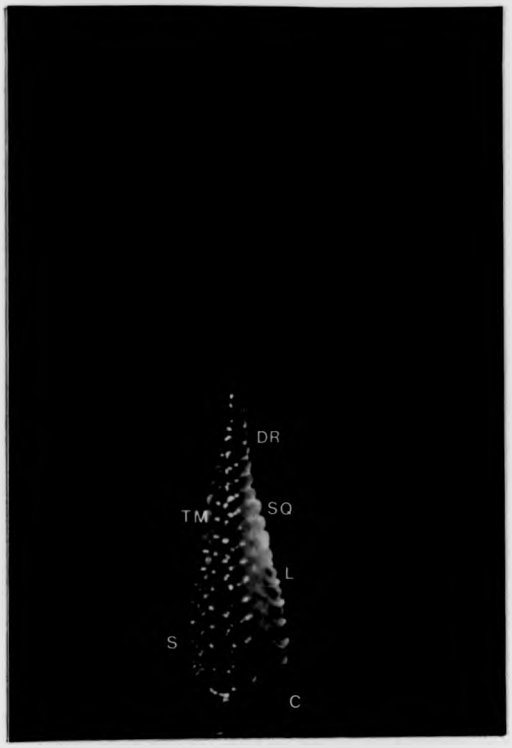


Plate 3. Main shoot apex of Golden Promise at Stamen initial (S) stage of development.

33 day old, spikelet primordium number = 32,

apex length = 1.95mm

DR = double ridge

SQ = square ridge

TM = triple mound

L = lemma initial

S = stamen initial

C = collar

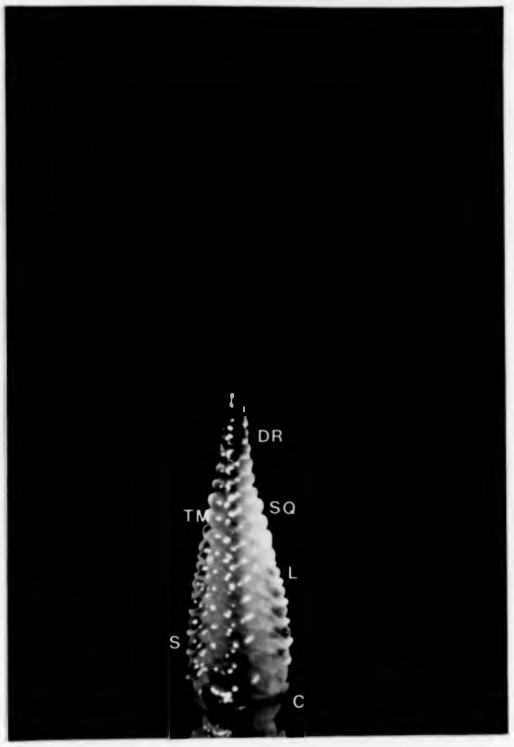


Plate 3. Main shoot apex of Golden Promise at Stamen initial (S) stage of development.

33 day old, spikelet primordium number = 32,

apex length = 1.95mm

DR = double ridge

SQ = square ridge

TM = triple mound

L = lemma initial

S = stamen initial

C = collar

the shoot apex until only the collar and the reproductive apex remained.

Each dissection had to be carried out quickly to prevent drying up of the shoot apex. Leaf number per main shoot (i.e. emerged leaves plus differentiated leaf primordia), total primordium and spikelet number per main shoot apex were then determined, and the apical developmental stage assessed according to the scoring technique described earlier.

The shoot apex was quickly excised from the shoot and placed in a drop of water on a clean microscope slide and the apex length and apex meristem length measured using an eyepiece graticule fitted in a stereoscopic microscope. During the period of apical development before the collar can be distinguished, the apex length was measured from the base of the undifferentiated primordium which just overlapped the primordium initial immediately acropetal to it on the same side of the apex to the meristem dome tip (Fig. 2). Once the collar was distinguishable, apex length was measured from the base of the collar to the tip of the meristem dome.

Length of the main shoot meristem dome was measured from the upper limit of the last-initiated primordium to the tip of the meristem dome (Fig. 2).

After degeneration of the distal spikelet primordia had occurred, the apex length was measured using an eyepiece graticule fitted in the binocular dissecting microscope. No measurement of meristem length was made.

The dry weight of the apex was obtained by carefully placing the excised apex in a small aluminium container and dried in an oven at 80^{o}C for 48h. The container was then placed in a desiccator until cool and the dry weight obtained

on a microforce balance (Beckman Microbalance LM 500). The procedure was repeated until constant dry weight was obtained.

If plant material had to be stored overnight, the samples were wrapped in moist tissue paper, placed in a polythene bag and kept in a refrigerator (0-5^{o}C) overnight. No noticeable deterioration in the shoot apex was observed.

Sowing date field trials in 1976 and 1977

(i) Plant culture

The influence of sowing date on the apical development and grain yield of 29 cultivars in 1976 and 15 cultivars in 1977 was examined in the field at the Scottish Plant Breeding Station, Pentlandfield, Edinburgh. These cultivars were selected from the one hundred cultivars examined in the initial glasshouse daylength experiment to show contrasted responses in spikelet number per main ear to daylength. A secondary criterion used for selection was the country of accession which allowed the selection of cultivars from different regions of the world and thus different growing conditions. The 29 cultivars selected in 1976 and the 15 cultivars selected in 1977 are presented in Table 4.

The three sowing dates used in 1976 were: 27 March (S.1), 20 April (S.2) and 17 May (S.3) and the two sowing dates in 1977 were: 15 March (S.1) and 20 May (S.2). The two sowing dates in 1977 thus correspond to the first and third sowings of 1976. A full description of the environmental conditions during the period of early plant growth and development is presented on page 53.

Both field trials were laid out in the form of a split plot design with three replicate blocks. The sowing dates (three in 1976 and two in 1977) were the main plot treatments

TABLE 4. Name, country of accession and daylength response in the glasshouse of 29 barley cultivars selected for sowing date field trial in 1976. Daylength response based on means of 6 to 8 plants in each daylength treatment. A negative value indicates an increase in spikelet number in long days. The cultivars underlined were also sown in the 1977 sowing date trial.

Cultivar	Country of accession	% spikelet no/main ear reduction in L.D.	Apex development
Early 12A Bonus	Sweden	46.7	
Clipper	Australia	46.5	**
Spartan	United States	30.5	**
Turkish 1106	Turkey	28.1	
CI 5791	Canada	19.1	*
Ingrid	Sweden	17.1	*
Banba	Eire	16.4	
Chevallier	Great Britain	15.8	*
Midas	Great Britain	9.9	
Bohmerwald	Austria	6.2	*
Heils Franken	W Germany	5.8	
Lami	Denmark	5.6	*
Mimi	Great Britain	5.2	
Charlottetown 80	Canada	2.9	
Domen	Norway	2.4	**
Scotch Common	Great Britain	2.1	
Tyra	Denmark	2.0	
Proctor	Great Britain	0.8	
Ark Royal	Great Britain	0.7	
Afghan R668	Afghanistan	-1.5	
Zephyr	Holland	-1.9	
Maris Mink	Great Britain	-3.0	*
Ariel	France	-3.7	
Golden Promise	Great Britain	-3.7	**
Abacus	Great Britain	-5.0	
Spratt	Great Britain	-10.2	*
Hillmarsh	Holland	-10.5	*
Uzu	Sweden	-14.4	*
Ymer	Sweden	-27.9	**

* cultivars selected for apex development examination in 1976

** " " " " " " " 1976 and 1977

and were randomised within each replicate block. Within each main plot, 29 and 20 subplot treatments for 1976 and 1977 respectively were completely randomised.

In 1976, each subplot consisted of one cultivar which was used for both apical development analysis (for 14 of the 29 cultivars) and for grain yield analysis (for all 29 cultivars). In 1977, 15 of the total 20 subplots corresponded to the 15 cultivars examined and these subplots were used for final grain yield analysis. The five remaining subplots corresponded to five of the 15 cultivars (Clipper, Spartan, Domen, Golden Promise and Ymer) for which apical development would be examined. As in 1976, each subplot consisted of one cultivar.

Each subplot consisted of six one-metre rows at 0.5m spacing. Twenty seeds were sown per row thus giving a final sowing density of 220 seeds per m^2. The sowing was carried out mechanically (Scottish plot seeder, designed at S.P.B.S.) and each sowing was completed within the one day.

The soil type was slightly different in the two field trials. In 1976, the soil type was of an alluvium soil series, silty loam and in 1977 was of a Winton-Macmerry soil type, medium heavy loam. Fertilizer treatment consisted of 29.4 kg N $hectare^{-1}$ in both field trials and was applied at the time of the first sowing on all plots.

Guard rows of the cultivar Maris Mink were sown around the perimeter of the replicate blocks in both trials. All plots were covered with netting to prevent bird damage and these were removed when the seedlings of the final sowing were established.

Weeding of the plots was carried out manually because of

the possible danger of spraying herbicides which may affect apical development. An infection of mildew (Erysiphe graminis f.sp. hordei) was noticed in the 1976 field trial and was effectively brought under control by an immediate single application of the commercial fungicide 'Calixin' (75% w/v tridemorph) at a rate of 4.0 $cm^3 l^{-1}$. Several small pustules of mildew were noticed in the 1977 field trial but the infection did not develop and no treatment was required for control.

(ii) Samples for apical dissection

The development of the main shoot apex was examined for 14 of the 29 cultivars in 1976 and for 5 of the 15 cultivars in 1977. The cultivars were selected to show a range of contrasted response in spikelet number per main ear to daylength in the glasshouse. The selected cultivars are denoted by an asterisk in Table 4.

In the 1976 field trial, sampling commenced three weeks after sowing for each of the three sowing dates and samples were taken thereafter at 14 day intervals. In the 1977 field trial, sampling commenced at the time of emergence of the first leaf from the coleoptile. This stage occurred 28 days after sowing for the early sowing date (15 March) but was reached after only 14 days for the late sowing (20 May). Samples were taken thereafter at 7 day intervals. In both years, sampling was continued until maximum spikelet primordium number had been reached for all cultivars.

The sampling technique was similar in both years. Each sample consisted of two plants of each cultivar from each of the three replicate blocks thus giving a total of six plants per cultivar for dissection at each sampling time. In 1976,

the two plants were randomly selected from rows 2 and 5 from each plot. In 1977, the two plants were randomly selected from rows 2, 3, 4 and 5 from the plots set aside specifically for apical dissection studies. Plants at the extreme ends of the rows were excluded from the samples.

Apical dissections in both years were performed as described on page 29 with the exception that dry weight of the main shoot apex was not measured.

(iii) Yield component analysis

The grain was defined as being mature and ready for harvest when the kernel could not be scratched by the thumbnail. The plots were harvested by individually removing the plants by hand from the central two rows of each plot excluding plants from the extreme ends of the row.

In 1976, the early sowing (S.1) was harvested between 1-10 September, second sowing (S.2) between 16-21 September and the third sowing (S.3) between 28 September - 15 October. The lateness of the S.3 harvest was due to the very heavy rainfall in October which resulted in severe lodging and, in extreme instances, germination in the ear.

The 1977 harvest was completed earlier than in 1976; the first sowing (S.1) was harvested between 29 August - 9 September and the late sowing (S.2) between 14-23 September. Samples were then stored in loose sheaths in a warm dry atmosphere until they could be analysed.

The data collected for each sample included the total and fertile tiller number per plant. Spikelet number and grain number per ear were measured separately for the main shoot and tillers. In the case of the main shoot all plants per plot were analysed but a subsample of 50 ears were

measured in the case of the tiller ears. The ears were then threshed on a laboratory threshing machine (F. Walter-H. Wintersteiger, K.G. LD 180 SH 4) and the 1000 grain weight measured separately for the main shoot and tillers.

RESULTS

Comparisons of response to daylength in the glasshouse

This sub-section is primarily concerned with the effect of daylength on spikelet number per main ear with a view to selecting cultivars which exhibited a range in the magnitude of their response in spikelet number to daylength for further study.

(i) Spikelet number per main ear

Spikelet number per main ear for each of the two daylength treatments is presented in Table 5 for 98 of the 100 cultivars examined. The other two cultivars have been omitted because of insufficient data due to high plant death. In the short day treatment (S.D.) there was a range in spikelet number from 14.0 (La Prevision 19) to 34.4 (Yugoslavian J895). The range was similar in the long day treatment (L.D.) although the final spikelet number was slightly reduced giving a range from 10.6 (Clipper) to 31.8 (Ymer). Cultivars differed in the magnitude of their response to long days. Eighteen of the 98 cultivars showed a significant decrease ($p \leq 0.05$) in spikelet number in L.D. compared with S.D., and four cultivars showed a significant increase in spikelet number in L.D. (Table 5). The remaining 76 cultivars were not significantly affected by daylength.

Cultivars exhibited a wide range in the percentage reduction of spikelet number per main ear in long days with a greated response being found in the percentage reduction in L.D. (e.g. Early 12A Bonus 46.7% and Clipper 46.5%) than the increase in L.D. (Cossack 28.8% reduction in L.D.)

The spikelet number attained in S.D. does not appear to be indicative of the cultivar's response to L.D. treatment

TABLE 5. Influence of daylength on spikelet number per main ear of 98 barley cultivars in the glasshouse. Each number is based on mean of 6 to 8 plants. A negative value for % reduction in L.D. denotes an increase in spikelet no. in L.D.

Cultivar	Spikelet no/main ear S.D.	sign. L.S.D.	L.D.	% reduction in L.D.	Selection for further study ☆
Early 12A Bonus	30.8	*	16.4	46.7	S
Clipper	19.9	*	10.6	46.5	X S SS
Spartan	20.1	*	14.0	30.5	X S SS
Turkish 1106	17.6	*	12.6	28.1	S
Jet	22.5	*	17.6	21.6	
La Prevision 19	14.0		11.3	19.6	
CI 5791	22.9	*	18.5	19.1	S SS
Julia	31.5	*	25.5	19.1	
Ingrid	25.5		22.1	17.1	S SS
Hiprody	20.7	*	17.3	16.7	
Banba	30.5	*	25.5	16.4	S
Yugoslavian J895	34.4	*	28.9	16.1	
Chevallier	26.1	*	22.0	15.8	S SS
Rene Guillemart	20.6		12.5	15.2	
Autotele	24.2	*	20.6	14.9	
Turkish 1823	26.1	*	22.5	13.9	
Russian (Mosdoksky)	20.5		17.8	13.4	
Mosane	28.0	*	24.3	13.4	
Maris Badger	28.4	*	24.9	12.3	
Long-eared Nottingham	31.1	*	27.4	12.1	
Russian (Kaluga)	29.8	*	26.3	12.0	
Archer	32.2	*	28.4	11.8	
Volla	26.5		23.8	10.4	
W 5414	26.6		24.0	9.9	
Midas	29.4		26.5	9.9	S
Freyman	24.7		22.4	9.4	
Kenia	27.8		25.3	9.0	
Lara	25.0		22.8	9.0	
Spratt Archer	30.6		28.1	8.2	
Minn 90-5	31.0		28.5	8.1	
Urais 062	29.5		27.1	8.0	

contd.

TABLE 5 (contd.)

Cultivar	Spikelet no./main ear S.D.	signif. L.S.D.	L.D.	% reduction in L.D.	Selection for further study
Yugoslavian 1	30.1		27.7	8.0	
Ethiopian (ST1746)	22.3		20.6	7.9	
Yugoslavian (Maksimis)	32.3		29.9	7.5	
Morgenrot	21.9		20.3	7.5	
Danpro	30.4		28.4	6.6	
Hemma	24.8		23.1	6.6	
Hannchen	27.0		25.3	6.5	
Bohmerwald	30.3		28.4	6.2	S SS
Union	24.5		23.0	6.1	
Heils Franken	23.1		26.5	5.8	S
Lami	21.5		20.3	5.6	S SS
Mimi	27.3		25.9	5.2	S
Arla	25.1		23.9	5.1	
Drusp	23.5		21.1	4.7	
Prior	16.5		15.8	4.6	
Sultan	25.9		24.8	4.4	
Gull Selection	28.0		26.9	4.0	
Ackermanns MGZ	25.3		24.3	4.0	
Hen Gymro A	29.6		28.5	3.6	
Charlottetown 80	27.3		26.5	2.9	S
German (MR 2)	29.8		29.0	2.5	
Domen	26.1		25.5	2.4	X S SS
Scotch Common	23.9		23.4	2.1	S
Tyra	24.6		24.1	2.0	S
Klages	26.0		25.6	1.4	
Zoe	21.7		21.5	1.0	
Moyjar	26.6		26.4	0.9	
Smyrnakorn	29.0		28.8	0.9	
Proctor	30.4		30.1	0.8	S
Ark Royal	27.4		27.3	0.7	S
Akka	27.0		26.9	0.4	
Golden Archer	30.1		30.0	0.4	
Wisa	24.6		24.5	0.3	
Dr Sauli (0192)	26.6		26.6	0.0	
Maythorpe	29.1		29.5	-1.2	
Afghan R668	22.3		22.6	-1.5	S SS
Zephyr	26.9		27.4	-1.9	S
Klintso	27.1		27.7	-2.1	
Betina	24.0		24.6	-2.5	

contd.

TABLE 5 (contd.)

Cultivar	Spikelet no./main ear S.D.	signif. L.S.D.	L.D.	% reduction in L.D.	Selection for further study
Malta	21.3		21.9	-2.8	
Naked 2-row	23.7		24.4	-2.8	
Maris Mink	20.6		21.3	-3.0	S SS
Ariel	24.0		24.9	-3.7	S
Golden Promise	27.0		28.0	-3.7	X S SS
Yugoslavian J mixture	30.4		31.6	-4.1	
Gold (Morayshire)	28.7		30.0	-4.6	
Nepal 1	26.1		27.4	-4.7	
Abacus	23.6		24.7	-5.0	S
Minn 84.7	25.0		26.3	-5.2	
Maris Baldric	25.4		26.8	-5.2	
Riff	27.3		28.8	-5.5	
Gunilla	24.3		25.6	-5.5	
Ruby	24.8		26.3	-6.1	
Alpha	25.0		26.7	-6.7	
Ethiopian (ST473)	25.6		27.4	-7.1	
Wieselburger	24.0		26.3	-9.5	
Georgie	21.7		23.8	-9.6	
Camion	28.0		30.7	-9.7	
Spratt	27.6		30.4	-10.2	S SS
Zarina	18.3		20.1	-10.3	
Hillmarsh	27.1		30.0	-10.5	S SS
Alfor	22.9		25.5	-11.5	
Short-awned mutant	25.4		28.8	-13.1	
Rogue A	27.1	*	30.9	-13.8	
Uzu	24.6	*	28.1	-14.4	S SS
Ymer	24.8	*	31.8	-27.9	X S SS
Cossack	21.6	*	27.9	-28.8	

Spikelet no/main ear mean of between 6 and 8 plants

* significant at $p \leq 0.05$

☆ X cultivars examined in growth room daylength study

S cultivars examined in 1976 sowing date field trial

SS cultivars examined in 1977 sowing date field trial

since they were not correlated ($r = 0.113$, N.S.). However, cultivars which have a low spikelet number per main ear in L.D. show a marked response to L.D. in the percentage spikelet reduction ($r = -0.560$, $p \leq 0.001$) and this relationship is depicted in Fig. 3 for the 29 cultivars selected to be examined in the 1976 sowing date field trial. Cultivars which have a high spikelet number in L.D. are cultivars which show little reduction in long days compared with short days.

(ii) Grain number per main ear

The response of grain number per main ear to daylength is available for only 46 of the initial 100 cultivars because many ears failed to emerge from the flag leaf sheath. Although it proved possible to excise the immature ear to determine the spikelet number, the grain set was considerably reduced and, in some cases, no grain was set. Because of the limited data available the results for grain number will not be described.

(iii) Spikelet and grain number per tiller ear

Analysis of the influence of daylength on spikelet and grain number per tiller ear is complicated by two factors: transfer of short day plants to long day growing conditions after maximum spikelet primordium number per main ear had been attained and secondly, poor grain set. Tiller development is slower than that of the main shoot and thus the time of transfer may have occured during the period of spikelet primordium production on the litters. Final spikelet number per tiller ear would therefore be a combination of S.D. during the early period of spikelet primordium production and L.D. during later development. Grain set was also poor in tiller ears and because of these factors, data for final spikelet and

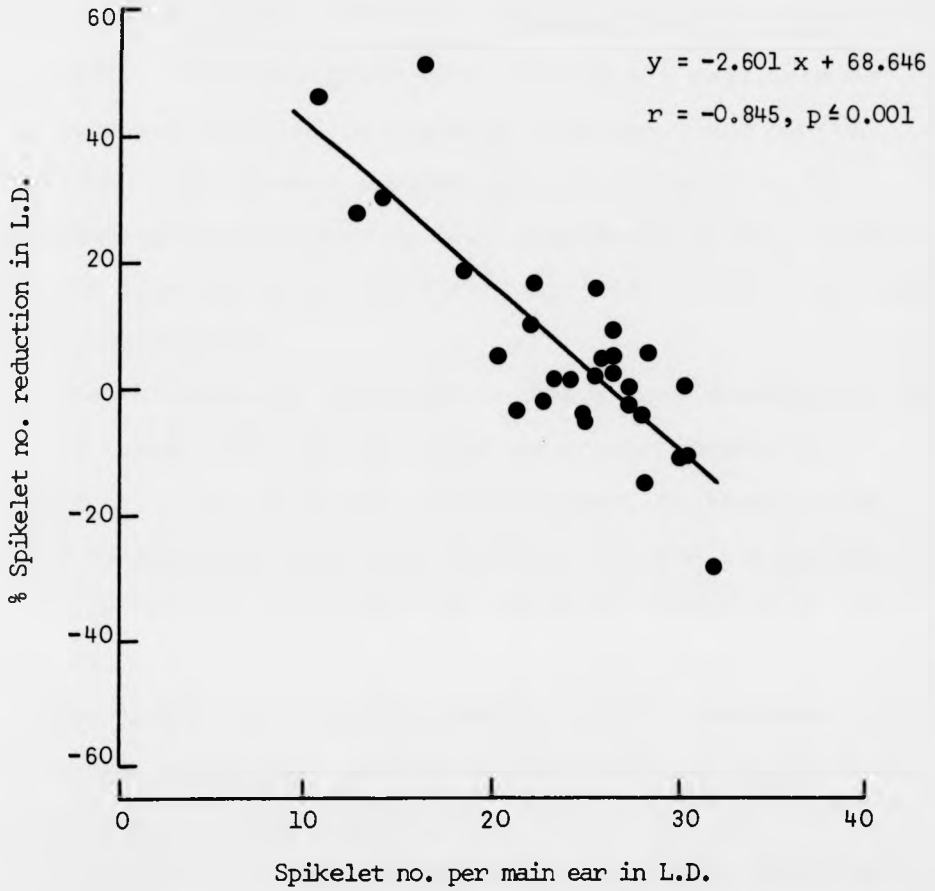


Fig. 3. Relationship between spikelet no./mean ear in L.D. and the percentage reduction of spikelet no./main ear in L.D. for 29 barley cultivars in the glasshouse.

Each point is a mean of between 6 and 8 plants.

grain number per tiller ear have not been included.

The cultivars examined in this study therefore show a wide range of response in spikelet number per main ear to daylength. The main group of cultivars (76 cvs) were not significantly affected by daylength treatment and of the remaining 22 cultivars, eighteen showed a significantly decreased spikelet number in L.D. compared to S.D. treatment and only four showed a significant increase in spikelet number in L.D. conditions.

The influence of daylength on the apical development of five of these cultivars was examined in the growth room experiment. The five cultivars (Clipper, Spartan, Domen, Golden Promise and Ymer) were selected to show contrasted responses in spikelet number of daylength (denoted 'X' in Table 5).

The influence of sowing date on apical development and final grain yield was examined in the field on 29 cultivars in 1976 and 15 cultivars in 1977, denoted 'S' and 'SS' in Table 5 for 1976 and 1977 respectively). These cultivars were again selected to show a range in the magnitude of the response of spikelet number to daylength.

Comparisons of apical response of selected genotypes to daylength in growth rooms.

The five cultivars examined in this study (Clipper, Spartan, Domen, Golden Promise and Ymer) were selected from the 100 cultivars examined in the previous glasshouse daylength study to show contrasted response in spikelet number per main ear to daylength. The response of the apical development of these cultivars to daylength is described in two parts. Firstly, the effect of daylength on main shoot apical development with

TABLE 6. Influence of daylength on final leaf number per main shoot of five barley cultivars in growth rooms. Each value is a mean of at least 10 plants.

Cultivar	Final leaf number per main shoot		
	S.D.	significant L.S.D.	L.D.
Clipper	11.3	***	7.0
Spartan	13.4	***	8.0
Domen	10.5	*	8.9
Golden Promise	13.1	**	11.1
Ymer	11.7	*	10.3

* significant at $p \leq 0.05$)
** $p \leq 0.01$) L.S.D. calculated following an analysis of variance for each cultivar separately.
*** $p \leq 0.001$)

time will be described in terms of the following parameters: final leaf number per main shoot, apical stage of development, spikelet primordium number, length and dry weight of the shoot apex and finally, apical meristem dome length. Particular emphasis will be placed on the response of spikelet primordium production to daylength and the aspects of apical development determining the spikelet primordium response. Secondly, comparisons of the cultivars' apical response to daylength in the growth room and the response of spikelet number per main ear to daylength in the glasshouse will be made. From this comparison it may be possible to evaluate the importance of the influence of daylength on early plant growth and development in determining final spikelet number.

1. Apical development in the growth room.

(i) Final leaf number per main shoot

The response of leaf number per main shoot to daylength for the five cultivars examined in this study is presented in Table 6. Cultivars exhibited a range in leaf number in both daylength conditions, from 10.5 (Domen) to 13.4 (Spartan) in S.D. and a slightly wider range in L.D. from 7.0 (Clipper) to 11.1 (Golden Promise).

The duration of leaf primordium production can be calculated from the graph of the change of total primordium number with time (Fig. 6) in which cessation of leaf primordium production occurs when total primordium number equals leaf number. Final leaf number was determined earlier in L.D. than in S.D. and the reduced period of leaf primordium production was reflected in the reduced leaf number for all cultivars in the L.D. treatment. This reduction was significant for all cultivars and, in particular, for Clipper and Spartan ($p \leq 0.001$) (Table 6).

(ii) Apical developmental stage

The effect of daylength on main shoot apical developmental stage with time for the five cultivars examined is presented in Fig. 4. The ten stages distinguished are described in Table 7. Apical development was accelerated in L.D. compared with S.D. treatment for all cultivars but cultivars differed in the magnitude of their response. This can be clearly seen if several stages of apical development are considered separately.

Although the double ridge stage (DR) is often assumed to correspond to the change from vegetative to floral development with the onset of spikelet primordium set down, this is clearly not the case in the cultivars examined (Fig. 4). In both daylength treatments for all cultivars, DR occurs after the onset of spikelet primordium production. The time taken to reach DR was reduced in L.D. treatment for all cultivars to 14 days after sowing (d.a.s.) for four cultivars (Spartan, Domen, Golden Promise and Ymer) and 11 d.a.s. for Clipper. The DR stage was delayed until 21 d.a.s. under S.D. conditions for all cultivars except Domen (14 d.a.s.).

The time taken to reach each subsequent stage was similarly reduced in L.D. treatment. The awn initial stage (stage A) was reached earlier for all cultivars in L.D. than S.D. treatment. The time taken was reduced to only three and four weeks for Clipper and Spartan respectively but was reached later in the other cultivars (Domen after five weeks, Golden Promise and Ymer after six weeks). This stage was not reached in S.D. treatment until 10-11 weeks after sowing (w.a.s.) for all cultivars.

TABLE 7. Developmental stages of main shoot apex

Stage	Apical stage of development	Description
ES	Simple ridge (early)	Meristem dome short and rounded <0.1mm
LS	Simple ridge (late)	Meristem dome elongated ≥ 0.1mm
DR	Double ridge	Spikelet primordium initial visible
SQ	Square ridge	Increased development of spikelet primordium initial
TM	Triple mound	Formation of lateral spikelet primordia
G	Glume initial	
L	Lemma initial	
S	Stamen initial	
A	Awn initial	
TD	Tip death	Degeneration of distal spikelet primordia

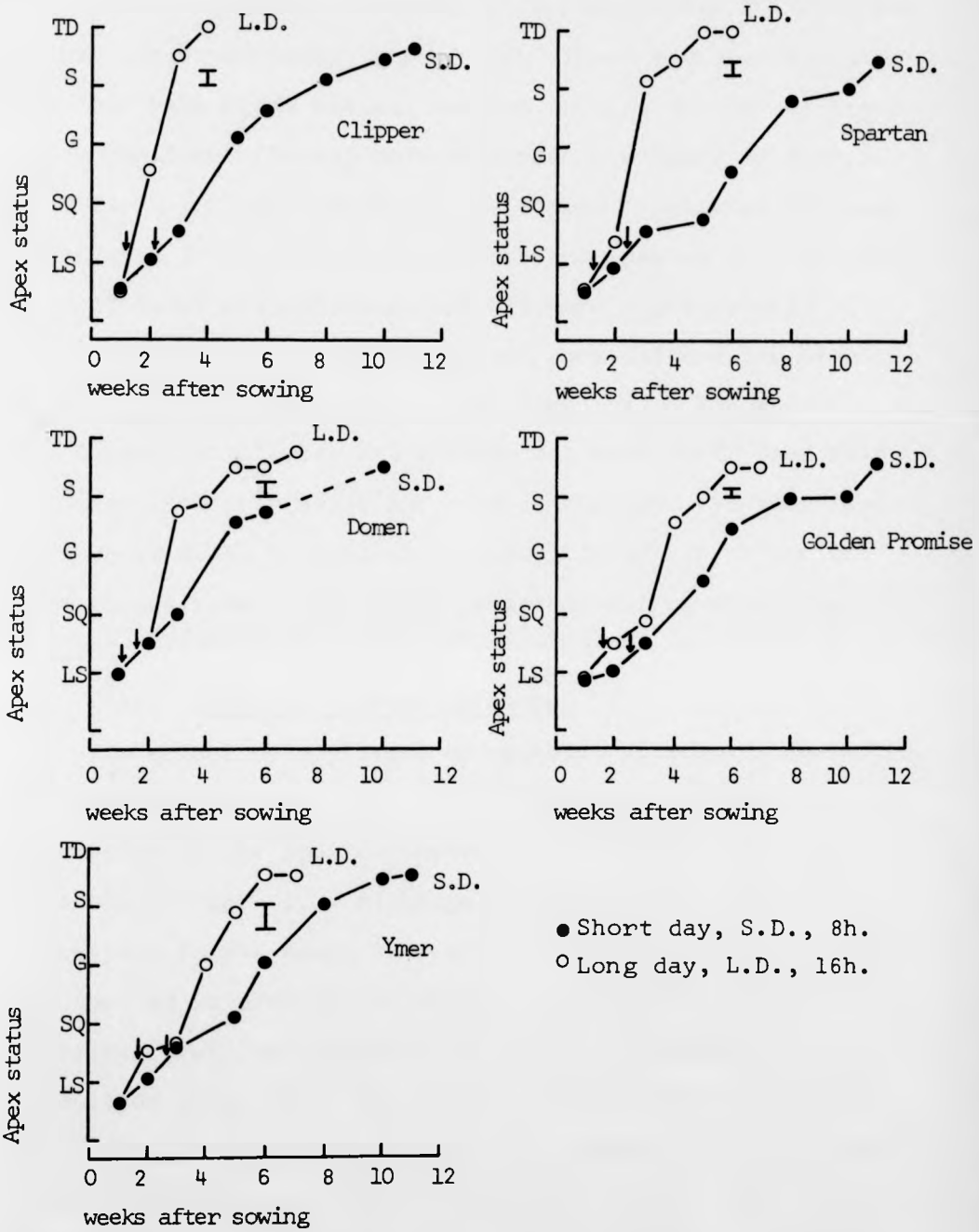


Fig. 4. Effect of daylength (8h S.D. and 16h L.D.) on apical developmental stage of 5 barley cultivars in growth rooms.

Each point is a mean of between 4 and 8 plants.
Vertical bars indicate L.S.D. significant at $p \leq 0.05$, calculated following an analysis of variance for each cultivar separately.
Arrows indicate onset of spikelet primordium production.
Only every second apical developmental stage is presented on y-axis - see Table 7.

Degeneration of distal primordia (stage TD) occurred within the experimental period for Clipper and Spartan in L.D. but this stage was not reached in L.D. for any of the other cultivars (Domen, Golden Promise and Ymer) or in S.D. conditions for any cultivar. This again indicates the very rapid apical development of Clipper and Spartan in long days.

Although all cultivars exhibit more rapid apical development in L.D. than S.D. there were differences between cultivars in the magnitude of the response. The apical development of Clipper and Spartan was more rapid than that of Domen, Golden Promise and Ymer in the L.D. treatment and further evidence to support this suggestion can be derived from an analysis of the other parameters of apex development studied.

(iii) Spikelet primordium number

The effect of daylength on spikelet primordium number is presented in Fig. 5. The onset of spikelet primordium production on the apex occurred earlier in L.D. than S.D. conditions (Fig. 5). Although the sample times do not correspond to the exact time of onset of spikelet primordium set down it is possible to estimate the time of onset retrospectively by reference to the total primordium production (Fig. 6). The first spikelet primordium occurs when the total primordium equals leaf number and collar plus one. The onset of spikelet primordium set down is, therefore, associated with the leaf number per main shoot. Cultivars which have a low leaf number also have an early onset of spikelet primordium production..

Maximum spikelet primordium number was reached during the awn initial stage of development before tip degeneration

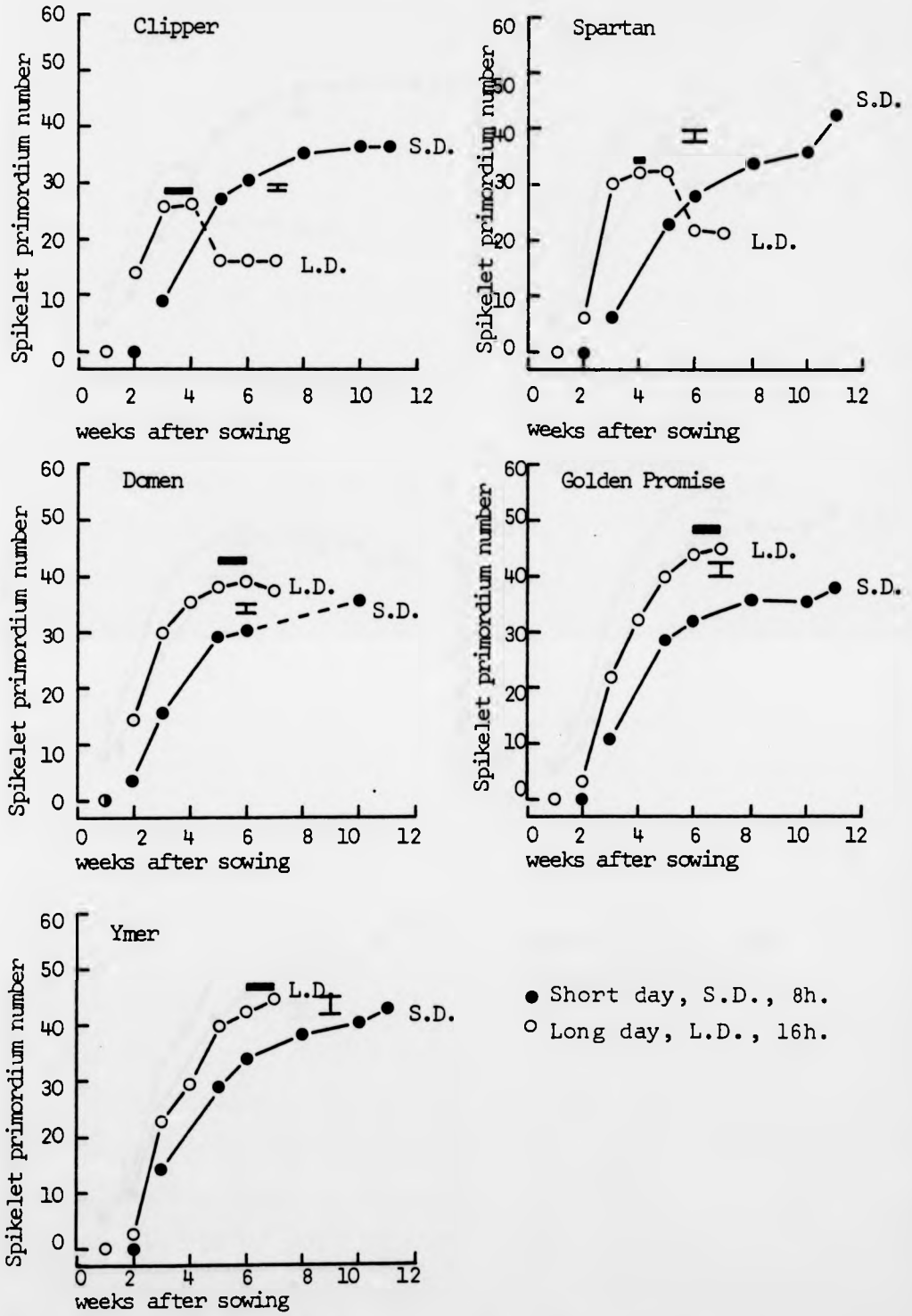


Fig. 5. Effect of daylength (8h S.D. and 16h L.D.) on spikelet primordium production of 5 barley cultivars in growth rooms.

Each point is a mean of between 4 and 8 plants.
Vertical bars indicate L.S.D. significant at $p \leq 0.05$, calculated following an analysis of variance for each cultivar separately.
Horizontal bar indicates period of awn initial stage of apical development for L.D. treatment.

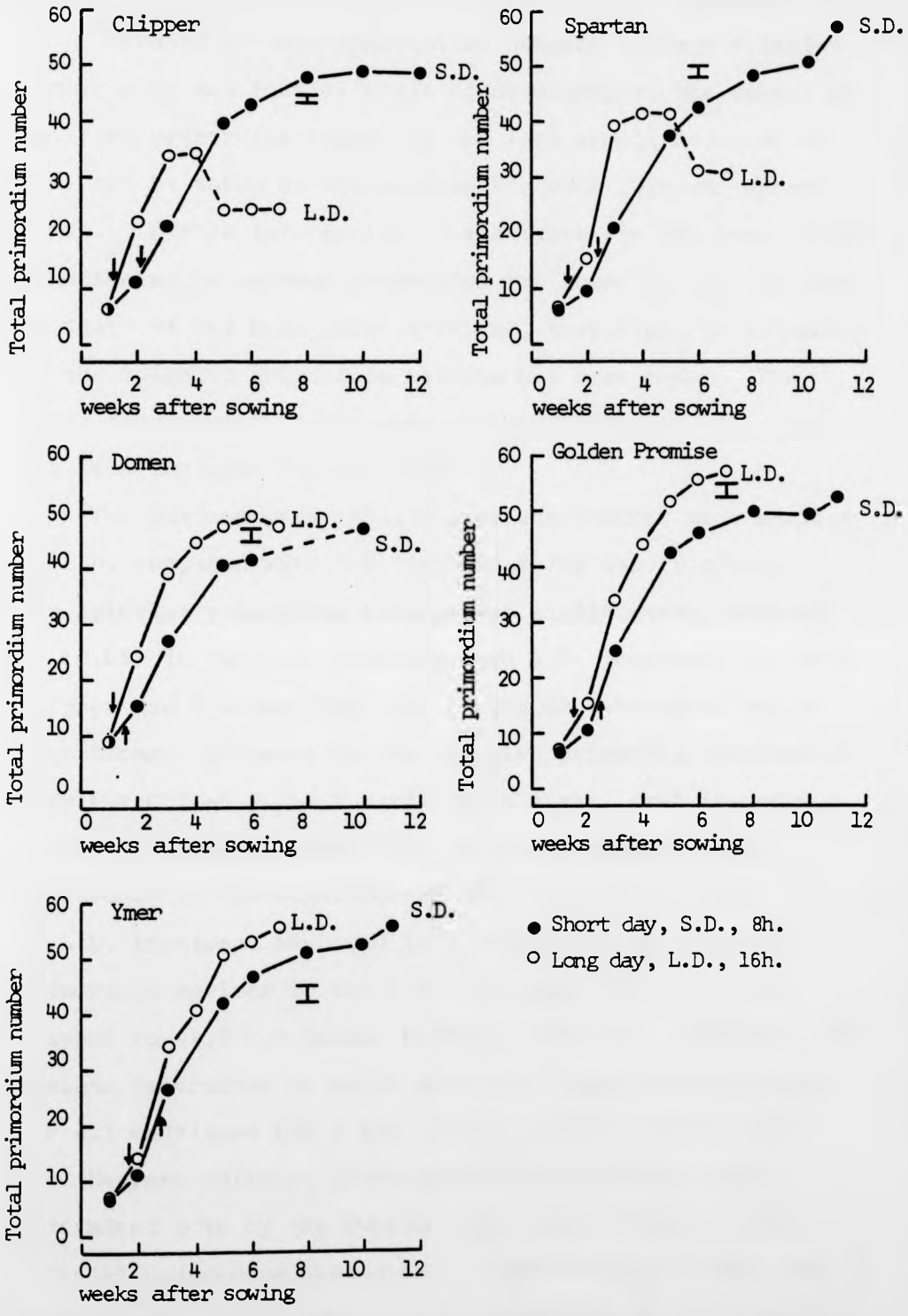


Fig. 6. Effect of daylength (8h S.D. and 16h L.D.) on total primordium production of 5 barley cultivars in growth rooms.

Each point is a mean of between 4 and 8 plants.
Vertical lines indicate L.S.D. significant at $p \leq 0.05$, calculated following an analysis of variance for each cultivar separately.
Arrows indicate onset of spikelet primordium production.

(Kirby 1977) and this can be seen in the L.D. treatment (Fig. 5). Because of this association between maximum spikelet number with awn initial stage of development, the values of spikelet primordium number at the last sample occasion in S.D. can be taken as the maximum for each cultivar except Domen. Little information is available for the later stages of spikelet primordium production for Domen in S.D. because of death of the main shoot apex and, therefore, no estimate of the spikelet primordium maximum has been made. The early development of the apex was unaffected and this data has been included for comparison.

The maximum primordium number was reached much earlier in L.D. compared with S.D. treatment for all cultivars. The spikelet primordium maximum was significantly reduced ($p \leq 0.05$) in the L.D. compared with S.D. treatment for both Clipper and Spartan (Fig. 5). Long day treatment had no significant influence on the spikelet primordium maximum of Ymer but Golden Primise exhibited a significant increase ($p \leq 0.05$) in the maximum attained in long days. The difference in the magnitude of the responses of these cultivars to L.D. treatment resulted in a wide range of spikelet primordium maximum in the L.D. treatment (from 26.5 for Clipper to 44.9 for Golden Promise; Table 8). However, the maximum determined in short days was comparatively similar for all cultivars (36.9 for Clipper to 42.6 for Spartan).

Maximum spikelet primordium number appears to be determined both by the duration and the initial rate of spikelet primordium production. The duration of set down is much longer in S.D. than in L.D. conditions for all cultivars (Table 8) and the period of set down in S.D. ranged from

55d (Clipper) to 62d (Ymer). The period of production was considerably reduced in L.D. treatment and the five cultivars exhibited a range in the magnitude of their response. For Clipper and Spartan, the duration of this period was very short (20 and 19 days respectively) but this period was much longer for Domen, Golden Promise and Ymer (35, 38 and 37 days respectively). The range in the response of the cultivars with respect to the duration of the period of set down is, therefore, greater in L.D. than in S.D. conditions.

The pattern of spikelet primordium production found in both daylength treatments is characteristic of plants grown in supplemental incandescent light (Paleg and Aspinall 1964) (Fig. 5). The initial rapid linear rate of spikelet primordium set down is followed by a slower, curvilinear pattern of set down until spikelet primordium maximum has been determined. This latter phase was very pronounced in the S.D. treatment for all cultivars but was found only in the L.D. treatment for Domen, Golden Promise and Ymer. Cessation of spikelet primordium production was more abruptly determined in Clipper and Spartan in L.D. treatment.

The rate of spikelet primordium production during this initial rapid set down period (3-4 week period after the onset of spikelet primordium production) is presented in Table 8. All five cultivars showed an increased rate of spikelet primordium set down in L.D. compared to S.D. treatment but this difference was significant ($p \leq 0.05$) only for Clipper and Spartan.

Long day treatment, therefore, has a marked influence on spikelet primordium production and two groups of cultivars can be distinguished on the basis of the magnitude of their response.

TABLE 8. Influence of daylength on some parameters of spikelet primordium production of five barley cultivars in growth rooms. Maximum spikelet primordium number based on mean of between 6 and 8 plants.

Cultivar	Spikelet primordium maximum			Duration of Production (days)		Initial rate of production (spikelet primordia per day)		
	S.D.		L.D.	S.D.	L.D.	S.D.		L.D.
Clipper	36.9x	* [a]	26.5	55	17	1.37	*[b]	1.98
Spartan	42.6x	*	32.5	60	12	1.13	*	2.59
Domen	-		39.0	-	14	1.21	N.S.	1.74
Golden Promise	37.9x	*	44.9	60	17	1.45	N.S.	2.00
Ymer	42.5x	N.S.	44.3	62	23	1.21	N.S.	1.74

x = apex at awn stage of development - see text

a = N.S. not significant) L.S.D. values calculated following an analysis of variance for each cultivar separately.
* significant at $p \leq 0.05$)

b = N.S. not significant) Significant differences calculated following comparison of regression coefficients for each cultivar separately.
* significant at $p \leq 0.05$)

In both Clipper and Spartan the onset of spikelet primordium set down occurred much earlier and the initial rate of set down was more rapid in L.D. than in S.D. conditions. However, the duration of production was greatly reduced in L.D. resulting in a low spikelet primordium maximum which was attained four weeks after sowing. If the percentage of the spikelet primordium maximum set down after three weeks is considered (Table 9), both Clipper and Spartan set down over 90% of the maximum within the first three weeks of plant growth and development in L.D. but less than 25% for the corresponding period under S.D. conditions. The percentage set down at three weeks is determined by both the earliness of the onset of spikelet primordium production, which is itself dependent on the duration of leaf primordium formation, and the initial rate of production.

Although cultivars: Domen, Golden Promise and Ymer, exhibited a slightly earlier onset of spikelet primordium production and a slightly faster initial rate of set down in L.D. compared with S.D. treatment, the response to long days was less pronounced than that found for Clipper and Spartan. The duration of set down is larger than the corresponding period for Clipper and Spartan and the spikelet primordium maximum attained was either similar in the two daylength conditions (Ymer) or greater in long days (Golden Promise). The maximum spikelet primordium number attained in long days was higher for Golden Promise and Ymer than the maxima for Clipper and Spartan although there was little difference in the S.D. maxima between any of the cultivars.

Spikelet primordium maximum is associated with the percentage spikelet primordia set down at three weeks and with

TABLE 9. Influence of daylength on spikelet primordium maximum and the percentage of the maximum set down at three weeks for five barley cultivars in growth rooms. Maximum spikelet primordium number based on mean of between 6 and 8 plants.

Cultivar	Spikelet primordium maximum		Percentage of spikelet primordium max. set down at 3 weeks		
	S.D.	L.D.	S.D.	L.D.	L.D.-S.D.
Clipper	36.9x	26.5	24.4	97.7	73.3
Spartan	42.6x	32.5	15.3	93.6	78.4
Domen	-	39.0	-	76.4	-
Golden Promise	37.9x	44.9	28.0	48.6	20.6
Ymer	42.5x	44.3	33.3	51.5	18.2

x = apex at awn initial stage of development - see text.

the overall duration of set down. The percentage of the maximum set down is higher in long days for both Golden Promise and Ymer than in S.D. treatment (Table 9) but the difference in the percentage set down between the two daylengths (20.6% and 18.2% respectively) was much smaller than the percentage set down for Clipper and Spartan (73.3% and 78.4% respectively). This seems to suggest that cultivars which produce a high proportion of the spikelet primordium maximum within the first three weeks of plant growth also produce a low maximum e.g. Clipper and Spartan in long days. This suggestion is confirmed by the significant and negative relationship ($r = -0.961$, $p \leq 0.01$) between the percentage set down at three weeks and the spikelet primordium maximum in long days. This relationship is depicted in Fig. 7. Spikelet primordium set down is much slower in the S.D. treatment and appears to have no determining influence on the maximum attained ($r = -0.127$, N.S.).

(iv) Apex length

The effect of daylength on the change of apex length with time is presented in Fig. 8. There are three distinct phases of apex length increase with time. The initial increase in apex length is very slow with little absolute increase in length. This phase is abruptly followed by a second, very rapid length increase when a maximum ear length is attained after which ear length remains constant.

The duration of the initial length increase was reduced in L.D. treatment for all cultivars although there were differences between cultivars in the magnitude of their response. For Clipper and Spartan, this initial period ceased after only two to three weeks but the abrupt change to the second phase

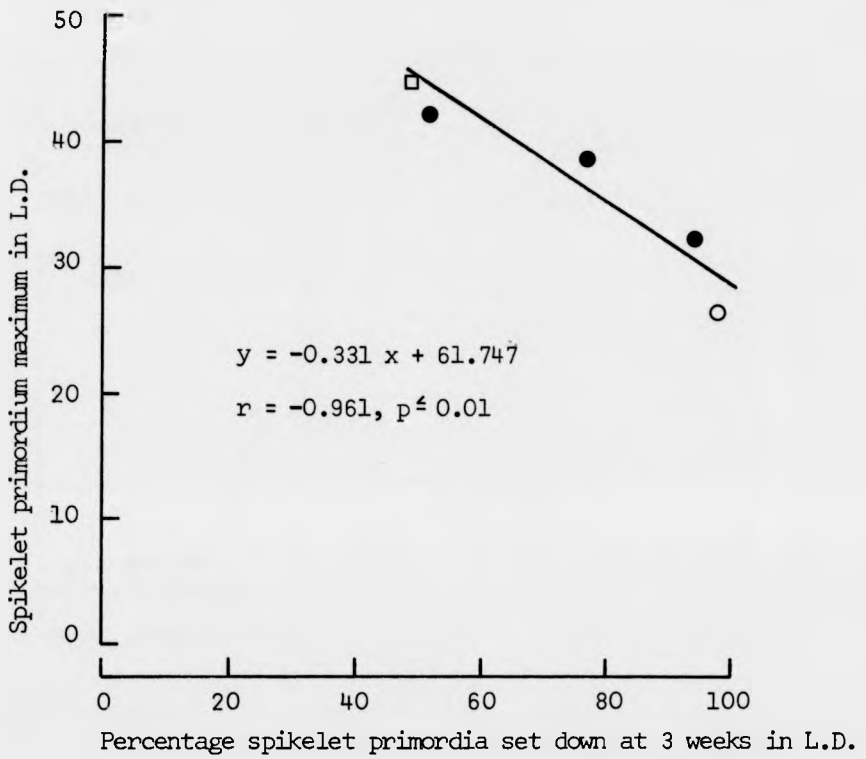


Fig. 7. Relationship between the percentage spikelet primordia set down at 3 weeks and the spikelet primordium maximum in L.D. in the growth room.

o Clipper

□ Golden Promise

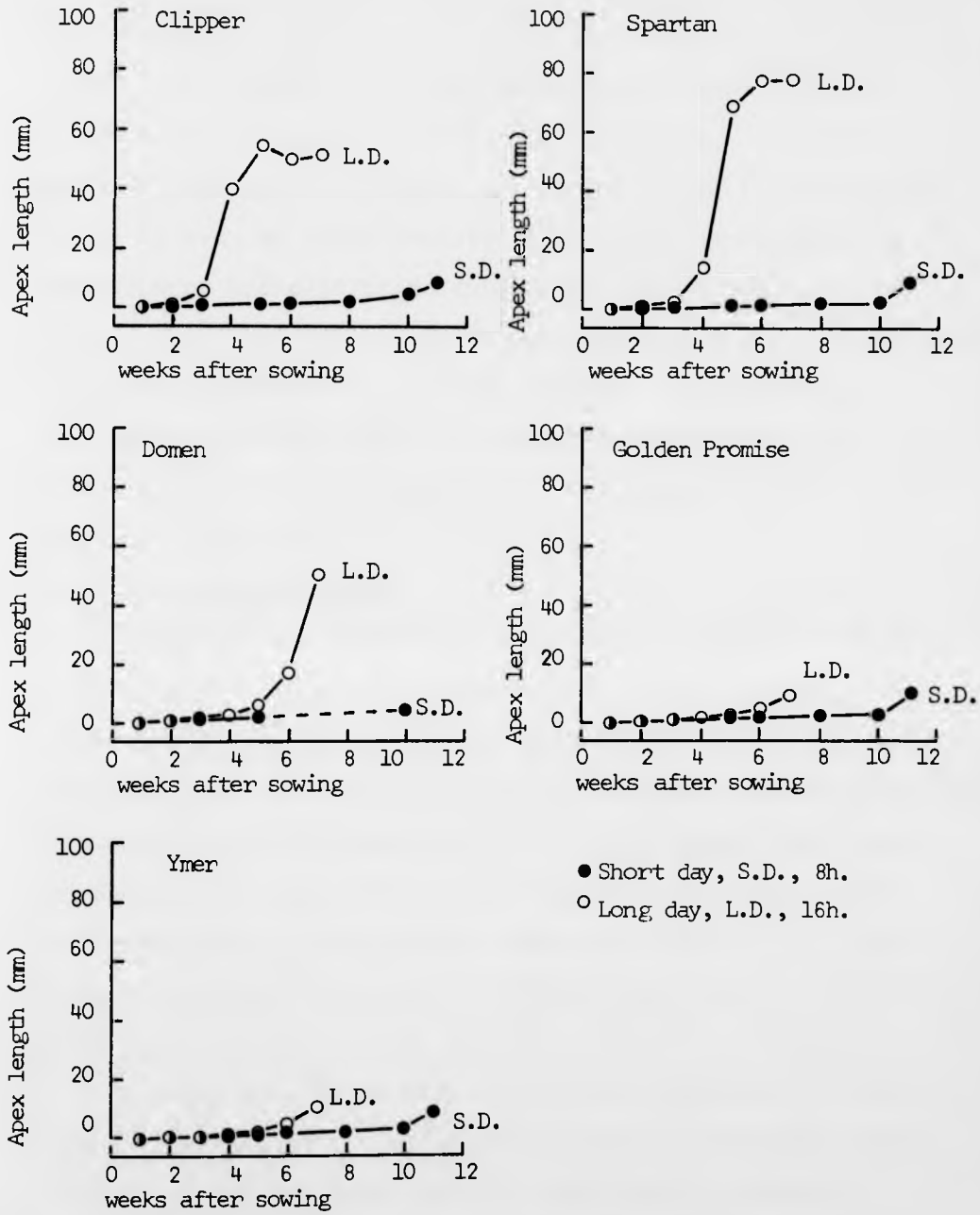


Fig. 8. Effect of daylength (8h S.D. and 16h L.D.) on apex length of 5 barley cultivars in growth rooms.
Each point is a mean of between 4 and 8 plants.

for Domen, Golden Promise and Ymer did not occur until weeks five to six. The duration of this initial period was prolonged in the S.D. treatment and the change to the phase of rapid length increase does not occur until week ten. This abrupt change occurs at the awn initial stage of apical development (stage A) and, as noted earlier, this stage corresponds to the cessation of spikelet primordium production. Thus at the time of this rapid increase in apex length most, if not all, of the spikelet primordia have been formed. It cannot be determined from the available data whether daylength has any influence on either the duration of this second phase or on the final length attained.

(v) Apex dry weight

The response of apex dry weight to daylength treatment for all five cultivars is presented in Fig. 9. Apical dry weight increased more rapidly in L.D. compared with S.D. treatment for all cutlivars and the difference between daylength treatments was more pronounced at an early stage for Clipper and Spartan than for Domen, Golden Promise and Ymer. The difference can be attributed to the early onset of the fast rate of dry matter increase for Clipper and Spartan under long days.

Three apical growth rates can be distinguished and are linked with the pattern of apical length increase described above. The first, slower rate of dry matter increase corresponds to the initial period of slow apex length increase and is associated with the set down of primordia on the apex. The second faster rate of dry matter accumulation coincides with the abrupt change in the pattern of apex length increase (Fig. 8) as a result of rachis internode elongation. The third

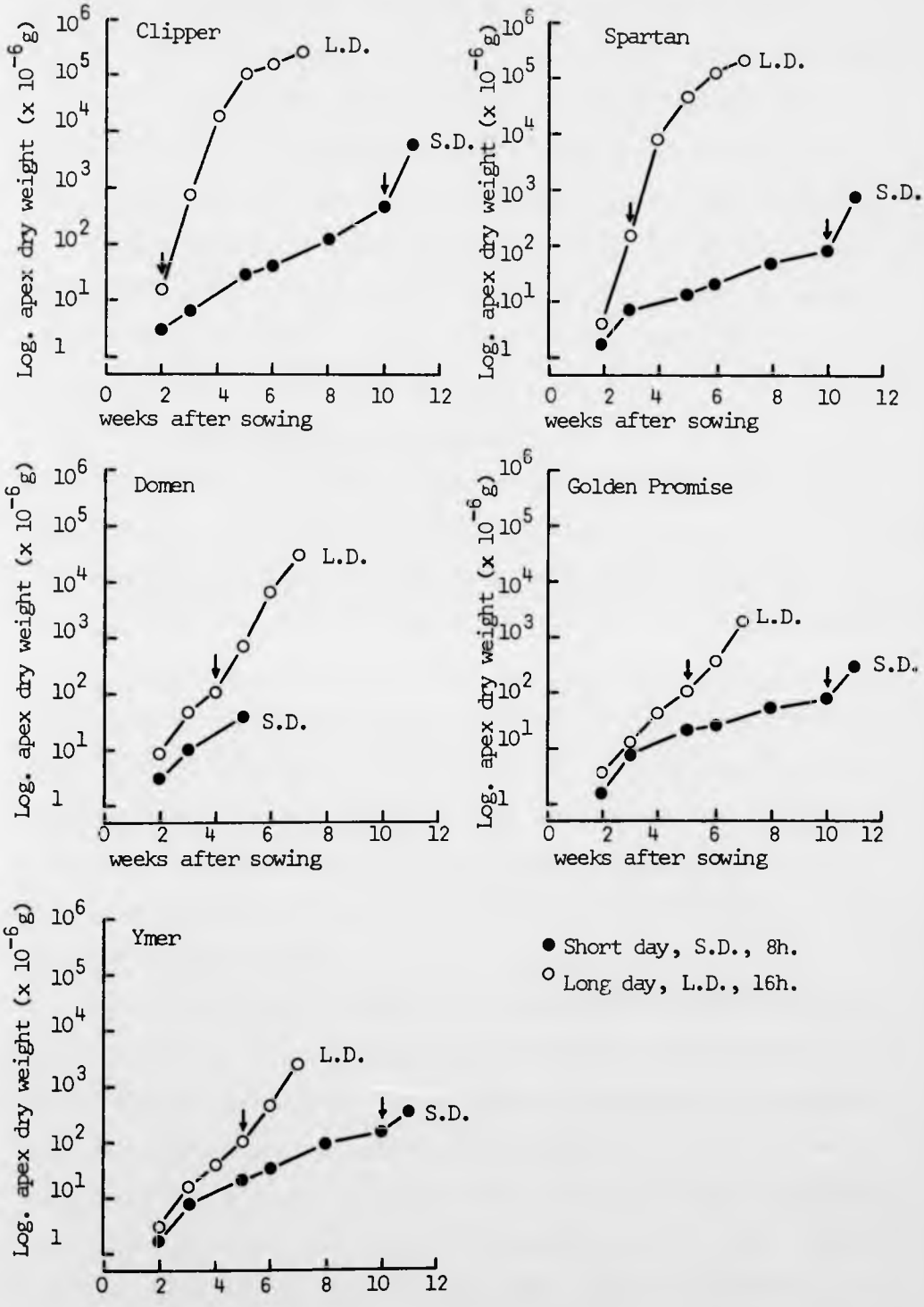


Fig. 9. Effect of daylength (8h S.D. and 16h L.D.) on apical dry weight of 5 barley cultivars in growth rooms.

Each point is a mean of between 4 and 8 plants.
Arrows indicate onset of rapid apical length increase.

period is characterised by a slower relative rate of dry matter accumulation although the absolute dry weight increase is large. This phase corresponds to the period of grain filling after ear emergence and was only found within the experimental period for Clipper and Spartan in long days.

The duration of the initial phase was prolonged in short days for all cultivars and the absolute dry weight increase was relatively small. The pattern of dry matter increase in short days was similar for all cultivars.

(vi) Apex meristem dome length

The change of meristem dome length with time exhibits three distinct phases of development (Fig. 10). The first phase is characterised by the elongation, during the first two to three weeks of apical development, of the initial hemispherical shaped meristem dome until a maximum length is attained. This maximum dome length was reached earlier in L.D. (week two) than in S.D. treatment (week three) for Clipper and Spartan but the time taken to reach maximum length was not affected by daylength treatment in any of the other cultivars. In all cases, maximum dome length occurred at or shortly before the time of double ridges.

The second phase consists of a gradual decrease in dome length until a minimum value is reached and this is followed by an abrupt increase in length after which both the dome and the last-formed distal primordia degenerate. This decrease in dome size is caused by the production of spikelet primordia in acropetal succession from the meristem dome. The duration of this phase was reduced in long days for all cultivars although there were differences in the magnitude of response. This phase was reduced to only seven days in Clipper and

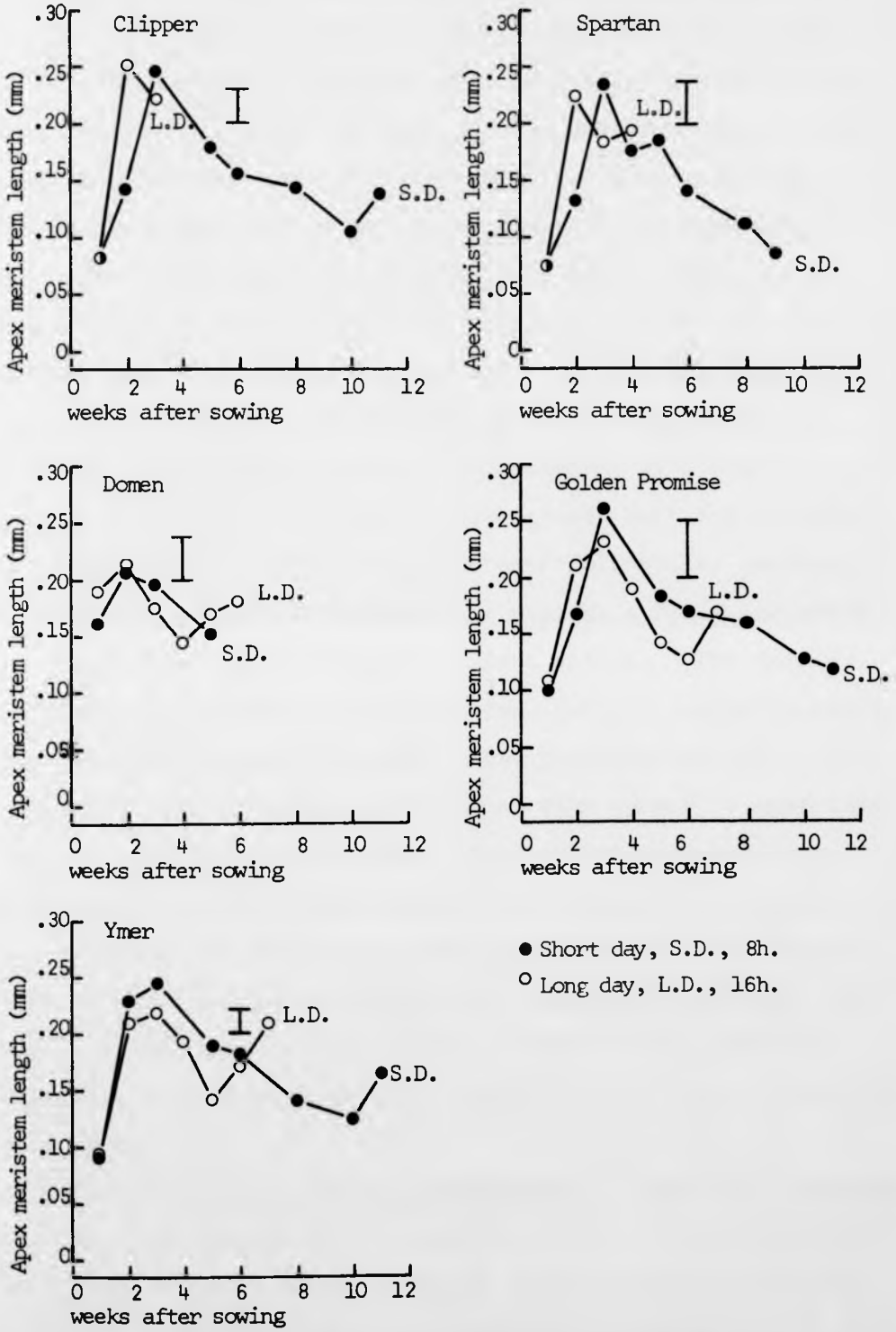


Fig. 10. Effect of daylength (8h S.D. and 16h L.D.) on apex meristem length of 5 barley cultivars in growth rooms.

Each point is a mean of between 4 and 8 plants.
Vertical lines indicate L.S.D. significant at $p \leq 0.05$, calculated following an analysis of variance for each cultivar separately.

Spartan and this was associated with only a small overall decrease in length. Domen, Golden Promise and Ymer on the other hand exhibited a longer and more gradual period of dome length decrease. The duration of this phase was considerably prolonged by short days and did not occur until week ten for Clipper and Ymer and was not reached within the sampling period of this study for the other cultivars. Both Clipper and Spartan showed a significant reduction ($p \leq 0.05$) in the minimum dome length in S.D. compared with L.D. treatment.

The two cultivars which exhibited the largest fall in spikelet primordium maximum in L.D. compared with S.D. treatment, Clipper and Spartan, also showed both a very short combined period of dome length increase followed by decrease in length and, associated with this period, a small reduction in dome length from maximum to minimum values. The duration of these two combined periods was considerably longer in short days and the decrease in length correspondingly greater, thus suggesting that a high spikelet primordium number is associated with long period of dome length increase followed by a long gradual decrease in length until a low minimum value is reached.

Spikelet primordium set down may still occur after this minimum value has been determined in long days (Spartan, Domen and Ymer) but the number is small. Insufficient data is available to determine whether this is also the case in the S.D. treatment.

(vii) Summary of apical developmental responses to daylength

The development of the main shoot apex of the five selected cultivars (Clipper, Spartan, Domen, Golden Promise and Ymer) examined in this study was more rapid in L.D. than in S.D. conditions. This was observed in all the parameters measured:

leaf number per main shoot, main shoot apical development stage, spikelet primordium number, length and dry weight of the apex and apex meristem length.

Cultivars differed in the magnitude of their responses to L.D. treatment and two groups could be distinguished. The first group (Clipper and Spartan) are characterised by exhibiting a much greater response to L.D. treatment than the second group (Domen, Golden Promise and Ymer).

Apical development is extremely rapid in Clipper and Spartan under L.D. conditions with an associated rapid spikelet primordium production during the first three weeks of growth and development resulting in a low maximum. The other parameters of apical development confirm the very rapid development of these two cultivars in L.D. conditions.

The second group (Domen, Golden Promise and Ymer) exhibit a less pronounced response to L.D. treatment in all parameters of apical development. Spikelet primordium production after three weeks is slower for all three cultivars than in group one resulting in either a similar maximum in both daylength treatments (Ymer) or an increased maximum in long days (Golden Promise).

2. Comparisons of the responses of spikelet primordium number (growth rooms) and spikelet number (glasshouse) to daylength.

In the growth room experiment it was not possible to sample beyond the stage of maximum spikelet primordium number because of space limitations. No direct comparison can therefore be made on how the apical response to daylength was manifested in final spikelet number per main ear. However, it is possible to compare the spikelet primordia response observed in the growth room with the spikelet number response found in the

glasshouse in which the same daylength treatments (8h S.D. and 16h L.D.) were used.

The effect of daylength on spikelet primordium maximum in the growth room and spikelet number per main ear in the glasshouse is presented in Table 10. The cultivars examined show a wide range of response in both spikelet primordium maximum and spikelet number to daylength.

It was suggested earlier that two groups of cultivars could be distinguished on the basis of the magnitude of the apical response to daylength. Both the spikelet primordium maximum and the spikelet number are greater in L.D. treatment for Domen, Golden Promise and Ymer (Group two) compared to Clipper and Spartan (Group one). This clearly suggests that cultivars which have a high spikelet primordium maximim will have a correspondingly higher spikelet number compared to cultivars with a lower spikelet primordium maximum. This is confirmed by the significant correlation ($r = 0.970$, $p \leq 0.01$) between these two parameters and this relationship is depicted in Fig. 11.

Apical development was slow in the S.D. treatment for all cultivars and, of the four cultivars for which the S.D. spikelet primordia maximum could be determined, only Golden Promise exhibited a higher maximum in L.D. compared with S.D. conditions. In the glasshouse S.D. treatment, only Ymer showed a significantly increased ($p \leq 0.05$) spikelet number per main ear compared with long days. No relationship between the spikelet primordium maximum and spikelet number in S.D. conditions ($r = -0.047$) was found.

TABLE 10 Influence of daylength on spikelet primordium max. (growth rooms) and spikelet number per main ear (glass-house). Values based on means of between 6 and 8 plants.

Cultivar	Growth room spikelet primordium maximum		Glasshouse spikelet no./ main ear	
	S.D.	L.D.	S.D.	L.D.
Clipper	36.9x	24.5	19.9	10.6
Spartan	42.6x	32.5	20.1	14.0
Domen	-	39.0	26.1	25.5
Golden Promise	37.9x	44.9	27.0	28.0
Ymer	42.5x	44.3	24.8	31.8

x = apex at awn initial stage of development - see text

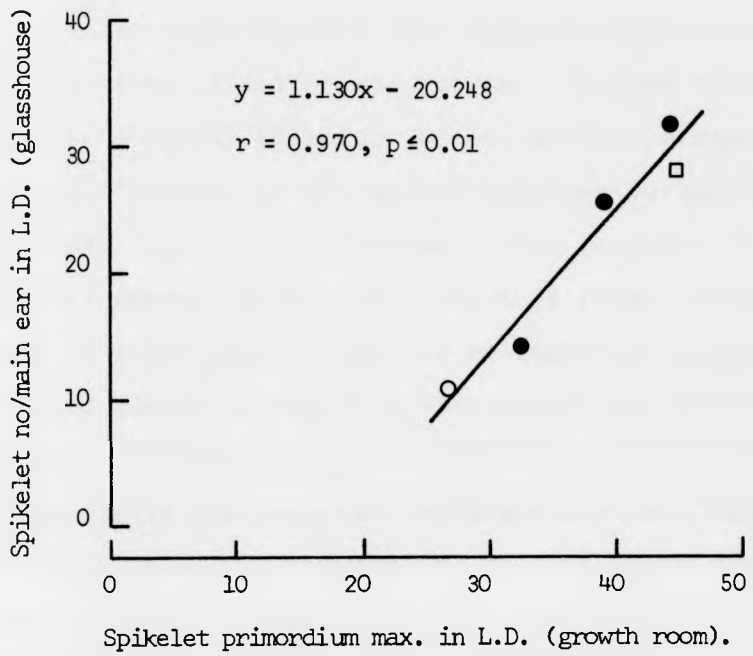


Fig. 11. Relationship between spikelet primordium max. (growth room) and spikelet no/main ear (glasshouse) in L.D. treatment.

○ Clipper
□ Golden Promise

It appears, therefore, that daylength has an important influence on apical development and final spikelet numbers. Long days accelerate development and reduce the maximum number of spikelet primordia set down compared with short days for same cultivars (Clipper and Spartan) whereas other cultivars are less markedly affected (Domen, Golden Promise and Ymer). These differences in the apical response to long days in the growth room were reflected in the response of final spikelet number to long days but this relationship was not found in short days. This is an important consideration in the field where sowing of spring barley may be delayed because of adverse weather conditions. It is suggested from the daylength results that cultivars may show differences in both the apical development and final spikelet and grain number to late sowings which are characterised by long days. This suggestion was examined in two sowing date field trials in 1976 and 1977 on 29 and 15 cultivars respectively (denoted 'S' and 'SS' in Table 5) and these cultivars were selected to show a range of response to daylength in spikelet number per main ear.

Comparisons of apical and final grain yield responses of selected genotypes to sowing date in the field.

The influence of sowing date on apical development and final grain yield in the field is described in five sub-sections. Firstly, an account of some of the environmental conditions in the field during the period of apical development is presented for both years and this is followed by a detailed description of the effect of sowing date on apical growth and development. This is considered in terms of the following parameters: final leaf number per main shoot,

apex developmental stage, spikelet primordium number, and apex length and apex meristem dome length. Several environmental factors are confounded in any comparison of sowing date treatments in the field including daylength and temperature. An attempt was made in the third sub-section to evaluate the possible importance of daylength in influencing apical development in the field by comparisons of the apical response to sowing date in the field with the growth room daylength response described above. The fourth sub-section examines the relationship between spikelet primordium number with spikelet and grain number, and, finally, the influence of sowing date on final grain yield is considered in the fifth sub-section.

1. Environmental conditions in the field during apical development.

Data for changes in some environmental parameters (daylength, air minimum and maximum temperatures, grass temperature and rainfall) from sowing to maximum spikelet primordium number are presented in Tables Ia and Ib in the Appendix for 1976 and 1977 respectively. Daylength values were estimated from Smithsonian Tables for latitude 56°N and are tabulated as the mean daily daylength for each week after sowing. Temperature and rainfall values were calculated from data collected from the weather station at Pentlandfield where the field trials were carried out.

The range of values for daylength and temperature from sowing to spikelet primordium maximum are presented in Table 11 for 1976 and 1977 respectively. Rainfall is presented as the average weekly rainfall during this period of apical development.

apex developmental stage, spikelet primordium number, and apex length and apex meristem dome length. Several environmental factors are confounded in any comparison of sowing date treatments in the field including daylength and temperature. An attempt was made in the third sub-section to evaluate the possible importance of daylength in influencing apical development in the field by comparisons of the apical response to sowing date in the field with the growth room daylength response described above. The fourth sub-section examines the relationship between spikelet primordium number with spikelet and grain number, and, finally, the influence of sowing date on final grain yield is considered in the fifth sub-section.

1. Environmental conditions in the field during apical development.

Data for changes in some environmental parameters (daylength, air minimum and maximum temperatures, grass temperature and rainfall) from sowing to maximum spikelet primordium number are presented in Tables Ia and Ib in the Appendix for 1976 and 1977 respectively. Daylength values were estimated from Smithsonian Tables for latitude 56^{o}N and are tabulated as the mean daily daylength for each week after sowing. Temperature and rainfall values were calculated from data collected from the weather station at Pentlandfield where the field trials were carried out.

The range of values for daylength and temperature from sowing to spikelet primordium maximum are presented in Table 11 for 1976 and 1977 respectively. Rainfall is presented as the average weekly rainfall during this period of apical development.

TABLE 11. Environmental conditions in the field during apical development.

a) 1976	S.1 (17 March)	S.2 (20 April)	S.3 (17 May)
Daylength (h) *	12.9-17.4	14.5-17.7	16.7-17.5
Air temp. max.(°C)*	8.5-20.4	10.2-16.1	14.9-25.3
Air temp. min.(°C)*	2.2-10.9	2.9- 8.3	7.7-12.5
Grass temp. (°C)*	2.4- 9.3	3.1- 7.3	5.9-11.2
Rainfall (mm)**	3.5	1.4	1.5

b) 1977	S.1 (15 March)	S.2 (20 May)
Daylength (h)*	12.0-17.5	16.8-17.4
Air temp. max.(°C)*	8.1-12.1	16.3-23.0
Air temp. min. (°C)*	3.9- 5.6	5.5-11.8
Grass temp. (°C)*	2.6- 4.7	4.0- 9.3
Rainfall (mm)**	2.2	2.3

* Range in mean daily values per week from sowing to spikelet primordium maximum.

** Average rainfall per week from sowing to spikelet primordium max.

Daylength, at the time of sowing, is increased with progressive delay in sowing although in any one year, the range of daylength conditions experienced by the plant is reduced with late sowing. In this case the plant is exposed to long days throughout its growth and development and is, therefore, directly comparable to plants sown under long day treatment. The daylength conditions for the first and last sowing in 1976 (S.1 and S.3) are equivalent to the two sowing dates used in 1977. However, it should be remembered that the daylength values are 'ideal' values calculated from daylength tables and may not represent the true daylength experienced by the plant.

Similarly, the three parameters of temperature measured (air maximum and minimum temperature and grass temperature) are increased with delay in sowing for both years. In general, the temperature was lower in 1977 than in 1976 in the first and final sowing dates.

The average weekly rainfall was higher in S.1 in 1976 than in the other sowing date treatments and this can be attributed to the heavy rainfall during weeks 10 and 11 after sowing.

2. Influence of sowing date on apical development in the field.

Before a description of the influence of sowing date on the apical development of cultivars in the field is presented, it should be noted that significant differences in plant number per plot were found between the two sowing dates in 1977 (Appendix, Table III). However, because of the very low plant density used in this study (220 seeds per m^2) it was

considered that little inter-plant competition would occur during early plant growth and development at the time of spikelet primordium production and, therefore, the results of apical development have been included.

Little is known about the effect of plant density on apical development of barley cultivars. Kirby and Faris (1970) observed that apical development was accelerated by increased density with a corresponding reduction in total primordium number per main shoot. However, there was little difference in the pattern of apical development at the lowest densities used in their study (50 and 100 plants per m^2) which corresponds to the observed plant number per plot for S.1 and S.2 respectively. This suggests that the comparisons drawn between the two sowing date treatments in 1977 are valid. The close similarities found between the influence of sowing date on apical development in the 1976 and 1977 field trials also support the reliability of the results presented for apical development.

i) Leaf number per main shoot.

The influence of sowing date on final leaf number per main shoot is presented in Table 12 for both 1976 and 1977 field trials. In 1976, cultivars exhibited a range in leaf number in S.1 (27 March) from 7.8 (Clipper) to 9.8 (Spratt). Eleven of the total 14 cultivars show a small reduction in leaf number in S.2 (20 April) compared with S.1 but this was only significant ($p \leq 0.05$) for Clipper and CI 5791. All 14 cultivars showed a decrease in leaf number in the final sowing (S.3, 17 May) compared with S.1 although this reduction was significant for only five cultivars (Table 12).

In 1977, the range of leaf number in the early sowing

TABLE 12 Influence of sowing date on final leaf number per main shoot of 14 and 5 barley cultivars in 1976 and 1977 respectively. Each value is a mean of at least 9 plants (1976) or 24 plants (1977).

		1976			1977		
Cultivar	sowing: date:	S.1 (27/3)	S.2 (20/4)	S.3 (17/5)	S.1 (15/3)	L.S.D.	S.2 (20/5)
Clipper		7.8a[x]	7.3b	6.9c	7.5	N.S.	7.1
Spartan		8.4a	8.0a	7.9a	8.2	N.S.	7.8
CI 5791		8.7a	8.4b	8.1c			
Ingrid		9.2a	8.9a	8.4b			
Chevallier		8.5a	8.1a	7.8b			
Bohmerwald		9.1a	9.2a	8.3b			
Lami		8.2a	8.0a	7.8a			
Domen		8.5a	8.6a	8.1a	9.2	N.S.	8.6
Maris Mink		9.3a	9.0a	8.5a			
Golden Promise		9.4a	9.4a	9.0a	9.6	N.S.	9.1
Spratt		9.8a	9.7a	9.4a			
Hillmarsh		9.2a	9.1a	8.8a			
Uzu		9.2a	9.0a	8.9a			
Ymer		8.8a	8.8a	8.1a	9.0	N.S.	8.3

x = Multiple range test, significant at $p \leq 0.05$, calculated following an analysis of variance for each cultivar separately. Means with same letters are not significantly different.

y = L.S.D. ($p \leq 0.05$) values, calculated following an analysis of variance for each cultivar separately.

N.S. = not significant.

(S.1, 15 March) was similar to that observed for the first sowing in 1976. Leaf number ranged from 7.5 (Clipper) to 9.6 (Golden Promise). All five cultivars showed a small but non-significant decrease in leaf number in S.2 (20 May) compared with S.1.

The reduced leaf number with progressively later sowing is associated with the more rapid vegetative development of the plant in late sowing conditions. This results in fewer leaves produced on the main shoot apex before the onset of spikelet primordium production.

ii) Apical developmental stage.

The effect of sowing date on the development of the main shoot apex for the 14 cultivars examined in 1976 and the five cultivars examined in 1977 are presented in Figs. 12 and 13 respectively. The ten developmental stages distinguished are as shown in Table 7.

For all cultivars in both field trials, the time taken for each developmental stage to be reached was reduced with progressively later sowing. This can be clearly seen if the following three developmental stages of: double ridge (DR), awn initials (A) and tip degeneration (TD) are discussed separately.

In 1976, all cultivars exhibited a reduction in the period from sowing to DR formation as sowing became progressively later. Double ridges were formed between four and five weeks after sowing (w.a.s.) in the early sowing (S.1) but this period was reduced to only three-four weeks in S.2 and, for Clipper and Lami, to only three weeks. Apical development was extremely rapid in the final sowing (S.3) and this stage occurred before the first sampling time (three w.a.s.) for all

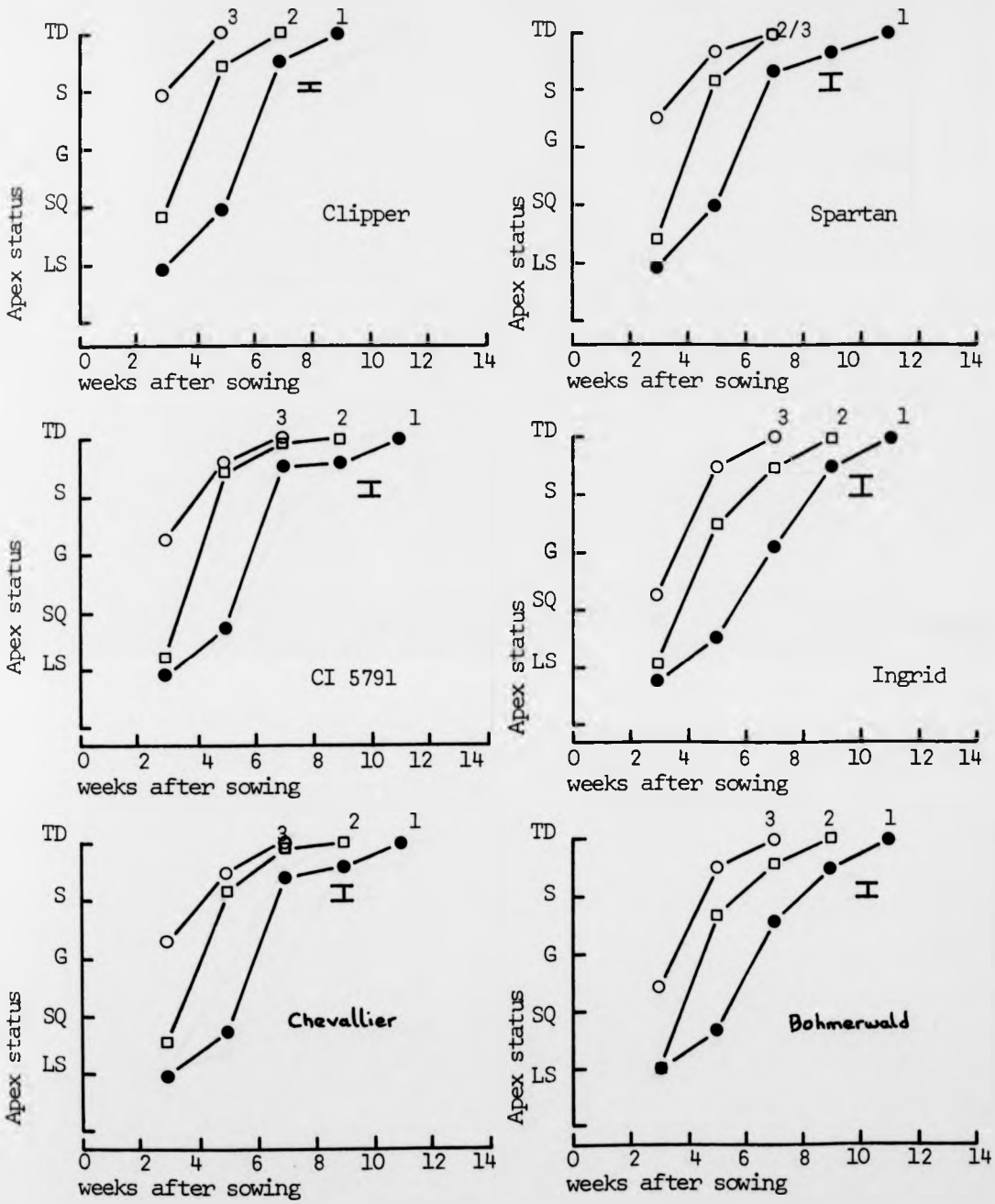


Fig. 12. Field Trial 1976.

Effect of sowing date (1) 27.3.76, (2) 20.4.76 and (3) 17.5.76 on apex development in 14 barley cultivars in the field.

contd.

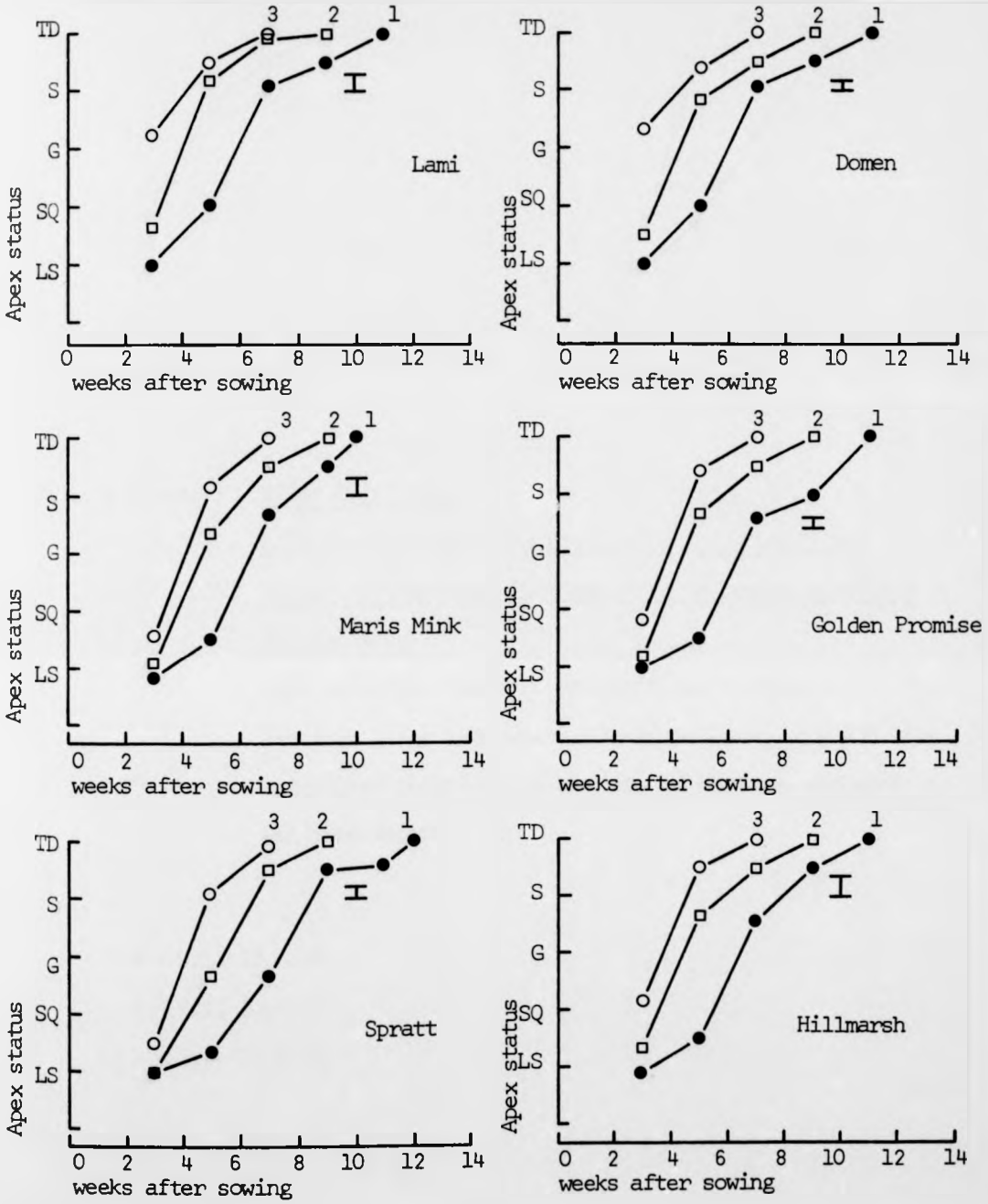


Fig. 12 (contd.) Field Trail 1976.
Effect of sowing date (1) 27.3.76, (2) 20.4.76 and (3) 17.5.76 on apex development in 14 barley cultivars in the field.

contd.

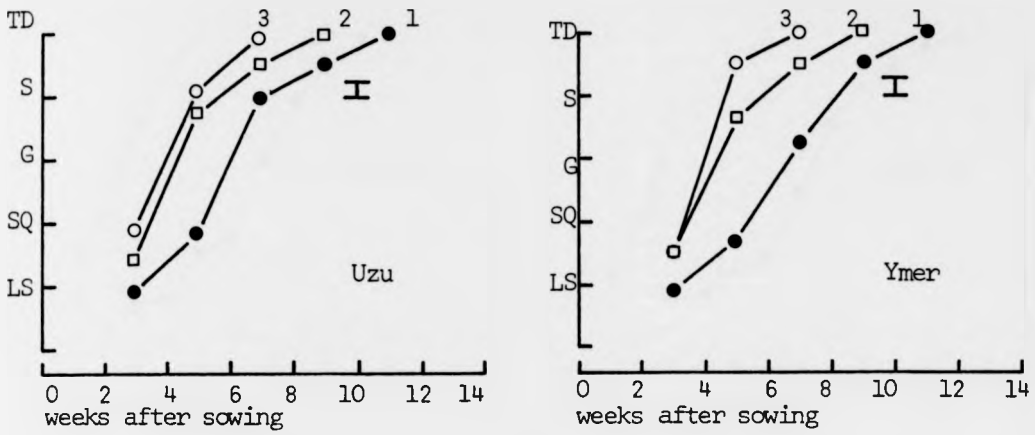


Fig. 12 (contd.) Field Trial 1976.

Effect of sowing date (1) 27.3.76, (2) 20.4.76 and (3) 17.5.76 on apex development in 14 barley cultivars in the field.

Each point is a mean of between 4 and 6 plants.

Vertical lines indicate L.S.D. significant at $p \leq 0.05$, calculated following an analysis of variance for each cultivar separately.

● = S.1, 27.3.76

□ = S.2, 20.4.76

○ = S.3, 17.5.76

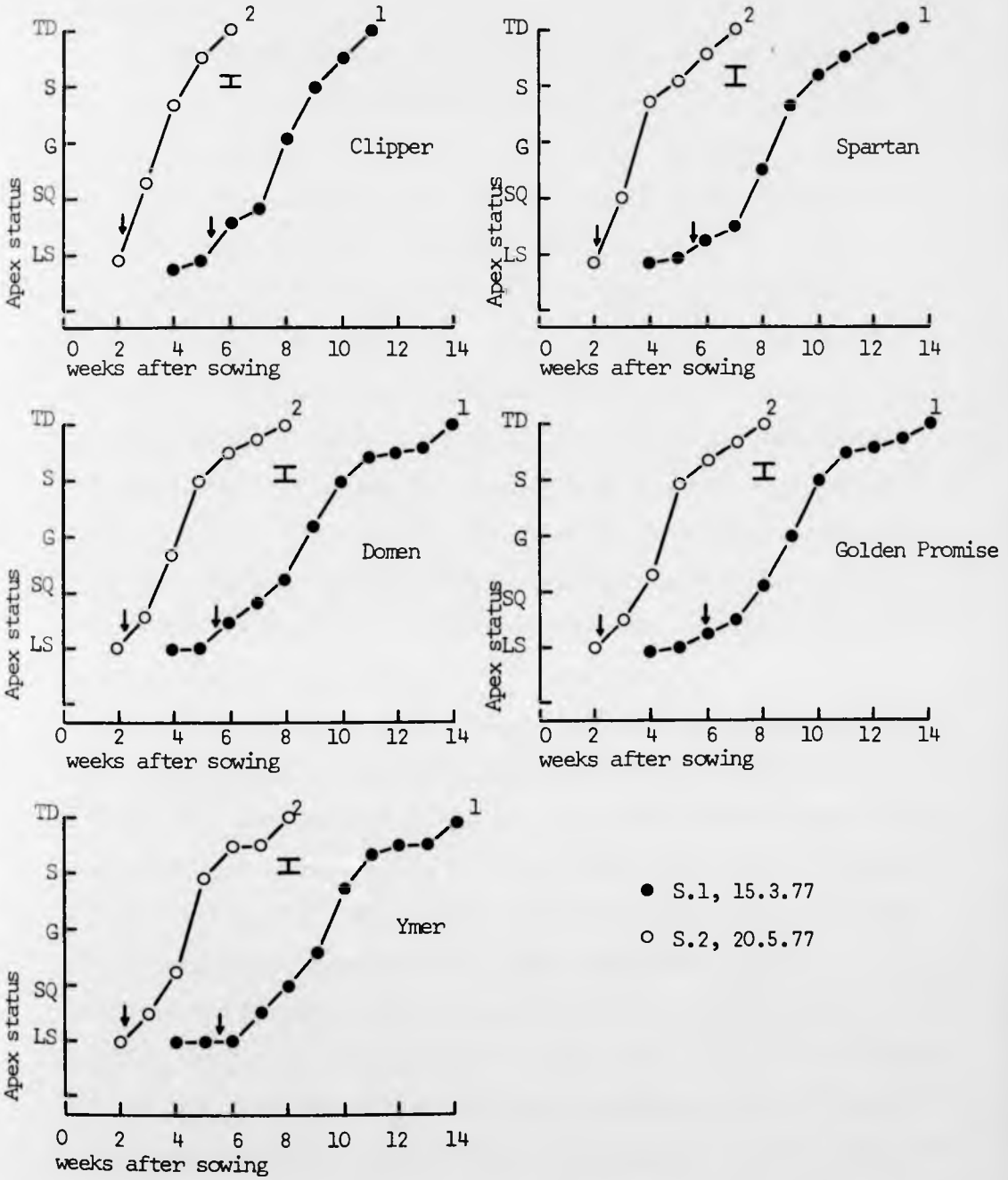


Fig. 13. Field Trial 1977

Effect of sowing date, (1) 15.3.77 and (2) 20.5.77 on apex development in 5 barley cultivars in the field.

Each point is a mean of 5 or 6 plants.
Vertical lines indicate L.S.D. significant at $p = 0.05$, calculated following an analysis of variance for each cultivar separately.
Arrows indicate onset of spikelet primordium production.

cultivars.

The hastening effect of late sowing on apical development can be clearly seen in the 1977 field trial (Fig 13). The DR stage occurred six to seven weeks after sowing for all cultivars in the early sowing (S.1) but commenced earlier in the late sowing (S.2). Although all cultivars showed accelerated apical development in the late sowing, there were differences between cultivars in the magnitude of their response. Double ridges were formed after only 10 to 11 d.a.s. for Clipper and Spartan but the response was less pronounced in Domen, Golden Promise and Ymer and this stage was reached after 14 days. It was indicated in the growth room daylength study that spikelet primordium production occurs before DR stage of development. Confirmation of this suggestion can be derived from the 1977 field trial (Fig. 13).

The time taken to reach each subsequent developmental stage was similarly reduced with progressively later sowing. In 1976, the awn initial stage (stage A) was reached after nine weeks for most cultivars in S.1 although there were differences between cultivars. The period between sowing and this stage was reduced with progressively later sowing and again cultivars exhibited differences in the magnitude of their response. For example, in S.3 the time taken to reach awn initials was reduced to less than five weeks for Clipper and Spartan but the apical development of the other cultivars was slightly slower and this stage was not reached until five to six w.a.s.

The accelerated apical development found in late compared with early sowing was confirmed in the 1977 field trial. The awn initial stage occurred 10 to 12 w.a.s. in S.1 for the five cultivars examined but this period was reduced to only six or

cultivars.

The hastening effect of late sowing on apical development can be clearly seen in the 1977 field trial (Fig 13). The DR stage occurred six to seven weeks after sowing for all cultivars in the early sowing (S.1) but commenced earlier in the late sowing (S.2). Although all cultivars showed accelerated apical development in the late sowing, there were differences between cultivars in the magnitude of their response. Double ridges were formed after only 10 to 11 d.a.s. for Clipper and Spartan but the response was less pronounced in Domen, Golden Promise and Ymer and this stage was reached after 14 days. It was indicated in the growth room daylength study that spikelet primordium production occurs before DR stage of development. Confirmation of this suggestion can be derived from the 1977 field trial (Fig. 13).

The time taken to reach each subsequent developmental stage was similarly reduced with progressively later sowing. In 1976, the awn initial stage (stage A) was reached after nine weeks for most cultivars in S.1 although there were differences between cultivars. The period between sowing and this stage was reduced with progressively later sowing and again cultivars exhibited differences in the magnitude of their response. For example, in S.3 the time taken to reach awn initials was reduced to less than five weeks for Clipper and Spartan but the apical development of the other cultivars was slightly slower and this stage was not reached until five to six w.a.s.

The accelerated apical development found in late compared with early sowing was confirmed in the 1977 field trial. The awn initial stage occurred 10 to 12 w.a.s. in S.1 for the five cultivars examined but this period was reduced to only six or

seven weeks for Domen, Golden Promise and Ymer. Again, Clipper and Spartan exhibited a faster apical development and this stage was reached less than six weeks after sowing.

The final stage of apical development distinguished, tip degeneration (stage TD), occurs after the maximum number of spikelet primordia had been determined and results in the subsequent loss of potential spikelets per ear. Tip degeneration occurred 11 w.a.s. for most cultivars in S.1 and this period was reduced with progressive delay in sowing.

A similar situation was found in the 1977 field trial, in which tip degeneration occurred six weeks earlier in S.2 compared with S.1 for Spartan, Domen, Golden Promise and Ymer (Fig. 13). As in 1976, Clipper was very responsive to late sowing and this period was reduced to only five weeks.

Although all cultivars showed accelerated apical development with progressively later sowing there were differences between cultivars in the magnitude of their response and this will be examined in the other parameters of apical development followed. The more rapid apical development in late sowing was identical to the effect of L.D. treatment on apical development in growth rooms described earlier. This relationship will be discussed more fully at the end of the section.

iii) Spikelet primordium number.

The influence of sowing date on spikelet primordium number per main shoot apex is presented in Fig. 14 for 1976 and Fig. 15 for 1977. In 1976, the time taken to reach maximum spikelet primordium number was reduced with progressive delay in sowing but cultivars differed in the magnitude of their response and this was particularly evident in S.3. Spikelet primordium maximum was not determined for Maris Mink

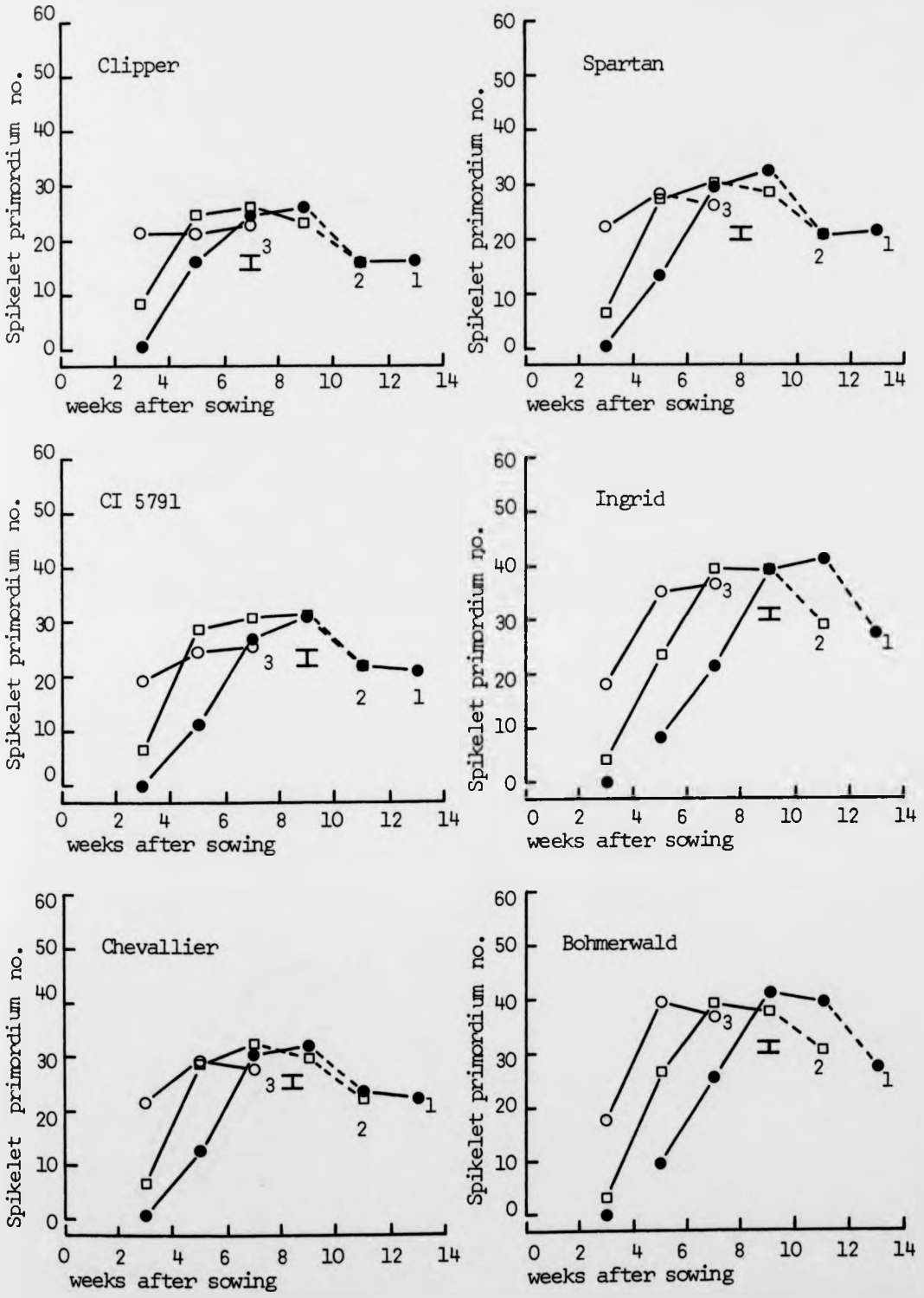


Fig. 14. Field trial 1976
Effect of sowing date (1) 27.3.76, (2) 20.4.76 and (3) 17.5.76 on spikelet primordia production in 14 barley cultivars in the field.

(contd.)

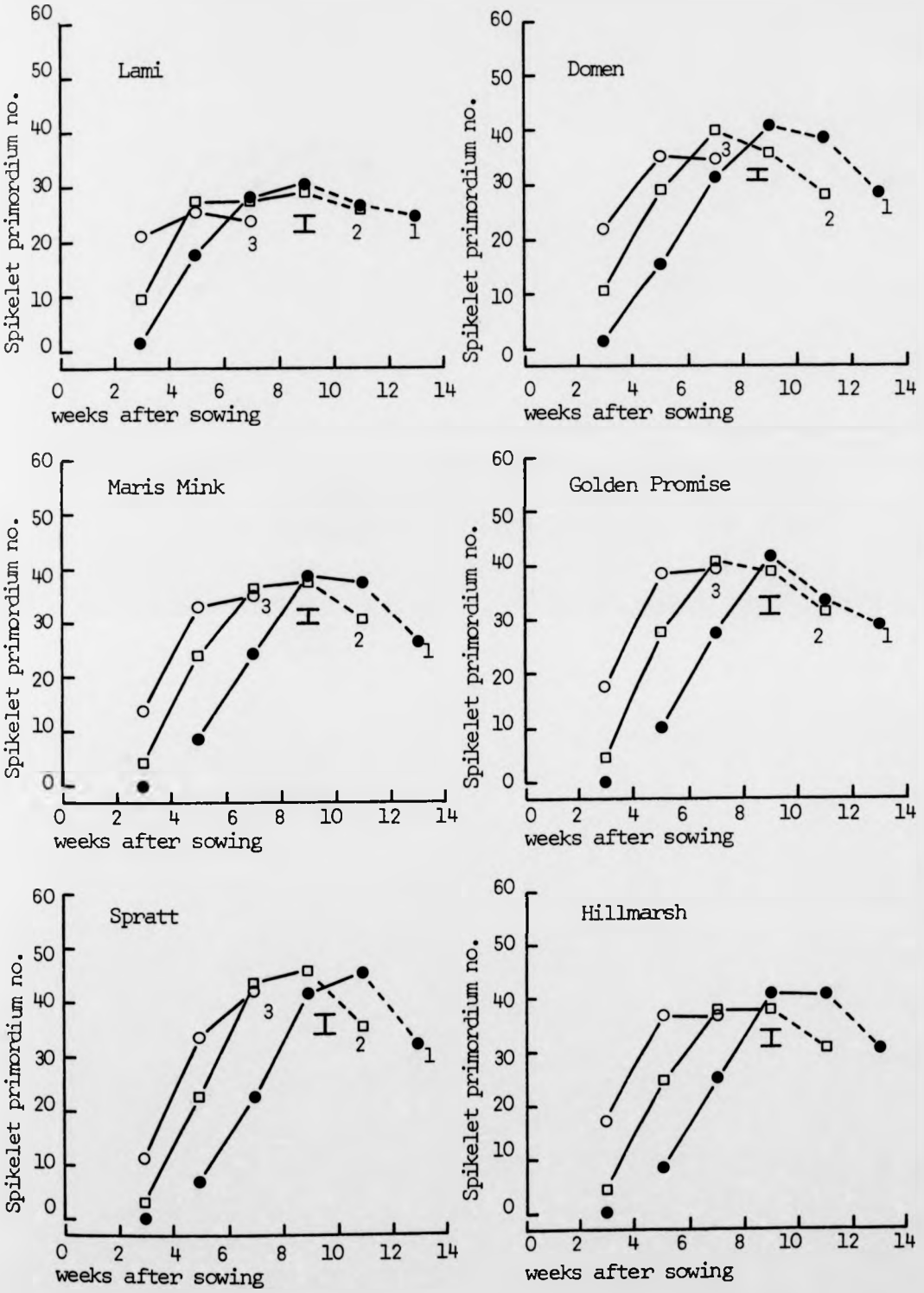


Fig. 14 (ccntd.) Field Trial 1976. Effect of sowing date (1) 27.3.76, (2) 20.4.76 and (3) 17.5.76 on spikelet primordia production in 14 barley cultivars in the field.

contd.

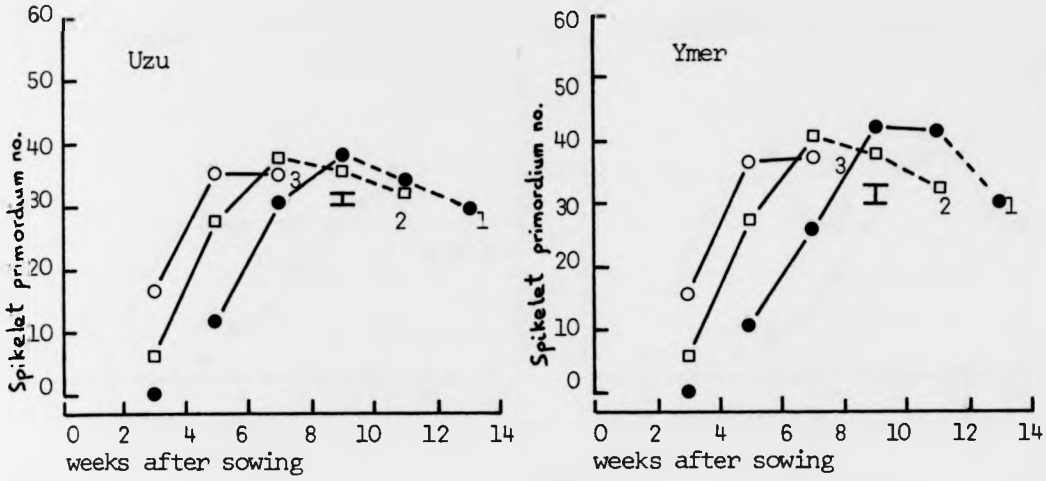


Fig. 14 (contd.) Field Trial 1976. Effect of sowing date (1) 27.3.76, (2) 20.4.76 and (3) 17.5.76 on spikelet primordia production in 14 barley cultivars in the field.

Each point is a mean of between 4 and 6 plants.

Vertical lines indicate L.S.D. significant at $p \leq 0.05$, calculated following an analysis of variance for each cultivar separately.

● = S.1, 27.3.76

□ = S.2, 20.4.76

○ = S.3, 17.5.76

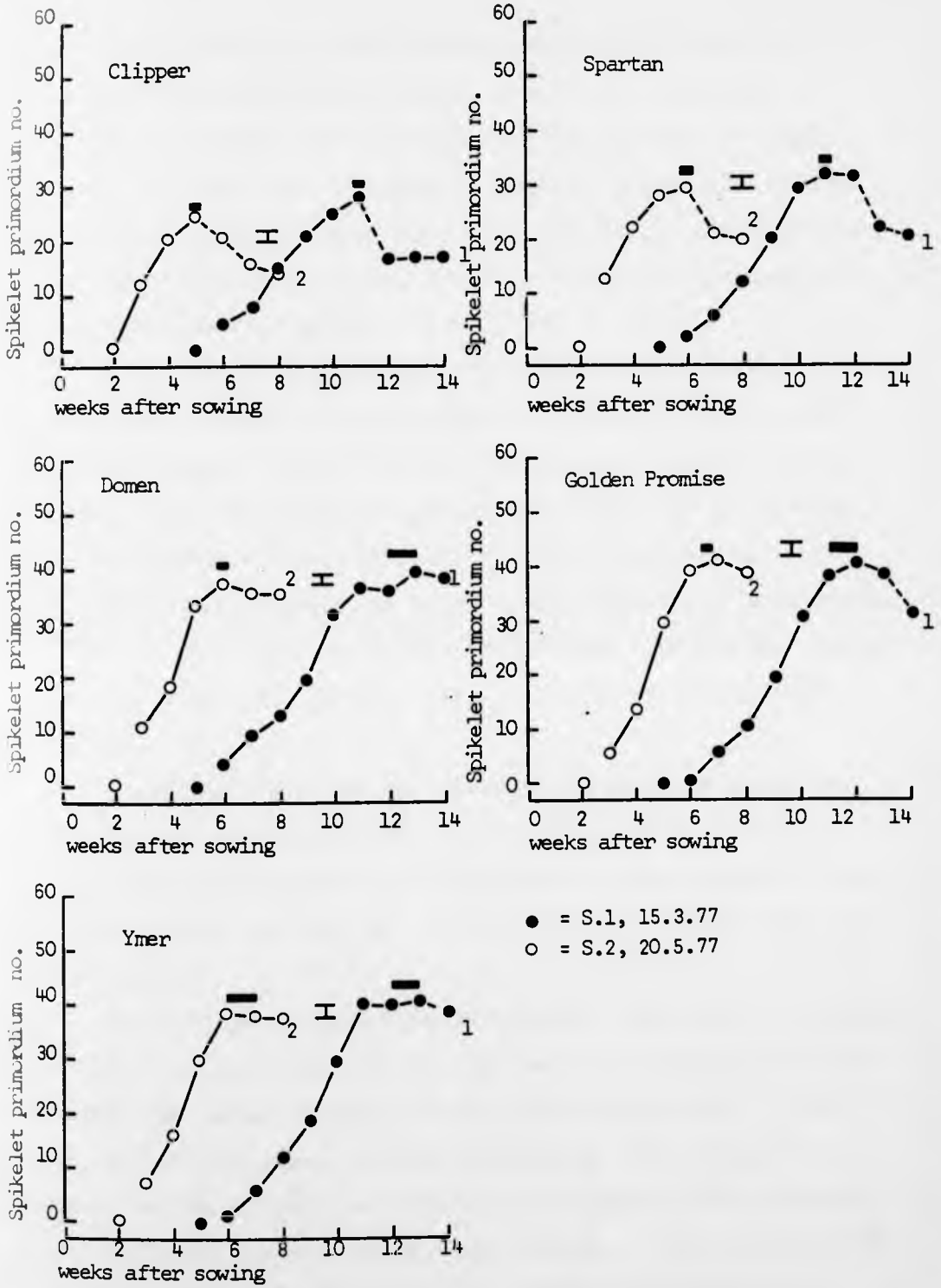


Fig. 15. Field trial 1977.

Effect of sowing date. (1) 15.3.77 and (2) 20.5.77 on spikelet promirdia production in 5 barley cultivars in the field.

Each point is a mean of 5 or 6 plants. Vertical lines indicate L.S.D. significant at $p \leq 0.05$, calculated following an analysis of variance for each cultivar separately. Horizontal bars indicate period of awn initial stage of development.

and Spratt during the seven-week sampling period but, in Spartan, the maximum was reached after five weeks and degeneration of the distal primordia had occurred at week seven. In the other cultivars, spikelet primordium maximum reached a plateau between five and seven w.a.s. although the data for Clipper is unusual in that this period extended from week three to week seven.

There was no significant difference in the spikelet primordium maximum attained between S.1 and S.2 for any of the cultivars. However, nine of the 14 cultivars (Clipper, Spartan, CI 5791, Ingrid, Lami, Domen, Maris Mink, Hillmarsh and Ymer) showed a significant ($p \leq 0.05$) decrease in the maximum in S.3 compared to S.1. Only Chevallier, Bohmerwald, Golden Promise, Spratt and Uzu, maintained a relatively stable spikelet primordium maximum over the range of sowing dates studied.

A similar situation was observed in 1977, in which the spikelet primordium maximum was determined 11 to 13 w.a.s. in S.1 but was reduced to six weeks in S.2 for Spartan, Domen, Golden Promise and Ymer and further reduced to only five weeks for Clipper.

The different magnitudes of response exhibited by cultivars to late sowing is clearly illustrated by the maximum spikelet primordium number attained in the two sowing dates. The maximum was not significantly affected by late sowing for Domen, Golden Promise and Ymer but was significantly reduced ($p \leq 0.05$) in S.2 for Clipper and Spartan. This confirms the results of the 1976 field trial in which both Clipper and Spartan showed a significant reduction in spikelet primordium maximum in the final compared to early sowing.

It was noted earlier (page 43) that the maximum spikelet primordium number was determined both by the duration and the rate of spikelet primordium production. A low spikelet primordium maximum was also associated with an early onset of spikelet primordium set down. The influence of sowing date on three parameters will be described below for both field trials.

In 1976, five of the 14 cultivars (Clipper, Spartan, Chevallier, Lami and Domen) had initiated spikelet primordium production at the time of the first sample (three w.a.s.) (Fig. 14). The onset of spikelet primordium production occurred earlier with progressively later sowing and all cultivars had initiated spikelet primordium production after three weeks in S.2 and S.3. Although it is possible to estimate the time of onset of production retrospectively by reference to the total primordium number as described on page 42, this cannot be calculated for S.2 and S.3 because of the high primordium number set down at three weeks.

Similarly, because the onset of spikelet primordium production cannot be determined for S.2 and S.3, it is not possible to determine either the duration or the rate of production. Although it is not possible to compare the rates of spikelet primordium production in the three sowing date treatments it is possible to examine the effect of sowing date on the early set down of spikelet primordia. Associated with both the onset and the initial rate of production is the percentage of the maximum set down during the first three weeks of plant growth and development.

The influence of sowing date on the maximum spikelet primordium number and the percentage of this maximum set down at three weeks is presented in Table 13. Only five of the 14

TABLE 13. Influence of sowing date on spikelet primordium max. and percentage set down at three weeks for 14 cultivars in the field in 1976.

Cultivar	Spikelet primordium max. x S.1	S.2	S.3	% of spikelet primordium max. set down at 3 weeks S.1	S.2	S.3
Clipper	26.2	26.3	23.2	3.4	32.2	93.9
Spartan	32.7	30.5	28.3	1.4	21.3	73.0
CI 5791	31.2	31.7	27.0	0	12.9	70.8
Ingrid	41.3	39.5	36.8	0	11.6	49.6
Chevallier	31.8	32.3	29.2	0.3	20.7	73.8
Bohmerwald	41.2	39.2	39.5	0	8.1	44.7
Lami	30.8	29.2	25.7	5.2	33.2	82.5
Domen	41.0	40.0	35.6	1.4	21.3	73.0
Maris Mink	38.7	37.7	35.7	0	11.6	39.3
Golden Promise	41.3	40.8	39.5	0	11.1	44.7
Spratt	45.3	45.8	42.2	0	6.9	27.0
Hillmarsh	40.7	37.8	36.8	0	11.7	46.6
Uzu	38.0	37.5	35.0	0	16.5	47.4
Ymer	42.0	40.7	37.5	0	14.5	42.0

x Each value is a mean of between 4 and 6 plants.

cultivars (Clipper, Spartan, Chevallier, Lami and Domen) had commenced spikelet primordium production after three weeks in S.1 but all cultivars had initiated spikelet primordia at this stage in S.2 and S.3. The percentage set down was increased with progressively later sowing for all cultivars thus indicating that either or both of the parameters determining the percentage set down (i.e. the onset and the initial rate of production) may be hastened by late sowing.

Cultivars exhibited differences in the magnitude of their response to late sowing such that the five cultivars which had initiated spikelet primordia at three weeks in S.1 plus CI 5791 exhibited the highest percentage set down in both S.2 and S.3. The other cultivars showed a less pronounced response to late sowing and the difference in the percentage set down between sowing date treatments was less marked than observed for the six cultivars described above.

It appears, therefore, that the range of magnitude of response between cultivars is increased as sowing date is delayed, i.e. cultivars which are responsive to late sowing become increasingly more responsive as sowing is progressively delayed compared with less sensitive cultivars.

Five of the six cultivars (Clipper, Spartan, CI 5791, Chevallier and Lami) which exhibit the highest percentage of the maximum spikelet primordium number set down at three weeks in S.3 also show the lowest maximum in S.3. This clearly suggests that cultivars which exhibit a high spikelet primordium percentage set down during the early growth and development of the plant will also have a low maximum. This suggestion is confirmed by the significant relationship ($r = -0.789$, $p \leq 0.001$) between the percentage set down at three weeks and the final

maximum attained in S.2 and a more marked correlation ($r = -0.916$, $p \leq 0.001$) in S.3. The relationship between the percentage spikelet primordia set down and the maximum for S.3 is depicted in Fig. 16. Cultivars which produce a large percentage of the spikelet primordium maximum within the first three weeks of development (e.g. Clipper) are also those cultivars which exhibit a low final maximum. Conversely, cultivars which exhibit a high maximum (e.g. Golden Promise) show a smaller percentage set down.

In the 1977 field trial, the onset of spikelet primordium production can be determined as described on page 42 and the duration of the period of set down and the initial rate of production have been calculated and the results presented in Table 14.

The period between sowing and the onset of spikelet primordium production was reduced from between 39 and 37 days to between 13 and 16 days for all cultivars. This observation corresponds to the reduced leaf number per main shoot with late sowing, i.e. a low leaf number is indicative of an early transition from negative to floral development associated with the early onset of spikelet primordium set down. The duration of the period of spikelet primordium production was similarly reduced with delay in sowing such that set down ceased for Clipper in S.2 after only 22 days but was slightly longer for the other cultivars (e.g. Golden Promise cessation occurred after 33 days).

The rate of spikelet primordium production is calculated for the initial period of linear set down before the onset of the curvilinear phase prior to maximum spikelet primordium number. The duration of this period is dependent on the genotype

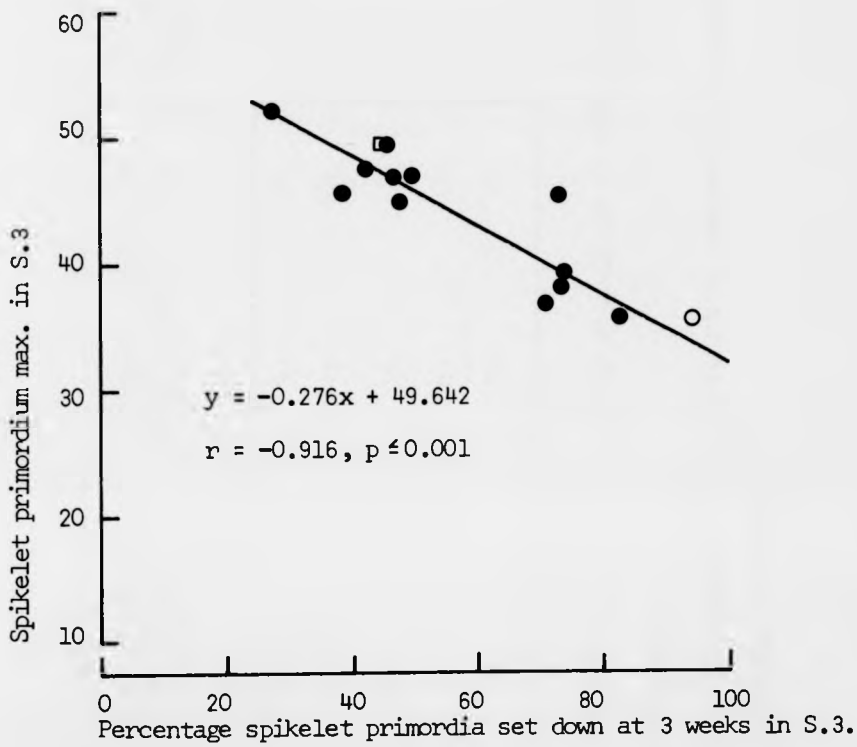


Fig. 16. Relationship between percentage spikelet primordia set down at 3 weeks and the spikelet primordium max. for 14 cultivars in S.3 in 1976.

○ Clipper
□ Golden Promise

TABLE 14. Influence of sowing date on parameters of spikelet primordium production for five barley cultivars in the field in 1977. Maximum spikelet primordium number based on means of 5 or 6 plants.

Cultivar	Spikelet primordium maximum			Onset of spikelet primordium production (d.a.s.)		Duration of spikelet primordium production (days)		Initial rate of production (spikelet primordia per day)		
	S.1		S.2	S.1	S.2	S.1	S.2	S.1		S.2
Clipper	28.0	*[a]	24.5	37	13	40	22	0.78	**[b]	1.39
Spartan	31.8	*	29.2	39	15	38	27	0.92	*	1.38
Domen	39.2	N.S.	37.0	37	15	54	27	0.92	**	1.59
Golden Promise	40.7	N.S.	41.2	39	16	43	23	1.07	**	1.56
Ymer	40.3	N.S.	38.5	39	15	38	27	1.04	*	1.47

a = N.S. not significant
* significant at $p \leq 0.05$
} L.S.D. ($p \leq 0.05$) calculated following an analysis of variance for each cultivar separately.

b = * significant at $p \leq 0.05$
** significant at $p \leq 0.01$
} Significant differences calculated following comparison of regression coefficients for each cultivar separately.

of the cultivar and the sowing date treatment and extends from three to six weeks after the onset of set down. This rate was significantly increased ($p \leq 0.05$) with late sowing for all cultivars but, in the case of Clipper and Spartan, the increase in rate was not sufficient to compensate for the reduced period of set down and thus a significantly lower maximum ($p \leq 0.05$) was attained in the late sowing.

It was suggested in the 1976 field trial that cultivars which set down a large percentage of the spikelet primordium maximum after three weeks of plant growth also determined a low maximum and confirmation of this suggestion can be derived from the 1977 field trial. The influence of sowing date on the percentage set down at three weeks and the maximum attained is presented in Table 15. Cultivars again differed in the magnitude of their response to late sowing and two groups may be distinguished. Group one (Clipper and Spartan) exhibited a more pronounced response to late sowing than the second group (Domen, Golden Promise and Ymer) and this was also reflected in the maximum spikelet primordium number. The relationship between these two parameters was significant in the late sowing ($r = -0.980$, $p \leq 0.001$) and is depicted in Fig. 17.

It was suggested earlier (page 42) that spikelet primordium maximum was attained during the awn initial stage of development. Confirmation of this suggestion can be derived from the 1977 field trial and is illustrated in Fig.15.

Final spikelet and grain number per ear is determined by both the spikelet primordium maximum and the proportion of this number which survive to form potential fertile spikelets per ear. Degeneration of the distal spikelet primordia is

TABLE 15. Influence of sowing date on maximum spikelet primordium number and the percentage of the maximum set down at three weeks for five barley cultivars in the field in 1977.

Cultivar	Spikelet primordium maximum [a]		Percentage spikelet primordia set down at 3 weeks	
	S.1	S.2	S.1	S.2
Clipper	28.0	24.5	0	49.7
Spartan	31.8	29.2	0	42.9
Domen	39.2	37.0	0	29.5
Golden Promise	40.7	41.2	0	14.3
Ymer	43.3	38.5	0	19.2

a = values based on means of 5 or 6 plants.

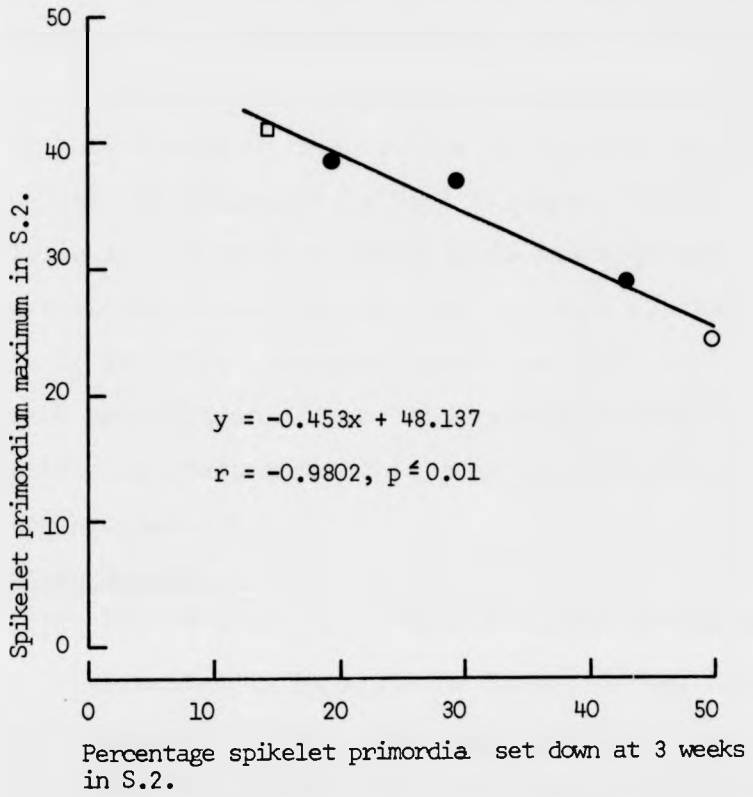


Fig. 17. Relationship between percentage spikelet primorida set down at 3 weeks and spikelet primordium max. for 5 barley cultivars in S.2 in 1976.

○ = Clipper

□ = Golden Promise

represented by the dashed line in Fig.14 for 1976 and Fig. 15 for 1977. Clearly, because the spikelet primordium maximum is determined earlier with progressively later sowing in both field trials, the time of onset of tip degeneration is hastened by late sowing. The decline in spikelet primordium number levelled out in some cultivars (Clipper, Spartan, CI5791 and Chevallier in S.1 in 1976 and Clipper and Spartan in S.1 in 1977) within the period of sampling and this plateau corresponds to the final spikelet number per main ear. A more detailed description of the influence of sowing date on final spikelet and grain number per main ear will be presented later in the section.

iv) Apex length.

The influence of sowing date on the length of the main shoot apex is presented in Fig. 18 for 1976 and Fig. 19 for 1977. Three distinct growth rates are evident for all cultivars in both years and these phases have been described earlier on page 46. The initial phase of apex length increase was very slow with little absolute increase in length. The duration of this period was reduced with progressive delay in sowing for all cultivars in both field trials but, again, Clipper and Spartan exhibited a more pronounced response to late sowing in both years than the other cultivars. The second phase is characterised by an abrupt change to a period of very rapid length increase and, as noted previously (page 47), this phase coincides with the cessation of spikelet primordium production and degeneration of the distal primordia. It cannot be readily determined from the available data whether sowing date has any influence on either the duration of this phase or on the final ear length attained. Comparisons of the first two

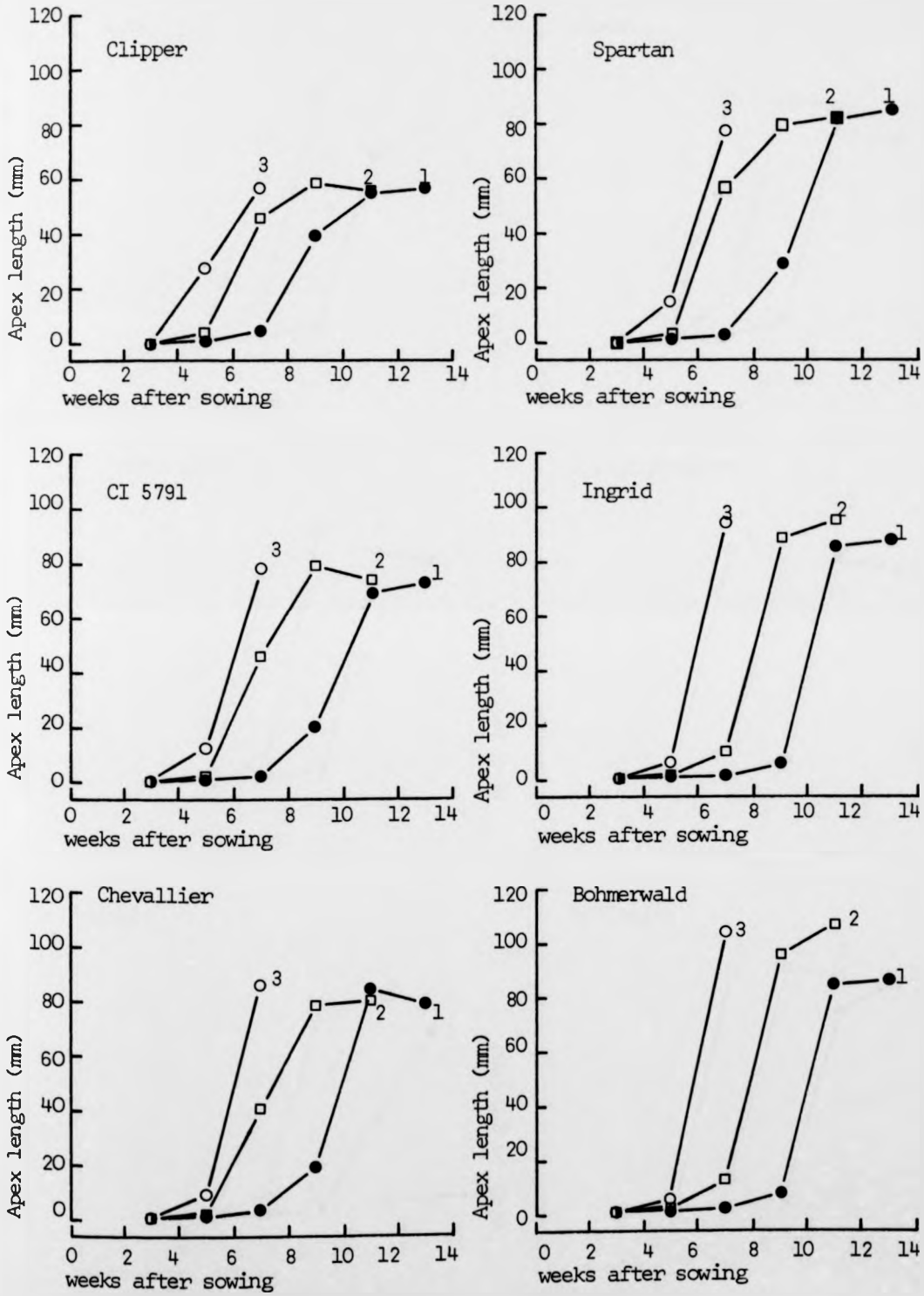


Fig. 18. Field Trial 1976
Effect of sowing date (1) 27.3.76, (2) 20.4.76 and (3) 17.5.76 on apex length in 14 barley cultivars in the field.

contd.

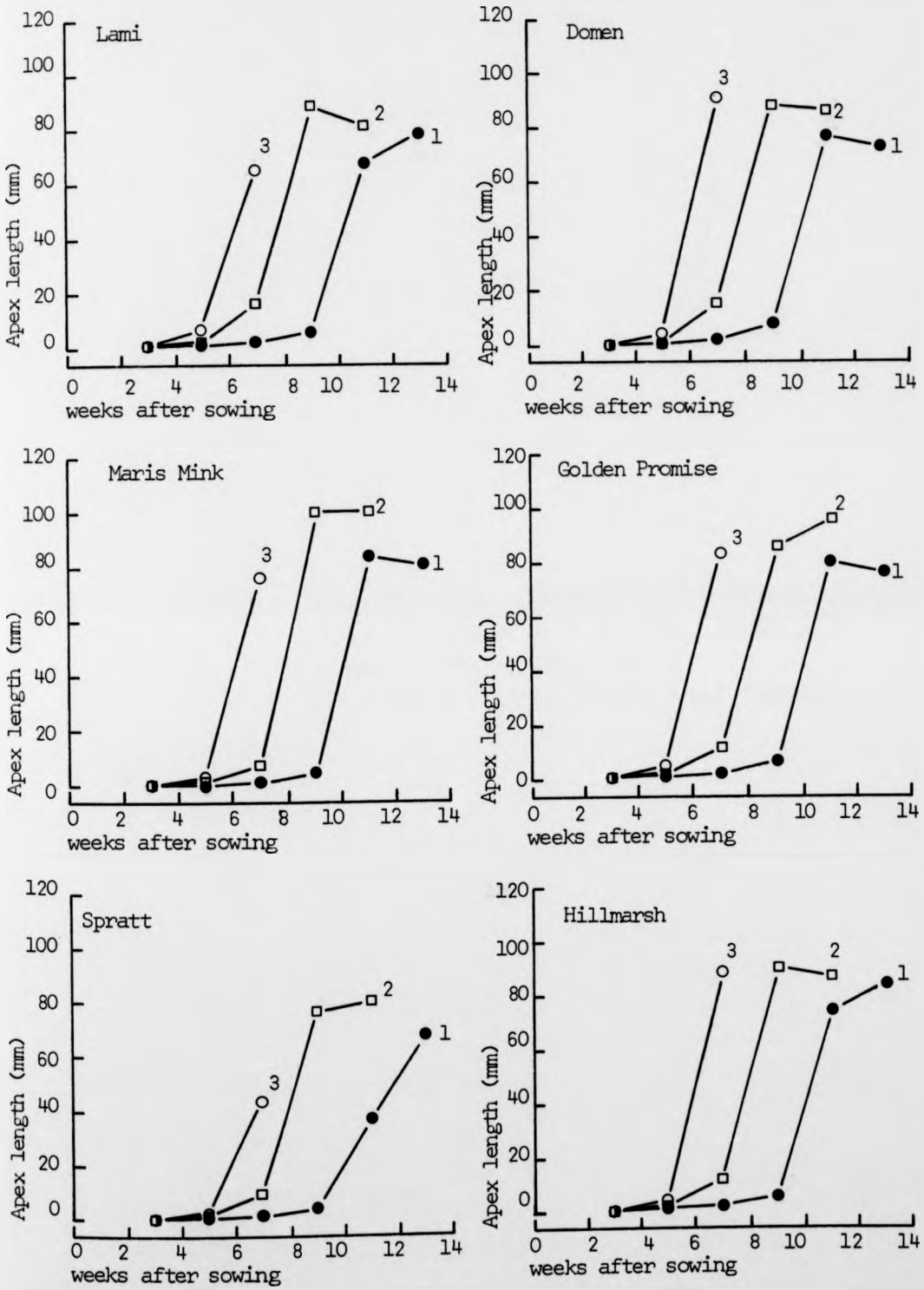


Fig. 18 (contd.) Field Trial 1976. Effect of sowing date (1) 27.3.76, (2) 20.4.76 and (3) 17.5.76 on apex length in 14 barley cultivars in the field.

contd.

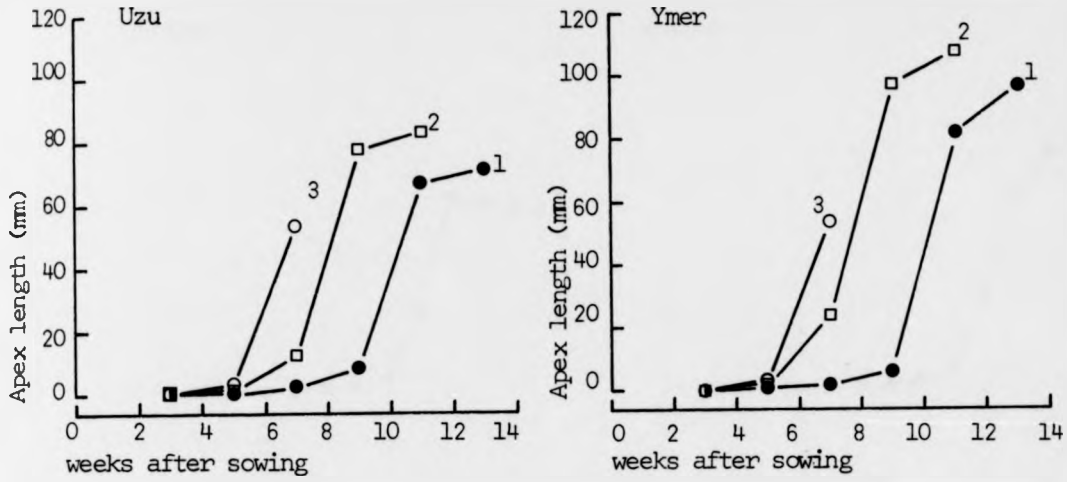


Fig. 18. (contd.) Field Trial 1976. Effect of sowing date (1) 27.3.76, (2) 20.4.76 and (3) 17.5.76 on apex length in 14 barley cultivars in the field.
Each point is a mean of between 4 and 6 plants.

● = S.1, 27.3.76
□ = S.2, 20.4.76
○ = S.3, 17.5.76

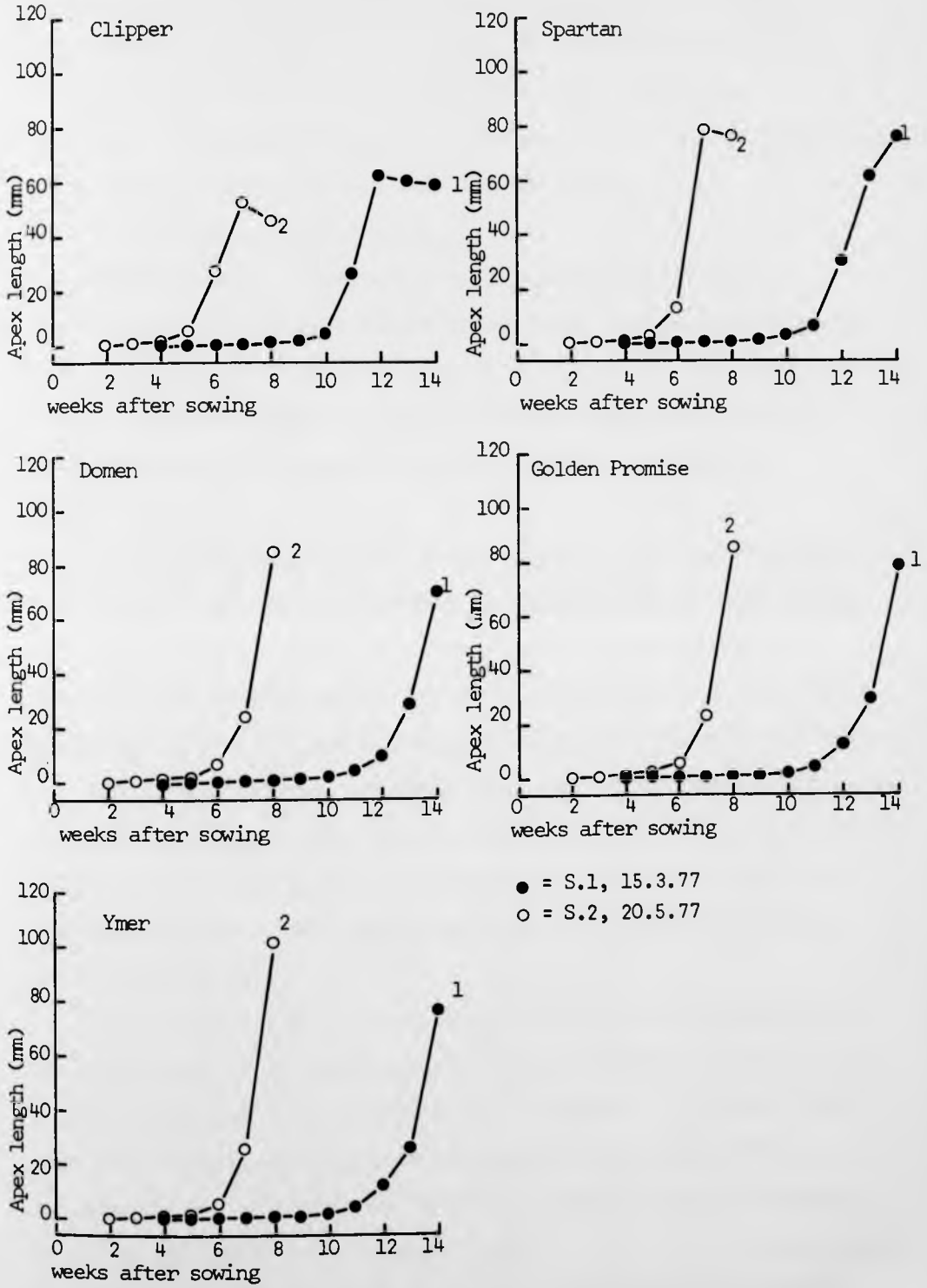


Fig. 19. Field trial 1977
Effect of sowing date, (1) 15.3.77 and (2) 20.5.77 on apex length in 5 barley cultivars in the field.
Each point is a mean of 5 or 6 plants.

sowing dates in 1976 suggests that the duration was not significantly reduced but this cannot be confirmed by the final sowing (S.3) in 1976 or by the 1977 field trial. Similarly, sowing date appears to have no consistent influence on final ear length in S.1 and S.2 in 1976.

v) Meristem dome length.

Because of the limited data available for meristem dome length in the 1976 field trial, the influence of sowing date on dome length is only presented for 1977 (Fig. 20). Three distinct phases of meristem dome development can be distinguished and these have been described previously (page 47).

The development of the meristem dome was accelerated by late sowing such that maximum dome length was attained after only two to three weeks although maximum length does not appear to be significantly affected for any of the cultivars. Meristem dome development at this stage was slightly different in Clipper and Spartan compared with the other three cultivars. Maximum dome length was usually determined earlier and the dome length lower in Clipper and Spartan than the other cultivars and these differences were more evident in the late sowing (S.2) than in S.1.

The second phase was characterised by a gradual decrease in dome length and the duration of this phase was reduced in S.2 for all cultivars except Golden Promise. However, this cultivar exhibited a protracted period of meristem dome elongation and the combined periods of elongation and length decrease was much greater in S.1 than in S.2. The final phase of dome development comprises the period between the abrupt increase in dome length after the minimum has been determined

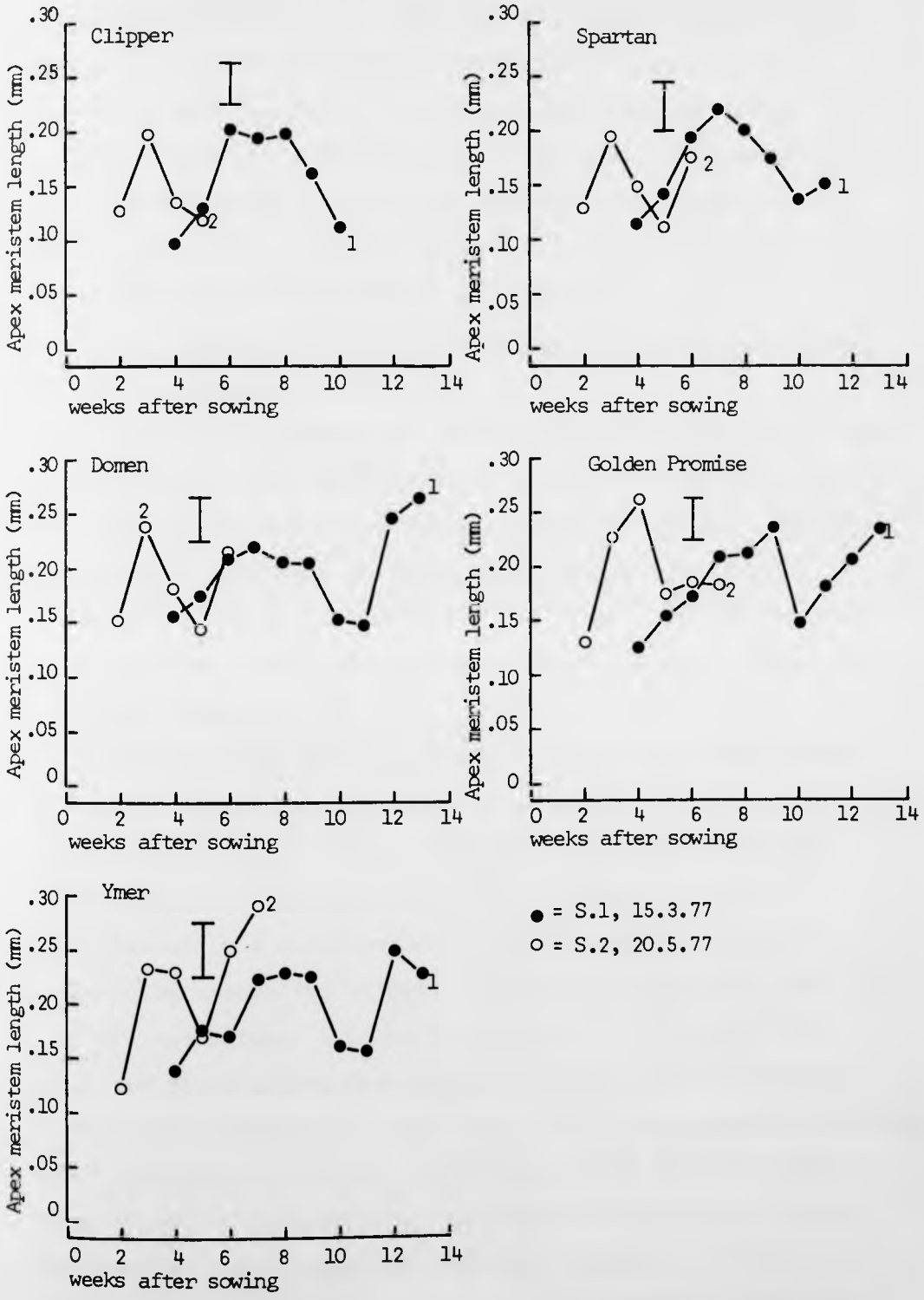


Fig. 20. Field trial 1977. Effect of sowing date (1) 15.3.77 and (2) 20.5.77 on apex meristem length in 5 barley cultivars in the field.

Each point is a mean of 5 or 6 plants. Vertical lines indicate L.S.D. significant at $p = 0.05$, calculated following an analysis of variance for each cultivar separately.

until tip degeneration. The period between sowing and the beginning of this phase was considerably reduced by late sowing. The increase in meristem length occurs before the maximum spikelet primordium number has been attained although none of the spikelet primordia produced after this stage will develop into fertile spikelets. This aspect will be discussed more fully later in the section.

vi) Summary of apical development in sowing date field trials.

Apical development was accelerated by progressively later sowing for all cultivars examined in the two field trials and this was reflected in all the parameters of apical development measured. Cultivars differed in the magnitude of their response to sowing date and, for the five cultivars examined in both years, two groups could be distinguished on the basis of their response.

The first group (Clipper and Spartan) are characterised by a more pronounced acceleration of apical growth and development in late sowing than the second group of Domen, Golden Promise and Ymer and this was reflected in the significant ($p \leq 0.05$) reduction in the maximum spikelet primordium number for Clipper and Spartan between S.1 and S.3 in 1976 and between S.1 and S.2 in 1977. Associated with the more rapid apical development of these two cultivars in late sowing conditions is the high percentage spikelet primordium set down during the first three weeks of plant growth and development. The second group exhibited a less pronounced response to late sowing and this was reflected in both the small but non-significant reduction in spikelet primordium maximum and in the lower percentage set down.

3. Comparison between cultivar's apical response to daylength (growth room) and to sowing date in the field.

It was suggested in the Introduction to this section that daylength may be one of the main environmental factors influencing growth and development of barley in the field. Comparisons of the spikelet primordium number response to daylength in the growth room with the influence of sowing date on spikelet primordium number in the field may enable the relative importance of daylength in influencing the sowing date response to be evaluated.

The influence of sowing date on the apical development of the five cultivars examined in 1976 and 1977 (Clipper, Spartan, Domen, Golden Promise and Ymer) was similar to the influence of daylength on the apical development of these cultivars in growth rooms. Clipper and Spartan exhibited a pronounced hastening of apical development in long day and late sowing treatments resulting in a significant reduction ($p \leq 0.05$) in spikelet primordium maxima in both treatments (cf Figs 5, 14 and 15). The apical development of Domen Golden Promise and Ymer was less responsive to L.D. and late sowing treatments and this was reflected in their spikelet primordium maxima which were not significantly affected by either treatment compared with short days or early sowing, with the exception of Golden Promise in L.D. conditions (Tables 8, 13 and 14).

These observations apparently suggest that the response of spikelet primordium maximum to L.D. and to late sowing treatment is similar. This is also suggested by the significant relationships between the spikelet primordium maximum in long days (growth room) and the maximum attained

in the final sowing dates in 1976 (S.3) and in 1977 (S.2) (Table 16 , and the relationship between the spikelet primordium maximum in L.D. and in S.3 in 1976 is illustrated in Fig. 21. However, there are also significant correlations between the maximum in L.D. treatment and the maxima determined in S.1 and S.2 in 1976 (Fig. 21), and in S.1 in 1977. Thus it appears that a high spikelet primordium number in long days is a feature of cultivars that produced a high maximum for all sowing dates in the two years of field trials. It may be that daylength during the period of set down for all plants is relatively long even in the early sowings (12.9h for S.1 in 1976 and 12.0h for S.1 in 1977) compared with the 8h S.D. period in the growth room such that plants are exhibiting a long day response for all sowings. Similarly, the period of spikelet primordium production is prolonged in the early sowing date treatments such that maximum spikelet primordium number is attained in daylengths of over 16h.

If the early stages of apical development are examined, there was a significant relationship between the percentage of the spikelet primordium maximum set down at three weeks in long days with the percentage set down in the final sowings in 1976 (S.3) and in 1977 (S.2) but this relationship was not found in the early sowing dates (Table 17 and Fig. 22).

No relationship was found between the maximum spikelet primordium number in short days and the maximum attained in any of the sowing date treatments in either field trial. This can presumably be attributed to the longer daylengths impinging on plant growth and development for all sowing dates as described above.

TABLE 16. Relationship between the response of spikelet primordium max. to daylength (growth room) and to sowing date (field) for five barley cultivars.

Spikelet primordium max. (field)	Spikelet primordium max. (growth room) S.D.	L.D.
1976 S.1	r = 0.378 N.S.	r = 0.965 **
S.2	0.261 N.S.	0.967 **
S.3	0.230 N.S.	0.991 ***
1977 S.1	0.133 N.S.	0.977 **
S.2	0.187 N.S.	0.986 **

N.S. Not Significant

** significant at $p \leq 0.01$

*** " " $p \leq 0.001$

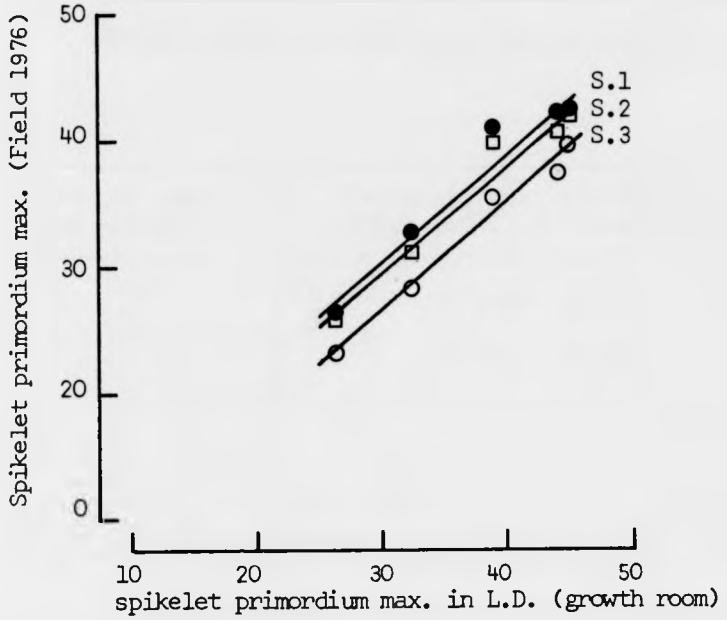


Fig. 21. Relationship between spikelet primordium max. in L.D. (growth room) and spikelet primordium max. in different sowing dates (in the field,1976)

● = S.1, 27.3.76
□ = S.2, 20.4.76
○ = S.3, 17.8.76

TABLE 17. Relationship between the percentage of the spikelet primordium max. set down at three weeks in long days (growth room) and in different sowing dates (field) for five barley cultivars.

Percentage max. set down at three weeks (field)		Percentage max. set down at three weeks L.D. (growth room)
1976	S.1	r = 0.588 N.S.
	S.2	0.761 N.S.
	S.3	0.910 *
1977	S.1	-
	S.2	0.985 **

N.S. Not significant

* significant at $p \leq 0.05$

** " " $p \leq 0.01$

\- not determined

TABLE 17. Relationship between the percentage of the spikelet primordium max. set down at three weeks in long days (growth room) and in different sowing dates (field) for five barley cultivars.

Percentage max. set down at three weeks (field)		Percentage max. set down at three weeks L.D. (growth room)
1976	S.1	r = 0.588 N.S.
	S.2	0.761 N.S.
	S.3	0.910 *
1977	S.1	-
	S.2	0.985 **

N.S. Not significant

* significant at $p \leq 0.05$

** " " $p \leq 0.01$

\- not determined

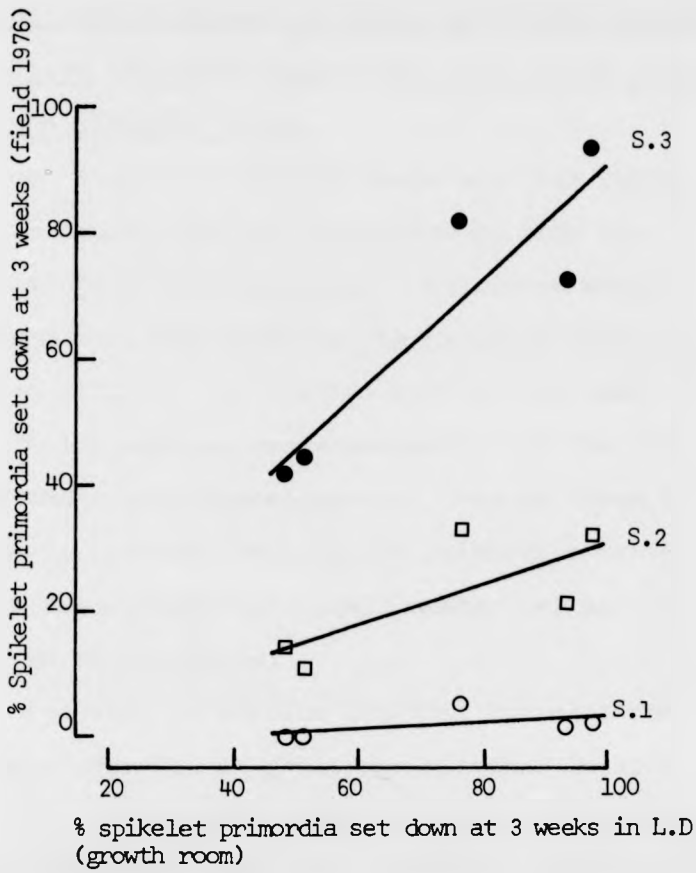


Fig. 22. Relationship between the percentage of the spikelet primordium max. set down at 3 weeks in L.D. (growth room) and the percentage set down in different sowing dates in the field (1976).

- ● S.1, 27.3.76, $y = 0.06x - 2.27$, $r = 0.585$ N.S.
- □ S.2, 20.4.76, $y = 0.33x - 2.09$, $r = 0.761$ N.S.
- ○ S.3, 17.5.76, $y = 0.91x - 0.03$, $r = 0.910$ $p \leq 0.05$

4. Relationship between spikelet primordium number, and spikelet and grain number per main ear of 14 genotypes in the field(in 1976).

It was suggested earlier (page 43) that spikelet primordium production was determined by both the duration and the initial rate of production. Cultivars which exhibited a low maximum were characterised by having a short period of production although the initial rate of set down was very rapid. A low maximum was associated with the early onset of set down and a high percentage set down at three weeks. The relationship between the spikelet primordium maximum per main shoot and the spikelet and grain number per main ear is examined in this section.

The spikelet primordium maximum, spikelet number and grain number for the 14 genotypes examined in sowing dates one and two in 1976 are presented in Table 18. The percentage reduction of these parameters with late sowing (S.2) is presented in Table 19. Data for the final sowing (S.3) in 1976 have been omitted because of the heavy rainfall immediately before harvest which resulted in severe lodging with subsequent grain loss.

The influence of sowing date on spikelet primordium maximum has been described earlier in the section (page 42). The 14 cultivars exhibited a wide range of spikelet number per main ear in S.1 and S.2 in 1976 and these values ranged from 17.1 (Clipper) to 30.7 (Spratt) in S.1 and from 18.5 (Clipper) to 31.9 (Spratt) in S.2. Sowing date appeared to have no consistent influence on spikelet number and differences between sowing dates are non-significant (Table 18).

Grain number per main ear was lower than the spikelet

TABLE 18. Influence of sowing date on spikelet primordium maximum spikelet number and grain number per main ear for 14 cultivars in the field in 1976.

Cultivar	Spikelet primordium maximum. a. S.1	S.2	Spikelet no/ main ear. b. S.1	S.2	grain no./ main ear. b. S.1	S.2
Clipper	26.2	26.3	17.1	18.5	14.7	15.9
Spartan	32.7	30.5	20.6	19.8	11.8	13.3
CI 5791	31.2	31.7	20.2	20.6	18.2 *	14.7
Ingrid	41.3	39.5	26.5	27.8	23.5	24.0
Chevallier	31.8	32.3	22.3	23.2	19.9	20.1
Bohmerwald	41.2	39.2	28.1	29.3	25.9	26.1
Lami	30.8	29.2	25.2	25.7	23.6	22.5
Domen	41.0	40.0	26.5	25.0	24.1 *	21.1
Maris Mink	78.7	37.7	26.1	28.4	24.2	25.8
Golden Promise	41.3	40.8	28.0	28.9	25.4	25.9
Spratt	45.3	45.8	30.7	31.9	27.8	26.4
Hillmarsh	40.7	37.8	28.3	27.8	26.2 *	24.0
Uzu	38.0	37.5	28.7	29.7	24.5 *	16.2
Ymer	42.0	40.7	29.4	29.7	26.7	26.2

a Values based on mean of 6 plants.

b Values based on mean of between 24 and 92 plants.

* L.S.D. significant at $p \leq 0.05$, calculated following an analysis of variance.

All other comparisons between S.1 and S.2 for: maximum spikelet primordium number, spikelet number per main ear, and grain number per main ear are not significantly different.

TABLE 19. The percentage reduction of spikelet primordium maximum, spikelet number and grain number per main ear in S.2 compared with S.1 for 14 cultivars in the field in 1976. A negative value denotes an increase in S.2

Cultivar	% reduction in S.2 of: spikelet primordia	spikelet number	grain number
Clipper	-0.01	-8.3	-7.9
Spartan	0.70	3.8	-13.4
CI 5791	-0.02	-1.7	19.3
Ingrid	0.04	-4.9	-2.0
Chevallier	-0.02	-4.0	-1.3
Bohmerwald	0.05	-4.5	-0.5
Lami	0.05	-1.8	4.8
Domen	0.02	5.7	12.5
Maris Mink	0.03	-8.8	-6.9
Golden Promise	0.01	-3.4	-1.8
Spratt	-0.01	-4.0	5.0
Hillmarsh	0.07	1.7	8.9
Uzu	0.01	-3.7	34.0
Ymer	0.03	-0.7	1.6

number for all cultivars and the values ranged from 11.8 (Spartan) to 27.3 (Spratt) in S.1 and from 13.3 (Spartan) to over 26 (Bohmerwald, Spratt and Ymer) in S.2. Later sowing has no consistent influence on grain number in the 14 cultivars examined (Table 18). Grain number was reduced in S.2 for seven cultivars and this reduction was significant ($p \leq 0.05$) for four of these but the increase in grain number for the other cultivars was not significant.

Sowing date in these field trials had no consistent influence on spikelet and grain number per main ear. It was suggested earlier (page 68) that the spikelet primordium maximum was not significantly different in S.2 compared with S.1 because of the prolonged period of set down in S.1 and thus the later stages of set down occurred in long days. The final sowing in 1976 (S.3) exhibited the most marked response of spikelet primordium production to late and thus may have been expected to show the most marked response of spikelet and grain number per main ear to late sowing, but this data is unfortunately not available.

It was noted earlier (page 51) that there was a significant relationship between the spikelet primordium maximum in long days (growth room) and final spikelet number in long days (glasshouse) and it was suggested that cultivars (e.g. Golden Promise) which exhibit a high maximum spikelet primordium maximum also exhibit a high final spikelet number. This suggestion is supported by the significant correlations between the spikelet primordium maximum and both spikelet and grain numbers for both sowing dates (Table 20) and their relationships are depicted in Figs. 23 and 24.

Maximum spikelet primordium number was much greater than

TABLE 20. Relationship between spikelet maximum, spikelet number and grain number per main ear with sowing date for 14 cultivars in the field in 1976.

	Sow. 1	Sow. 2
Spikelet primordia max./ main ear v. spikelet no/ main ear	r=0.912 ***	r=0.864 ***
Spikelet primordia max./ main ear v. grain no/main ear	0.812 ***	0.721 **
Spikelet no/main ear v. grain no/main ear	0.933 ***	0.865 ***

** significant at $p \leq 0.01$

*** " " $p \leq 0.001$

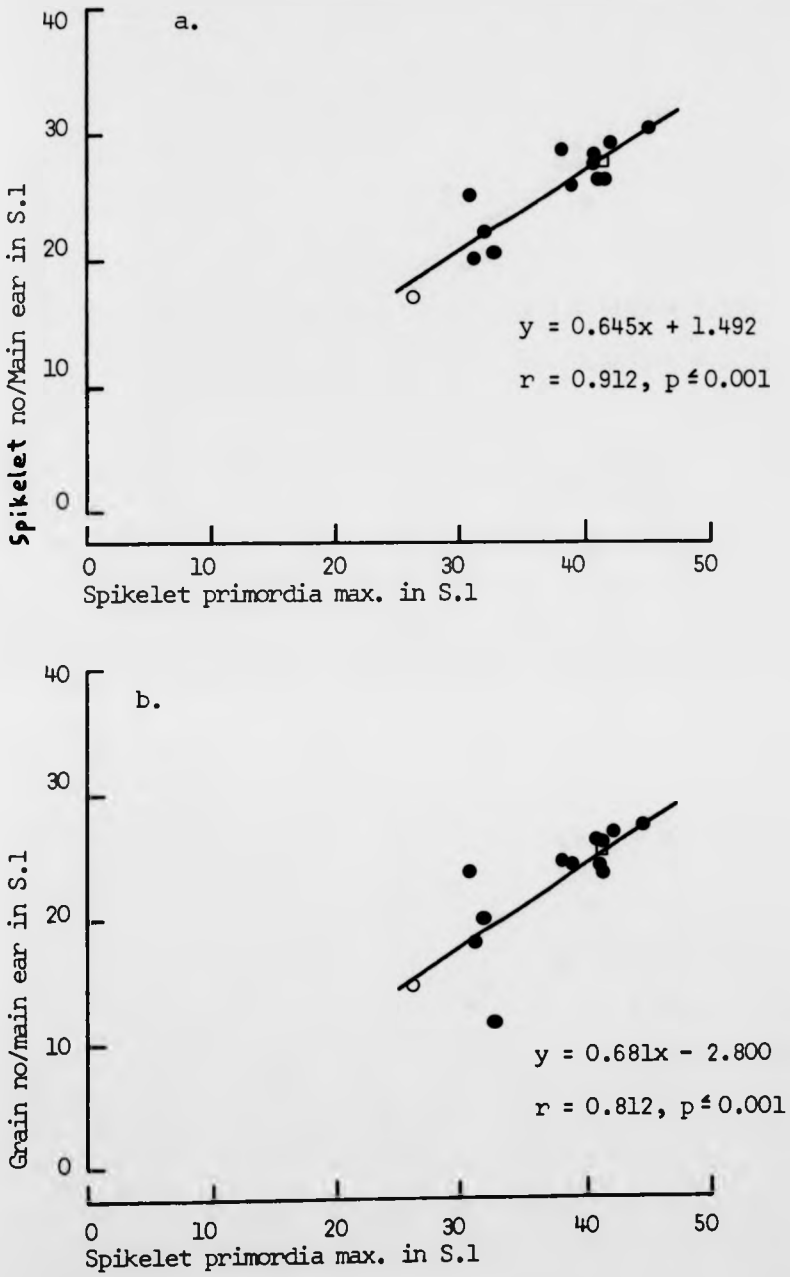


Fig. 23. Relationship between spikelet primordia max. and (a) spikelet no. and (b) grain no. per main ear in S.1 in 1976.

o = Clipper
□ = Golden Promise

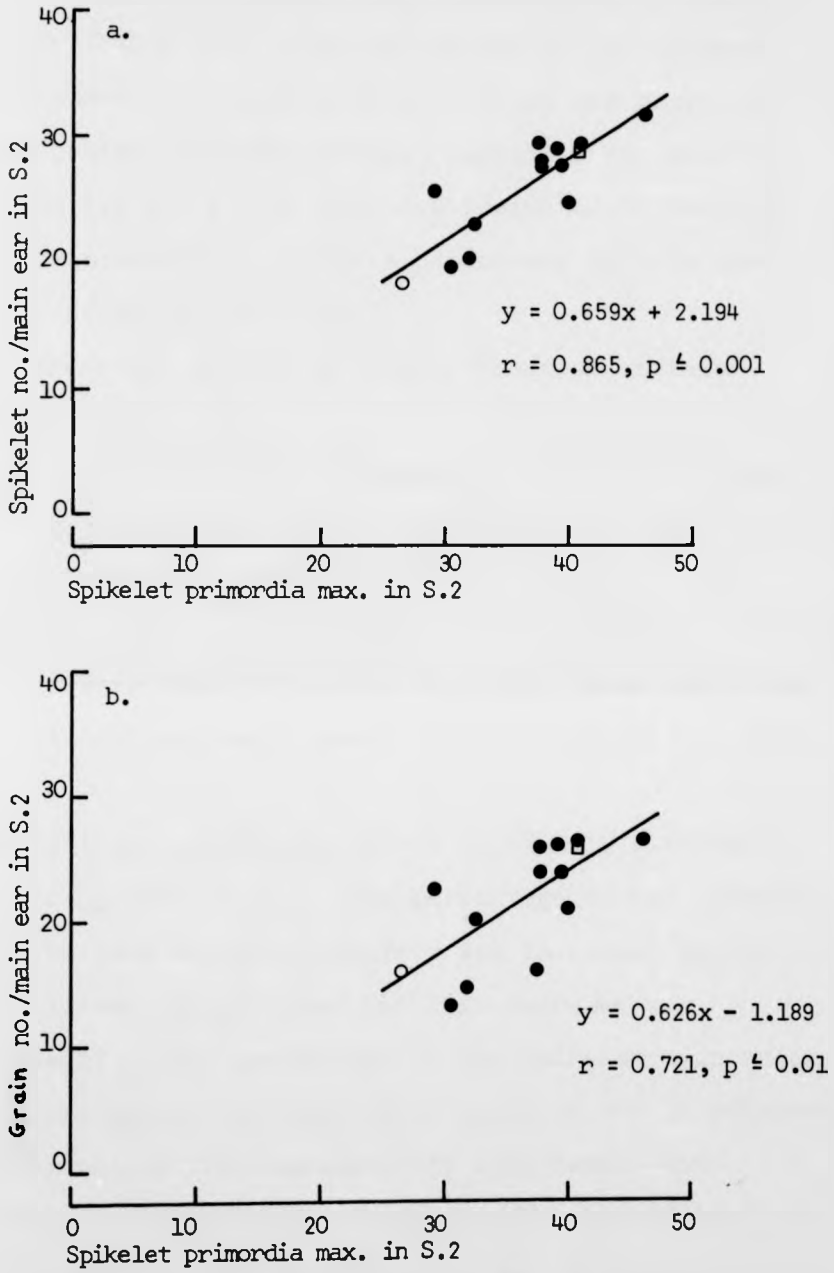


Fig. 24. Relationship between spikelet primordia max. and (a) spikelet no. and (b) grain no. per main ear in S.2 in 1976.

o = Clipper
□ = Golden Promise

the spikelet and grain numbers for all cultivars in both sowing dates (Table 18). The percentage of the maximum spikelet primordia which form spikelets and the proportion which form grains, and the spikelet fertility for the 14 cultivars in S.1 and S.2 in 1976 are presented in Table 21. The percentage reduction of these parameters in late sowing (S.2) is presented in Table 22.

The percentage of the spikelet primordium maximum which set spikelets and grains was low in both sowing dates, generally between 60 to 80% for spikelet number and between 50 to 70% for grain number for both sowing dates. The percentage of the spikelets which set grain was comparatively high. In S.1, all cultivars except Spartan (53.0%) exhibited a spikelet fertility greater than 85% and in S.2, only three cultivars (Spartan, CF 5791 and Uzu) showed a spikelet fertility less than 80%.

None of these parameters were consistently affected by delay in sowing (Table 22). The percentage of the spikelet primordium maximum to form spikelets was increased in S.2 for all cultivars except Domen but this increase was generally small. The percentage of the spikelet primordium maximum to set grains was reduced in eight of the 14 cultivars but the response of this parameter to late sowing was inconsistent and the range of response was large, from 33.1% (Uzu) to -21.4% for Spartan (i.e. an increased value in late sowing). All cultivars except Domen showed a reduction in spikelet fertility with late sowing and although this reduction was generally small, it was more marked in CI 5791 (20.7%) and Uzu (36.3%).

It may have been expected that cultivars which exhibit

TABLE 21. Influence of sowing date on the percentage of (a) spikelet primordium maximum which formed spikelets, (b) spikelet primordium max. which formed grains, and (c) spikelet number which set grains per main shoot ear for 14 cultivars in the field in 1976.

Cultivar	Percentage of spikelet primordium max. which form spikelets		Percentage of spikelet primordium max. which set grains		Percentage of spikelets which set grains	
	S.1	S.2	S.1	S.2	S.1	S.2
Clipper	65.2	70.2	56.1	60.2	86.1	85.8
Spartan	63.1	65.0	36.0	43.7	53.0	67.2
CI 5791	64.9	65.0	58.5	46.4	90.0	71.4
Ingrid	64.1	70.4	56.9	60.7	38.8	86.3
Chevallier	70.1	71.7	62.4	62.2	89.1	86.8
Bohmerwald	68.1	74.8	63.0	66.5	92.4	88.9
Lami	81.7	88.0	76.6	72.4	93.7	87.6
Domen	64.6	62.5	58.7	52.6	90.8	84.3
Maris Mink	67.4	75.3	62.8	68.5	92.6	91.0
Golden Promise	67.7	70.9	61.6	63.4	90.9	89.5
Spratt	67.7	69.6	61.3	57.6	90.6	82.8
Hillmarsh	69.6	74.5	64.5	67.3	92.6	86.3
Uzu	75.4	79.2	64.5	43.2	85.6	54.5
Ymer	67.8	72.9	63.5	57.5	90.6	88.5

TABLE 22. Percentage reduction of the percentage of (a) spikelet primordium maximum which formed spikelets, (b) spikelet primordium max. which formed grains, and (c) spikelet number which set grains per main shoot ear in S.2 compared with S.1 for 14 cultivars in the field in 1976.

A negative value denotes an increased percentage in S.2.

Cultivar	Percentage reduction in S.2 in the percentage of:		
	spikelet primordium max. - spikelet no.	spikelet primordium max. - grain no.	spikelet no. -grain no.
Clipper	-7.6	-7.3	0.4
Spartan	-3.0	-21.4	-17.9
CI 5791	-0.1	20.6	20.7
Ingrid	-9.7	-6.7	2.8
Chevallier	-2.4	0.3	2.6
Bohmerwald	-9.8	-5.6	3.8
Lami	-7.6	5.4	6.5
Domen	3.3	10.3	7.2
Maris Mink	-11.7	-9.7	1.8
Golden Promise	-4.5	-3.0	1.5
Spratt	-2.8	6.0	8.6
Hillmarsh	-7.1	-4.3	6.8
Uzu	-5.1	33.1	36.3
Ymer	-7.6	9.4	2.3

rapid spikelet primordium production may show a reduced capacity of the spikelet primordium maximum to set spikelets and grains (Kirby and Faris 1971 and Williams, R.H. personal communication 1979). However, consideration of the relationships between the difference between S.2 and S.1 in the percentage spikelet primordium set down at three weeks and the percentage reduction of the spikelet primordium capacity above, suggests that this is not the case ($r = 0.138$ and -0.028 respectively, both non-significant). This appears to indicate that the pattern of spikelet primordium production during the early stages of apical development is not an important determinant of the ability of the spikelet primordium number to set spikelets and grains. However, the largest difference in the pattern of spikelet primordium set down was observed between S.3 and S.1 in 1976. It may be possible that very rapid set down of spikelet primordia during early development, found in S.3, may result in a marked reduction in the proportion of the spikelet primordia which form spikelets and grains.

5. Influence of sowing date on grain yield.

i) 1976 field trial

Plant number per plot.

Plant numbers per plot for the 29 cultivars sown in S.1 and S.2 are presented in Table 23. Plant number (and final yield data) for S.3 has been omitted because of the heavy rainfall before harvest which resulted in severe lodging and subsequent yield reduction. Cultivars showed a large variation in plant number per plot in both sowing dates with a range between 20.7 (Early 12A Bonus) to 32.7 (Abacus) in S.1

TABLE 23. The effect of sowing date on plant number per plot for 29 barley cultivars in the field in 1976. A negative value denotes an increase in plant number in S.2

Cultivar	Plant no. per plot S.1	signif. L.S.D.	S.2	% reduction in S.2 compared with S.1
Early 12A Bonus	20.7		24.3	-17.7
Clipper	24.3		28.0	-15.1
Spartan	23.3		27.0	-15.7
Turkish 1106	25.7		27.0	- 5.2
CI 5791	24.0	*	29.7	-23.6
Ingrid	26.3		26.0	1.3
Banba	26.7		21.7	18.8
Chevallier	28.0		29.3	-4.8
Midas	30.7		25.7	16.3
Bohmerwald	29.0		28.7	1.1
Heils Franken	27.0		25.3	6.2
Lami	25.3		29.0	-14.5
Mimi	26.3		28.3	-7.6
Charlottetown 80	27.3		24.3	11.0
Domen	26.3		28.7	-8.9
Scotch Common	23.7		21.0	11.3
Tyra	31.7		27.3	13.7
Proctor	31.0		33.0	-6.5
Ark Royal	25.3		29.7	-17.1
Afghan R668	23.0		26.0	-13.0
Zephyr	25.7		27.7	-3.8
Maris Mink	27.7		25.3	8.5
Ariel	29.3		27.0	7.9
Golden Promise	27.7		25.7	7.2
Abacus	32.7		29.0	11.2
Spratt	23.7		27.0	-14.1
Hillmarsh	25.7		28.3	-10.4
Uzu	25.7		23.3	9.1
Ymer	27.3		28.0	-2.5

* significant at $p \leq 0.05$ L.S.D. calculated following an analysis of variance.

and between 21.0 (Scotch Common) to 33.3 (Proctor) in S.2. The effect of sowing date on plant number was inconsistent and only one cultivar (CI 5791) showed a significant response ($p \leq 0.05$) to late sowing. Clearly, plant establishment was not significantly influenced by sowing date and variations which existed may be due to soil conditions.

Grain yield per plant.

The separate components of grain yield per plant:ear number per plant; grain number and 1000 grain weight per main ear; and grain number and 1000 grain weight per tiller ear for the 29 cultivars in S.1 and S.2 were measured separately and are presented in Tables III a, b in the Appendix. The computed grain number per ear, grain number per plant and 1000 grain weight for each sowing are included in these tables. The percentage reduction of these parameters in S.2 are presented in Table IV in the Appendix.

Final grain yield is calculated as the grain yield per plant and the results for the 29 cultivars in S.1 and S.2 are presented in Table 24. Cultivars exhibited a wide range in grain yield per plant in each sowing date from 2.51 g plant^{-1} (Spartan) to 6.1 (Lami in S.1 and from 2.23 (Spartan) to 4.66 g plant^{-1} (Ymer) in S.2. Grain yield per plant was reduced in the late sowing (S.2) for all cultivars (Table 25) and this decrease was significant ($p \leq 0.05$) for 22 of the 29 cultivars. Cultivars exhibited a wide range in the magnitude of the response of grain yield to sowing date and the percentage reduction of grain yield per plant in S.2 compared with S.1 ranged from 5.6% (Midas) to a reduction of over 40% (CI 5791, Charlottetown 80 and Uzu).

TABLE 24. Influence of sowing date on grain yield per plant of 29 barley cultivars in the field in 1976. All values of grain yield per plant in g plant^{-1}.

Cultivar	Grain yield per plant S.1	signif. L.S.D.	S.2	% reduction in S.2 compared with S.1
Early 12A Bonus	4.62	*	3.80	17.8
Clipper	4.34	*	2.93	32.5
Spartan	2.51		2.23	11.2
Turkish 1106	4.40	*	3.12	29.1
CI 5791	3.98	*	2.24	43.7
Ingrid	5.27	*	3.57	32.6
Banba	4.54	*	3.26	28.2
Chevallier	4.87	*	3.42	29.8
Midas	4.45		4.20	5.6
Bohmerwald	4.23		3.74	11.6
Heils Franken	4.85	*	3.26	32.8
Lami	6.10	*	4.67	23.4
Mimi	4.20	*	2.98	29.1
Charlottetown 80	4.18	*	2.45	41.4
Domen	3.83		3.34	12.8
Scotch Common	4.11		3.55	13.6
Tyra	5.46	*	4.33	20.7
Proctor	4.52		3.86	14.6
Ark Royal	5.62	*	4.36	22.4
Afghan R668	4.61	*	2.78	39.7
Zephyr	4.68	*	3.68	21.4
Maris Mink	4.71		3.74	15.2
Ariel	4.77	*	3.69	22.6
Golden Promise	3.85	*	2.80	27.3
Abacus	5.43	*	3.57	37.9
Spratt	5.10	*	3.14	38.4
Hillmarsh	4.71		4.03	14.4
Uzu	4.62	*	2.27	55.2
Ymer	6.06	*	3.97	34.5

* Significant at $p \leq 0.05$, L.S.D. calculated following an analysis of variance.

TABLE 25. Percentage reduction of grain yield per plant and grain yield components in S.2 compared with S.1 in 1976. A negative value denotes an increase in S.2

Cultivar	Percentage reduction in S.2 of: grain yield per plant	ear no. per plant	grain no. per ear	grain no. per plant	1000 grain weight
Early 12A Bonus	17.8	14.8	-4.3	11.0	8.7
Clipper	32.5	31.4	-7.3	26.5	8.7
Spartan	11.2	12.0	-7.7	5.3	6.5
Turkish 1106	29.1	22.8	2.9	25.1	7.2
CI 5791	43.7	22.0	28.8	44.4	0.3
Ingrid	32.6	25.7	-6.7	20.7	15.2
Banba	28.2	18.1	7.8	24.5	6.2
Chevallier	29.8	22.0	-1.3	21.9	12.0
Midas	5.6	6.9	2.1	8.8	-2.8
Bohmerwald	11.6	8.5	0.9	9.2	2.4
Heils Franken	22.8	6.4	13.7	19.2	15.9
Lami	23.4	22.6	5.8	27.1	-0.6
Mimi	29.1	29.4	-0.1	29.0	0.9
Charlotte Town 80	41.4	25.5	6.3	30.2	17.5
Domen	12.8	3.0	7.6	10.4	0.8
Scotch Common	13.6	2.8	2.4	5.1	7.1
Tyra	20.7	32.6	-14.4	22.7	-3.4
Proctor	14.6	19.8	-6.3	14.7	-1.7
Ark Royal	28.4	19.0	-11.1	10.0	15.3
Afghan R668	39.7	2.2	23.7	25.4	21.0
Zephyr	21.4	20.0	0.8	20.6	1.4
Maris Mink	15.2	13.9	-3.8	10.7	6.3
Ariel	22.6	13.4	-3.5	10.4	10.8
Golden Promise	27.3	31.4	-6.6	26.8	-1.8
Abacus	37.9	30.4	1.1	31.2	9.8
Spratt	38.4	27.5	13.7	37.4	8.6
Hillmarsh	14.4	0.9	8.1	8.9	6.8
Uzu	55.2	26.1	30.4	48.6	5.1
Ymer	34.5	31.1	-0.4	30.2	6.2

Components of grain yield.

The percentage reduction of the components of grain yield per plant:ear number per plant, grain number per ear and 1000 grain weight in late sowing (S.2) compared with early sowing (S.1) are presented in Table 25. The percentage reduction of grain number per plant in S.2 is also included. Late sowing caused a marked decrease in ear number per plant in all 29 cultivars and there was a wide range in the magnitude of the cultivar's response to late sowing from a percentage reduction in S.2 of 2.0% (Afghan R668) to over 30% (e.g. Clipper). Ear number per plant is clearly influenced by late sowing and was significantly correlated ($p \leq 0.01$) with the percentage grain yield per plant reduction in S.2 (Table 26).

Grain number per ear was reduced with delay in sowing for 16 of the 29 cultivars (Table 25). Cultivars again exhibited a range in the magnitude of their response to late sowing from 30.4% reduction in S.2 to an increase in grain number per ear (i.e. -14.4% reduction in S.2, for Tyra). Although the results appear inconsistent there was a significant correlation ($p \leq 0.01$) (Table 26) between the percentage reduction in grain yield per plant and the percentage grain number per ear reduction in S.2.

Grain number per plant is derived from the combination of the two above components of grain yield per plant:ear number per plant and grain number per ear. The response of grain number per plant to late sowing therefore follows a similar pattern to than observed for the two component parameters. Grain number per plant was decreased in S.2 for all cultivars and the percentage reduction varied from

TABLE 26. Relationship between the percentage reduction of grain yield per plant with the percentage reduction of the components of grain yield per plant in S.2 compared with S.1 for 29 genotypes in 1976.

Percentage reduction of components of grain yield per plant in S.2	Percentage reduction of grain yield per plant in S.2
ear number per plant	r = 0.518 **
grain number per ear	0.573 **
grain number per plant	0.902 ***
1000 grain weight	0.405 *

significant at:

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

around 5% (Spartan and Scotch Common) to over 40% (CI 5791 and Uzu). This parameter was significantly correlated ($p \leq 0.001$) with the percentage reduction in grain yield per plant (Table 26) and this relationship is depicted in Fig. 25.

The third component of grain yield per plant, 1000 grain weight was generally decreased with late sowing although five cultivars (Midas, Lami, Tyra, Proctor and Golden Promise) showed a slight increase in grain weight in S.2 (Table 25). Cultivars again exhibited a range in the magnitude of their response to late sowing from 21.0% reduction in S.2 (Afghan R668) to an increase in S.2 (-3.4% reduction, Tyra). The percentage reduction of 1000 grain weight in S.2 was just significantly correlated ($p \leq 0.05$) with the percentage grain yield reduction (Table 26).

The decrease in grain yield per plant with late sowing was primarily associated with the reduced grain number per plant ($r = 0.902$, $p \leq 0.001$). Both components of grain yield contributing to this parameter (ear number per plant and grain number per ear) were also correlated ($p \leq 0.01$) with the grain yield reduction. Grain weight, although influenced by sowing date, was not a major determinant of the grain yield reduction in late sowing in this study.

ii) 1977 field trial.

Plant number per plot.

Plant number per plot for both sowing dates in 1977 are presented in Table II, Appendix. There was a significant decrease ($p \leq 0.05$) in plant number per plot for all cultivars in S.2. Seedling establishement was poor in S.1 because of the heavy rainfall at the time of sowing and this was reflected in the final plant number per plot. Because of

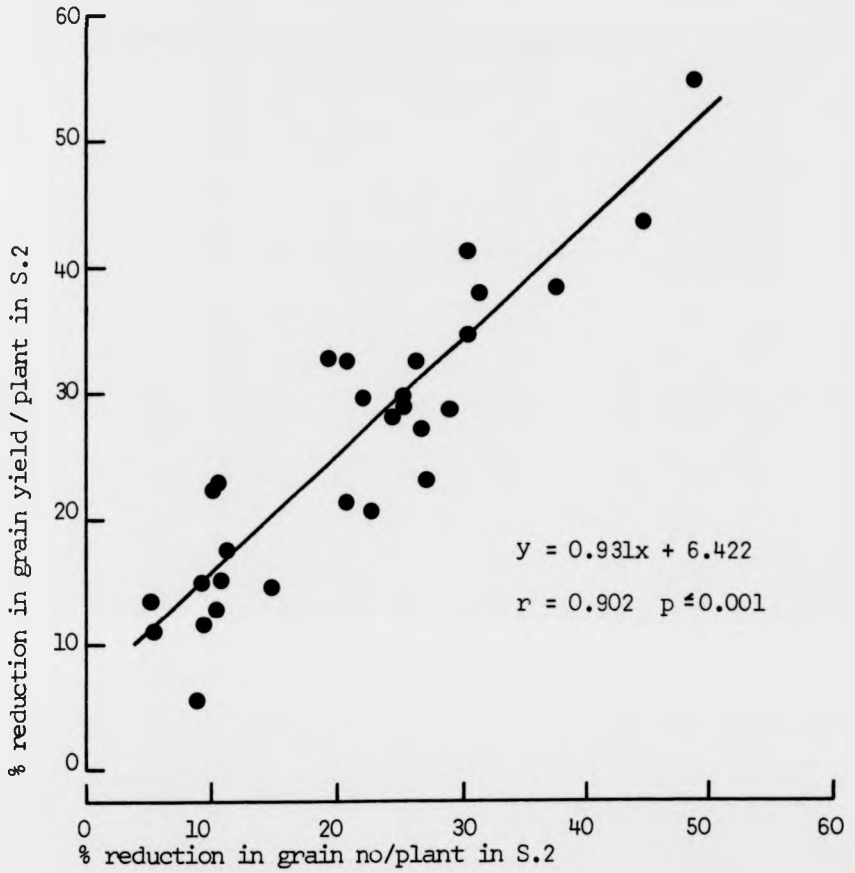


Fig. 25. Relationship between percentage reduction in grain no/plant in S2 and percentage reduction in grain yield/plant in S.2 in the field in 1976.

the significant reduction in plant number, the effect of sowing date is confounded by density and therefore the results of grain yield will not be presented.

DISCUSSION

Previous studies on the effect of environmental factors such as daylength and sowing date on barley growth and development have tended to concentrate on mature plant morphological characters. In this study, emphasis has been placed on the effect of these factors on apical development of the main shoot and the subsequent effect on spikelet and grain number per main ear and final grain yield per plant.

The discussion is divided into five sub-sections which follow the style of presentation used in the Results section. The first two parts consider the influence of daylength on spikelet number and apical development under controlled environment conditions and the next two consider the influence of sowing date on apical development and final grain yield in the field. The final sub-section discusses the importance of daylength in determining the apical response to sowing date in the field.

Influence of daylength on spikelet number

Barley has been described as a quantitative long day plant in terms of the increased rate of plant growth, and earlier heading and maturity in long days compared with short days (Takahashi and Yasuda 1960; Ormrod 1963; Kirby and Eisenberg 1966 and Kirby 1969a). Cultivars differ, however, in the magnitude of their response to daylength; some exhibit a marked response to daylength treatment, and others are virtually day-neutral. The glasshouse daylength study confirms the wide range between cultivars in the magnitude of their response to long day treatment. Although plant growth and development was accelerated in L.D. compared with S.D. treatment,

the final spikelet number per main ear was generally not significantly influenced by daylength regime. However, 18 of the 98 cultivars did exhibit a significant decrease ($p \leq 0.05$) in spikelet number in long days and four cultivars showed a significant increase in the L.D. treatment.

The second daylength study carried out in growth rooms in which the response of apical development to daylength was examined, indicated that maximum spikelet primordium number was determined about 84 days after sowing (84 d.a.s.) in the S.D. treatment. The time of the switch of the S.D. plants to L.D. conditions in this glasshouse study (90 d.a.s.) therefore coincides with the cessation of spikelet primordium production. Studies on barley in which daylength has been altered at different stages of plant growth have shown that optimum spikelet number is attained as a result of S.D. treatment during the period of spikelet primordium production followed by long days until maturity (Guitard 1960, and Thorne et al 1967). The observed high spikelet number of Ymer and several other cultivars in S.D. conditions may be the result of the optimal combination of the two daylength regimes for spikelet primordium production.

Final grain number per ear could not be determined for many of the cultivars because of poor grain set and, in many instances, the ears failed to emerge from the flag leaf sheath. Reduced fertility in short days has been found by other workers (Borthwick et al 1941 and Guitard 1960) especially if combined with low light intensity. This suggests that the reduction in spikelet survival may be caused by insufficient assimilate supply to maintain a high spikelet number. Short days have also been shown to reduce spikelet

fertility as a result of male sterility (Batch and Morgan 1974) and this effect was greatest when S.D. treatment given during the period of apical development.

Floret fertility may also be affected by the low nutrient availability and restricted root growth often associated with pot experiments carried out in controlled environment conditions. Low nutrient levels has been shown to decrease both leaf and spikelet number (Aspinall 1961 and Holmes 1973) and Single (1964) has suggested that spikelet fertility may be reduced by low nitrogen levels at ear emergence. Although liquid nutrient ('Vitafeed 101') was supplied to the plants 80 days after sowing, this may not have been sufficient for the continued normal growth and development of the plants until maturity.

Several workers have attempted to link the cultivar's response to daylength with the latitude of origin but no consistent relationship has been suggested (Kirby and Eisenberg 1966 and Kirby 1969a). From the glasshouse data it is possible to distinguish certain broad trends between the daylength response and the latitude of accession but the picture is confused because some cultivars do not fit the pattern.

Cultivars from N.W. European latitudes (e.g. Norway, Sweden and Great Britain) tend to be less responsive to daylength than cultivars from Mediterranean and Australian growing conditions. For example, Clipper (Australia), Spartan (America), Turkish 1106 (Turkey), Jet (Ethiopia) and La Prevision 19 (Argentian) show a marked response to L.D. compared with S.D. treatment with a marked reduction in spikelet number. N.W. European cultivars, on the other hand, tended to be less responsive to daylength and determined a similar spikelet number in both S.D. and L.D. treatments. This

suggestion finds support in the review by Kirby (1969) who noted that there was a closer link between Mediterranean-Australian cultivars than between British-Australian genotypes. However, several cultivars do not fit into this pattern, e.g. Early 12A Bonus (Sweden) was sensitive to L.D. treatment but Nepal and Ethiopian ST.473 were not influenced by daylength. Not all the cultivars examined in this study are commercially sown in the country of accession which itself may not be the country of origin. No direct relationship between the response to daylength and the latitude of the country of origin can, therefore, be suggested. However, the response to daylength can still be used to predict how a cultivar may behave in a new area and this aspect will be discussed later.

Influence of daylength on apical development

The cultivars examined in this study (Clipper, Spartan, Domen, Golden Promise and Ymer) exhibited accelerated apical development in L.D. compared with S.D. treatment and thus confirms the earlier study by Aspinall (1966). Cultivars differed in the magnitude of their apical response to long days and these differences were reflected in the spikelet primordium production. Clipper and Spartan exhibited a marked response to L.D. treatment with a significant reduction in the spikelet primordium maximum. The other cultivars were less responsive to daylength; Ymer attained a similar maximum in both daylength treatments, and Golden Promise exhibited an increase in spikelet primordium maximum in long days.

It has generally been assumed that environmental conditions such as long days which lead to more rapid apical development also result in a lower maximum spikelet primordium

number. The result for Golden Promise would appear to contradict this assumption but Aspinall (1966) found that two cultivars in his study (Proctor and Piroline) also attained a higher maximum in 16h than 8h daylength in spite of the faster apical development. A possible explanation for this observation will be discussed later (Section 3, page 118).

Maximum spikelet primordium number was found to be determined by both the duration and initial rate of production. Although the initial rate of production was increased in L.D. compared with S.D. treatment the duration of set down was reduced and thus a lower spikelet primordium maximum was often determined. This has also been found by Aspinall and Paleg (1963) and Paleg and Aspinall (1964) for barley, and Rawson (1971) and Lucas (1972) for wheat. The duration of set down of Golden Promise and Ymer was less responsive to daylength than that of Clipper and Spartan and, therefore, a higher maximum was determined.

A low spikelet primordium maximum was associated with early onset of spikelet primordium production and this is itself determined by the final leaf number per main shoot. Many studies have associated the rapid plant growth and development in long days with reduced leaf number and have suggested that the response of leaf number to daylength is a good indication of the cultivar's response to daylength (Gott et al 1955; Aspinall 1966; Pugsley 1966 and Rawson 1970, 1971).

This is clearly confirmed in this study; cultivars which were responsive to L.D. treatment and attained a low spikelet primordium maximum also determined a low leaf number. For

example, Clipper produced only 7.0 leaves per main shoot in L.D. conditions and this agrees well with Dale and Wilson (1978) who found a final leaf number of 6.0 at high nutrient levels under L.D. conditions. It is known that the number of primordia in the dry grain is between three and four and thus at least two further leaf primordia have to be set down before spikelet primordium formation can occur (Kirby 1974).

Associated with the early onset of spikelet primordium production was the percentage of the maximum set down during the first three weeks of plant growth and development. This parameter is determined by both the onset and the initial rate of production and was closely correlated ($p \leq 0.001$) with the final maximum attained. The five cultivars examined showed marked differences in their response to daylength and two physiological groups could be distinguished. Clipper and Spartan exhibited a higher percentage set down at three weeks in L.D. compared to the second group of Domen, Golden Promise and Ymer resulting in a low spikelet primordium maximum.

Aspinall (1966) in his study of ten barley cultivars also distinguished two groups on the basis of the magnitude of their response to daylength. Although none of the cultivars examined in his study were duplicated in this present study, it is interesting to note that the two Australian cultivars examined (Noyep and Prior) were very responsive to daylength (cf. Clipper in this study) and Proctor and Freja (Great Britain and Sweden respectively) were less responsive (cf. Domen-Norway, Golden Promise-Great Britain and Ymer-Sweden).

Previous studies have attempted to link cessation of spikelet primordium production with certain apical developmental stages. Aspinall and Paleg (1963) and Nicholls and

May (1963) have suggested tha maximum spikelet primordium number coincides with the formation of stamen initials but data from this study and the 1977 field trial suggests that the maximum occurs at awn initial stage of development and is, therefore, in agreement with Kirby and Faris (1970) and Kirby (1971).

Because the response of apical development and spikelet primordium production to daylength are similar Aspinall and Paleg (1963) and Nicholls and May (1963) have suggested that both are under the same endogenous control. Several authors have implicated gibberellins in the control of apical development and floral organogenesis (Nicholls and May 1964 and Kirby and Faris 1970).

Gibberellic acid (GA) concentration within the shoot apex is known to be greater in L.D. compared with S.D. plants both at double ridges and at stamen initial stages of apical development (Nicholls and May 1964). Further work by James and Lund (1965) and Nicholls (1974, 1978) has shown that a single application of GA to a young barley plant resulted in enhanced apical growth which Nicholls (1978) suggested could be caused either by a direct effect on meristem growth or an effect on the diffusivity of nutrients to the meristem.

Radley (1970) found that G.A. stimulated apical growth of tall but not dwarf wheat cultivars and she suggested that this could be caused by a block on the utilization of GA in dwarf genotypes. Similarly, Holmes (1973) suggested that the regulation of development of both apical and lateral meristems in the wheat shoot apex may involve the relative rates of utilization of GA and inhibitor(s) such as abscissin

rather than their relative levels. He further suggested that apices of dwarf wheats contained high levels of GA with a corresponding reduction in the GA gradient within the apex. The low level of utilization would delay formation and development of spikelet primordia and result in the synchronous development of the primordia and a high maximum spikelet primordium number. For the other wheat cultivar examined in his study (Marquis, tall cultivar) he suggested that the rapid development in long days was due to the steep gradient of GA within the apex and high rate of utilization resulting in rapid spikelet development with a low final spikelet number. He suggested that the apical development of this cultivar in short days was, therefore, limited by the endogenous GA level.

Similarly, Kirby and Faris (1970) linked the rapid apical development of barley at high plant densities with high GA levels. The authors proposed that during the early stages of apical development, assimilates for spikelet primordium set down and for spikelet growth resulted from diffusion through the apex but that, after a period, the demand for assimilates by the growing spikelets would establish a gradient within the apex and new primordium set down would stop. At high plant densities, the more rapid floret organogenesis may give rise to earlier competition for assimilates thereby causing a reduction in the supply to the meristem dome, and thus an early cessation of primordium set down would result with a correspondingly low maximum number. The low spikelet number may therefore be caused by either an increase in GA concentration resulting in accelerated apical development and/or a reduction in assimilate supply to the apex.

Both Kirby and Faris (1970) and Holmes (1973) have suggested that endogenous gibberellic acid concentration may be increased because of differences in the light environment such as daylength or light intensity.

Although it seems likely that apical development is under some form of hormonal control, further investigation is required before the mechanism of endogenous control is fully understood.

The effect of daylength on the early development of the plant was also reflected in final spikelet number per main ear ($r = 0.970$, $p \leq 0.01$) in the L.D. treatment although this relationship was not found under short days. As indicated earlier, this suggests that a cultivar's response to daylength is linked with its response to long days; the range of spikelet primordium maximum and final spikelet number between cultivars being greater in L.D. compared with S.D. treatment.

Degeneration of the distal spikelet primordia involves the death of a comparatively large number of primordia with a loss of potential spikelets of between 10 and 15 (growth room daylength study and 1976 sowing date field trial; and Kirby 1973, 1977). It has been suggested that tip degeneration may be caused by increased concentrations of endogenous gibberellic acid (GA) in the shoot apex resulting in more rapid floret morphogenesis (Kirby and Faris 1970) or as a result of different levels in the rate of utilization of GA (Holmes 1973). This may then give rise to an earlier competition for assimilates with a subsequent reduction in assimilate supply to the apical dome and distal primordia.

During the early stages of apical development, undifferentiated leaf and spikelet primordia will be dependent

on diffusates from the ends of phloem tubes (Kirby and Rymer 1974). Inflorescence procambial traces are first formed in the lower-mid region of the apex and differentiation then proceeds both acropetally and basipetally. Procambial connections to the rest of the plant were not completed until later in development and protophloem was again formed initially in the lower-mid region of the apex but was not formed in the terminal 10 to 16 spikelets which subsequently aborted. The authors suggested, therefore, that the relative growth rates found in the ear and the death of the terminal spikelet primordia may be related to vascular differentiation.

It is interesting to note that both these suggestions to explain tip degeneration are linked to the supply of assimilate to the developing apex. Both studies associate death of the distal spikelet primordia with a reduced carbohydrate supply to the meristem dome and although this was not examined in the present study this suggestion will be discussed later in this thesis (Section 4.).

The extent of the variation of the response of maximum spikelet primordium number between cultivars to daylength (in growth rooms, Table 8) reflected that of spikelet number (in the glasshouse, Table 5) and is thus in agreement with the earlier work of Aspinall (1966, cf. Fig.3 and Table 2). Maximum spikelet primordium number was significantly correlated with final spikelet numbers ($r = 0.970$, $p \leq 0.01$) in long days although no such relationship was found in short days. Cultivars which have a high spikelet primordium maximum in long days similarly attain a high final spikelet number compared with cultivars with a lower maximum number of spikelet primordia. This has been found by other workers

both for barley (Aspinall 1966) and for wheat (Rawson 1971 and Holmes 1973) over a range of genotypes thus indicating the generality of this relationship. Environmental factors such as daylength which affect the apical development of the plant, therefore, have an important influence on final spikelet numbers and, therefore, on potential grain yield. The effect of sowing date treatment in the field on apical development, and on spikelet and grain number per main ear and grain yield per plant is discussed in the following three sub-sections.

Influence of sowing date on apical development in the field.

Apical development and spikelet primordium production was hastened with progressive delay in sowing in both field trials and the magnitude of the accelerated apical development was reflected in the maximum spikelet primordium number attained. Nine of the 14 cultivars in 1976 showed a significant reduction ($p \leq 0.05$) in the maximum in the final sowing (S.3) compared with early sowing (S.1). In 1977, two of the five cultivars (Clipper and Spartan) exhibited a significant reduction ($p \leq 0.05$) in the maximum with late sowing (S.2) compared with S.1 whereas the other cultivars (Domen, Golden Promise and Ymer) were unaffected.

No comparable study has examined the effect of sowing date on apical development of barley cultivars in the field. In a night break study carried out in the field, Paleg and Aspinall (1966) found that light treatment accelerated apical development and spikelet primordium production with a subsequent reduction in the maximum spikelet primordium number. The reduced maximum was caused by a reduction in the

period of set down and is thus in agreement with the present study in suggesting that the duration of spikelet primordium production is an important parameter determining the final maximum number attained. The determining influence of the duration of the set down period on the maximum has also been noted by Kirby and Faris (1970). In their study, the low spikelet number of barley plants sown at high densities was caused by the earlier cessation of spikelet primordium production; the rate of production was unaffected by density treatment.

The similarities between the apical response of the five cultivars to daylength and the apical response of these cultivars to sowing date in the field suggested that daylength was an important environmental factor determining the influence of sowing date on plant growth and development. This is in agreement with other workers (Aspinall 1966, Kirby and Eisenberg 1966 and Kirby 1969a) who have also suggested that daylength is one of the main environmental factors influencing plant growth.

However, many other environmental factors including light intensity and temperature also influence plant growth and both are confounded with daylength in the sowing date response. Both environmental factors are known to accelerate apical development and spikelet primordium production for both barley and wheat. High light intensity, however, results in a higher spikelet number per ear (Aspinall and Paleg 1963 for barley, and Friend et al 1963 and Friend 1965 for wheat) whereas high temperature results in a reduction in spikelet number (Aspinall 1965 for barley, and Friend et al 1963; Friend 1965 and Wall and Cartwright 1974 for wheat).

All three environmental factors of daylength, light intensity and temperature will influence apical development in the field and all three are confounded in the sowing date treatment. Several workers (Aspinall 1969 for barley, and Rawson 1970, 1971 and Wall and Cartwright 1974 for wheat) have indicated that the second-order interactions between these factors and their effect on apical development is complex. However, the significant relationship found between the apical response to daylength and to sowing date ($r = 0.991$, $p \leq 0.001$, for S.3 in 1976) indicates that daylength is an important environmental influence on apical development in the field and this relationship is discussed more fully on page 92. The influence of temperature on apical development of two cultivars which contrasted in their response to sowing date treatment in the field (Clipper and Golden Promise) is examined in the next section (Section 2). A comparison of the apical response to daylength and to temperature with the response found to sowing date treatment may enable the relative importance of daylength and temperature on apical development in the field to be evaluated.

Influence of sowing date on grain number and final grain yield in the field.

The extent of the variation between genotypes in the response of spikelet primordium maximum to sowing date (S.1 and S.2 in 1976) in the field was reflected in the wide range of spikelet and grain numbers per main ear (Table 18). Spikelet and grain numbers were again closely linked with the spikelet primordium maximum such that cultivars with a high maximum number also attained a high spikelet and grain number compared with cultivars with a lower maximum, and thus confirmed

the earlier suggestion of this relationship (page 51). Sowing date treatment (S.1 and S.2 in 1976) appeared, however, to have no influence on spikelet or grain numbers but, as noted earlier (page 68), maximum spikelet primordium number was similar in these two sowing dates because of the long period of set down in S.1 such that the later stages of spikelet primordium production and subseuqent tip degeneration occurred under the same environmental conditions as S.2. Maximum spikelet primordium number was reduced in the final sowing (S.3) in 1976 for some genotypes and this reduction might have been expected to be reflected in a decreased spikelet and grain number. Unfortunately, this data is not available and further work is required before the influence of sowing date on the degeneration of distal primordia and the parameters determining the subsequent spikelet and grain numbers in the field is fully understood.

Grain yield (defined as grain yield per plant) was reduced with late sowing for all cultivars and thus confirms the previous studies on barley of Kirby (1969b); Jessop and Ivins (1970); Davies (1973) and Nass et al (1974). The reduction in yield was more closely correlated with ear number per plant and grain number per ear than 1000 grain weight and this indicated the importance of sink capacity in determining yield. However, because of the compensation which occurs between these components of grain yield it is not possible to consistently associate reduction in grain yield with any one component. Kirby (1969b) and Davies (1973) found that the grain yield reduction with late sowing was caused by a reduction in grain number per ear and 1000 grain weight. Ear number per m^2 was either unaffected by sowing date (Davies 1973)

or increased with late sowing (Kirby 1969b). Studies by Jessop and Ivins (1970) on the other hand indicated that reductions in grain yield of barley and wheat were correlated with ear number per m^2 and grain weight was relatively constant. It is difficult to reconcile the differences between the above studies.

Many workers including Willey and Holliday (1969) and Langer and Dougherty (1976) have suggested that grain number per unit area rather than 1000 grain weight is the main determinant of grain yield. In a series of shading studies on barley and wheat, Willey and Holliday (1971a,b) found that grain yield was generally more closely related to grain number per m^2 than to grain weight. The effect of shade treatment on grain yield and the components of grain yield was dependent on the stage of treatment.

In barley, shade treatment between seedling establishment and ear initiation decreased yield by reducing ear number per m^2, and shading between ear initiation and anthesis caused marked reductions in yield due to a large decrease in grain number per ear although grain weight was also slightly decreased. Shading after anthesis did not reduce yield as might have been expected and they suggested that this was due to compensation by stored pre-anthesis carbohydrate transported to the grain during the post-anthesis period. These results indicate the importance of sink capacity in determining grain yield and, because of the effect of late pre-anthesis shading on grain weight, the authors suggested that the potential grain size may be partly determined by environmental factors during the early growth of the plant.

In wheat, early pre-anthesis shading caused a slight

decrease in spikelet number per ear. Later shading during the pre-anthesis period decreased yield by a reduction in grain number per spikelet. In contrast to the barley study however, post-anthesis shading did result in decreased grain weight which they suggested may be due to the limited compensatory ability of wheat compared with barley. Thinning of the wheat plants produced a slight increase in grain yield, and yield per ear decreased as thinning was progressively delayed and decreased most rapidly at high populations. Because grain weight was little affected by time of thinning, they suggested that both source and sink factors operate in limiting yield.

In a study on the two-row barley cultivar, Proctor, Gallagher et al (1975) found that grain weight was relatively constant over a wide range of environmental conditions and grain yield was more closely associated with grain number per m^2 than grain weight. Recent studies by Williams and Hayes (1977) on barley, and Bremner and Davidson (1978) and Pinthus and Millett (1978) on wheat also confirmed the importance of grain number per m^2 in determining grain yield. Williams and Hayes (1977) noted that a plateau in yield was not reached in their study even with high grain number and suggested, therefore, that sink capacity rather than assimilate supply during grain filling was limiting grain yields.

Relationship between daylength (growth room) and sowing date (field) studies.

The similarities between a cultivar's apical response to daylength in the growth room and the apical response to sowing date in the field (page 67) suggested that daylength

was an important environmental factor in determining the influence of sowing date on apical growth and development in the field. This is in agreement with other workers (Kirby and Eisenberg 1966 and Kirby 1969a,b) who have also suggested that daylength is one of the main environmental factors influencing plant growth in the field in Britain. This relationship was, however, more noticeable when only the early apical development was considered, and it was suggested that the later period of spikelet primordium production occurred in long days in all sowing date treatments as a result of the protracted period of development in early sowings. The effect of late sowing compared with early sowing on the maximum spikelet primordium number was, therefore, greatest as late sowing was progressively delayed, i.e. as the daylength during the early period of development became longer. A cultivar sensitive to long days (e.g. Clipper) would produce a high proportion of this maximum after only three weeks in late sowing and would subsequently attain a low final maximum. Such a cultivar would be described as an early genotype in British conditions and would be characterised by the pattern of apical development outlined in Table 27. A cultivar relatively unresponsive to daylength (e.g. Golden Promise) exhibits a less pronounced acceleration of apical development with late sowing and would therefore be considered to be a late genotype compared with the above group (Table 27). It is suggested that such a cultivar would attain a high spikelet primordium maximum over a wide range of sowing dates.

As indicated above, a high spikelet primordium maximum is associated with higher spikelet and grain numbers than a lower maximum and thus it is suggested that late genotypes

TABLE 27. Characteristics of early and late barley genotypes.

Genotype	Leaf primordium production	Final leaf number per main stem	Spikelet primordium production	Spikelet primordium maximum	Time to ear emergence [a]	Final spikelet and grain number
Early	short duration fast rate	low	early onset, short duration, rapid initial rate, high % set down at 3 weeks	low	short duration	low
Late	prolonged duration, slow rate	high	later onset, prolonged duration, slower initial rate, lower % set down at 3 weeks	high	prolonged duration	high

a Data not presented, derived from both 1976 and 1977 sowing date field trials.

would generally attain higher spikelet and grain numbers than early genotypes (Table 27).

The direct influence of daylength in determining final spikelet and grain numbers is, however, less readily distinguishable than that for early apical development. The only data available for spikelet and grain numbers, in S.1 and S.2 in 1976, was found to be unaffected by sowing date treatment and it was suggested that this is because the later stages of spikelet primordium production occurred in long days for both sowing dates and thus the spikelet primordium maximum attained was similar in both treatments. Maximum spikelet primordium number was, however, reduced for some cultivars in the final sowing (S.3) in 1976 and it was suggested that this decrease resulted from long days during early apical development. Unfortunately, no data is available for final spikelet and grain numbers and it is suggested that these components might have been expected to show a decrease compared with S.1 thereby confirming the importance of daylength in influencing both maximum spikelet primordium number and final grain number per ear in the field.

Daylength studies may be used to predict how new barley genotypes are likely to behave in new areas and this will be examined in the General Discussion. Particular reference will be made to Scottish growing conditions because of the wider range of daylength found between early and late sowing dates compared with English conditions.

SECTION 2. The influence of temperature on apical development of two selected genotypes in growth rooms.

INTRODUCTION

Long day treatment has been shown to accelerate apical growth and development and spikelet primordium production compared with short days (Section 1) and cultivars exhibited differences in the magnitude of their response. Cultivars, Clipper and Spartan, exhibited a more pronounced hastening of spikelet primordium production in L.D. compared with S.D. conditions than the second group consisting of Domen, Golden Promise and Ymer, and this was reflected in a significantly lower maximum spikelet primordium number.

A similar response was observed in two sowing date field trials in 1976 and 1977 in which Clipper and Spartan again exhibited a more marked acceleration of apical development with delay in sowing than the other cultivars. It was suggested that, because of the similarities of the apical response to daylength (growth room) and to sowing date (field) that daylength was an important environmental factor in influencing the magnitude of the sowing date response. However, many other environmental factors are confounded in sowing date treatments including temperature.

Most of the studies which have examined the effect of temperature on barley and wheat have tended to concentrate on the morphological development of the plant and the period of grain filling rather than on apical development (e.g. Takahashi and Yasuda 1960 and Thorne et al 1967 on barley, and Thorne et al 1968 and Marcelles and Single 1971 and 1972

on wheat). Temperature is known to affect spikelet number in wheat (Friend et al 1963, Friend 1965, Thorne et al 1968 and Rawson 1970) but few studies have examined the effect of temperature on the apical development of barley (Aspinall 1969 and Kirby 1973).

In this section, the influence of temperature on the apical development and spikelet primordium number is examined for two cultivars (Clipper and Golden Promise) known to exhibit contrasted responses to both daylength and sowing date. Comparisons of the influence of daylength and temperature on apical development in growth rooms may give an indication of the relative importance of temperature in influencing the sowing date response in the field.

MATERIALS AND METHODS

i) Plant culture.

The influence of temperature on the apical development of two two-row spring barley cultivars (Clipper and Golden Promise) was examined in growth rooms. Two temperature treatments were used in this study: low temperature (14°C ±2°C) and high temperature (20°C±1°C) and growing conditions were as described in the growth room daylength study (Section 1, page 27) except that only long daylength (16h) conditions were used. Sowing and plant culture methods were carried out as described earlier (page 28).

ii) Samples for apical dissection.

For each cultivar, each sample consisted of randomly selecting two replicate pots per temperature treatment as described previously (Section 1, page 28). Sampling

commenced seven days after sowing for both treatments and continued at seven-day intervals until the spikelet primordium maximum had been attained (week seven for 20°C and week eight for 14°C).

Apical dissections were performed as described in Section 1, page 29, and the following parameters were measured: final leaf number per main shoot, and apical developmental stage and spikelet primordium number of the main shoot apex. Apex developmental stage was assessed according to Table 7 with the exception that meristem dome elongation was assessed visually.

RESULTS

i) Final leaf number per main shoot.

Leaf number was greater in Golden Promise than Clipper in both temperature treatments (Table 28) but was not significantly affected by temperature increase from 14°C to 20°C for either cultivar. However, temperature did have a slight effect on leaf primordium production. The duration of set down can be calculated from the graph of the change in total primordium number with time (not presented) as described on page 42, and was reduced from 9 and 13 days after sowing (d.a.s.) for Clipper and Golden Promise respectively at 14°C to 7 and 11 d.a.s. respectively at 20°C.

ii) Apical developmental stage.

Apical development was hastened by increased temperature for both cultivars and this was particularly evident for Clipper (Fig. 26). As indicated earlier (page 41), double ridge stage (DR) occurs before the onset of spikelet primordium production and this stage was reached 14 and 11 d.a.s. for

TABLE 28. Influence of temperature on final leaf number per main shoot of Clipper and Golden Promise (growth room). Each value is a mean of at least 16 plants.

Cultivar	Leaf number per main shoot		
	14°C	signif. L.S.D.	20°C
Clipper	7.6	N.S.	7.8
Golden Promise	10.5	N.S.	11.0

N.S. Not significant, $L.S.D._{0.05}$ calculated following an analysis of variance for each cultivar separately.

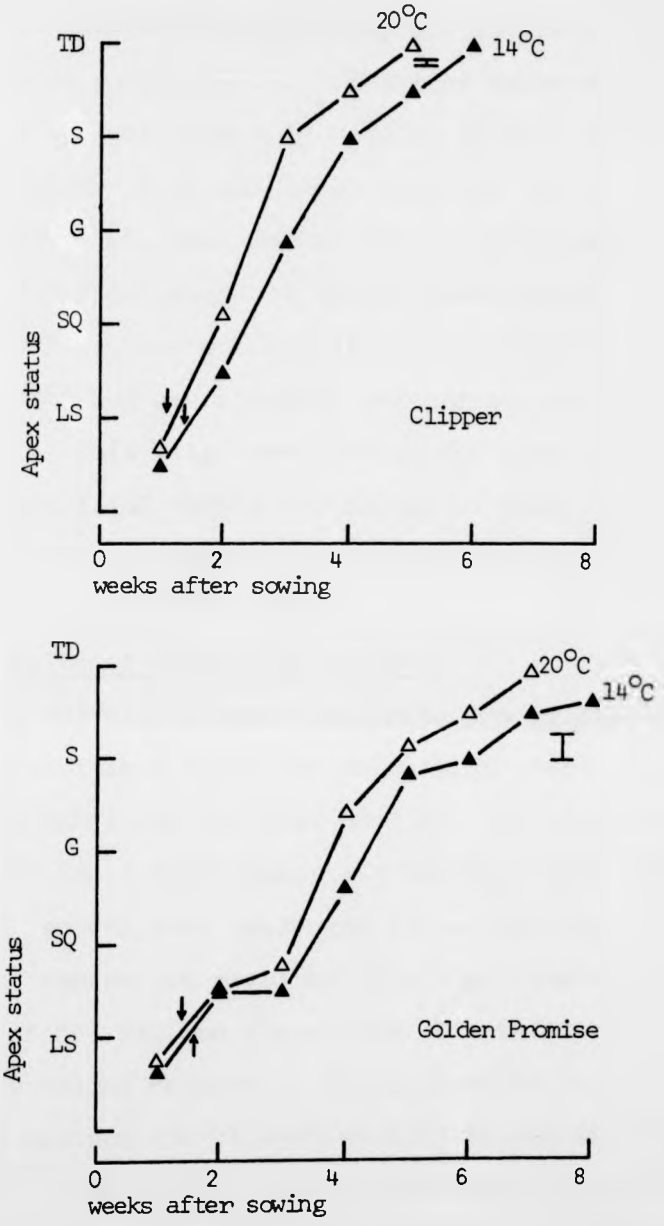


Fig.26. Effect of temperature (14°C and 20°C) on apical developmental stage of Clipper and Golden Promise (growth room).

Only alternate apical developmental stages are shown on y-axis, see Table 7. Each point is a mean of 7 or 8 plants. Vertical bars indicate L.S.D. significant at $p \leq 0.05$, calculated following an analysis of variance for each cultivar separately. Arrows indicate onset of spikelet primordium production.

▲ = 14°C

△ = 20°C

Clipper at 14 and 20°C respectively and 14 d.a.s. for Golden Promise at both remperatures. The time taken to reach each subsequent stage was similarly reduced at 20°C compared with 14°C treatment for both cultivars although the response to high temperature was more marked for Clipper than Golden Promise. The final stage of apical development distinguished, tip degeneration (TD) occurred after only five weeks for Clipper at 20°C but was slightly delayed at the cooler temperature. This stage was reached for some of the plants comprising the final sample for Golden Promise (seven and eight weeks after sowing, w.a.s., for 20°C and 14°C respectively).

iii) Spikelet primordium number.

Maximum spikelet primordium number was greater in Golden Promise than Clipper for both temperature treatments (Fig. 27 and Table 29) and thus confirms the close relationship found between final leaf number and spikelet primordium maximum (cf. growth room daylength study, Section 1). An increase in temperature resulted in a significant decrease ($p \leq 0.05$) in the maximum for Clipper but this was not observed for Golden Promise. It is possible to attribute the reduced maximum for Clipper at 20°C to the much reduced period of set down rather than to the initial rate of production which, although increased at 20°C, was not significantly affected (Table 29). The duration of production was not markedly affected by temperature treatment for Golden Promise although the rate was just significantly increased ($p \leq 0.05$) at the higher temperature (Table 29).

The percentage of the spikelet primordium maximum set down at three weeks was increased with increase in temperature

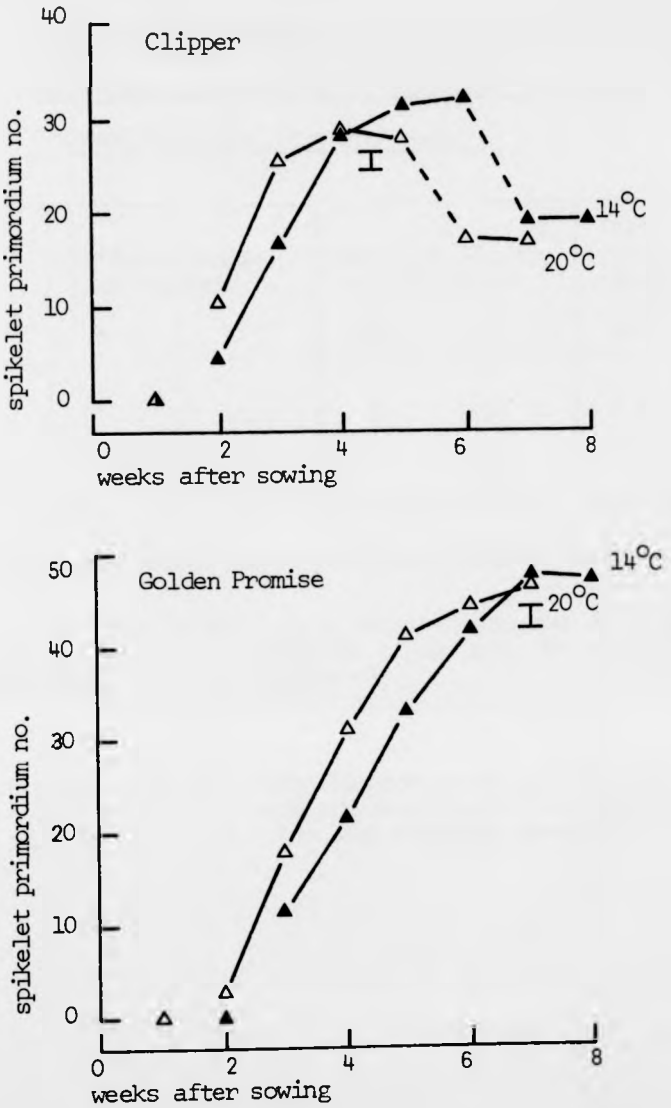


Fig. 27. Effect of temperature (14°C and 20°C) on spikelet primordium no. of Clipper and Golden Promise (growth room).

Each point is a mean of 7 or 8 plants. Vertical bars indicate L.S.D. significant at $p \leq 0.05$, calculated following an analysis of variance for each cultivar separately.

▲ = 14°C

△ = 20°C

TABLE 29. Influence of temperature on some parameters of spikelet primordium production of Clipper and Golden Promise (growth room).

Cultivar	Spikelet primordium maximum		Duration of production (days)		Initial rate of production (spike. primordia per day).	
	14°C	20°C	14°C	20°C	14°C	20°C
Clipper	32.5 *[a]	28.8	32	20	1.57 N.S.[b]	1.97
Golden Promise	47.8 N.S.	46.6	75	37	1.49 *	1.72

Maximum spikelet primordium number based on a mean of 8 plants.

a * significant at $p \leq 0.05$) L.S.D. values calculated following an analysis of variance for each cultivar separately.
N.S. not significant)

b.* significant at $p \leq 0.05$) significance calculated following comparison of regression coefficients for each cultivar separately.
N.S. not significant)

for both cultivars (52.1% and 89.2% for Clipper at 14°C and 20°C respectively and 24.0% and 38.7% respectively for Golden Promise). The increased percentage set down is due to both the earlier onset of spikelet primordium set down and the slightly faster initial rate of set down. As in the earlier growth room daylength study (Section 1), a large percentage set down at three weeks is associated with a low spikelet primordium maximum (e.g. Clipper at 20°C).

DISCUSSION

The discussion is divided into two sub-sections. First, the results described above on the influence of temperature on apical development of barley will be discussed in relation to previous work on both barley and wheat. Secondly, the relationship between the response to daylength and temperature in the growth room is examined with a view to evaluating the possible importance of temperature in influencing the sowing date response in the field.

The influence of temperature on apical development (growth rooms)

Leaf primordium production was influenced by an increase in temperature from 14°C to 20°C for both cultivars and, although the duration of production was reduced, this was not reflected in final leaf number because of the slightly slower rate of set down. Studies by Friend et al (1965) and Hasle and Weir (1970) on wheat have also suggested that leaf number was not significantly influenced by temperature and Kirby (1973) only noticed a slight decrease in leaf

number of barley at the lowest temperature (7°C) used in his study.

Apical development and spikelet primordium production were hastened by increased temperature for both cultivars although the response was greater for Clipper than for Golden Promise. Spikelet primordium maximum was decreased with increase in temperature for both cultivars although this increase was only significant ($p \leq 0.05$) for Clipper. Other studies have also indicated that spikelet number is reduced with increase in temperature (Borthwick et al 1941 and Guitard 1960 for barley, and Friend 1965 and Wall and Cartwright 1974 for wheat). However, Rawson (1970) in his study on 12 wheat cultivars found that spikelet number was lower at day/night temperature of 15/10°C compared with 21/16°C. He suggested that the low spikelet number in the 15/10°C treatment may be caused by the low temperature partially fulfilling any cold requirement of the cultivars examined.

The cold requirement of barley and wheat appears to be quantitative rather than qualitative in character and Chujo (1961) and Gott (1961) have found that temperatures of around 10°C may be sufficient to vernalize several cultivars of barley and wheat respectively. Rao and Witcombe (1977) have similarly found that barley and wheat cultivars differ in the magnitude of their response to vernalization treatment. Cold treatment has been shown to hasten apical development of the plant with a subsequent reduction in the period of spikelet production resulting in a low spikelet number (Rawson 1970 and Wall and Cartwright 1974) for wheat. Clearly, vernalization treatment confounds the effect of temperature on ear development and a cultivar's response to temperature can be

altered by prior vernalization treatment (Hasle and Weir 1970, and Wall and Cartwright 1974).

In this study, increased temperature resulted in an earlier onset of spikelet primordium production together with an increased rate of set down but the significant reduction in the maximum for Clipper at 20°C was associated with the short duration of set down. This confirms the work by Friend (1965) and Wall and Cartwright (1974) on wheat who also stressed the importance of the duration of this period of set down in influencing final spikelet number.

Because of the close relationship between spikelet primordium maximum and final spikelet and grain number per ear (Section 1 of this study), the effect of temperature on apical development and spikelet primordium production may also influence final grain number per ear and final grain yield. Confirmation of this suggestion can be derived from the studies by Thorne et al (1967 and 1968) on barley and wheat. These workers found that the decrease in grain yield resulting from increased temperature during the early growth of the plant could be attributed to the reduction in grain number per ear.

Relationship between the influences of daylength, temperature and sowing date on apical development.

Apical development and spikelet primordium production were hastened in long day and 20°C treatments compared with short day and 14°C treatments respectively and cultivars differed in the magnitude of their response. Apical development and spikelet primordium production of Clipper was more responsive to L.D. and 20°C treatments than Golden Promise and this was reflected in a significant ($p \leq 0.05$) reduction in

maximum spikelet primordium number in these treatments.

Although daylength and temperature have similar effects on apical development it does not necessarily follow that their action is mediated through the same control mechanism. It was suggested earlier (page 86) that daylength may exert an effect on apical growth and development either by influencing assimilate movement to the apex and /or by influencing the production or utilization of hormones within the apex. Friend et al (1963) have similarly suggested that the more rapid apical development as a result of increased temperature may be caused by either an increase in the rate of production or rate of utilization of a flower-inducing substance.

The contrasted differences between Clipper and Golden Promise in the magnitude of their responses to daylength and temperature confirms an earlier study on barley by Takahashi and Yasuda (1960). They suggested that early cultivars (e.g. Clipper in this study) were more responsive to both L.D. and high temperature treatments than late cultivars (e.g. Golden Promise in this study) which tended to be day-neutral and relatively unresponsive to temperature. However, because of the limited number of cultivars used in these studies (the present study and Takahashi and Yasuda 1960) it cannot be assumed that all cultivars which are responsive to daylength will also be sensitive to temperature.

In the previous section, it was suggested that daylength was one of the main environmental factors influencing the effect of sowing date on apical development in the field. However, the similarities of the response of apical development to temperature in growth rooms and to sowing date in the field

suggests that temperature may also contribute to the accelerated apical development with late sowing. Temperature increased with progressive delay in sowing (Table 10) and thus paralleled the increase in daylength conditions. The apical response to increased temperature (growth room) for both Clipper and Golden Promise was less than that found for differences in daylength (Section 1, growth room study) but it should be noted that two extreme daylengths were used (8h S.D. and 16h L.D.) and this range was greater than that found in the field (Table 10). The air temperature difference between early and late sowing date treatments in the field (Table 10) was similar to the difference in temperatures used in the growth room ($14^{o}C$ and $20^{o}C$) although the absolute temperatures were generally lower in the field particularly when minimum air and grass temperatures are considered. These low temperatures may have fulfilled any cold requirement of the cultivars examined and thus would confound the effect of temperature on apical development in the field. More physiological work is required to gain a better understanding of the influence of temperature and cold treatment on apical development in the field. It is clear, however, that both daylength and temperature are important environmental influences in the field and act simultaneously on apical development.

SECTION 3. The influence of photoperiod on apical development of selected genotypes under controlled environment conditions.

INTRODUCTION

Daylength (8h S.D. and 16h L.D.) was shown to influence the apical development and spikelet primordium production of barley genotypes in the growth room (Section 1). All cultivars exhibited an accelerated apical development in L.D. compared with S.D. conditions but cultivars differed in the magnitude of their response. Two cultivars, Clipper and Spartan, were particularly responsive to long days compared with the other three cultivars examined: Domen, Golden Promise and Ymer and a lower spikelet primordium maximum was subsequently determined in L.D. compared with S.D. conditions for the responsive cultivars.

No attempt was made in the daylength experiments of the first section to separate the two components of daylength, photoperiod and radiation. Either or both of these components may influence apical development and the studies in this section examine the relative contributions of these components to the apical response of cultivars to daylength.

The relative influences of the photoperiod and radiation components of daylength may be separated either by means of a Night Interruption study (N.I.) in which the long dark period (16h) is broken by a short period of supplemental light (Fig. 28) or by a Day extension treatment (D.E.) in which the 8h high light intensity period is followed by a period of low intensity supplemental light (Fig. 28). Night interruption and Day extension treatments are, therefore, photoperiodically similar to the L.D. treatment but have only the short high

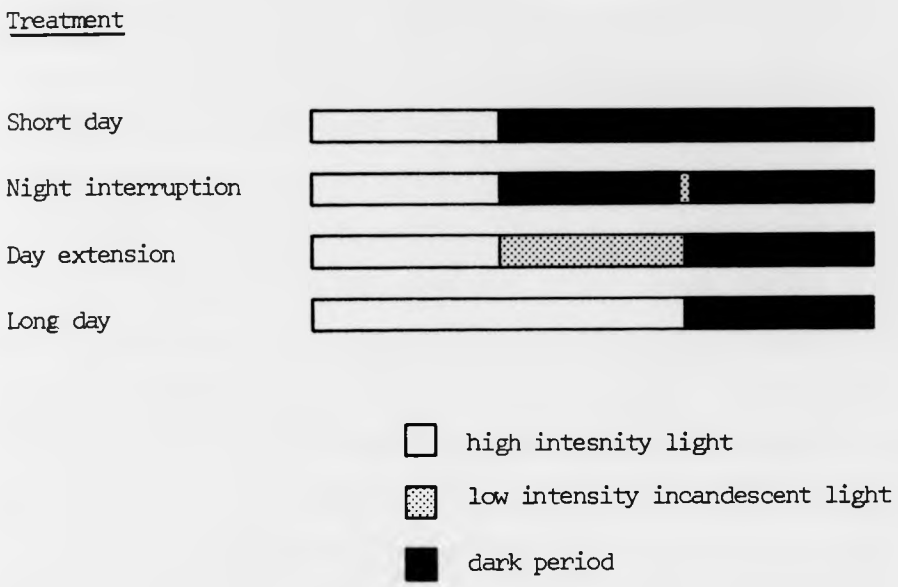


Fig. 28. Night Interruption (N.I.) and Day Extension (D.E.) photoperiod treatments.

energy radiation period associated with S.D. conditions.

Both N.I. and D.E. treatments have been employed to examine the effects of photoperiod on cereal development (Borthwick et al 1948 and Downs et al 1959 among others) and both methods will be used in this section.

Barley cultivars have been shown by Borthwick et al (1948) to be sensitive to an incandescent light break during the dark period resulting in an earlier onset of floral initiation compared with S.D. treatment. Incandescent light is more effective than fluorescent light in evoking a photoperiodic response when used either as a N.I. treatment (Friend et al 1959) or to extend the light period (Downs et al 1959 and Friend et al 1961). The magnitude of the photoperiodic response has been shown to increase with increased levels of incandescent light whether used by itself or in conjunction with fluorescent light (Friend 1964 and Paleg and Aspinall 1964) although Aspinall and Paleg (1966) found that even low intensities of incandescent light (1 Foot candle, 10.8 lux) are sufficient to promote apical development in a N.I. study in the field.

Many studies on the influence of photoperiod on the growth and development of barley and wheat cultivars have examined only a limited number of cultivars and have not necessarily included cultivars which exhibit a contrasted response to daylength. The influence of N.I. treatment in this study was, therefore, examined on five cultivars (Clipper, Spartan, Domen, Golden Promise and Uzu) which showed a contrasted response to daylength in the initial glasshouse experiment. The apical response of four of these cultivars (Clipper, Spartan, Domen and Golden Promise) to daylength has been

examined in the growth room experiment and the fifth cultivar, Uzu, was selected to show a similar daylength response to Ymer.

The relative effectiveness of D.E. treatment in separating the two daylength components was examined in a second study for two cultivars, Clipper and Golden Promise, in growth rooms. Plants used in this study were retained for radio-isotope feeding and distribution assays which will be described in the following section.

The influence of photoperiod on apical development was examined in a further experiment to determine whether the pattern of apical development and spikelet primordium production could be altered by change in photoperiod treatment. Studies by Lucas (1972) and Allison and Daynard (1976) have indicated that the pattern of apical development of wheat can be changed by transferring plants from one photoperiod treatment to another. Although several workers (Guitard 1960 and Thorne et al 1967) have shown that the growth pattern of barley plants may be changed by changes in daylength conditions, no comparable study has examined the effect of photoperiod transfer on the apical development of barley. The effect of transferring plants from D.E. to S.D. conditions at various stages of apical growth was examined for one cultivar, Clipper, shown by the above studies to be photoperiodically sensitive.

MATERIALS AND METHODS

Night interruption experiment

i) Plant culture.

The influence of photoperiod on apical development of five two-row spring barley cultivars was examined using a Night interruption treatment (N.I.) in the glasshouse. The five cultivars examined were selected from the one hundred cultivars sown in the initial glasshouse daylength experiment to show a known contrasted response to daylength (Table 30). The apical response to daylength of four of these cultivars has been previously examined in the growth room study and the response of spikelet primordium maximum to daylength of these cultivars is also presented in Table 30. The fifth cultivar used in the above study, Ymer, was not sown in this N.I. study because of insufficient seed and Uzu was selected as a suitable replacement exhibiting a similar response to daylength (Table 5).

The experiment was designed as a split plot trial with the three photoperiod treatments (8h S.D., 16h L.D. and N.I. treatment consisting of 8h high intensity light with the 16h dark period interrupted by 30 min. light break in the middle of the night). Within each main plot, 14 pots of each of the five cultivars were completely randomised giving a final total of 80 subplots per main plot treatment. The L.D. treatment was replicated three times and the N.I. and S.D. treatments twice. In order to minimize the effects of variation of temperature and light intensity within the glasshouse, the main treatments and the subplots were re-randomised at weekly intervals.

Short day and long day treatments were obtained by using high intensity light (20,000 lux, 250 Wm^{-2}) of 8h and 16h duration respectively as described earlier (Section 1,

TABLE 30. Spikelet number and spikelet primordium maximum per main shoot ear of five barley cultivars examined in Night Interruption study (glasshouse). Values based on the mean of between 6 and 8 plants.

	Spikelet no./ main ear		Spikelet primordium maximum	
	S.D.	L.D.	S.D.	L.D.
Clipper	19.9	10.6	36.9x	26.5
Spartan	20.1	14.0	43.6x	32.5
Domen	26.1	25.5	-	39.0
Golden Promise	27.0	28.0	37.9x	44.9
Uzu	24.6	28.1	-	-

x = awn stage of apical development (see text)

- = not determined

page 24). The artificial lighting was controlled by time switches and was used to supplement the natural daylight at the time of the experiment (summer-autumn 1976). The N.I. treatment remained under the same 8h photoperiod conditions as the S.D. plants but each replicate block was transferred to separate garages at the end of the light period and positioned directly under one 100W incandescent light bulb situated in the ceiling of the garage. This provided a light intensity of 2.8 Wm^{-2} measured at pot level and the light break treatment given in the middle of the night period from 24.00 to 24.30h. Temperature was maintained at approximately 20°C during the day but fell to c. 10°C min. during the dark period in both glasshouse and garages.

Two days prior to sowing the soil in all pots was treated with 'Diazitol' (containing Diazinon, supplied by Ciba-Geigy, Agrochemical Division) at a rate of 2.0 $cm^3 l^{-1}$ to prevent insect damage. Sowing was carried out on 11 June 1976 and completed within the day. Six seeds were sown per 15.3 cm diameter plastic pot containing J. Innes No. 2 compost at a depth of 2.5 cm. Once the seedlings were established they were thinned to give a final number of four plants per plot. Plant culture was then carried out as described previously (Section 1, page 25).

Several plants showed signs of a slight infection of mildew (Erysiphe graminis f. sp. hordei) after 25 days and all plants were immediately treated with sulphur which prevented spread of the infection. When all plants had developed five fully-emerged leaves on the main stem, the infection was treated with a single spray of 'Calixin' (75% w/v tridemorph) at a concentration of 2.0 $cm^3 l^{-1}$ which proved

completely effective.

ii) Samples for apical dissection.

Eight sample occasions were possible for each of the three photoperiod treatments and sampling commenced seven days after sowing. Sampling continued at seven-day intervals in the L.D. treatment until the spikelet primordium maximum had been attained for all cultivars but, because of the slower apical development in both N.I. and S.D. treatments, it occasionally proved necessary to sample at 14-day intervals to enable a value for the maximum to be determined.

For each cultivar, each sample consisted of randomly selecting one pot per replicate treatment thus providing a total of three replicate pots for the L.D. treatment and two replicate pots for the N.I. and S.D. treatments. All four plants per pot were carefully and individually removed for apical dissection which were performed as described in Section 1, page 29.

The following parameters of the development of the main shoot apex were measured at each sample occasion: apical developmental stage (assessed according to Table 7), total and spikelet primordium number and apex length. Apex dry weight was measured from sample two onwards in the L.D. treatment and from sample three in the N.I. and S.D. treatments. As soon as the final leaf number per main shoot could be determined, this parameter was also counted.

Day extension experiment

i) Plant culture.

The influence of photoperiod (using Day extension treatment) on the apical development (and on the movement

of ^{14}C-assimilates to the developing apex, Section 4) was examined in growth rooms for two cultivars, Clipper and Golden Promise, known to exhibit a contrasted response to daylength treatment (Table 30).

Three daylength treatments were employed: 8h short day (S.D.) and 16h long day (L.D.) as in the earlier growth room daylength study (Section 1) plus a day extension treatment (D.E.) in which the 8h high radiation period was immediately followed by 8h low intensity incandescent light (cf. Fig. 28). Temperature was maintained at $20\pm1^{\circ}C$ for all treatments.

Two days prior to sowing, all pots were treated with the commercial pesticide 'Diazitol' (containing Diazinon) at a rate of 2.0 $cm^{3}\ l^{-1}$. Each of the three daylength treatments were sown on consecutive days and plant culture was then carried out as described for the earlier growth room study (Section 1, page 28). As only three growth rooms were available and space within each growth room was limited, Golden Promise and Clipper were sown in two separate experiments. No infection by mildew (Erysiphe graminis f. sp. hordei) or other foliar pathogens was present in any of the growth room plants.

ii) Samples for apical dissection.

For each cultivar, four replicate pots (for L.D. and D.E. treatments) or three replicate pots (for S.D. treatment) were randomly selected at each sample occasion. Three of the four plants per pot were carefully and individually removed for apical dissections thus giving a final total of 12 plants (in L.D. and D.E. conditions) and nine plants (in short days) per sample. The remaining single plant was

retained in the pot for subsequent net photosynthesis measurement by Infra-red gas analysis and for radio-isotope labelling.

Sampling commenced seven d.a.s. for each treatment for both cultivars and, in Clipper, continued at seven day intervals until the experiment was terminated 42 d.a.s. (49 d.a.s. in short days). Maximum spikelet primordium number was determined within the sampling period under L.D. and D.E. conditions but had not been reached in short days. For Golden Promise, the second and third samples for all three treatments were taken 14 and 24 d.a.s. respectively and continued thereafter at seven-day intervals. Sampling stopped 53 d.a.s. by which time, spikelet primordium maximum had been determined under L.D. conditions but not in the other treatments.

Apical dissections were carried out as described in Section 1 (page 29) and the following parameters of apical growth were measured: main shoot apical developmental stage (assessed according to Table 7) and total and spikelet primordium number. Apex length was measured using a calibrated eyepiece graticule as before and apex dry weight was measured from sample two onwards in all treatments. As soon as the final leaf number could be determined on the main shoot, this parameter was also measured.

Photoperiod transfer experiment

i) Plant culture.

The influence of photoperiodic switch from day extension (D.E.) to short day (S.D.) conditions was examined in this growth room study for one cultivar, Clipper. The two

The two photoperiod treatments were obtained as described above (page 110) and temperature in both growth rooms was maintained at 20±1°C.

Sowing and plant culture methods were performed as described for the growth room daylength experiment (Section 1, page 28). Initially, 80 and 20 pots were sown in the D.E. and S.D. treatments respectively and, at weekly intervals, 14 pots were randomly selected from the D.E. treatment and transferred to S.D. conditions for the remainder of the experimental period. All pots were completely re-randomized within each photoperiod treatment after each transfer. The transfer from D.E. to S.D. conditions continued until the maximum spikelet primordium number had been determined in the D.E. treatment (week four), giving a final total of three transfer treatments (D.E.1, D.E.2 and D.E.3).

No infection of mildew (Erysiphe graminis f. sp. hordei) or other foliar pathogens was present in any of the growth room plants.

ii) Samples for apical dissection.

On each sampling occasion, two replicate pots were randomly selected from the D.E. and S.D. treatments and from the appropriate photoperiod switch treatments. Sampling commenced seven d.a.s. for the D.E. and S.D. photoperiod treatments and continued at seven-day intervals until the experiment was terminated seven weeks after sowing. Samples of the photoperiod transfer treatments were taken seven days after transfer to S.D. conditions, thus plants transferred seven d.a.s. (D.E.1) were first sampled 14 d.a.s.

Apical dissections were carried out as described in Section 1 (page 29) and the following parameters were

measured: final leaf number per main shoot, apical developmental stage, and total and spikelet primordium number per main shoot apex. Apex developmental stage was assessed according to Table 7 with the exception that meristem dome development (stages E.S. and L.S.) was assessed visually.

RESULTS

The response of apical growth and development to photoperiod was similar in both Night interruption and Day extension experiments. The results of the five cultivars examined in the N.I. study are described in detail and data from the D.E. study used as confirmation of this response for Clipper and Golden Promise. Part two of the Results section examines the effect of photoperiod transfer from D.E. to S.D. conditions on the apical development of one of these cultivars, Clipper.

Night interruption and Day extension photoperiod experiments

i) Final leaf number per main shoot.

The influence of photoperiod on final leaf number for all five cultivars examined in the N.I. study and for Clipper and Golden Promise in the D.E. study is presented in Tables 31 a,b respectively. As in the earlier growth room daylength experiment (Section 1, Table 6) all cultivars showed a significant reduction ($p \leq 0.05$) in leaf number in L.D. compared to S.D. conditions in both photoperiod studies but cultivars differed both in the magnitude of the difference of their response to daylength and in their response to N.I. and D.E. treatments.

Clipper and Spartan determined an intermediate leaf number

TABLE 31. Influence of photoperiod on final leaf number per main shoot of selected genotypes.

a. Night interruption experiment (glasshouse).

Cultivar	Short day	Night inter.	Long day
Clipper	10.4 a[x]	80.6 b	6.3 c
Spartan	12.6 a	9.5 b	6.9 c
Domen	10.2 a	10.3 a	7.6 b
Golden Promise	12.0 a	12.6 a	9.0 b
Uzu	13.4 a	13.2 a	9.2 b

b. Day extension experiment (growth room).

Cultivar	Short day	Day extn.	Long day
Clipper	11.3 a[x]	7.7 b	7.0 b
Golden Promise	12.6 a	12.5 a	11.3 b

Each value is a mean of at least 12 plants.

x = Multiple range test significant at $p \leq 0.05$, calculated for each cultivar separately. Means with same letters are not significantly different.

in N.I. compared to L.D. and S.D. conditions thus suggesting that leaf number in these cultivars is sensitive to both the photoperiodic and radiation components of daylength. Final leaf number was not significantly different between the N.I. and S.D. treatments for Domen, Golden Promise and Uzu indicating that leaf number was determined by the light energy available for photosynthesis rather than the longer photoperiod.

The reduced leaf number in L.D. conditions tends to be associated with the reduced duration of leaf primordium production before the onset of spikelet primordium set down (Fig. 29). Similarly, the increased leaf number in S.D. compared with N.I. treatment for Clipper and Spartan is linked with the delayed onset of spikelet primordium production whereas the cessation of leaf primordium set down in both treatments for the other cultivars occurs at the same time.

The contrasted response of final leaf number for Clipper and Golden Promise to photoperiod treatment was confirmed in the Day extension study (Table 31b) although the difference between D.E. and L.D. treatments was less pronounced than between N.I. and L.D. treatments. Final leaf number could again be linked with the duration of leaf primordium set down with a large leaf number being associated with a prolonged period of production (cf. Fig. 30 and Table 31b).

ii) Apical developmental stage.

The influence of photoperiod on the apical development of selected genotypes is presented in Fig. 29 for the Night interruption study and Fig. 30 for the Day extension study. The ten developmental stages distinguished are described in Table 7.

in N.I. compared to L.D. and S.D. conditions thus suggesting that leaf number in these cultivars is sensitive to both the photoperiodic and radiation components of daylength. Final leaf number was not significantly different between the N.I. and S.D. treatments for Domen, Golden Promise and Uzu indicating that leaf number was determined by the light energy available for photosynthesis rather than the longer photoperiod.

The reduced leaf number in L.D. conditions tends to be associated with the reduced duration of leaf primordium production before the onset of spikelet primordium set down (Fig. 29). Similarly, the increased leaf number in S.D. compared with N.I. treatment for Clipper and Spartan is linked with the delayed onset of spikelet primordium production whereas the cessation of leaf primordium set down in both treatments for the other cultivars occurs at the same time.

The contrasted response of final leaf number for Clipper and Golden Promise to photoperiod treatment was confirmed in the Day extension study (Table 31b) although the difference between D.E. and L.D. treatments was less pronounced than between N.I. and L.D. treatments. Final leaf number could again be linked with the duration of leaf primordium set down with a large leaf number being associated with a prolonged period of production (cf. Fig. 30 and Table 31b).

ii) Apical developmental stage.

The influence of photoperiod on the apical development of selected genotypes is presented in Fig. 29 for the Night interruption study and Fig. 30 for the Day extension study. The ten developmental stages distinguished are described in Table 7.

in N.I. compared to L.D. and S.D. conditions thus suggesting that leaf number in these cultivars is sensitive to both the photoperiodic and radiation components of daylength. Final leaf number was not significantly different between the N.I. and S.D. treatments for Domen, Golden Promise and Uzu indicating that leaf number was determined by the light energy available for photosynthesis rather than the longer photoperiod.

The reduced leaf number in L.D. conditions tends to be associated with the reduced duration of leaf primordium production before the onset of spikelet primordium set down (Fig. 29). Similarly, the increased leaf number in S.D. compared with N.I. treatment for Clipper and Spartan is linked with the delayed onset of spikelet primordium production whereas the cessation of leaf primordium set down in both treatments for the other cultivars occurs at the same time.

The contrasted response of final leaf number for Clipper and Golden Promise to photoperiod treatment was confirmed in the Day extension study (Table 31b) although the difference between D.E. and L.D. treatments was less pronounced than between N.I. and L.D. treatments. Final leaf number could again be linked with the duration of leaf primordium set down with a large leaf number being associated with a prolonged period of production (cf. Fig. 30 and Table 31b).

ii) Apical developmental stage.

The influence of photoperiod on the apical development of selected genotypes is presented in Fig. 29 for the Night interruption study and Fig. 30 for the Day extension study. The ten developmental stages distinguished are described in Table 7.

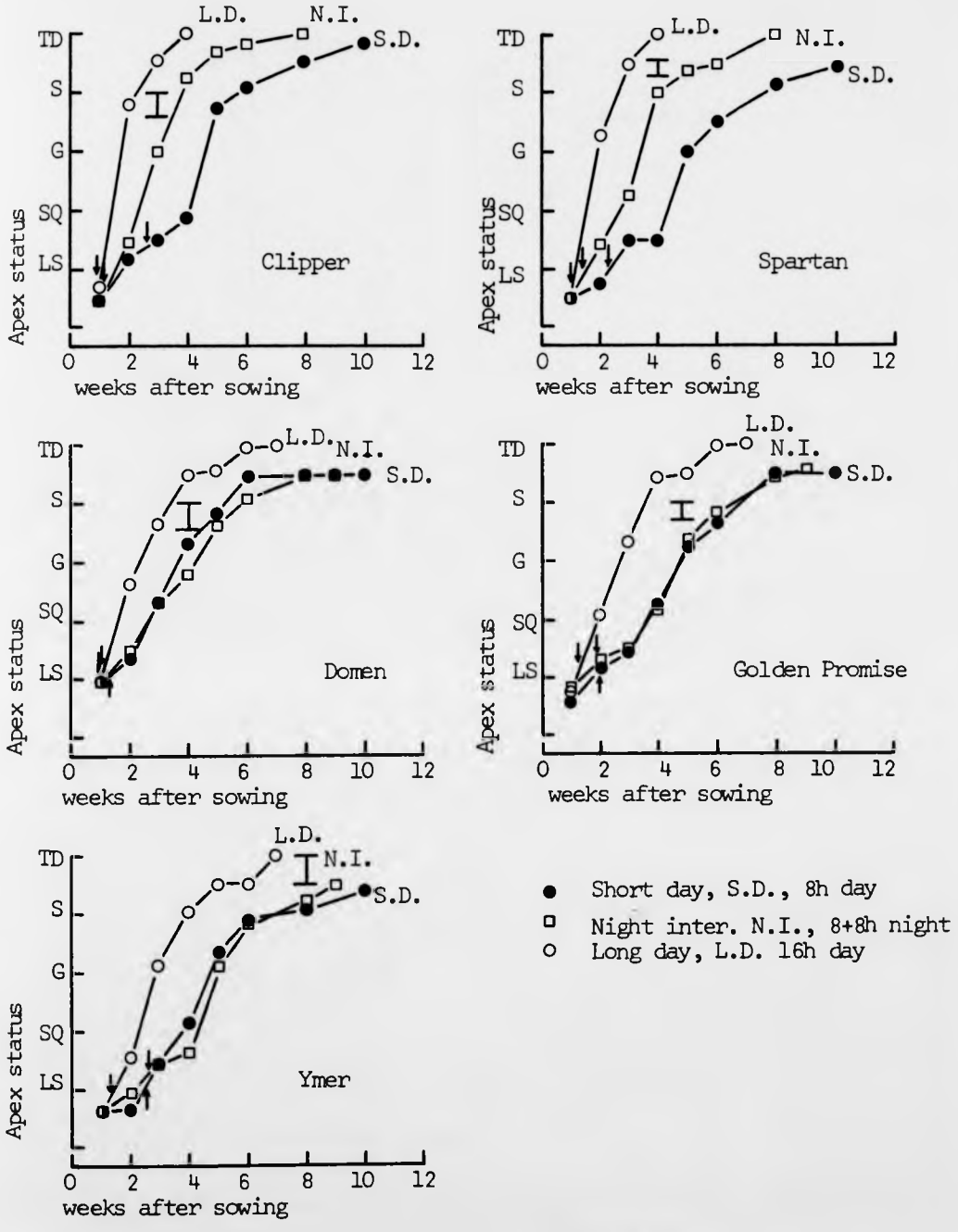
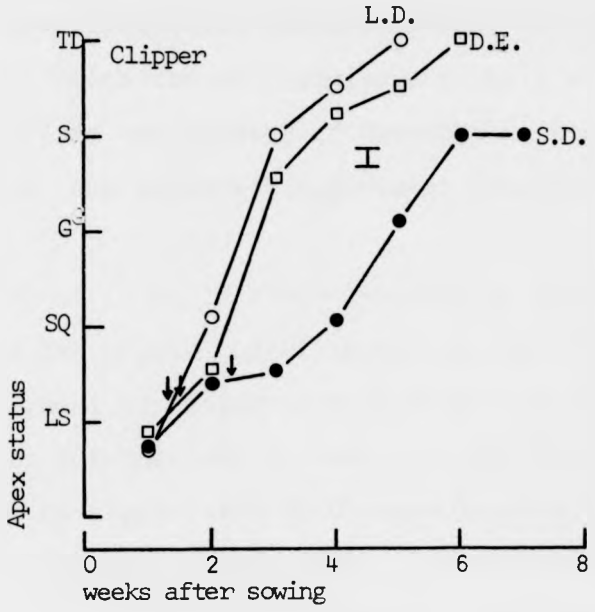


Fig. 29. Effect of photoperiod (night interruption) on apical developmental of five barley cultivars.

Only alternate apical developmental stages are shown on y-axis, see Table 7. Each point is a means of between 4 and 12 plants. Vertical lines indicate L.S.D. significant at $p=0.05$, calculated following an analysis of variance for each cultivar separately. Arrows indicate onset of spikelet primordium production.



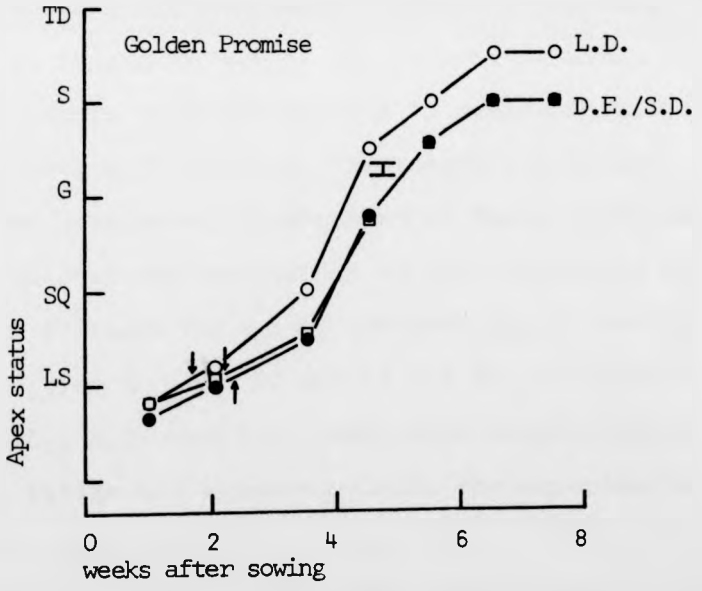


Fig. 30. Effect of photoperiod (day extension) on apical developmental of Clipper and Golden Promise (growth room)

Only alternate apical developmental stages are shown on y-axis, see Table 7. Each point is a mean of between 9 and 12 plants. Vertical bars indicate L.S.D. significant at $p \leq 0.05$, calculated following an analysis of variance for each cultivar separately. Arrows indicate onset of spikelet primordium production.

● = short day, S.D., 8h day
□ = Day extn., D.E., 8+8h day
○ = Long day, L.D., 16h day

Apical development was accelerated in L.D. compared with S.D. conditions for all cultivars in both studies and therefore confirms the pattern of development found in the earlier growth room daylength experiment (Section 1, Fig. 4).

Cultivars differed in their response to photoperiod treatment and two physiological groups can be distinguished. Apical development of Clipper and Spartan under N.I. conditions was intermediate between L.D. and S.D. conditions but there was no significant difference between the pattern of apical development in N.I. and S.D. treatments for the other cultivars. If the two contrasted cultivars, Clipper and Golden Promise, are considered, double ridge stage (DR) was reached 9, 14 and 21 d.a.s. for Clipper in L.D., N.I. and S.D. treatments respectively but 11 d.a.s. in L.D. and 22 d.a.s. in both N.I. and S.D. treatments for Golden Promise. The contrasted development of these cultivars with N.I. treatment was maintained in the subsequent stages such that awn initials (stage A) occurred 20, 32 and 56 d.a.s. for Clipper and 35, 60 and 56 d.a.s. for Golden Promise in L.D., N.I. and S.D. treatments respectively. Tip degeneration (stage TD) occurred within the experimental period for all cultivars in L.D. conditions and in N.I. treatment for Clipper and Spartan but did not occur in the other treatments.

The contrasted pattern of apical development between cultivars with N.I. treatment clearly indicates the promotive influence of photoperiod on Clipper and Spartan and confirmation of the photoperiodic sensitivity of Clipper can be derived from the Day extension study (Fig. 30). Apical

development of both Clipper and Golden Promise was accelerated in long days compared with the D.E. and S.D. treatments because of the increased radiation energy for photosynthesis. However, the response was less pronounced than found above (cf. Fig. 29) and this may be due to the lower light intensity in the growth rooms compared with the natural daylight during summer-autumn in the glasshouse Night interruption study. The influence of the radiation component of daylength on apical growth and development is discussed in more detail in Section 4.

iii) Spikelet primordium number.

Spikelet primordium production was accelerated in L.D. compared with S.D. treatment for all cultivars in both N.I. (Fig. 31) and D.E. (Fig. 32) studies (cf. Section 1, Fig. 5). Cultivars exhibited differences in the magnitude of their response to daylength treatment (long days) and this was reflected in their response to photoperiod treatment.

The pattern of spikelet primordium production for Clipper and Spartan under N.I. treatment was intermediate between the S.D. and L.D. treatments but no significant difference was found in the pattern of set down between N.I. and S.D. treatments for Domen, Golden Promise and Uzu. The contrasted response of these cultivars to light break is reflected in the maximum determined (Table 32). The maximum was not reached within the experimental period in several treatments and the number attained at the final sample in these cases has been taken to be the maximum (cf. page 42). This number may underestimate the potential maximum but it is suggested that this would involve a limited number of primordia and would not invalidate any comparisons. The

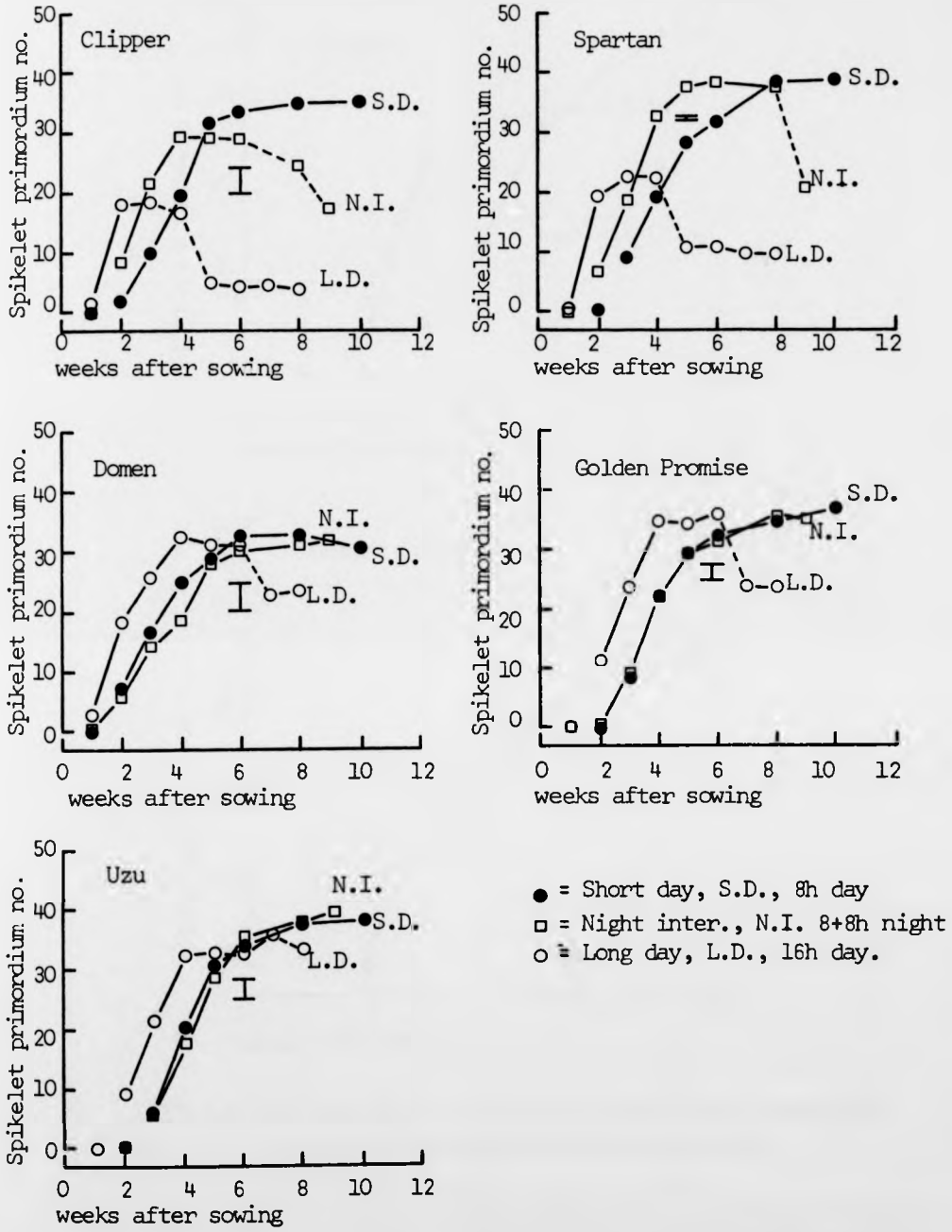


Fig. 31. Effect of photoperiod (night interruption) on spikelet primordium number of five barley cultivars.

Each point is a mean of between 4 and 12 plants. Vertical lines indicate L.S.D. significant at $p \leq 0.05$, calculated following an analysis of variance for each cultivar separately.

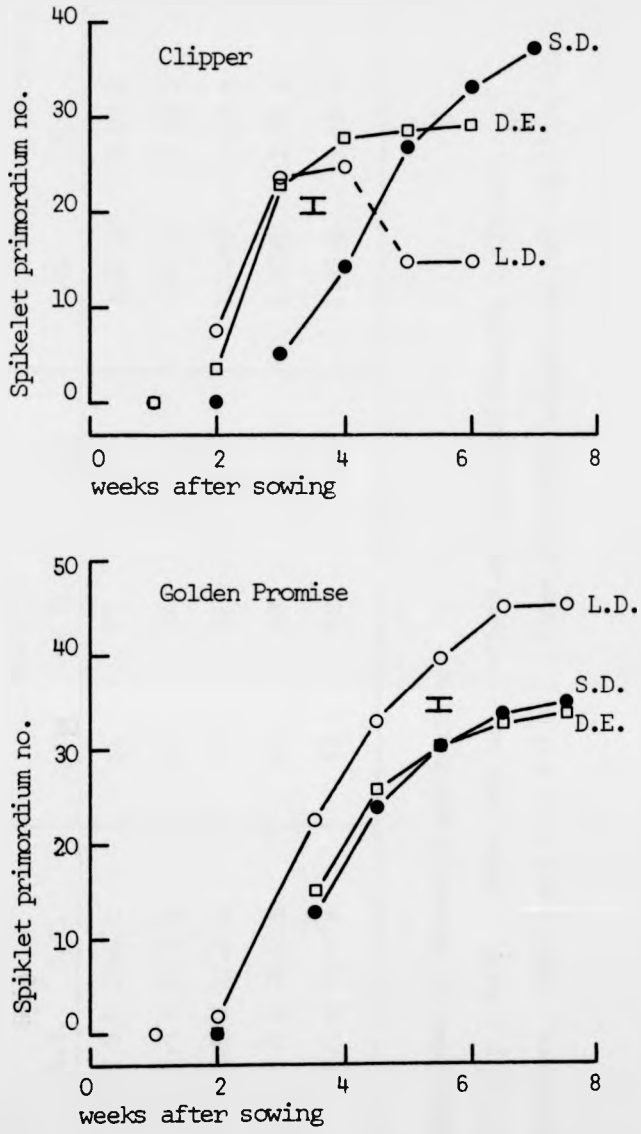


Fig. 32. Effect of photoperiod (day extension) on spikelet primordium number of Clipper and Golden Promise (growth room).

Each point is a mean of between 9 and 12 plants.
Vertical bars indicate L.S.D. significant at $p \leq 0.05$, calculated following an analysis of variance for each cultivar separately.

● = Short day, S.D., 8h day
□ = Day extn., D.E., 8+8h day
○ = Long day, L.D., 16h day

TABLE 32. Influence of photoperiod (Night interruption) on some parameters of spikelet primordium production of five barley cultivars (glasshouse).

Cultivar	Spikelet primordium maximum			Duration of production (days)			Initial rate of production (spikelet primordia/day)		
	S.D.	N.I.	L.D.	S.D.	N.I.	L.D.	S.D.	N.I.	L.D.
Clipper	35.3 a*	29.3 b	18.4 c	51	27	15	1.37 a*	1.49 a	2.30 b
Spartan	38.9 a	38.4 a	22.5 b	54	32	14	1.48 a	1.81 b	2.51 c
Domen	32.5 a	35.0 a	32.3 a	47	56	22	1.13ab	1.00 a	1.47 b
Golden Promise	37.0 a	35.9 a	36.0 a	56	43	33	1.45ab	1.40 a	1.82 b
Uzu	38.2 a	39.1 a	35.6 a	52	45	40	1.82 a	1.68 a	1.70 a

Values of spikelet primordium maximum mean of between 4 and 8 plants.

x = Multiple range test significant at $p \leq 0.05$. Means with same letters are not significantly different.

y = Comparison of regression coefficients, significant at $p \leq 0.05$. Rates with same letters are not significantly different.

maximum number of spikelet primordia was significantly reduced ($p \leq 0.05$) in L.D. compared with N.I. and S.D. treatments for Clipper and Spartan although the decrease found in N.I. compared with S.D. treatment was not significant. The spikelet primordium maximum was not significantly different in N.I. compared with the L.D. and S.D. treatments for the other cultivars (Table 32).

It has been shown that the maximum is determined by both the duration and the initial rate of set down (page 43). These parameters have been calculated using the method of analysis described on page 42 and are presented in Table 32.

The duration of set down was reduced in L.D. compared with S.D. conditions for all cultivars and this difference was particularly evident for Clipper and Spartan (cf. Table 8). The period of production with light break treatment was intermediate between S.D. and L.D. conditions for all cultivars except Domen which exhibited a slightly longer period of set down in N.I. treatment. However, the effect of photoperiod was greatest for Clipper and Spartan than for the other cultivars.

The initial rate of spikelet primordium production for the period of linear increase in numbers following the onset of set down was increased for all cultivars in L.D. compared with S.D. conditions but this increase was significant ($p \leq 0.05$) only for Clipper and Spartan (cf. Table 8). The influence of night interruption on the rate of production for both cultivars was intermediate between S.D. and L.D. conditions with significant differences between N.I. with both S.D. and L.D. conditions for Spartan. The effect of N.I. treatment was less pronounced in the other cultivars and

was not significantly different from either S.D. or L.D. conditions except for Domen and Golden Promise in long days. Confirmation of the contracted responsiveness between these cultivars to photoperiod can be derived from the magnitude of the difference between N.I. and S.D. treatments in the percentage of the spikelet primordium maximum set down at three weeks from sowing, for example between the cultivars Clipper and Golden Promise (Table 33). The high percentage set down at three weeks in N.I. and L.D. conditions for Clipper compared with Golden Promise is due to both the early onset of set down and the rapid initial rate of set down.

In the Day extension experiment, the pattern of spikelet primordium production for Clipper under S.D. and L.D. conditions (Fig. 32) was similar to that found in the N.I. study above but the pattern of set down was different for Golden Promise. The spikelet primordium maximum for Golden Promise was higher in L.D. than D.E. and S.D. conditions (Fig. 32 and Table 34) (cf. growth room daylength study, Fig. 5) whereas the maximum was unaffected by daylength treatment in the glasshouse. It is suggested that the relatively low maximum attained under S.D. and D.E. conditions may be attributed to the low light intensity used in the growth room. Supplemental light intensity in the growth rooms was 15,000 lux, 120 Wm^{-2} compared with a light intensity of 20,000 lux, 200 Wm^{-2} in the glasshouse and this value does not include the natural daylight intensity at the time of the experiment (summer-autumn 1977).

Under these conditions assimilate production may not be sufficient to maintain apical growth and development with a

TABLE 33. Influence of photoperiod (Night Interruption) on spikelet primordium maximum and percentage set down at three weeks for five barley cultivars (glasshouse).

Cultivar	Spikelet primordium max.			% of spikelet primordium max. set down at 3 weeks		
	S.D.	N.I.	L.D.	S.D.	N.I.	L.D.
Clipper	35.3	29.3	18.4	28.4	73.5	100
Spartan	38.9	38.4	22.5	23.8	48.6	100
Domen	32.5	35.0	32.3	50.8	40.5	79.8
Golden Promise	37.0	35.9	36.0	23.6	25.8	66.2
Uzu	38.2	39.1	35.6	16.0	13.8	60.0

Each value for spikelet promordium maximum is a mean of between 4 and 8 plants.

TABLE 34. Influence of photoperiod (Day extension) on some parameters of spikelet primordium production of Clipper and Golden Promise (growth room).

Cultivar	Spikelet primordium maximum			Duration of production (days)			Initial rate of production (spikelet primordia/day)		
	S.D.	D.E.	L.D.	S.D.	D.E.	L.D.	S.D.	D.E.	L.D.
Clipper	37.2[x]a	29.1 b	25.0 c	33[x]	31	19	1.46 a[z]	2.18 b	1.98 b
Golden Promise	35.0[x]a	33.8[x]a	45.0 b	37[x]	38[x]	34	1.55 a	1.51 a	2.18 a

Values of spikelet primordium max. mean of between 9 and 12 plants.

x = spikelet primordium number at final sample - see text.

y = multiple range test, significant at $p \leq 0.05$, calculated for each cultivar separately. Means with same letters are not significantly different.

z = comparison of regression coefficients, significant at $p \leq 0.05$. Rates with same letters are not significantly different.

subsequently early cessation of spikelet primordium production and a lower final spikelet primordium number. It may be suggested that with increased light intensity, the increased photosynthesis possible would prolong set down and allow a higher maximum to be determined. This confirms the sensitivity of Golden Promise to the radiation component of daylength and this explanation would explain the low spikelet primordium maximum attained in the D.E. treatment.

Spikelet primordium production of Clipper was accelerated by increased photoperiod and the final maximum attained was intermediate between L.D. and S.D. conditions (Table 34). It may again be suggested that the difference between L.D. and D.E. treatments was less pronounced than might have been expected because of the low radiation energy in the growth rooms. The pattern of spikelet primordium set down of Golden Promise was unaffected by photoperiod treatment and the maximum was similar in both D.E. and S.D. treatments (Table 34).

The influence of photoperiod (Day extension treatment) on the time of onset of spikelet primordium production (Fig. 30) and on the duration and initial rate of set down (Table 34) was similar to that found in the Night interruption study (Fig. 29 and Table 34) and will therefore not be described in detail. The contrasted response between Clipper and Golden Promise to photoperiod is evident from all parameters and it should be noted that in all treatments marked 'x' in Table 34, the duration of production will be longer than the value given (see above).

iv) Apex length.

The influence of photoperiod treatment on apical length for the five cultivars examined in the Night interruption

subsequently early cessation of spikelet primordium production and a lower final spikelet primordium number. It may be suggested that with increased light intensity, the increased photosynthesis possible would prolong set down and allow a higher maximum to be determined. This confirms the sensitivity of Golden Promise to the radiation component of daylength and this explanation would explain the low spikelet primordium maximum attained in the D.E. treatment.

Spikelet primordium production of Clipper was accelerated by increased photoperiod and the final maximum attained was intermediate between L.D. and S.D. conditions (Table 34). It may again be suggested that the difference between L.D. and D.E. treatments was less pronounced than might have been expected because of the low radiation energy in the growth rooms. The pattern of spikelet primordium set down of Golden Promise was unaffected by photoperiod treatment and the maximum was similar in both D.E. and S.D. treatments (Table 34).

The influence of photoperiod (Day extension treatment) on the time of onset of spikelet primordium production (Fig. 30) and on the duration and initial rate of set down (Table 34) was similar to that found in the Night interruption study (Fig. 29 and Table 34) and will therefore not be described in detail. The contrasted response between Clipper and Golden Promise to photoperiod is evident from all parameters and it should be noted that in all treatments marked 'x' in Table 34, the duration of production will be longer than the value given (see above).

iv) Apex length.

The influence of photoperiod treatment on apical length for the five cultivars examined in the Night interruption

study is presented in Fig. 33 and for the two selected genotypes in the Day extension study in Fig. 34. The pattern of apical length increase with time in the S.D. and L.D. in both studies was similar to the response found in the earlier growth room daylength study (Section 1, Fig. 8). The duration of the initial slow rate of length increase was reduced in long days for all cultivars in both studies and apical length was significantly greater ($p \leq 0.05$) under L.D. compared with the other treatments 14 d.a.s. for all cultivars in the N.I. study and at 14 and 24 d.a.s. for Clipper and Golden Promise respectively in the D.E. study (significant differences calculated from Multiple range test following an analysis of variance).

Cultivars exhibited differences in the magnitude of their response to long days and this difference was reflected in their response to photoperiod. In the N.I. study, the onset of the period of rapid length increase with light break treatment was intermediate between S.D. and L.D. treatments for Clipper and Spartan (significant, $p \leq 0.05$, five and six w.a.s. respectively) and this pattern of apical length increase for Clipper with increased photoperiod was confirmed in the Day extension study (Fig. 34). Apical length of the other cultivars was not affected by increased photoperiod either with night interruption or day extension.

The longer period of the initial slow growth rate for Clipper and Spartan in N.I. compared with L.D. treatment was reflected in a correspondingly longer period of rapid increase attaining a greater ear length at emergence. This may be due to either the increased spikelet number determined in N.I. compared with L.D. treatment or to differences in rachis

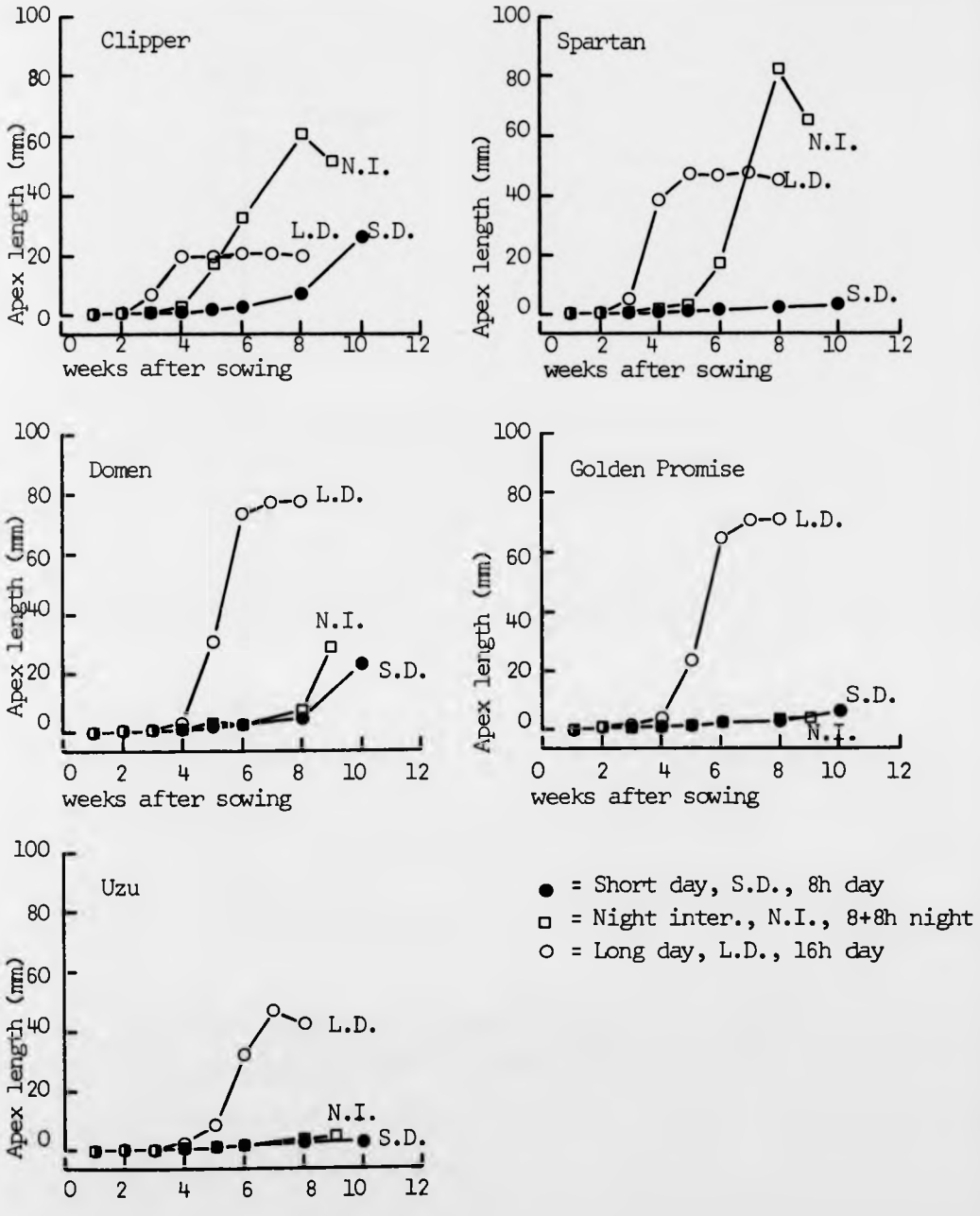


Fig. 33. Effect of photoperiod (night interruption) on apex length (mm) of five barley cultivars.

Each point is a mean of between 4 and 12 plants.

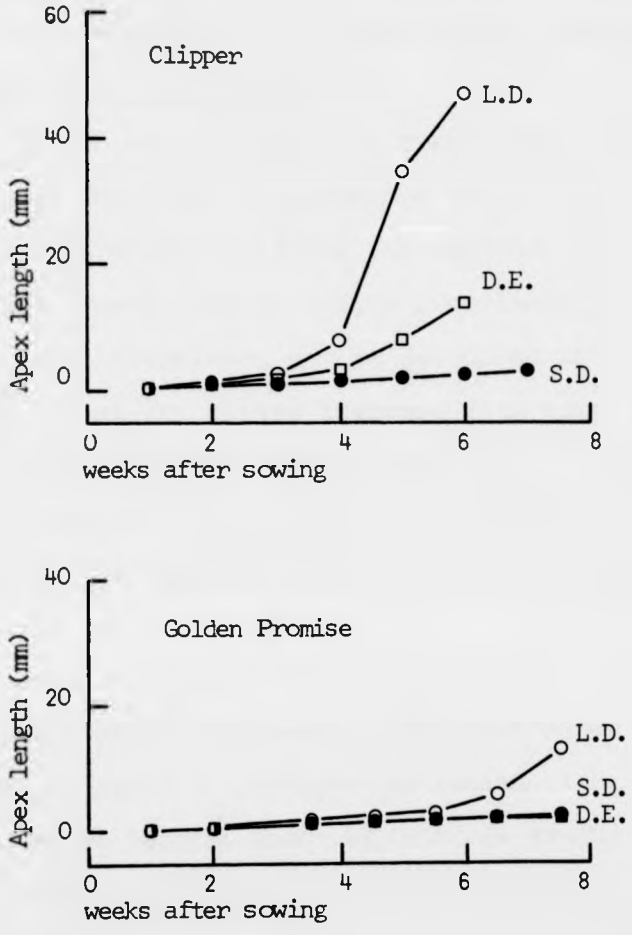


Fig. 34. Effect of photoperiod (day extension) on apex length of Clipper and Golden Promise (growth room).

Each point is a mean of between 9 and 12 plants.

● = Short day, S.D., 8h day
□ = Day extn., D.E., 8+8h day
○ = Lond day, L.D., 16h day

internode length but this was not measured in this study. Final ear length was not determined in the other treatments in either study because of the slower apical development.

v) Main apex dry weight.

The influence of S.D. and L.D. treatments on apex dry weight (Fig. 35 for Night interruption study and Fig. 36 for Day extension study) confirms the response pattern found in the earlier growth room daylength experiment (Section 1, Fig. 9) and will, therefore, not be described in detail.

The pattern of dry matter increase with time for Clipper and Spartan with increased photoperiod (N.I. treatment) was intermediate between S.D. and L.D. conditions and was associated with the earlier onset of the phase of rapid dry matter increase compared with short days. Increased photoperiod had no effect on the pattern of dry weight increase for the other cultivars. The contrasted response of dry matter increase to photoperiod treatment between Clipper and Golden Promise was confirmed in the Day extension study (Fig. 36) again indicating the photoperiodic sensitivity of Clipper.

The onset of the phase of rapid apical dry weight increase corresponded to the period of rapid length increase (Figs. 35 and 36) again suggesting that their two parameters are under the same endogenous control. The effect of photoperiod treatment (either night interruption or day extension) on final ear dry weight cannot be determined from the available data although the pattern of dry matter increase for Clipper in L.D. and N.I. conditions suggests that the duration of increase is prolonged with N.I. treatment culminating in a heavier final dry weight. This would,

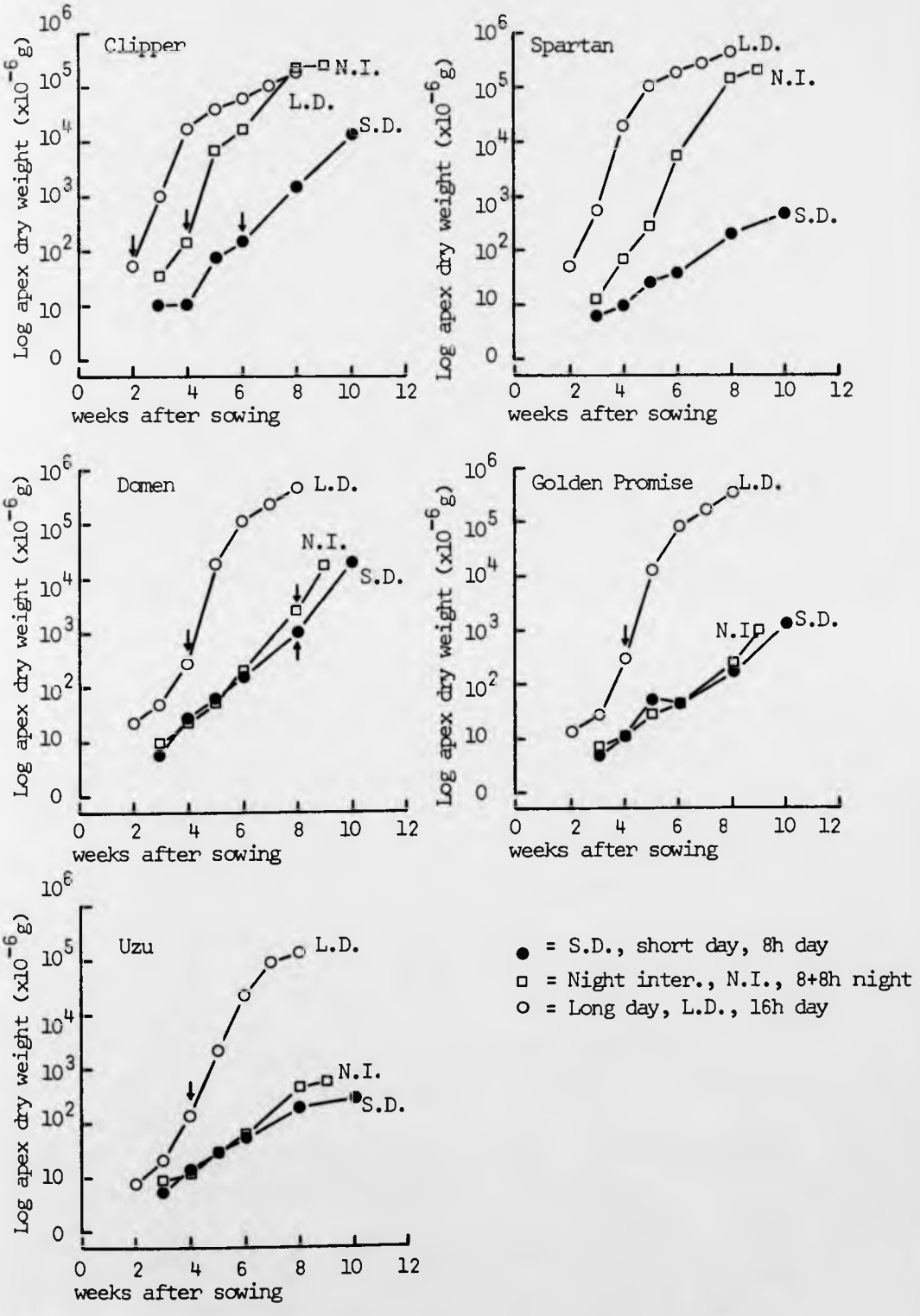


Fig. 35. Effect of photoperiod (night interruption) on apical dry weight of five barley cultivars (glass-house)

Each point is a mean of between 4 and 12 plants.
Arrows indicate onset of rapid apex length increase.

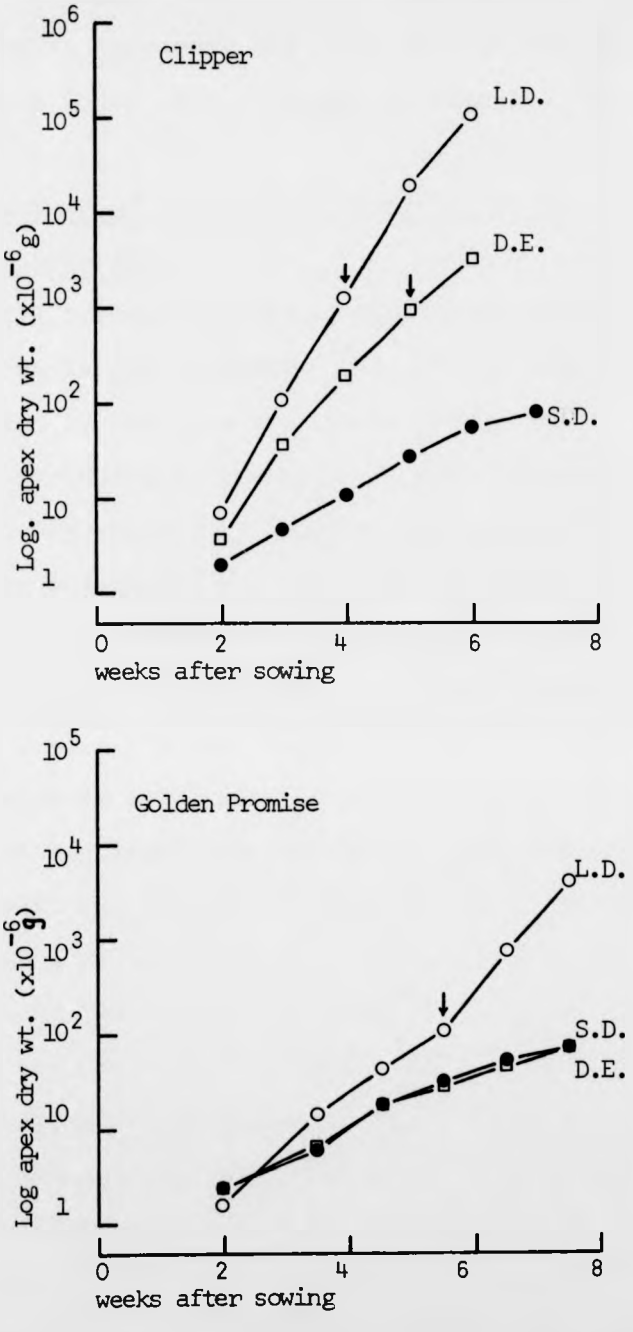


Fig. 36. Effect of photoperiod (day extension) on apex dry weight of Clipper and Golden Promise (growth room).

Each point is a mean of between 8 and 12 plants.
Arrows indicate onset of rapid length increase.

● = Short day, S.D., 8h day
□ = Day extn., D.E., 8+8h day
○ = Long day, L.D., 16h day

therefore, be in agreement with the greater ear length observed for Clipper in N.I. compared with L.D. treatment (Fig. 33).

vi) Summary of apical developmental responses to photoperiod.

Cultivars differed in the magnitude of their apical response to daylength treatment (cf. growth room daylength study, Section 1) and this was reflected in their contrasted response to photoperiod treatment. The pattern of apical growth and development for Clipper and Spartan with N.I. treatment was intermediate between the response to S.D. and L.D. treatments but light break appeared to have no effect on apical development for the other cultivars (Domen, Golden Promise and Uzu). It was suggested that Clipper and Spartan were responsive to both the photoperiodic and radiation components of daylength whereas apical development of the other cultivars was influenced only by the light energy available for photosynthesis and was unresponsive to photoperiod. Confirmation of the contrasted response of these cultivars to photoperiod treatment can be similarly derived from the accelerated spikelet primordium production with N.I. treatment for Clipper and Spartan resulting in a lower maximum but which was unaffected by increased photoperiod for the other cultivars.

Apical growth and development was similarly affected by increased photoperiod when given by a day extension treatment and the contrasted photoperiodic sensitivity between Clipper and Golden Promise was confirmed.

Photoperiod transfer experiment

The influence of photoperiod on apical development was examined further in this study. Plants of one photoperiodically-sensitive cultivar, Clipper, were transferred from one photoperiod treatment to another (D.E. to S.D.) and the pattern of apical development followed. This cultivar has been shown to be responsive to photoperiod treatment (see above).

i) Final leaf number per main shoot.

Leaf number was significantly reduced under D.E. conditions and in all photoperiod transfer treatments, D.E.1, D.E.2 and D.E.3 (i.e. plants transferred one, two and three w.a.s. respectively) compared with S.D. treatment (Table 35). Early transfer (D.E.1) resulted in an intermediate leaf number between D.E. and S.D. conditions whereas later transfer (D.E.2 and D.E.3) had no effect on the final number.

Cessation of leaf primordium production in Clipper under D.E. treatment occurred seven d.a.s. (see page 40) and final number was determined after 14 days. Transfer of plants to S.D. conditions within this period (D.E.1) resulted in an increase in leaf number thus indicating that some of the primordia set down during this period may be induced to develop into either spikelet or leaf primordia depending on the subsequent treatment. Photoperiod transfer after 14 days (D.E.2 and D.E.3), therefore, had no effect on final number because this had already been determined. Duration of leaf primordium production was prolonged in short days and cessation did not occur until 15 d.a.s. with a correspondingly high leaf number.

ii) Apical developmental stage.

TABLE 35. Influence of photoperiod transfer from D.E. to S.D. conditions on final leaf number per main shoot of Clipper (growth room).

Treatment	Final leaf number per main shoot
D.E.	6.88 a [x]
S.D.	11.46 b
D.E.1	10.84 c
D.E.2	6.98 a
D.E.3	6.77 a

D.E.1, D.E.2 and D.E.3 - plants transferred from D.E. to S.D. conditions one, two and three weeks after sowing respectively.

Each value is a mean of at least 24 plants.

x = multiple range test, significant at $p \leq 0.05$. Means with same letters do not differ significantly.

The effect of photoperiod on apical development of Clipper under D.E., S.D., D.E.1 and D.E.2 treatments is presented in Fig. 37. The pattern of apical development in D.E.3 was identical to D.E. treatment and has not been included.

Apical development was accelerated in D.E. compared with S.D. conditions and the final stage of development distinguished, tip degeneration (TD) occurred four w.a.s. in D.E. treatment but was not reached within the experimental period (seven weeks) in short days. Transfer of plants after seven days (D.E.1) resulted in a slower rate of development similar to that observed for S.D. plants and this pattern was maintained throughout the experimental period. Apical morphogenesis was again prolonged after transfer to short days in D.E.2 photoperiod treatment and tip degeneration did not occur until seven w.a.s. The change in the pattern of apical development in both D.E.1 and D.E.2 treatments was noticeable at the time of the first sample after transfer although it cannot be determined whether the change was immediate or occurred after a delay of several days.

iii) Spikelet primordium number.

The influence of photoperiod transfer treatment on spikelet primordium production of Clipper is shown in Fig. 38 and the maximum number (or number at the final sample for S.D. and D.E.1 treatment) is presented in Table 36. The duration and rate of set down was calculated as described earlier (page 42) and these parameters are also included in the Table.

Spikelet primordium maximum was significantly reduced ($p \leq 0.05$) in D.E. compared with S.D. conditions and this

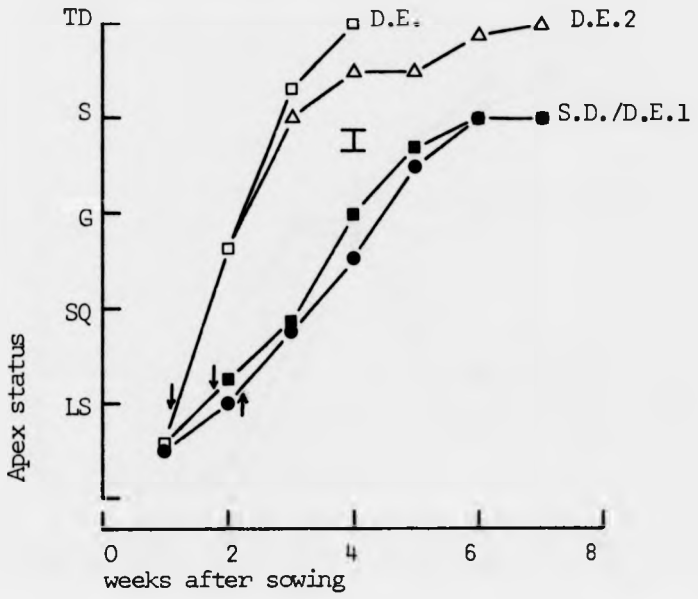


Fig. 37. Effect of photoperiod transfer from day extension (D.E.) to short day (S.D.) treatment on apex developmental stage of Clipper (growth room).

Only alternate apical developmental stages are shown on y-axis, see Table 7.

Each point is a mean of between 6 and 8 plants.
Vertical bar indicates L.S.D. significant at $p \leq 0.05$, calculated following an analysis of variance.
Arrows indicate onset of spikelet primordium production.

● = Short day, S.D., 8h day
□ = Day extn., D.E., 8+8h day
■ = D.E.1) Plants transferred from S.D. to D.E. conditions one
△ = D.E.2) and two weeks after sowing respectively.

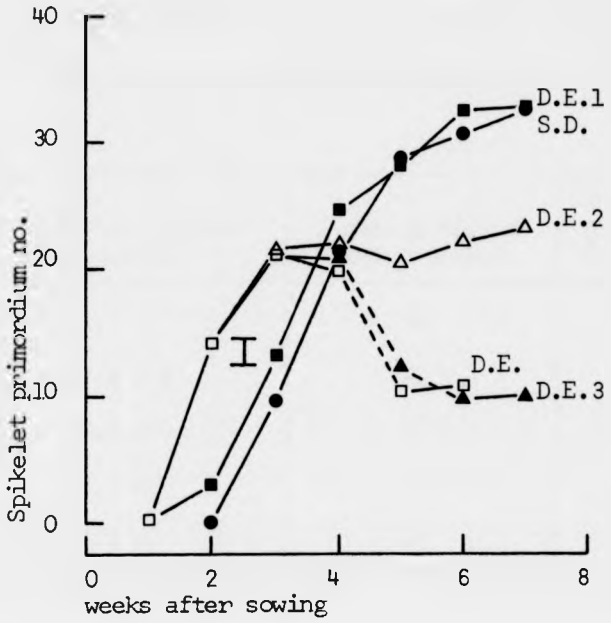


Fig. 38. Effect of photoperiod transfer from day extension (D.E.) to short day (S.D.) treatment on spikelet primordium number of Clipper (growth room).

Each point is a mean of between 6 and 8 plants.
Vertical bar indicates L.S.D. significant at $p = 0.05$, calculated following an analysis of variance.

● = Short day, S.D., 8h day
□ = Day extn., D.E., 8+8h day
■ = D.E.1)
△ = D.E.2) Plants transferred from S.D. to D.E. conditions
▲ = D.E.3) 1, 2 and 3 weeks after sowing respectively.

TABLE 36. Influence of photoperiod transfer from D.E. to S.D. conditions on several parameters of spikelet primordium production of Clipper (growth room).

Treatment	Spikelet primordium maximum	Duration of production (days)	Initial rate of production (sp. primordia/day)
D.E.	21.1 a[y]	14	2.02 a[z]
S.D.	32.8 x b	33 x	1.53 ab
D.E.1	32.9 x b	37 x	1.54 b
D.E.2	23.3 a	42	-
D.E.3	21.1 a	14	-

D.E.1, D.E.2 and D.E.3 - plants transferred from D.E. to S.D. conditions one, two and three weeks after sowing respectively.

Each value of spikelet primordium max. is a mean of 8 plants.

x = spikelet primordium number at final sample - see text.

y = multiple range test, significant at $p \leq 0.05$. Means with same letters are not significantly different.

z = comparison of regression coefficients, significant at $p \leq 0.05$. Rates with same letters are not significantly different. Rates were not calculated for D.E.2 and D.E.3 treatments.

decrease was caused by the reduced duration of the period of production although the rate was slightly but not significantly increased (Table 36). Early photoperiod transfer (D.E.1) resulted in the later onset of set down (Fig. 38) combined with both a longer period and a significantly ($p \leq 0.05$) reduced rate of production (Table 36) compared with D.E. treatment and the subsequent pattern was similar to S.D. plants. The curvilinear phase of production was prolonged by D.E.2 treatment although the maximum attained was not significantly affected. Similarly, increased delay in the time of transfer (D.E.3) had no effect on the maximum determined although there was a slightly longer period of set down of the last-formed primordia.

Clipper is clearly influenced by changes in photoperiod during apical development but because of the rapid development under promotive photoperiod treatments (i.e. photoperiodically long days), the transfer of plants to shorter photoperiods must occur during the very early growth of the plant to significantly affect spikelet primordium number.

DISCUSSION

Apical development and spikelet primordium production was accelerated in L.D. compared with S.D. treatment for all cultivars in both Night interruption and Day extension studies (cf. growth room daylength experiment, Section 1) and cultivars differed in the magnitude of their response. This difference was reflected in their apical response to photoperiod treatment using either night interruption or day extension treatment. For example, apical growth and development of the daylength highly-sensitive cultivar,

Clipper, with either N.I. or D.E. treatment was intermediate between L.D. and S.D. conditions with a subsequent reduction in the spikelet primordium maximum attained. Apical development of Golden Promise on the other hand was similar in N.I. and D.E. treatments compared with short days and the maximum number was unaffected by photoperiod treatment.

Aspinall (1966) and Paleg and Aspinall (1966) similarly found apical development and spikelet primordium production to be accelerated for most cultivars examined with N.I. treatment, e.g. CI 5611 and Prior with a subsequent decrease in the maximum attained, but other cultivars, e.g. Proctor, were relatively unresponsive. Aspinall suggested that the response to night interruption was a good indication of its response to daylength and confirmation of this can be derived from the present study. Clipper and Spartan exhibited a greater response to L.D. and N.I. treatment compared with Domen, Golden Promise and Uzu (cf. CI 5611 and Proctor respectively, Aspinall 1966).

Two physiological groups can, therefore, be distinguished on the basis of their response to night interruption. Group one (Clipper and Spartan) appeared to be sensitive to both the photoperiodic and radiation components of daylength whereas group two (Domen, Golden Promise and Uzu) appeared to be unresponsive to photoperiod and apical development and spikelet primordium production was determined by the light energy for photosynthesis.

The contrasted photoperiodic sensitivity of Clipper and Golden Promise was confirmed in the Day extension study thus suggesting that both night interruption and day extension treatments may be used to evaluate the photoperiodic

responsiveness of barley genotypes. This contradicts the earlier work by Lane et al (1965) on Wintex barley which was unresponsive to light break but was sensitive to photoperiod if provided by day extension period.

As in the previous growth room daylength study, there is a close relationship between both the duration of leaf primordium production and final leaf number and the duration of spikelet primordium set down and the maximum attained in both photoperiod studies. All parameters were influenced by night interruption for Clipper and Spartan (and for Clipper with D.E. treatment). The duration of the period of leaf primordium set down with N.I. and D.E. treatments was intermediate between S.D. and L.D. conditions and the subsequent final leaf number was intermediate between the two daylength regimes. Consequently, the onset of spikelet primordium production was earlier with increased photoperiod and the period of set down was markedly reduced with a resulting decrease in the maximum number determined by Clipper despite the increased rate of production. Aspinall (1966) also found cessation of set down occurred earlier with light break treatment than in short days and that the duration of the period of set down was more important than the rate of set down in determining the final number. In this study, however, maximum spikelet primordium number of Spartan was unaffected by N.I. compared with S.D. treatment because the reduced period of set down was compensated by the increased rate of production.

Many other studies using day extension treatments have similarly indicated that photoperiod treatment reduces the period of both leaf and spikelet primordium production of wheat

cultivars although the rate of set down is increased (Rawson 1970, Lucas 1972, Holmes 1973, Wall and Cartwright 1974 and Allison and Daynard 1976). Spikelet number is generally reduced with increased photoperiod although cultivars differ in the magnitude of their response. Holmes (1973) found that Marquis wheat was sensitive to photoperiod and was characterised by a short duration of set down compared with Pitic wheat which was relatively unresponsive to photoperiod treatment (cf. Clipper and Golden Promise in this study and CI 5611 and Proctor in Aspinall 1966).

The effect of photoperiod transfer from D.E. to S.D. conditions on apical development and spikelet primordium number for Clipper depended on the apical stage at time of transfer and thus confirms the earlier work by Lucas (1972) and Allison and Daynard (1976) on wheat. Early transfer reduces the rate of both leaf and spikelet primordium production with a subsequent increase in both leaf and spikelet number. Late transfer has no effect of leaf number and only the later stages of spikelet primordium production are affected. Clearly, the earlier the change to photoperiodically-different conditions the greater the potential for the photoperiod to be manifested in final spikelet number. It is suggested, therefore, that an early change from short to long photoperiods would result in decreased leaf and spikelet number and an associated prolonged period of apical growth and development. Aspinall (1969) and Allison and Daynard (1976) have suggested that several days may elapse before apical development is affected and although this seems likely, the present study cannot clarify this point.

The contrasted sensitivity of apical development and

spikelet primordium production to photoperiod between Clipper and Golden Promise was also reflected in the pattern of response for apex length and dry weight. The rapid increase in dry weight coincided with the onset of rapid rachis internode elongation (Fig. 35, Night interruption study and Fig. 36, Day extension study) which similarly occurred at around the time of the cessation of spikelet primordium formation. The close relationships between the patterns of leaf and spikelet primordium production with apical growth and development indicates control by the same endogenous mechanism (cf. Section 1, page 83). It may also be possible that the effect of photoperiod on apical growth, leaf and spikelet primordium set down and floret development of Clipper and Spartan may also be mediated by the same mechanism of control.

However, the marked apical response of Clipper to photoperiod treatment compared with Golden Promise may also be caused by a possible differential response of these cultivars to incandescent light used for the light break and day extension period. Barley and wheat cultivars are known to be more responsive to incandescent than fluorescent light when given either as a Night interruption or day extension treatment due to the higher level of far-red light in incandescent light (Borthwick et al 1948, Downs et al 1959, Friend et al 1959, 1961). Similarly, it has been shown that the apical response is further accelerated with increased levels of incandescent light energy (Friendet al 1961, Paleg and Aspinall 1966 and Aspinall 1969).

In Aspinall's later study, he found that cultivars exhibited differences in the magnitude of their response to

increased levels of incandescent light used as an extension period such that Prior and CI 5611 were more responsive than CI 3576. It may, therefore, be possible that, in this study, Clipper and Spartan are not only more responsive to daylength than the other cultivars but are also more responsive to both the photoperiod and spectral quality of the light-source.

It is suggested, however, that because plants in N.I. treatment would only receive 30 mins. of low intensity incandescent light more than S.D. plants, the marked difference in the response of Clipper and Spartan to these treatments could not be attributed to the accelerated apical development in incandescent light alone. However, Friend (1964) has suggested that the promotive effect of far-red light was quantitative and partly dependent on the duration of the period of illumination and thus the promotive effect of incandescent light may be more important in the D.E. treatment. However, the similarities in the magnitude of the apical response of Clipper and Golden Promise to both N.I. and D.E. treatment (this study and Section 4) suggests the importance of photoperiod rather than spectral quality in determining the response of Clipper to those treatments whereas Golden Promise appears to be unresponsive to both daylength factors.

It is suggested, therefore, that Clipper and Spartan are long day or short night cultivars photoperiodically. Phytochrome has been implicated in the photoperiodic response of cereals (Borthwick et al 1948, Downs 1956 among many others) such that the inactive red-absorbing form (Pr) undergoes photoconversion by red light to produce the active

far-red absorbing form (Pfr) until a dynamic photo-stationary equilibrium is reached.

$$Pr \underset{\text{far-red}}{\overset{\text{red}}{\rightleftharpoons}} Pfr$$

Apical development of Clipper and Spartan was accelerated in long days implying that apical development was promoted by enhanced levels of P_{fr} but the light source for L.D. treatment was supplemented by incandescent light which has a high proportion of its energy in the far-red region of the spectrum (730nm). Similarly, apical development was also hastened with incandescent light supplied either as a N.I. or D.E. photoperiod treatment and these treatments could only have resulted in decreased levels of P_{fr} at the start of the dark period.

Mohr (1962) has suggested that plants may have two photoreactive systems - a photoreversible phytochrome system and a non-reversible high energy system with peaks in the blue and far-red regions of the spectrum and that both systems may mediate the same photoresponse. This has also been suggested by other workers both for barley (Paleg and Aspinall, 1964) and wheat (Friend 1964). Paleg and Aspinall (1964) suggested that in intermediate photoperiods (16h), the large apical response exhibited by barley cultivars to incandescent light was due to the activation of the high energy system but in short days, the phytochrome system dominated the response. Friend (1964) similarly argued that far-red would normally inhibit floral development but if given in high intensity light or in long photoperiods then a small but significant absorption of Pr may occur with far-red light and this may over-ride the photoreversible

phytochrome system. Further work by Aspinall (1969) has confirmed the sensitivity of barley cultivars to far-red light and has indicated that blue light is relatively ineffective in accelerating apical development compared with far-red. This mechanism would also help explain the increased response found with increased far-red energy found by many workers suggesting that it is the absolute amount of energy in red/far-red which determined the magnitude of the response rather than the ratio.

The apparent non-responsiveness of Domen, Golden Promise and Uzu to incandescent light supplied as a light break may, therefore, be due to a higher threshold for activation of this photoreactive system than Clipper and Spartan. Similarly, the 30 minute light break may not have been sufficiently long for activation, and the photoreversible phytochrome system dominated the response. The lack of photoperiodic response of these cultivars may also be due to a block on the sequence of biochemical events following the photo-activation of the high energy system.

Some phytochrome controlled responses may involve changes in the level of some hormones (Galston and Davies 1969, Kendrick and Frankland 1976) and it may be suggested that the flowering stimulus may involve a hormone, florigen, although this has not yet been isolated and identified.

Other growth substances have also been implicated in the flowering response and Galston and Davies (1969) have suggested that photoperiods favourable to flowering may perhaps affect the ratio of GA to inhibitor(s) such as abscissin. Other studies implicating GA in apical development (Nicholls and May 1964, Kirby and Faris 1970, Kirby 1971,

Holmes 1973 and Nicholls 1974, 1978) have been discussed earlier (Section 1).

Zeevart (1971) indicated that in spinach (Spinacia oleracea) there was both an increased biosynthesis of GA in long days and also an increased sensitivity to GA. This confirms suggestions by Kirby and Faris (1970) and Holmes (1973) that under certain treatments, such as long photoperiod regimes, the increased levels of GA in the apex as a result of these treatments will usually cause increased apical development with a subsequent reduction in spikelet primordium maximum. This would suggest that apical development of Clipper and Spartan was sensitive to changes in endogenous GA level and thus any environmental treatment which increases this level will result in accelerated apical development and a lower spikelet primordium number.

Some cultivars, however, (such as Pitic in Holmes' study and Golden Promise in the present study) may have a low level of utilization or sensitivity to GA with slower apical development and spikelet primordium production resulting in the concurrent establishment of primordia leading to a high final spikelet number. Under short days it may be suggested, therefore, that the low levels of endogenous GA will result in slower apical development and spikelet primordium production with a subsequently high maximum.

All cultivars were influenced by the radiation component of daylength thus suggesting that the delayed apical development in short days was at least partly due to the limited photosynthate supply to the apex. This is in agreement with the earlier suggestion that the reduced spikelet primordium

maximum for Golden Promise in D.E. and S.D. treatments in the Day extension study was due to the low light intensity used in the growth room. Both apical development and spikelet number has been shown to be decreased by both low light intensity treatment (Aspinall and Paleg 1963, 1964 for barley, and Friend et al 1963, Friend 1964 and Lucas 1972 for wheat) and also by shade treatment (Dale, Felippe and Fletcher 1972 and Dale and Felippe 1972). The effect of low light intensities has similarly been shown to be more pronounced when used in conjunction with S.D. treatment (Aspinall and Paleg 1963 for barley, and Williams and Williams 1968 for wheat). The combination of the slow apical development of Golden Promise in S.D. and D.E. treatments with their associated short high light intensity period plus the delayed development with low radiation levels may have resulted in a protracted period of spikelet primordium production such that assimilate production may not have been sufficient to supply the required carbohydrate for continued growth. It was suggested that this would result in both an earlier cessation of the initial linear period of production and a prolonged subsequent curvilinear period of increase resulting in a comparatively low spikelet primordium maximum.

The increased light energy present in long days compared with S.D., N.I. and D.E. treatments may, therefore, exert its effect through the increased photosynthate availability to the developing apex with a subsequent increase in apical growth and development. Conversely, long days, either by photoperiod or radiation level, may accelerate apical growth, say by increased endogenous GA level described above, thereby

increasing the competitive strength of the main shoot apex with respect to other sinks such as tiller buds. This, in turn, may then regulate the pattern and rate of assimilate distribution to the apex.

The effect of photoperiod (using day extension treatment) on assimilate movement to the apex using radio-isotope labelling and distribution assay for two cultivars, Clipper and Golden Promise, is examined in the following section. This experiment was carried out concurrently with the Day extension apical study described above.

increasing the competitive strength of the main shoot apex with respect to other sinks such as tiller buds. This, in turn, may then regulate the pattern and rate of assimilate distribution to the apex.

The effect of photoperiod (using day extension treatment) on assimilate movement to the apex using radio-isotope labelling and distribution assay for two cultivars, Clipper and Golden Promise, is examined in the following section. This experiment was carried out concurrently with the Day extension apical study described above.

SECTION 4. The influence of photoperiod on ^{14}C-labelled assimilate movement to the apex of selected genotypes.

INTRODUCTION

Barley cultivars appear to show two types of physiological response to daylength conditions (8h S.D. and 16h L.D.). Group one cultivars (Clipper and Spartan) appear to be influenced by both the photoperiod and radiation components of daylength with an accelerated pattern of apical growth and development resulting in a subsequent reduction in spikelet primordium number in long photoperiods compared with short days. Group two cultivars (Domen, Golden Promise and Uzu) were unaffected by photoperiod treatment and apical growth and development appeared to be controlled only by the radiation level available for photosynthesis.

It has been suggested that the effect of daylength on apical development may either be directly mediated through the increased supply of assimilates to the apex caused by the increased photosynthesis possible in long days or through an initial effect on apical development. Assimilate supply to the developing apex will subsequently be increased due to the increased sink strength of the larger apex.

The movement of ^{14}C-labelled assimilates to different parts of the plant has been examined by several workers both for barley (Felippe and Dale 1972, 1973) and wheat (Quinlan and Sagar 1962, Doodson et al 1964, Lupton 1966 and Rawson and Holstra 1969) as well as other grass species such as Lolium multiflorum (Sagar and Marshall 1966, Ryle 1970, 1972 and Ryle and Powell 1972, 1974).

During the early stages of growth, assimilates move

freely from the expanded leaves to the different parts of the plant and accumulate in regions of meristematic activity (expanding leaves, apical meristem, tiller buds and roots) (Quinlan and Sagar 1962, Doodson et al 1964, Lupton 1966, Rawson and Hofstra 1969 and Felippe and Dale 1972, 1973). The assimilate supply to the expanding leaves reaches a maximum around the time of full expansion but then decreases as the rate of leaf expansion falls. The supply from the lower leaves and the increased supply from the expanding leaf is then switched to the next leaf in sequence (Doodson et al 1964, Rawson and Hofstra 1969 and Felippe and Dale 1972). At this time, reciprocal transfer of assimilates between main shoot and tillers freely occurs although once internode elongation of the main stem occurs, the tillers become independent (Quinlan and Sagar 1962, and Lupton 1966). However, Rawson and Hofstra (1969) suggested that full independence is never attained and studies by Marshall and Sagar (1968), Clifford et al (1973) and Nyahoza et al (1974) for Lolium multiflorum and Poa pratensis have indicated that reciprocal transfer of carbohydrate may still occur even at ear emergence.

During the later stages of plant growth of wheat, translocate movement becomes polarized and each recently expanded leaf supplies carbohydrate preferentially to the expanding leaves, stem and inflorescence whereas the lower leaves supply the lower parts of the stem, tillers and roots (Quinlan and Sagar 1962; Lupton 1966 and Rawson and Hofstra 1969) although transfer from the upper leaves to the roots is still possible. The preferential distribution of assimilates in wheat becomes even more sharply polarized at

grain filling during which the ear derives almost all its carbohydrate from the flag leaf, penultimate leaf and top stem internode (Stoy 1963, 1965 and Austin and Edrich 1975 among many others). This preferential pattern of assimilate distribution to the nearest actively-growing meristematic region of the plant is confirmed by the detailed series of studies by Ryle on Lolium multiflorum (Ryle 1970, 1972 and Ryle and Powell 1972, 1974).

These studies have generally followed the pattern of assimilate movement to the different parts of the plant under only one set of environmental conditions. In this section, the influence of daylength (S.D. and L.D. conditions) and day extension treatment on ^{14}C-labelled assimilate movement to the main shoot apex is followed for the two photoperiodically-contrasted cultivars, Clipper and Golden Promise. The response of apical growth and development to day extension photoperiod treatment was examined in a parallel study and has been described previously (Section 3).

Many of the earlier radio-isotope labelling studies have expressed the data in terms of the percentage supply of assimilates to the different regions of the plant and although this provides information on the qualitative distribution of carbohydrate it gives no indication of the absolute amount involved. In the present study, the net photosynthesis of a single barley plant was measured immediately prior to ^{14}C-labelling and thus the absolute amount of labelled carbohydrate present in the apex could be measured.

MATERIALS AND METHODS

i) Plant culture.

This radio-isotope labelling and distribution study was carried out in conjunction with the apical response to day extension treatment discussed previously and thus sowing and plant culture methods are as described earlier (Section 3).

ii) Measurement of net photosynthesis by single plants.

For both cultivars, net photosynthesis of single plants was measured for the plants retained following the removal of samples for apical dissection (Section 3, page 110). As far as possible the plants selected were of uniform external morphological appearance. The carbon dioxide uptake of plants was measured at different times during the photoperiod: one, four, seven and ten hours into the L.D. and D.E. photoperiods and at: one, four and seven hours under short day conditions.

Net photosynthesis of single plants was determined using an open circuit, differential infra-red gas analyser (IRGA; Grubb-Parsons, model SB2 connected to a Servoscribe 15 chart recorder) (Fig. 39). Air was pumped into a 25 litre reservoir to buffer the effect of small variations in temperature and atmospheric CO_2 levels and to saturate the air with water vapour before passing through a rate-meter to regulate the air flow. The flow rate was normally maintained at 800 $cm^3 min^{-1}$ but was increased to 1600 $cm^3 min^{-1}$ if CO_2 depletion exceeded 50ppm. Air was then passed through a secondary humidifier before entering the reference tube of the IRGA and finally through an assimilation chamber (6867 cm^3 capacity) sealed onto the outer rim of a pot

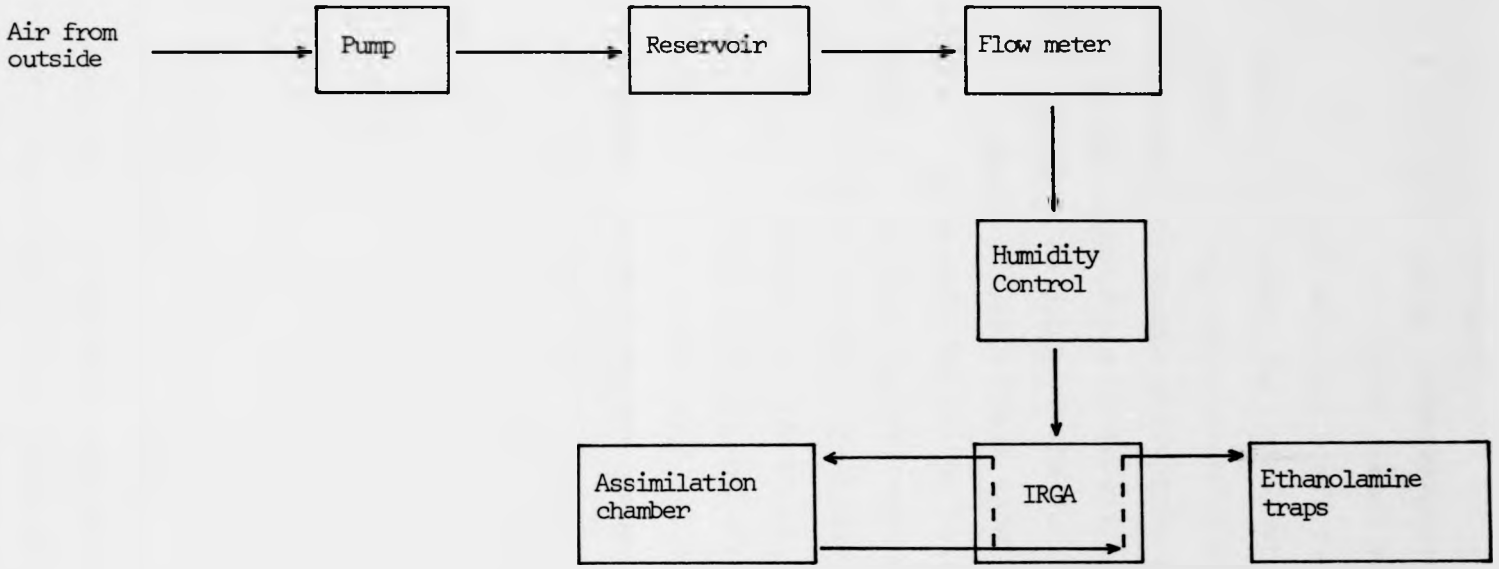


Fig. 39. Circuit employed for measurements of net photosynthesis and ^{14}C-assimilate movement to the apex of single barley plants.

containing a single plant (Fig. 40).

The assimilation chamber consisted of a glass bell-jar clamped onto a 5mm thick perspex base-plate and the seal made air-tight with petroleum jelly. The base-plate contained two hollow glass tubes (8mm internal diameter - inlet and outlet pipes) and a 5cm diameter hole was cut in the plate for the plant shoot. The base of the pot was sealed to prevent leakage and it was also found necessary to seal off the soil surface to prevent respiratory carbon dioxide from the soil entering the chamber. This was achieved using a 13cm diameter circular perspex disc designed to fit tightly onto the inner rim of the pot and sealed with petroleum jelly. The perspex discs were cut in half and contained a small central hole of different diameters designed to fit plant stems of increasing age and the shoot sealed in the central hole with petroleum jelly.

Air was circulated within the chamber by means of a small fan and then passed via a second humidifier to the analysis tube of the IRGA and then vented. A second flow meter could be situated in the air flow prior to venting to ensure that no leaks were present in the circuit.

Artificial lighting was provided by a single 500W incandescent bulb positioned directly above the assimilation chamber and a highly reflective convex aluminium shield positioned around the chamber to provide more equal illumination of the leaves. The light intensity was 12,500 lux (120 Wm^{-2}) at soil level and thus equivalent to the intensity used in the growth rooms.

Plants were maintained under these conditions for 45 minutes or until a steady photosynthesis reading could be

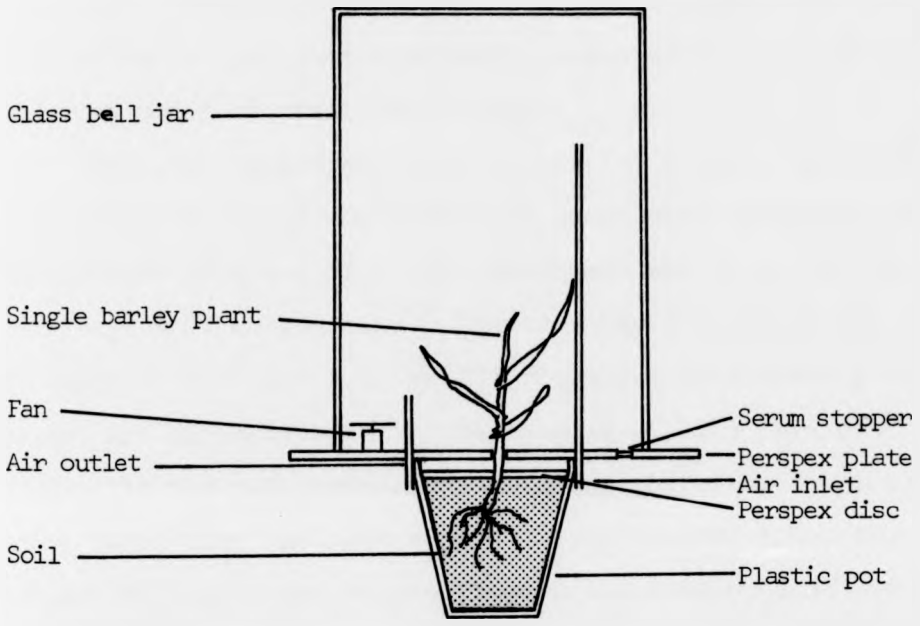


Fig. 40. Diagram of photosynthesis assimilation chamber.

obtained. The assimilation chamber was sealed off from the rest of the circuit and the plant exposed to $^{14}CO_2$ for 30 minutes as described in the following section. After this presentation period, the chamber was reconnected to the IRGA and a second photosynthesis reading obtained as above. The values of net photosynthesis presented (in mg C $h^{-1}plant^{-1}$) are the means of these two readings.

Sampling commenced seven d.a.s. for Clipper and continued thereafter at seven day intervals until the experiment was terminated 28 d.a.s. for L.D. treatment and 35 d.a.s. under D.E. and S.D. conditions. The very rapid plant growth of Clipper in L.D. and D.E. conditions meant that older plants could not be positioned in the chamber without physical damage to the main stem and leaves and therefore fewer samples were taken than had been hoped. Samples were taken seven, 14 and 24 d.a.s. for Golden Promise and continued at seven day intervals until 46 d.a.s.

iii) ^{14}C-labelled assimilate movement to the main shoot apex.

The circuit and chamber described above were modified to allow the plant to be labelled with $^{14}CO_2$. Two ethanolamine traps, each containing 5.0 cm^3 of an ethanolamine: 2-methoxyethanol solution (1:1 v/v), were positioned in series prior to venting in order to absorb $^{14}CO_2$ not assimilated by the plant both during the initial period of photosynthesis and after feeding. These were emptied into 10.0 cm^3 graduated conical flasks at the end of both periods and each trap flushed with a further 5.0 cm^3 aliquot of the ethanolamine: 2-methoxyethanol solution. The efficiency of these traps was estimated to be 96.9% (S.E. ± 0.8%).

Five µl of ^{14}C-sodium bicarbonate (equivalent to 10.0 µCi) was placed in a small watch glass inside the chamber at the beginning of the experiment. After the initial net photosynthesis value had been determined, the air flow was disconnected and the chamber sealed off from the rest of the circuit. A small quantity of 0.1N lactic acid was added by syringe through a serum stopper to liberate the $^{14}CO_2$ for a presentation period of 30 minutes. The chamber was then reconnected to the circuit and the residual $^{14}CO_2$ flushed into the series of ethanolamine traps as described above.

For each of the four flasks of absorbent per plant, 2.0 cm^3 aliquots were incorporated into 15.0 cm^3 of toluene-based scintillation fluid (containing 5.5g PPO, 0.5g dimethyl POPOP, 200 cm^3 2-methoxyethanol and 800 cm^3 toluene) in a glass counting vial and counted on a Packard scintillation spectrometer. A calibration curve was constructed for counting efficiency (Fig. 41) using ^{14}C-hexadecane as an internal standard (10µl = 1.7492×10^4 DPM) and the counts (minus background level) expressed as disintegrations per minute (DPM).

Radio-isotope ($^{14}CO_2$) uptake by the plant was calculated from the following equations:

Total $^{14}CO_2$ in chamber at start of expt. = 10 (µCi) x 3.7×10^4 DPM = A

Total $^{14}CO_2$ fed to plant = A - (DPM trap 1 + DPM trap 2) = B

Total $^{14}CO_2$ left after feeding = B - (DPM trap 3 + DPM trap 4) = C

$\therefore$ Total $^{14}CO_2$ fixed = B - C = D

The fed plant was removed from the assimilation chamber and returned to the appropriate photoperiod treatment for 24h.

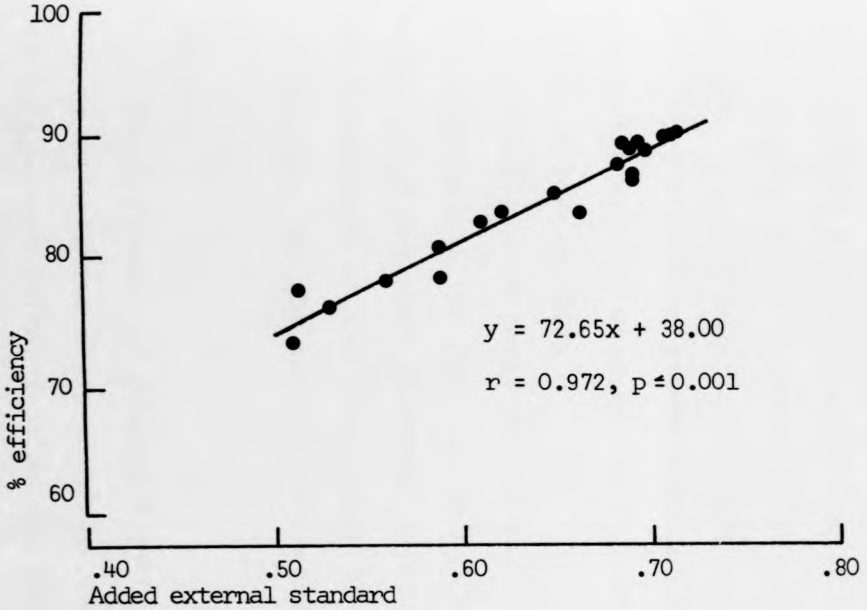


Fig. 41. Calibration curve - counting efficiency.

The main shoot apex was dissected out as described in Section 1 (page 29) and placed in 1.0 cm^3 'Soluene 350', a tissue solubiliser, in a glass counting vial for 24h at 50°C. Fifteen ml of toluene-based scintillation fluid (containing 5.0g PPO, 0.5g dimethyl POPOP and one litre toluene) and the radioactivity determined as previously. The radioactivity of the apex (minus background level and computed as DPM), E, was then used to determine the percentage of the plant $^{14}CO_2$ uptake transported to the main shoot apex (E/D x 100%). It should be noted, however, that this value is not equivalent to the proportion of the 14-carbon available for incorporation. Loss of $^{14}CO_2$ will occur during the 24h period following feeding and this may differ between cultivars and daylength-photoperiod treatments. This parameter was not measured in this study and will be discussed later in the section.

Finally, the total amount of ^{14}C-labelled assimilate incorporated in the apex was calculated by multiplying the whole plant net photosynthesis (from IRGA measurements) by the percentage of the $^{14}CO_2$ fixed by the plant accumulated in the apex and the results expressed as mg C h^{-1}.

RESULTS

The influence of daylength and photoperiod treatment (using an extended day period) on apical growth and development of Clipper and Golden Promise has been discussed previously (Section 3) and will not be commented upon further. The Results section will concentrate on the effect of these treatments on the movement of ^{14}C-labelled assimilate to the main shoot apex for Clipper and Golden Promise (Fig. 42)

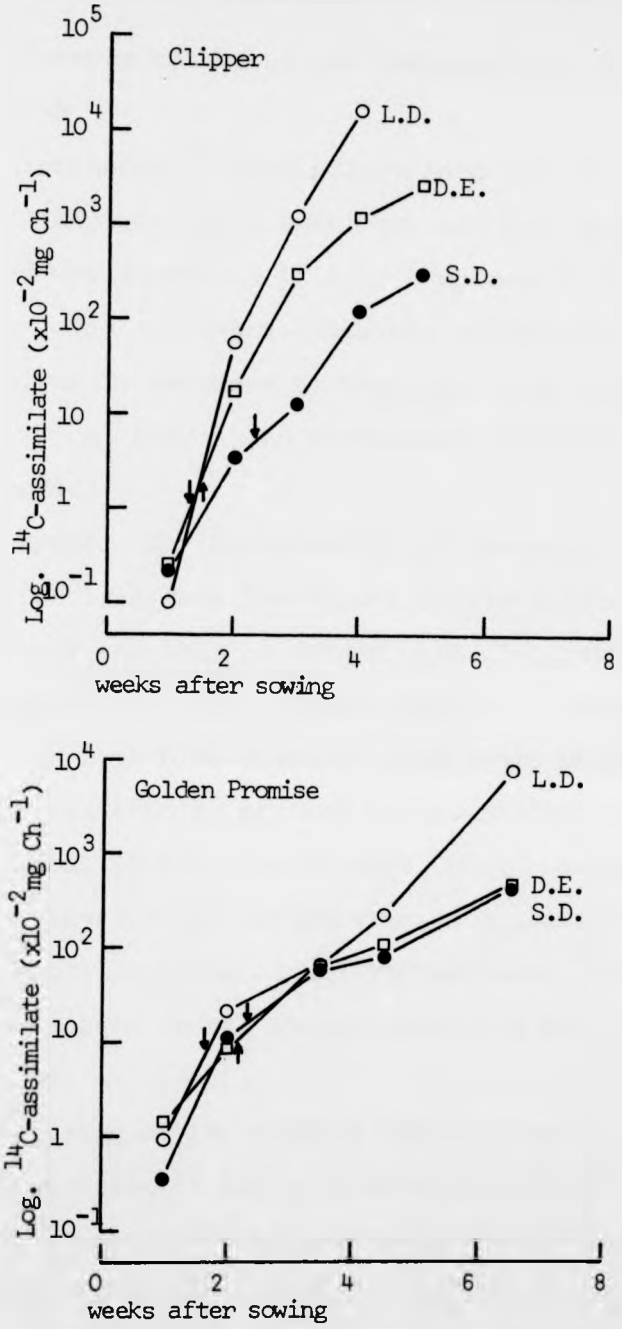


Fig. 42. Effect of photoperiod (day extension) on ^{14}C-assimilate movement to the main shoot apex in Clipper and Golden Promise (growth room).

Each point is a mean of between two and four plants.

Arrows indicate onset of spikelet primordium production.

● = Short day, S.D., 8h day

□ = Day extn., D.E., 8+8h day

○ = Long day, L.D., 16h day

although reference to the apical response will be made in the Discussion.

Accumulation of ^{14}C-assimilate into the apex increased with age of plant for both cultivars and the amount incorporated was increased in L.D. compared to S.D. conditions. The cultivars exhibited differences in the magnitude of their response to long days thus confirming the pattern of apical growth and development described in previous studies.

For Clipper, the incorporation of 14-carbon into the apex under long days was significantly greater ($p \leq 0.05$) after two weeks and this coincided with the increased apical growth observed earlier. Accumulation of ^{14}C-assimilate was similar in both L.D. and S.D. treatments during the early growth of Golden Promise and was not significantly increased ($p \leq 0.05$) until plants were 22 days old. Labelled material continued to be accumulated at a constant but slow rate under short days for both cultivars and, after five weeks, the absolute amount incorporated was similar (2.0×10^{-5} mg C h^{-1}).

The influence of photoperiod (Day extension treatment) on the incorporation of labelled material into the apex again reflected the difference between the two cultivars in the magnitude of their response to daylength. For Clipper, assimilate movement increased with increase in photoperiod (significant, $p \leq 0.05$, at three weeks) and the subsequent pattern of accumulation was intermediate between that found in L.D. and S.D. conditions. Photoperiod had no effect on the amount of 14-carbon present in the apex of Golden Promise, however, and the pattern of accumulation was similar

in both treatments throughout the experimental period.

The influence of daylength and photoperiod on the absolute amount of ^{14}C-assimilate incorporated into the apex may be caused by either or both a change in net photosynthesis of the plant or by a change in the pattern of ^{14}C-assimilate distribution. The effect of these treatments on net carbon dioxide uptake per plant and the percentage of the $^{14}CO_2$ uptake translocated to the apex is shown in Figs. 43 and 44 respectively.

The increased ^{14}C-assimilate accumulation in the apex of Clipper in L.D. and D.E. treatments is more clearly attributable to the increased proportion of translocate to the apex than to any differences in plant net photosynthesis. In contrast, the increased incorporation of ^{14}C-assimilate in the apex of Golden Promise in L.D. compared with D.E. and S.D. treatments appears to be caused by increased plant net photosynthesis in long days rather than to any differences in assimilate movement. For Clipper, the net carbon dioxide uptake was slightly higher in L.D. than in D.E. or S.D. conditions for all sample occasions but was only just significant ($p \leq 0.05$) at week three. The large L.S.D. value (26.0), however, indicates that the measurements obtained were rather variable (cf. Golden Promise, 41.6) and this may have obscured any small but important differences between treatments. Similarly, no measurement of net photosynthesis of L.D. plants of Clipper was taken 35 d.a.s. when greater differences in CO_2 uptake between treatments as plants aged may have been expected (cf. Golden Promise). The data suggests, therefore, that assuming the photosynthetic efficiency (i.e. the conversion of carbon dioxide uptake

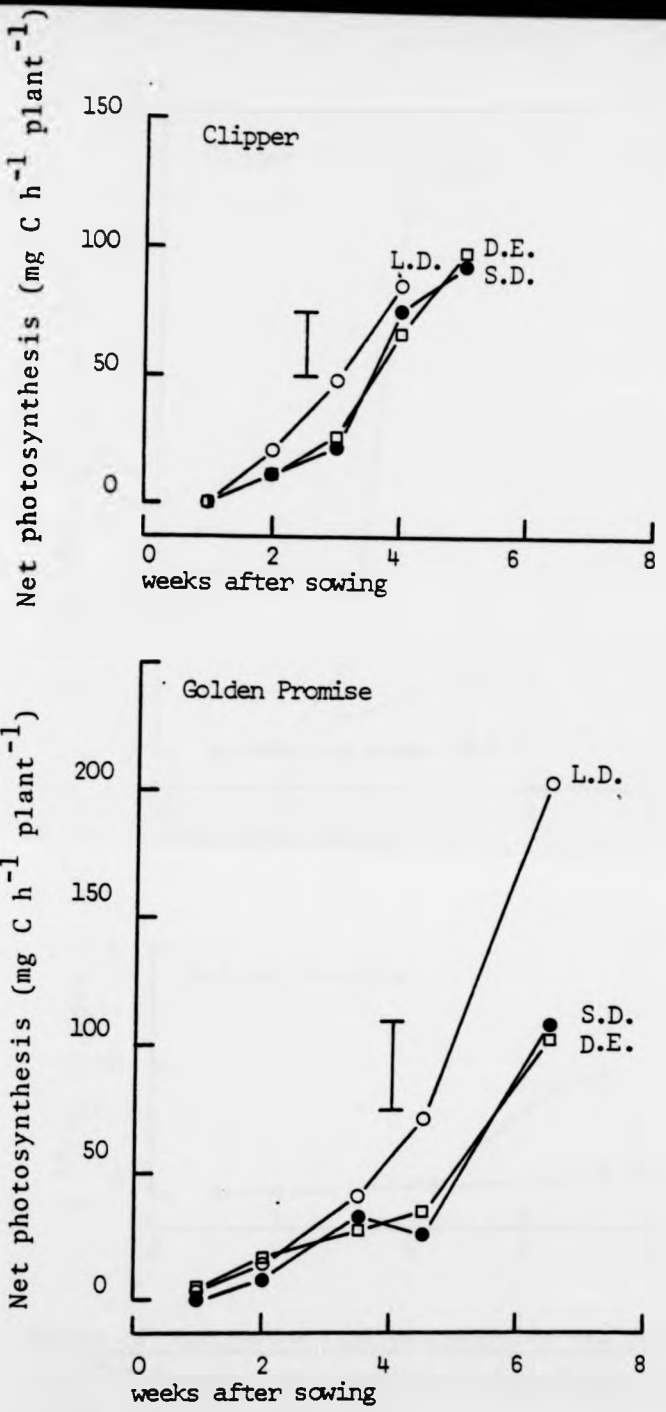


Fig. 43. Effect of photoperiod (day extension) on net photosynthesis of single barley plants of Clipper and Golden Promise (growth room).

Each point is a mean of between 2 and 4 plants.
Vertical bars indicate L.S.D. significant at $p \leq 0.05$, calculated following an analysis of variance for each cultivar separately.

● = Short day, S.D., 8h day
□ = Day extn., D.E., 8+8h day
○ = Long day, L.D., 16h day

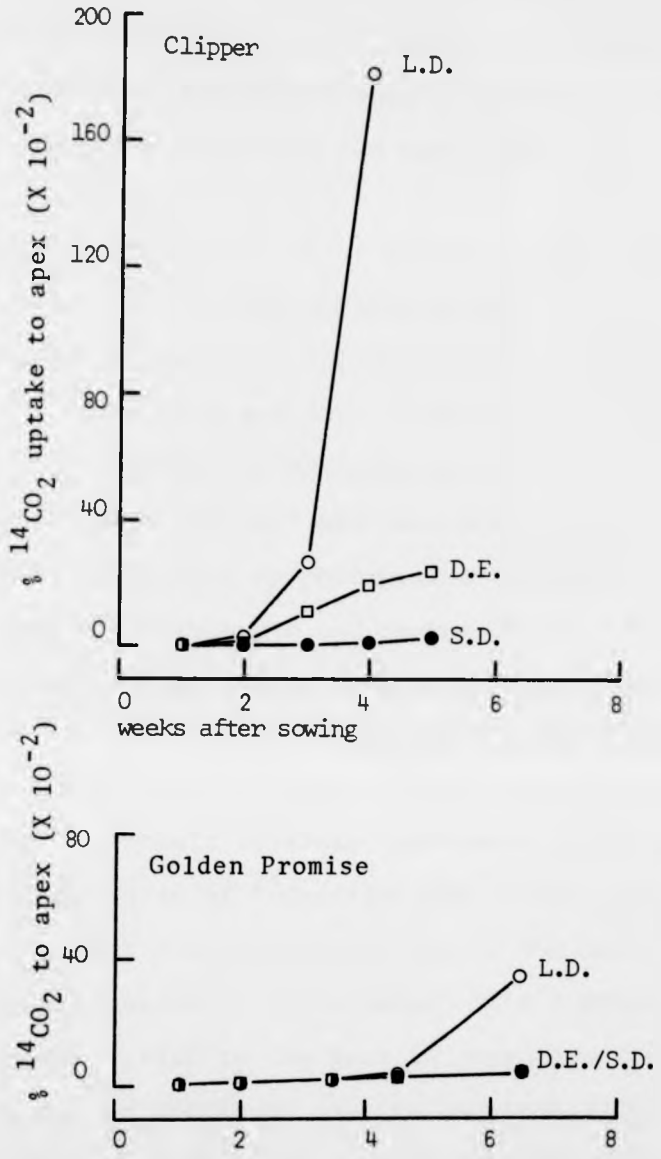


Fig. 44. Effect of photoperiod (day extension) on the percentage of the $^{14}CO_2$ uptake found in the apex for Clipper and Golden Promise (growth room).

Each point is a mean of between 2 and 4 plants.

● = Short day, S.D., 8h day
□ = Day extn., D.E., 8+8h day
○ = Long day, L.D., 16h day

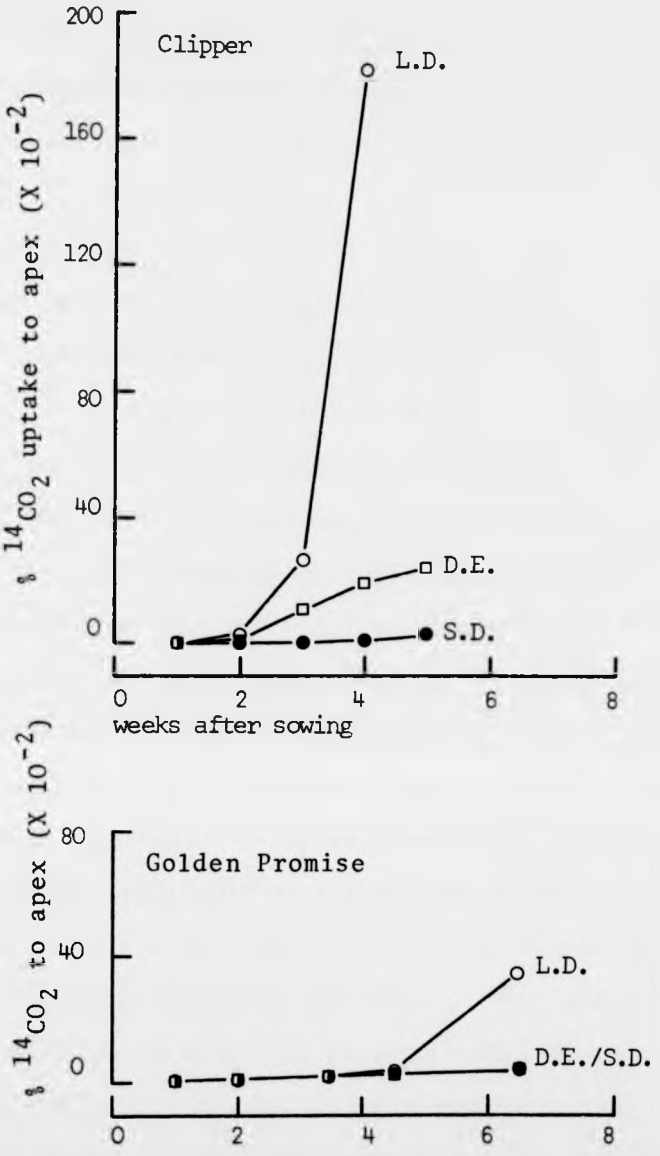


Fig. 44. Effect of photoperiod (day extension) on the percentage of the $^{14}CO_2$ uptake found in the apex for Clipper and Golden Promise (growth room).

Each point is a mean of between 2 and 4 plants.

● = Short day, S.D., 8h day
□ = Day extn., D.E., 8+8h day
○ = Long day, L.D., 16h day

into assimilate) was similar for Clipper in all three treatments, the potential assimilate supply to the meristematic regions of the plant including the main shoot apex would also be similar.

Net plant photosynthesis of Golden Promise was similar in all three treatments during early growth (Fig. 43) but later increased 32 d.a.s. ($p \leq 0.05$) in L.D. compared with D.E. and S.D. treatments and this difference was maintained throughout the remainder of the experimental period. The increase in the rate of plant net photosynthesis with time appeared to be unaffected by photoperiod treatment.

The effect of daylength and photoperiod on the partitioning of labelled material for Clipper (Fig. 44) paralleled the response pattern showed by the accumulation of ^{14}C-assimilate in the apex (Fig. 42). In view of the limited response of net plant photosynthesis to these treatments it is suggested that the incorporation of ^{14}C-assimilate in the apex of Clipper in L.D. and D.E. conditions may be due to increased percentage distribution of assimilate. The increased percentage distribution to the apex in long days occurred after two weeks and continued to rise exponentially until nearly two percent of the $^{14}CO_2$ uptake was transported to the developing apex after four weeks. Distribution of labelled material to the apex was significantly increased ($p \leq 0.05$) three w.a.s. in D.E. compared with S.D. treatment but continued to increase at a slower rate than in long day plants. The percentage movement to the apex was maintained at a constant but slow rate in short days and this was reflected in the low absolute incorporation of labelled material (Fig. 42).

For Golden Promise, the percentage distribution of

labelled material increased initially at a slow, constant rate in all treatments (Fig. 44) but subsequently increased in L.D. conditions (32 d.a.s.) and was significantly greater ($p \leq 0.05$) after 46 days. Although the exact timing of this increase cannot be determined, it would appear that it occurred after the increased rate of net plant photosynthesis (Fig. 43). It is suggested, therefore, that the increased ^{14}C- accumulation in the apex was due to the increased assimilate supply to the apex as a result of greater plant net photosynthesis. The larger sink size subsequently increased the demand for assimilates and hence altered the partitioning of carbohydrate such that a larger proportion was translocated to the main shoot apex.

DISCUSSION

The influence of daylength and photoperiod on the pattern of ^{14}C-labelled assimilate accumulation in the apex for both Clipper and Golden Promise reflected the response of apical growth and development to these treatments (Section 3). Incorporation of labelled material increased significantly after two weeks in long days for Clipper and after three weeks with day extension treatment. It was suggested that the increased 14-carbon accumulation resulted from the increased proportion of assimilate distribution to the apex rather than to any immediate change in plant net photosynthesis. For Golden Promise, incorporation of labelled material did not increase in L.D. compared with D.E. and S.D. treatments until 32 d.a.s. and appeared to be due to increased CO_2 uptake rather than to differences in the partition of assimilates.

The potential assimilate supply to the main shoot apex

is determined by the photosynthetic capacity of the plant (which is itself dependent on the number, surface area, position and age of the expanded leaves of the plant), the photosynthetic efficiency (here, defined as the efficiency of conversion of CO_2 uptake by the plant to assimilate available for transport to the apex) and on the pattern of translocation. The distribution of assimilate may be controlled either directly by environmental factors (e.g. by affecting the loading of assimilate into the phloem, cf. Wardlaw 1968) or by competitive demand from the actively growing meristematic regions such as expanding leaves, main shoot apex, internode meristems, tiller buds and root meristems.

During the early growth of the plant, assimilates are translocated freely about the plant (Quinlan and Sagar 1962, Doodson et al 1964 and Rawson and Hofstra 1969). The main shoot apex will, therefore, be in competition from the other meristematic regions and, in particular, from the expanding leaves (Dale and Felippe 1972, and Felippe and Dale 1972, 1973) and thus the supply to the apex will be very small (Fig. 42, cf. Felippe and Dale 1973). Assimilate supply will increase with age due to both the increased plant photosynthesis (Fig. 43) as a result of increased leaf surface area per plant as the plant ages (due to both increased leaf and tiller number) and due to a change in the partitioning of assimilate (Fig. 44) as a result of increased sink size and thus greater demand. In later growth, assimilates tend to be translocated preferentially to the nearest actively-growing sink such that upper mature leaves supply expanding leaves, stem and terminal meristem whereas lower leaves supply the base of the stem, roots and tillers.

The influence of daylength and photoperiod treatment on the incorporation of 14-carbon into the apex of Clipper and Golden Promise paralleled the observed contrasted apical response pattern. ^{14}C-accumulation was affected by both the photoperiodic and radiation components of daylength in Clipper but Golden Promise responded only to the radiation component. The contrasted response may be due to the different relative influences of the two physiological determinants of carbohydrate accumulation in the apex - photosynthetic capacity and assimilate distribution.

The greater 14-carbon incorporation for Golden Promise under L.D. compared to D.E. and S.D. conditions was associated with the higher net carbon dioxide uptake thereby increasing the assimilate 'pool' for translocation. Partitioning of ^{14}C-assimilate to the apex did not increase until after apical growth had been accelerated, i.e. after apical size and, therefore, demand had been increased.

The increased plant net photosynthesis under long days for both cultivars (significant for Golden Promise after 32 days but only slightly increased for Clipper), may be caused by either an increased leaf surface area per plant (either due to higher leaf number, leaf surface area or tiller number) or to an increased photosynthetic efficiency.

Leaf surface area was not measured but data for leaf number per main shoot and tiller number (not presented) indicate that both parameters are increased in L.D. compared with D.E. and S.D. conditions after 24 days for Golden Promise and these differences were maintained throughout the experimental period. In Clipper, leaf number was greater in L.D. than D.E. or S.D. treatments from week three until

flag-leaf emergence at week five, however, tillering was inconsistently affected by treatment.

Similarly, Friend et al (1967) working with wheat also noted an increased leaf area per plant with increased photoperiod treatment and this was caused by both an increased leaf and tiller number. Friend et al (1962) on wheat and Kirby and Eisenberg (1966) on barley, however, found that leaf surface area increased in long days until leaf three but later decreased. It can be suggested, therefore, that the significantly increased net photosynthesis of Golden Promise can be attributed to the increased leaf surface area per plant as a result of increased leaf number per main shoot and tiller number. Neither component may have been sufficiently increased in Clipper to offset the presumed reduction in leaf area to significantly increase net photosynthesis.

Dale and Felippe (1972) and Felippe and Dale (1972) examined the effect of shade treatment on young barley plants (cv. Proctor) and suggested that shading reduced carbon dioxide uptake both directly through an effect on the photosynthetic rate and also through a morphogenic system which reduced the photosynthetic efficiency of the leaves. A similar situation may occur as a result of short day treatment or as a result of low total light energy in a given photoperiod with a subsequent reduction in assimilate supply.

The increased ^{14}C-assimilate accumulation under L.D. and D.E. conditions for Clipper on the other hand was attributed to the increased percentage distribution of 14-carbon to the apex rather than to the slightly increased plant net photosynthesis. The increased partitioning to the apex may be

due to either a direct effect of light on translocation, e.g. loading on translocate from leaves into phloem traces (cf. Wardlaw 1968) or through an effect of daylength on apical growth resulting in increased sink size and therefore increased demand for assimilates.

Felippe and Dale (1972) have suggested it unlikely that light directly affects the loading of assimilate into the translocate system and it seems more probable that assimilate movement was increased to the apex as a result of increased demand due to increased sink size.

Seedling emergence occurred five d.a.s. in all three treatments and the influence of daylength and photoperiod treatments on apical development was observed shortly after the time of the first sample (seven d.a.s.) with the earlier onset of spikelet primordium set down. Clearly, the increased daylength and photoperiod stimulus was rapidly perceived resulting in accelerated apical development and spikelet primordium production which was reflected in a significantly greater 14-carbon accumulation in the apex after only 14 days. Little difference in the magnitude of the ^{14}C-assimilate incorporation between treatments would be expected at seven days because the first leaf does not supply the apical region until day six (Felippe and Dale 1973). Ryle and Powell (1976) found that there was only a slight delay of one to two days between differences in the light treatment (as a result of contrasting light intensities) being reflected in the translocation pattern of Lolium temulentum although complete adaptation may not occur until day seven.

A similar situation is envisaged for Clipper in which the accelerated apical development and spikelet primordium

production resulted in a greater proportion of the assimilate being transported to the main shoot apex because of increased sink strength.

The absolute amount of ^{14}C-assimilate incorporation will also be determined by the amount of $^{14}CO_2$ lost by respiration during the 24h period following feeding. Various attempts have been made to estimate this loss and values include: 20% for wheat (Rawson and Hofstra 1969 and Rawson and Evans 1971), 33% for barley (Birecka et al 1967) and 35% for Lolium temulentum (Ryle 1972). In a detailed study, Ryle et al (1976) on the uniculm barley cultivar, Kindred, found that the loss of ^{14}C-assimilate through respiration after 24h could be as high as 50%, of which most occurred after the first three hours. He distinguished two types of respiratory loss: an initial high rate of biosynthetic respiration loss (as a result of translocation to meristems) of 25 to 35% over the first 24h followed by a second, constant but slow rate of efflux, maintenance loss (due to respiration of mature tissues) of 12 to 27%.

No measurement of respiratory loss was made in this study but it should be noted that Ruckenbauer (1975) has suggested that respiratory losses may differ between cultivars and it has been shown (Hofstra et al 1969 and Ryle et al 1976) that light intensity and daylength may also affect this parameter. Clearly the incorporation of labelled material may be due to differences in respiration rate between the treatments rather than to simply differences in net photosynthesis or in dry matter distribution. Further physiological research is required to elucidate the response of ^{14}C-assimilate incorporation to daylength treatments with respect

to this parameter.

The effect of daylength on apical development may either be direct, resulting from an increase in net photosynthesis or indirect, as a result of influencing the rate of development and spikelet primordium production say, by affecting hormonal levels within the shoot apex. As a result of the greater sink strength, an increased proportion of the available assimilate will be transported to the apex. In view of the contrasted response between Clipper and Golden Promise, it is suggested that daylength may control the absolute amount of assimilate available for translocation while superimposed on this, is the effect of photoperiod on the growth and development of the actively-growing tissues such as the main shoot apex and thus the relative sink strength. In the case of the photoperiodically-sensitive Clipper, both factors will influence the incorporation of assimilate into the apex whereas, for Golden Promise, only the availability of assimilate will influence apical growth. It is envisaged that the two patterns of assimilate incorporation described above would apply to all barley genotypes although only photoperiodically-responsive cultivars would exhibit the second pattern of incorporation.

GENERAL DISCUSSION

The one hundred barley cultivars examined in the initial glasshouse daylength study exhibited a wide range in the magnitude of the response of spikelet number per main ear to daylength. This suggested that barley genotypes could be regarded as quantitative long day plants in that the growth and development of the plant was hastened by long days. Spikelet number per main ear was generally unaffected by daylength treatment but 18 of the 98 cultivars for which results are available showed a significant reduction ($p \leq 0.05$) in spikelet number in long days and four cultivars exhibited a significant increase in long days.

From this initial study, the effect of daylength on apical development of a selected number of genotypes which contrasted in their spikelet number response to daylength was examined in growth rooms. The effect of daylength in the field was carried out using sowing date treatments in 1976 and 1977 on a further number of selected genotypes which again contrasted in their spikelet number response to daylength. The influence of sowing date on spikelet and grain number per main ear, and on grain yield was also examined in these cultivars.

Apical development was accelerated for all cutlivars in long days compared with short days (growth rooms) and by late sowing compared to early sowing (in the field). Cultivars differed in the magnitude of their apical response to daylength and to sowing date and it was suggested that cultivars could be broadly divided into two groups on the basis of this response. Group one cultivars were characterised by showing

a marked sensitivity to long day and late sowing treatments and were considered to be early genotypes (Table 27). Group two cultivars were less responsive to daylength and sowing date treatments and were considered to be late genotypes (Table 27). This is in agreement with earlier work by Bell (1939) who suggested that genotypes which reach anthesis relatively early from a late spring sowing exhibit a more marked sensitivity to daylength than later cultivars.

It was suggested that Group one cultivars consisted mainly of Mediterranean and Australian cultivars whereas Group two cultivars consisted generally of N.W. European genotypes (cf. Aspinall 1966). In Mediterranean and S. Australian environments, the optimal date of ear emergence is governed principally by the onset of soil moisture stress in spring and therefore cultivars are sown in a daylength from 10 to 13.5h during the period of spikelet primordium production. Although final spikelet numbers are lower than in Britain, the accelerated plant growth and development results in higher yields than would be obtained with British cultivars which would ear later and thus be subject to drought conditions. Scottish growing conditions, however, require genotypes which are relatively insensitive to environmental factors including daylength during the period of spikelet primordium production and thus have the ability to maintain comparatively high yields even from later sowings. From this point of view it is interesting to note that the two cultivars which were least responsive to daylength in the growth room (Golden Promise and Ymer) are particularly associated with Scotland. Ymer was formerly the most popular cultivar and Golden Promise currently is the most widely-grown cultivar occupying nearly

70% of the barley acreage in Scotland.

A high spikelet primordium maximum was associated with correspondingly higher spikelet and grain numbers than a lower maximum under both controlled environment daylength studies and in sowing date treatments in the field. Grain yield (per plant) was clearly linked with ear number per plant and with grain number per ear, thus indicating the importance of sink capacity in determining final grain yield. It has been suggested that modern cultivars have higher yields than older varieties because of better dry matter distribution rather than greater total dry weight (Thorne 1966, 1974; Holliday and Willey 1969 and Bingham 1969, 1971). Kirby (1973a) has suggested that the more efficient partitioning of carbohydrate may be attributed to the larger ears of modern genotypes and to reduced competition from non-productive high-order tillers. This study has stressed the importance of grain number per ear in determining final grain yield and many other studies have also reported the physiological desirability of having a large grain number per ear for both barley (Kirby 1973a and Dyson 1977) and for wheat (Donald 1968, Rawson 1970, 1971 and Kirby 1974).

Grain number per ear may be increased either by increasing maximum spikelet primordium number or by increasing the proportion of the maximum which eventually form spikelets and set grain. Maximum spikelet primordium number is determined by the duration of the period of set down and by the initial rate of production (page 43). Maximum spikelet primordium number could be increased by a longer period of set down either as a result of an earlier onset of initiation or a delay in the cessation of production.

However, in this study, an earlier onset was associated with a small leaf number and selecting for this feature is, therefore, probably inadvisable in view of the limited photosynthetic capacity during later growth. A delay in the cessation of spikelet primordium production may also be inadvisable because of the reduced period for optimal grain filling during the long days and high radiation levels in June and July. Similarly, a late harvest as a consequence of the extended period of set down may result in grain loss due to heavy rainfall during autumn.

A high spikelet primordium number may be attained following a rapid rate of set down but this is normally associated with an earlier cessation of production and a comparatively low final number. Spikelet primordium number would be increased, however, if a high rate of production could be maintained over a long period and Rawson (1971) observed that these features were characteristic of Triticale wheat. He attributed the high spikelet number to the concurrent development of spikelets along the apex and other workers (Pinthus 1967; Fisher 1973 and Holmes 1973) have also found this to be a characteristic of high-yielding Mexican dwarf wheats. Holmes (1973) has suggested that the pattern of spikelet organogenesis may be linked to the low rate of GA utilization within the apex as described previously (page 83). No marked difference in the pattern of spikelet development within the apex was noticed between cultivars in short days in this study but the contrasted apical development between, for example, Clipper and Golden Promise with L.D. treatment confirms the importance of concurrent spikelet development in attaining a high maximum. Maximum spikelet primordium

number could, therefore, be increased if the sink strength of the shoot apex could be increased early on in apical development with a corresponding increased assimilate supply to the apex but without rapid spikelet organogenesis in relation to spikelet primordium set down. The importance of maintaining a large assimilate supply during apical development especially in British genotypes is discussed later.

This study (Section 1) has stressed the importance of daylength in influencing apical growth and development in the field but other environmental factors including temperature are confounded with daylength in the different sowing date treatments used in the field. The influence of temperature on apical development was examined in growth rooms (Section 2) for two cultivars, Clipper and Golden Promise, which contrasted in their apical response to sowing date. Increased temperature (20^{o}C compared with 14^{o}C) accelerated apical development for both cultivars but the two cultivars differed in the magnitude of their response and this paralleled the response observed to both daylength and sowing date treatments. This cannot be taken, however, to indicate that cultivars sensitive to daylength will be equally responsive to temperature and it has been shown that the second order interaction between daylength, temperature and cultivar on apical development is complex (Aspinall 1969 and Rawson 1970, 1971). The similarities of the apical response to temperature and to sowing date treatment suggested that temperature also influences apical development in the field. Takahashi and Yasuda (1960) have suggested that early cultivars of barley were responsive to temperature but not later genotypes. It may be suggested that early and late

genotypes with regard to their temperature response may be similarly characterised by the patterns of development outlined in Table 27 although there is no reason, per se, to suggest that temperature and daylength influence apical development through the same system of control. Further work is required in this area to elucidate the physiological response of apical development to variations in temperature.

More detailed physiological analyses of the effect of daylength on apical development was carried out in Sections 3 and 4 on a limited number of genotypes which contrasted in their spikelet number response to daylength in the glasshouse (Section 1). Daylength contains both a photoperiodic and a radiation component and the relative influences of these components on apical development was evaluated using both Night interruption and Day extension treatments. Cultivars which were highly sensitive to long days (e.g. Clipper) responded to both the photoperiodic and radiation components whereas cultivars which were less responsive to daylength treatment (e.g. Golden Promise) were only sensitive to the light energy available for photosynthesis.

It was suggested that, for the photoperiodically-sensitive genotypes e.g. Clipper, photoperiod accelerates apical development and spikelet primordium production resulting in greater sink strength and thus in increased distribution of assimilates to the main shoot apex. The very rapid apical development results, however, in an earlier cessation of set down and a low spikelet primordium maximum. It is envisaged that the earlier cessation of set down is a result of either competition within the apex for assimilates or in different rates of utilization of endogenous gibberellic acid similar to

that outlined by Kirby and Faris (1970) and Holmes (1973) (cf. page 83).

Radiation level (either by increased light intensity within one photoperiod regime or higher radiation level within different photoperiods) appears to affect apical development by influencing photosynthesis and thus assimilate supply to the apex. It is suggested that if there is a large 'pool' of available assimilate then apical development and spikelet primordium production will proceed at a fast rate and continue over a comparatively long period. However, if the radiation level is low, apical growth and development will be delayed and spikelet primordium production will cease earlier (cf. Dale and Felippe 1973). It may be that all barley cultivars examined in this study would respond to increased radiation levels in this way.

The effects of photoperiod and radiation level on apical development and assimilate movement to the apex described above have two important implications for plant breeding. It is suggested that the 'earliness' of a cultivar (Table 27) is partly determined by its photoperiodic sensitivity (cf. Clipper - early genotype, and Golden Promise - late genotype). In view of the greater contrast in daylengths with progressively later sowing in Scottish compared with English growing conditions, it is suggested that new genotypes for Scotland should be selected which are insensitive to photoperiod. Photoperiodically-insensitive cultivars may be rapidly selected by examining the apical development of the new genotype in two photoperiod treatments (8h S.D. coupled with either a Night interruption of Day extension treatment) until maximum spikelet primordium number is attained.

Genotypes which determine a high spikelet primordium maximum in both treatments may be regarded as photoperiodically-insensitive and, providing other morphological characters are optimal, may be sown in areas which show marked differences in daylength conditions (e.g. different sowing dates in North Scotland) and will maintain a relatively high spikelet number per ear.

Secondly, Sections 3 and 4 have stressed the importance of maintaining an adequate supply of assimilate to the apex in order to attain a high maximum spikelet primordium number and thus also a high spikelet number, and this was particularly evident for the photoperiodically-insensitive Golden Promise. Maintaining a high assimilate supply to the apex is particularly important for Britain as a whole, and for Scotland in particular, because radiation levels may be quite low and are generally lower than say, in Australia (Thorne 1974). Williams and Hayes (1977) noted a strong correlation between final spikelet number per ear and the area and duration of the F-2 leaf (i.e. second leaf before the flag leaf) thus suggesting the importance of a large leaf area per plant during the pre-anthesis period of plant growth and development. Although this was not examined directly in this study, results for leaf number per plant (not presented) indicate that the F-2 leaf emerged shortly before the spikelet primordium maximum per main shoot apex was determined. This leaf would, therefore, supply the main shoot apex during the critical period of development including the determination of the spikelet primordium maximum and subsequent tip degeneration.

It is clearly important to optimise assimilate movement to the apex during this period of development and it may be

possible to achieve this by selecting for a large leaf-area during the pre-anthesis period. Although it has long been recognised by plant breeders that optimal carbohydrate supply to the ear during grain filling is important, few studies have examined the range in pre-anthesis leaf area between genotypes. Cultivars with a high leaf area may have an increased potential supply of assimilate available to be transported to the developing apex and therefore potentially more able to maintain a high spikelet number. A greater assimilate supply to the apex may also be achieved by increased distribution of assimilate and, in this context, it is important to supply only the apices which will eventually be fertile and contribute to final grain yield. Increased carbohydrate movement to these apices could therefore be achieved at the expense of high-order tillers.

The underlying objective of this thesis has been to develop a better understanding of the influence of one environmental factor, daylength, on the apical development and subsequent grain number per ear both in controlled environment conditions and in the field, as a means of helping plant breeders gain a better insight into the physiological parameters affecting ear development in the field. The influence of daylength on spikelet number per ear was examined in the glasshouse for a large number of cultivars and, from the range of response exhibited, cultivars were selected for more detailed physiological analyses of the response of apical development to daylength both in controlled environment conditions and in the field using sowing date treatments. These studies have enabled us to gain a better understanding of the physiological response of apical development to daylength

and have also drawn attention to other areas which require further study. A feature of this thesis has been an examination of the implications of these physiological studies for plant breeding, with particular regard to genotypes which are appropriate to Scottish growing conditions.

BIBLIOGRAPHY

ALLISON, J.C.S. and DAYNARD, T.B. (1976). Effect of photoperiod on development and number of spikelets of a temperate and some low latitude wheats. Ann.appl.Biol., 83: 93-102.

ARCHBOLD, H.K. (1942). Physiological studies in plant nutrition XIII. Experiments with barley on defoliation and shading of the ear in relation to sugar metabolism. Ann.Bot., 6: 487-531.

ASPINALL, D. (1961). The control of tillering in the barley plant: 1. The pattern of tillering and its relation to nutrient supply. Aust.J.Biol.Sci., 14: 493-505.

ASPINALL, D. (1963). The control of tillering in the barley plant. II. The control of tiller-bud growth during ear development. Aust.J.biol.Sci., 16: 285-304.

ASPINALL, D. (1966). Effects of daylength and light intensity on growth of barley. IV. Genetically controlled variation in response to photoperiod. Aust.J.biol.Sci., 19: 517-534.

ASPINALL, D. (1969). The effects of daylength and light intensity on the growth of barley. VI. Interactions between the effects of temperature, photoperiod and the spectral composition of the light source. Aust.J.biol.Sci., 22: 53-67.

ASPINALL, D. and PALEG, L.G. (1963). Effects of daylength and light intensity on the growth of barley. I. Growth and development of apex with a fluorescent light source.. Bot.Gaz., 124: 429-437.

ASPINALL, D. and PALEG, L.G. (1964). Effects of daylength and light intensity on growth of barley. III. Vegetative development. Aust.J.biol.Sci., 17: 807-822.

AUSTIN, R.B. and EDRICH, I. (1975). Effects of ear removal on photosynthesis, carbohydrate accumulation and on the distribution of assimilated ^{14}C in wheat. Ann.Bot., 39: 141-152.

BARNARD, C. (1955). Histogenesis of the inflorescence and flower of Triticum aestivum, L., Aust.J.Bot., 3: 1-20.

BATCH, J.J. and MORGAN, D.G. (1974). Male sterility induced in barley by photoperiod. Nature, Lond., 250: 165-167.

BELL, G.D.H. (1939). A study on the date of ear emergence in barley. J.agric.Sci., Camb., 29: 175-228.

BELL, G.D.H. and KIRBY, E.J.M. (1966). Utilization of growth responses in breeding new varieties of cereals. In The growth of cereals and grasses. Proceedings of 12th Easter School of Agricultural Science, University of Nottingham, pp: 308-319, Butterworths, London.

BERGAL, P. and CLEMENCET, M. (1962). The botany of the barley plant. In Barley and malt. Biology, biochemistry, technology, pp: 1-23. Ed. E.H. Cook. Academic Press, New York.

BIDINGER, F., MUSGRAVE, R.B. and FISCHER, R.A. (1977). Contribution of stores pre-anthesis assimilate to grain yield in wheat and barley. Nature, Lond., 270: 431-432.

BINGHAM, J. (1964). Paternal effect on grain size in wheat. Nature, Lond., 209: 940-941.

BINGHAM, J. (1967). Investigations on the physiology of yield in winter wheat by comparison of varieties and by artificial variation in grain number. J.agric.Sci., Camb., 68: 411-422.

BINGHAM, J. (1969). The physiological determinants of grain yield in cereals. Agric.Prog., 44: 30-42.

BINGHAM, J. (1971). Physiological objectives in breeding for grain yield in wheat. Proc. 6th Eucarpia Congress, Cambridge, pp: 15.29.

BIRECKA, H. and DAKIC-WLODKOWSKA, L. (1966). Photosynthetic activity and productivity before and after ear emergence in spring wheat. Acta Soc.Bot.Pol., 35: 637-662.

BIRECKA, H., SKUPINSKA, I. and BERNSTEIN, I. (1964). Photosynthesis, translocation and accumulation of assimilate in cereals during grain development. V. Contribution of products of current photosynthesis after heading to the accumulation of organic compounds in the grain of barley. Acta Soc.Bot.Pol., 33: 601-608.

BIRECKA, H., SKUPINSKA, J. and BERSTEIN, I. (1967). Photosynthetic activity and productivity before and after ear emergence in spring wheat. Acta Soc.Bot.Pol., 36: 387-409.

BONNETT, O.T. (1966). Inflorescence of maize, wheat, rye, barley and oats. Their initiation and development. University of Illinois College of Agriculture. Agriculture Experimental Station Bulletin 721.

BORTHWICK, H.A., HENDRICKS, S.B. and PARKER, M.W. (1948). Action spectrum for photoperiodic control of floral initiation of a long-day plant, Wintex barley (Hordeum vulgare). Bot.Gaz., 110: 103-118.

BORTHWICK, H.H., PARKER, M.W. and HEINZE, P.H. (1941). Effect of photoperiod and temperature on the development of barley. Bot.Gaz., 103: 326-341.

BOYD, D.A. (1952). The effect of seed rate on yield of cereals. Emp.J.Exp.Agric., 20: 115-122.

BREMNER, P.M. (1972). Accumulation of dry matter and nitrogen by grains in different positions of the wheat ear as influenced by shading and defoliation. Aust.J.biol.Sci., 25: 657-668.

BREMNER, P.M. and DAVIDSON, J.L. (1978). A study of grain number in two contrasting wheat cultivars. Aust.J. agric.Res., 28: 431-441.

BREMNER, P.M. and RAWSON, W.M. (1972). Fixation of $^{14}CO_2$ by flowering and non-flowering glumes of the wheat ear, and the pattern of transport of label to individual grains. Aust.J.biol.Sci., 25: 921-930.

BREMNER, P.M. and RAWSON, H.M. (1978). The weight of individual grains of the wheat ear in relation to their growth potential, the supply of assimilate and the interaction between grains. Aust.J.Plant Physiol., 5: 60-72.

BROCKLEHURST, P.A. (1977). Factors controlling grain weight in wheat. Nature, Lond., 266: 348-349.

BROCKLEHURST, P.A. (1979). Control of grain morphogenesis in wheat and its relation to grain yield. Eucarpia workshop on Crop physiology and cereal breeding, Wageringen, 1978. To be published.

BUTTROSE, M.S. and MAY, L.H. (1959). Physiology of cereal grain 1. The source of carbon for the developing barley kernel. Aust.J.biol.Sci., 12: 40-52.

CANNELL, R.Q. (1969). The tillering pattern in barley varieties. I. Production, survival and contribution to yield by component tillers. J.agric.Sci.,Camb., 72: 405-422.

CARR, D.J. and WARDLAW, I.F. (1965). The supply of photosynthetic assimilates to the grain from the flag leaf and ear of wheat. Aust.J.biol.Sci., 18: 711-719.

CHIJO, H. (1961). The effect of temperature on the low temperature vernalization of barley. Bull.Univ.Osaka Pref. Ser. B. Agric.Biol., 12: 55-64.

CLIFFORD, P.E., MARSHALL, C. and SAGAR, G.R. (1973). The reciprocal transfer of radiocarbon between a developing tiller and its parent shoot in vegetative plants of Lolium multiflorum, Lam. Ann.Bot., 37: 777-785.

DALE, J.E. and FELIPPE, G.M. (1972). Effects of shading the first leaf on growth of barley plants. II. Effects on photosynthesis. Ann.Bot., 36: 397-409.

DALE, J.E., FELIPPE, G.M. and FLETCHER, G.M. (1972). Effects of shading the first leaf on growth of barley plants. I. Long term experiments. Ann.Bot., 36: 385-395.

DALE, J.E. and WILSON, R.G. (1978). A comparison of leaf and ear development in barley cultivars as affected by nitrogen supply. J.agric.Sci.Camb., 90: 503-508.

DAVIES, D.H.K. (1973). Physical and economic optima in sowing densities of spring barley in Scotland, PhD thesis, University of Stirling.

DONALD, C.M. (1968). The breeding of ideotypes. Euphytica, 17: 385-403.

DOODSON, J.K., MANNERS, J.G. and MYERS, A. (1964). The distribution pattern of ^{14}C assimilated by the third leaf of wheat. J.exp.Bot., 15: 96-103.

DOWNS, R.J. (1956). Photoreversibility of flower initiation. Pl. Physiol., 31: 279-284.

DOWNS, R.J., PIRINGER, A.A. and WEIBE, G.A. (1969). Effects of photoperiod and kind of supplemental light on growth and reproduction of several varieties of wheat and barley. Bot.Gaz., 120: 170-177.

DYSON, P.W. (1977). An investigation into the relations between some growth parameters and yield of barley. Ann.appl.Biol., 87: 471-483.

ENGLEDOW, F.L. and WADHAM, S.M. (1923). Investigations on yield of cereals. 1. J.agric.Sci.Camb., 13: 390-439.

EVANS, L.T. and RAWSON, H.M. (1970). Photsynthesis and respiration by the flag leaf and components of the ear during grain development in wheat. Aust.J.biol.Sci., 23: 245-254.

FELIPPE, G.M. and DALE, J.E. (1972). The uptake of $^{14}CO_2$ by developing first leaves of barley and partition of the labelled assimilates. Ann.Bot., 36: 411-418.

FELIPPE, G.M. and DALE, J.E. (1973). Effects of shading the first leaf of barley plants on growth and carbon nutrition of the stem apex. Ann.Bot., 37: 45-56.

FISCHER, R.A. and KOHN, G.D. (1966). The relationship of grain yield to vegetative growth and post-flowering leaf area in the wheat crop under conditions of limited soil moisture. Aust.J.agric.Res., 17: 281-295.

FISCHER, J.E. (1973). Developmental morphology of the inflorescence in hexaploid wheat cultivars with and without the cultivar Norin 10 in their ancestry. Can.J.Pl.Sci., 53: 7-15.

FLETCHER, G.M. and DALE, J.E. (1974). Growth of tiller buds in barley: effects of shade treatment and mineral nutrition. Ann. Bot., 38: 63-76.

FRIEND, D.J.C. (1964). The promotion of floral initiation of wheat by far-red radiation. Physiologia Pl., 17: 909-920.

FRIEND, D.J.C. (1965). Ear length and spikelet number of wheat grown at different temperatures and light intensities. Can.J.Bot., 43: 345-353.

FRIEND, D.J.C. (1966). The effects of light and temperature on the growth of cereals. In The growth of cereals and grasses, pp. 181-199. Proceedings 12th Easter School of Agricultural Science, University of Nottingham, Butterworths, LOndon.

FRIEND, D.J.C., FISCHER, J.E. and HELSON, V.A. (1963). The effect of light intensity and temperature on floral initiation and inflorescence development of Marquis wheat. Can.J.Bot., 41: 1663-1674.

FRIEND, D.J.C., HELSON, V.A. and FISCHER, J.E. (1959). The relative effectiveness of standard cool white fluorescent and incandescent light in the photoperiodic response of Marquis wheat, Garnet wheat, and Wintex barley. Can.J.Pl.Sci., 39: 229-240.

FRIEND, D.J.C., HELSON, V.A. and FISCHER, J.E. (1961). The influence of the ratio of incandescent fluorescent light on the flowering response of Marquis wheat grown under controlled conditions. Can.J.Pl.Sci., 41: 418-427.

FRIEND, D.J.C., HELSON, V.A. and FISCHER, J.E. (1962). Leaf growth in Marquis wheat, as regulated by temperature, light intensity and daylength. Can.J.Bot., 40: 1299-1311.

FRIEND, D.J.C., HELSON, V.A. and FISCHER, J.E. (1965). Changes in leaf area duration and net assimilation rate during growth of Marquis wheat as affected by temperature and light intensity. Can.J.Bot., 43: 15-28.

FRIEND, D.J.C., HELSON, V.A. and FISCHER, J.E. (1967). Effects of daylength on growth of wheat. Can.J.Bot. 45: 117-131.

GALLAGHER, J.N., BISCOE, P.V. and SCOTT, R.K. (1975). Barley and its environment. V. Stability of grain weight. J.appl.Ecology, 12: 319-336.

GALSTON, A.W. and DAVIES, P.J. (1969). Hormonal regulation in higher plants. Science (Wash.), 163: 1288-1297.

GIFFORD, R.M. (1974). Photosynthetic limitations to cereal yield. In Mechanisms of regulation of plant growth, pp: 887-893. Ed. Bieleski, R.L., Ferguson, A.R. and Cresswell, M.M. R.Soc. N.Z. Bull. 12.

GOTT, M.B. (1961). Flowering of Australian wheats and its relation to frost injury. Aust.J.agric.Res., 12: 547-565.

GOTT, M.B., GREGORY, F.G. and PURVIS, O.N. (1965). Studies in vernalization of cereals. XIII. Photoperiodic control of stage in flowering between initiation and ear formation in vernalized and unvernalized Petkus winter rye. Ann.Bot., 19: 87-126.

GUITARD, A.A. (1960). The influence of variety, temperature and stage of growth on the response of spring barley to photoperiod. Can.J.Pl.Sci., 40: 65-80.

HALSE, N.J. and WEIR, R.N. (1970). Effects of vernalization, photoperiod, and temperature on phenological development and spikelet number of Australian wheat. Aust.J.agric. Res., 21: 383-393.

HOFSTRA, G., RYLE, G.J.A. and WILLIAMS, R.F. (1969). Effects of extending the daylength with low intensity light on the growth of wheat and cocksfoot. Aust.J. biol.Sci., 22: 333-341.

HOLMES, D.P., (1973). Inflorescence development of semi-dwarf and standard height wheat cultivars in different photoperiod and nitrogen treatments. Can.J.Bot., 51: 941-956.

JAMES, N.I. and LUND, S. (1965). Shoot apex development of winter barley as influenced by potassium gibberellate Am.J.Bot., 52: 877-882.

JENNER, C.F. and RATHJEN, A.J. (1972a). Factors limiting the supply of sucrose to the developing wheat grain. Ann.Bot., 36: 729-741.

JENNER, C.F. and RATHJEN, A.J. (1972b). Limitations to the accumulation of starch in the developing wheat grain. Ann.Bot., 36: 743-752.

JENNER, C.F. and RATHJEN, A.J. (1975). Factors regulating the accumulation of starch in ripening wheat grain. Aust.J.Pl.Physiol., 2: 311-322.

JESSOP, R.S. and IVINS, J.D. (1970). The effect of date sowing on the growth and yield of spring cereals. J.agric.Sci.Camb., 75: 553-557.

JEWISS, O.R. (1972). Tillering in grasses - its significance and control. J.Br.Grassld.Soc., 27: 65-82.

JONES, H.G. and KIRBY, E.J.M. (1977). Effects of manipulation of number of tillers and water supply on grain yield of barley. J.agric.Sci.,Camb., 88: 391-398.

KENDRICK, R.E. and FRANKLAND, B. (1976). Phytochrome and plant growth. Institute of Biology, Studies in Biology No. 68, Arnold Publ. Ltd., London.

KING, R.W., WARDLAW, I.F. and EVANS, L.T. (1967). Effect of assimilate utilization on photosynthetic rate in wheat. Planta, 77: 261-276.

KIRBY, E.J.M. (1967). The effect of plant density upon the growth and yield of barley. J.agric.Sci., Camb., 68: 317-324.

KIRBY, E.J.M. (1969a). The effects of daylength upon the development and growth of wheat, barley and oats. Field Crop Abstr., 22: 1-7.

KIRBY, E.J.M. (1969b). The effect of sowing date and plant density on barley. Ann.appl.Biol., 63: 513-521.

KIRBY, E.J.M. (1971). Abnormalities included in barley ears by gibberellic acid. J.exp.Bot., 22: 411-419.

KIRBY, E.J.M. (1973a). The control of leaf and ear size in barley. J.exp.Bot., 24: 567-578.

KIRBY, E.J.M. (1973b). Effect of temperature on ear abnormalities in uniculm barley. J.exp.Bot., 24: 935-947.

KIRBY, E.J.M. (1974). Ear development in spring wheat. J.agric.Sci., Camb., 82: 437-447.

KIRBY, E.J.M. (1977). The growth of the shoot apex and the apical dome of barley during ear initiation. Ann.Bot., 41: 1297-1308.

KIRBY, E.J.M. and EISENBERG, B.E. (1966). Some effects of photoperiod on barley. J.exp.Bot., 17: 204-213.

KIRBY, E.J.M. and FARIS, D.G. (1970). Plant population induced growth correlations in the barley plant main shoot and possible hormonal mechanism. J.exp.Bot., 21: 787-798.

KIRBY, E.J.M. and FARIS, D.G. (1972). The effect of plant density on tiller growth and morphology in barley. J.agric.Sci., Camb., 78: 281-288.

KIRBY, E.J.M. and JONES, H.G. (1977). The relations between the main shoot and tillers in barley plants. J.agric.Sci., Camb., 88: 381-390.

KIRBY, E.J.M. and RYMER, J.L. (1974). Development of the vascular system in the ear of barley. Ann.Bot., 38: 565-573.

LANE, H.C., CATHEY, H.M. and EVANS, L.T. (1965). The dependence of flowering in several long day plants on the spectral composition of light extending the photoperiod. Am.J.Bot., 52: 1006-1014.

LANGER, R.H.M. (1967). Physiological approaches to yield determination in wheat and barley. Field.Crop.Abstr., 20: 101-106.

LANGER, R.H.M. and DOUGHERTY, C.T. (1976). Physiology of grain yield in wheat. In Perspectives in experimental biology (Vol. 2 Botany), pp: 59-67. Ed. Sunderland, N. Pergamon Press, London.

LAST, F.T. (1957). The effect of date of sowing on the incidence of powdery mildew on spring sown cereals. Ann.appl.Biol., 45: 1-10.

LUCAS, D. (1972). The effect of daylength on primordia production on the wheat apex. Aust.J.biol.Sci., 25: 649-656.

LUPTON, F.G.H. (1966). Translocation of photosynthetic assimilates in wheat. Ann.appl.Biol., 57: 355-364.

LUPTON, F.G.H. (1968). The analysis of grain yield of wheat in terms of photosynthetic ability and efficiency of translocation. Ann.appl.Biol., 61: 109-119.

LUPTON, F.G.H. (1969). Estimation of yield in wheat from measurements of photosynthesis and translocation in the field. Ann.appl.Biol., 64: 363-374.

LUPTON, F.G.H. (1972). Further experiments on photosynthesis and translocation in wheat. Ann.Appl.Biol., 71: 69-79.

LUPTON, F.G.H. and KIRBY, E.J.M. (1968). Applications of physiological analysis to cereal breeding. Rep.Plant breed.Inst., Camb., 1967: 5-26.

LUPTON, F.G.H. and WHITEHOUSE, R.N.H. (1961). Development in wheat breeding methods. Rep.plant breed.Inst., Camb., 1960: 5-18.

MARCELLOS, H. and SINGLE, W.V. (1971). Quantitative responses of wheat to photoperiod and temperature in the field. Aust.J.agric.Res., 22: 343-357.

MARCELLOS, H. and SINGLE, W.V. (1972). The influence of cultivar, temperature and photoperiod on post-flowering development of wheat. Aust.J.agric.Res., 23: 533-540.

MARSHALL, C. and SAGAR, G.R. (1968). The interdependence of tiller of Lolium multiflorum Lam. - a quantitative assessment. J.exp.Bot., 19: 785-794.

MOHR, H. (1962). Primary effects of light on growth. A Rev.Pl.Physiol., 13: 465-488.

NASS, H.G., JOHNSTON, H.W., MacLEOD, J.A. and STERLING, J.D.E. (1974). Effects of seeding date, seed treatment and foliar sprays on yield and other agronomic characters of wheat, oats and barley. Can.J.Pl.Sci., 55: 41-47.

NICHOLLS, P.B. (1974a). Interrelationship between meristematic regions of developing inflorescences for four cereal species. Ann.Bot., 38: 827-837.

NICHOLLS, P.B. (1974b). The effect of daylength on the development of the barley inflorescence and the endogenous gibberellin concentration. R.Soc.N.Z. Bull. 12: 305-309.

NICHOLLS, P.B. (1978). Response of barley shoot apices to application of gibberellic acid: initial response pattern. Aust.J.Pl.Physiol., 5: 311-320.

NICHOLLS, P.B. and MAY, L.H. (1963). Studies on the growth of the barley apex. I. Interrelationships between primordium formation, apex length and spikelet development. Aust.J.biol.Sci., 16: 561-571.

NICHOLLS, P.B. and MAY, L.H. (1964). Studies on the growth of the barley apex. II. On the initiation of internode elongation in the inflorescence. Aust.J.biol.Sci., 17: 619-630.

NYAHOZA, F., MARHSALL, C. and SAGAR, G.R. (1974). Assimilate distribution in Poa pratensis L. - a quantitative study. Weed.Res., 14: 251-256.

ORMROD, D.P. (1963). Photoperiodic sensitivity of head differentiation, culm elongation, and heading in some spring wheat and spring barley varieties. Can.J.Pl.Sci., 43: 323-329.

PALEG, L.G. and ASPINALL, D. (1964). Effects of daylength and light intensity on growth of barley. II. Influence of incandescent light on apical development. Bot.Gaz., 125: 149-155.

PALEG, L.G. and ASPINALL, D. (1966). Effects of daylength and light intensity on growth of barley. V. Response by plants in the field to night interruption. Aust.J. biol.Sci., 19: 719-731.

PINTHUS, M.J. (1967). Evaluation of winter wheat as a source of high yield potential for the breeding of spring wheat. Euphytica, 16: 231-251.

PINTHUS, M.J. and MILLETT, E. (1978). Interactions among number of spikelets, number of grains and grain weight in the spikes of wheat. Ann.Bot., 42: 839-848.

PORTER, H.K., PAL, I. and MARTIN, R.V. (1950). Physiological studies in plant nutrition. XV. Assimilation of carbon by the ear of barley and its relation to the accumulation of dry matter in the grain. Ann.Bot., 14: 55-68.

PUCKRIDGE, D.W. and DONALD, C.M. (1967). Competition among wheat plants sown at a wide range of densities. Aust.J.agric.Res., 18: 193-211.

PUGSLEY, A.T. (1966). The photoperiodic sensitivity of some spring wheats with special reference to the variety Thatcher. Aust.J. agric.Res., 17591-599.

QUINLAN, J.D. and SAGAR, G.R. (1962). An autoradiographic study of the movement of ^{14}C-labelled assimilates in the developing wheat plant. Weed.Res., 2: 264-273.

RADLEY, M. (1970). Comparison of endogenous gibberellins and response to applied gibberellin of some dwarf and tall wheat cultivars. Planta, 92: 292-300.

RAO, A.R. and WITCOMBE, J.R. (1977). Genetic adaption for vernalization requirement in Nepalese wheat and barley. Ann.appl.Biol., 85: 121-130.

RAWSON, H.M. (1970). Spikelet number, its control and relation to yield per ear in wheat. Aust.J.biol.Sci., 23: 1-15.

RAWSON, H.M. (1971). An upper limit for spikelet number per ear in wheat, as controlled by photoperiod. Aust. J.agric.Res., 22: 537-546.

RAWSON, H.M. and EVANS, L.T. (1970). The pattern of grain growth within rhe ear of wheat. Aust.J.biol.Sci., 23: 753-764.

RAWSON, H.M. and EVANS, L.T. (1971). The contribution of stem reserves to grain development in a range of wheat cultivars of different height. Aust.J.agric.Res., 22: 851-863.

RAWSON, H.M. and HOFSTRA, G. (1969). Translocation and remobilization of ^{14}C assimilated at different stages by each leaf of the wheat plant. Aust.J.biol.Sci., 22: 321-331.

RUCKENBAUER, P. (1975). Photosynthetic and translocation patterns in contrasting winter wheat varieties. Ann. appl.Biol., 79: 351-359.

RYLE, G.J.A. (1970). Distribution patterns of assimilated ^{14}C in vegetative and reproductive shoots of Lolium perenne and Lolium temulentum. Ann.appl.Biol., 66: 155-168.

RYLE, G.J.A. (1972). A quantitative analysis of the uptake of carbon and of the supply of ^{14}C labelled assimilates to areas of meristematic growth in Lolium termulentum. Ann.Bot., 36: 497-512.

RYLE, G.J.A., COBBY, J.M. and POWELL, C.E. (1976). Synthetic and maintenance respiratory losses of $^{14}CO_2$ in uniculm barley and maize. Ann.Bot., 40: 571-587.

RYLE, G.J.A. and POWELL, C.E. (1972). The export and distribution of ^{14}C-labelled assimilates from each leaf on the shoot of Lolium temulentum during resproductive and vegetative growth. Ann.Bot., 36: 363;375.

RYLE, G.J.A. and POWELL, C.E. (1974). The utilization of recently assimilated carbon in graminaceous plants. Ann.appl..Biol., 77: 113-211.

RYLE, G.J.A. and POWELL, C.E. (1976). Effect of rate of photosynthesis on the pattern of assimilate distribution in the graminaceous plant. J.exp.Bot., 27: 189-199.

SAGAR, G.R. and MARSHALL, C. (1966). The grass plant as an integral unit - some studies on assimilate distribution in Lolium multiflorum. Proc.9th int. Grassl.Cong., : 493-497.

SINGLE, W.V. (1964). Influence of nitrate supply on the fertility of the wheat ear. Aust.J.exp.Agric.Anim.Husb., 4: 165-168.

SOFIELD, I., EVANS, L.T., COOK, M.G. and WARDLAW, I.F. (1978). Factors influencing the rate and duration of grain filling in wheat. Aust.J.Pl.Physiol., 4: 785-797.

STOY, V. (1963). The translocation of ^{14}C labelled photosynthetic products from the leaf to the ear in wheat. Physiologia Pl., 16: 851-866.

STOY, V. (1965). Photosynthesis, respiration and carbohydrate accumulation in spring wheat in relation to yield. Physiologia Pl. Suppl. IV: 1-125.

TAKAHASHI, R. and YASUDA, S. (1960). Varietal differences in responses to photoperiod and temperature in barley. Ber.d.Ohara Lust.Landw.Biol., 11: 365-384.

THORNE, G.N. (1962). Survival of tillers and distribution of dry matter between ear and shoot of barley varieties. Ann.Bot., 26: 37-54.

THORNE, G.N. (1963), Varietal differences in photosynthesis of ears and leaves of barley. Ann.Bot., 27: 154-174.

THORNE, G.N. (1965). Photosynthesis of ears and flag leaves of wheat and barley. Ann.Bot., 29: 317-329.

THORNE, G.N. (1966). Photosynthesis of flag leaf laminae of cereals. Rep.Rothamsted exp.Stn., 1965: 100-101.

THORNE, G.N. (1974). Physiology of grain yield of wheat and barley. Rep.Rothamsted exp.Stn., 1973: 5-25.

THORNE, G.N., FORD, M.A. and WATSON, D.J. (1967). Effects of temperature variation at different times on growth and yield of sugar beet and barley. Ann.Bot., 31: 71-101.

THORNE, G.N., FORD, M.A. and WATSON, D.J. (1968). Growth, development and yield of spring wheat in artificial climates. Ann.Bot., 32: 425-445.

THORNE, G.N. and WATSON, D.J. (1955). The effect on yield and leaf area of wheat of applying nitrogen as a top dressing in April or in sprays at ear emergence. J.agric.Sci.Camb., 46: 449 - 456.

WALL, P.C. and CARTWRIGHT, P.M. (1974). Effects of photoperiod temperature and vernalization on the phenology and spikelet numbers of spring wheats. Ann.appl.Biol., 76: 299-309.

WARDLAW, I.F. (1965). The velocity and pattern of assimilate translocation in wheat plants during grain development. Aust.J.biol.Sci., 18: 269-281.

WARDLAW, I.F. (1968). The control and pattern of movement of carbohydrate in plants. Bot.Rev., 34: 73-105.

WARDLAW, I.F., CARR, D.J. and ANDERSON, M.J. (1965). The relative supply of carbohydrate and nitrogen to wheat grains, and an assessment of the shading and defoliation techniques used for these determinations. Aust.J. agric.Res., 16: 893-901.

WATSON, D.J. (1952). The physiological basis of variation in yield. Adv. Agronomy, 4: 101-145.

WATSON, D.J. (1971). Size, structure and activity of the productive system of crops. In Potential crop production, pp. 76-88. Ed. Cooper, J.F. and Wareing, P.F. Heinemann, London.

WATSON, D.J., THORNE, G.N. and FRENCH, S.A.W. (1958). Physiological causes of differences in grain yield between varieties of barley. Ann.Bot., 22: 321-352.

WATSON, D.J., THORNE, G.N. and FRENCH, S.A.W. (1963). Analysis of growth and yield of winter and spring wheat. Ann.Bot., 27: 1-22.

WELBANK, P.J., FRENCH, S.A.W. and WITTS, K.J. (1966). Dependence of yields of wheat varieties on their leaf area durations. Ann.Bot., 30: 291-289.

WHEELER, A.W. (1972). Changes in growth-substance contents during growth of wheat grains. Ann.appl.Biol., 72: 327-334.

WHEELER, A.W. (1976). Some treatments affecting growth substances in developing wheat ears. Ann.appl.Biol., 83: 455-462.

WILLEY, R.W. and DENT, J.D. (1969). The supply and storage of carbohydrate in wheat and barley. Agric.Prog., 44: 43-55.

WILLEY, R.W. and HOLLIDAY, R. (1971a). Plant population and shading studies in barley. J.agric.Sci.Camb., 77: 445-452.

WILLEY, R.W. and HOLLIDAY, R. (1971b). Plant population, shading and thinning studies in wheat. J.agric. Sci., Camb., 77: 453-461.

WILLIAMS, R.F. (1960). The physiology of growth in the wheat plant. I. Seedling growth and the pattern of growth at the shoot apex. Aust.J.biol.Sci., 13: 401-428.

WILLIAMS, R.F. (1966). The physiology of growth in the wheat plant. III. Growth of the primary shoot and inflorescence. Aust.J.biol.Sci., 19: 949-966.

WILLIAMS, R.F. (1974). The shoot apex and leaf growth. A study in quantitative biology. Cambridge University Press, Cambridge.

WILLIAMS, R.F. and WILLIAMS, C.N. (1968). Physiology of growth of the wheat plant. IV. Effects of daylength and light energy level. Aust.J.biol.Sci., 21: 835-854.

WILLIAMS, R.H. and HAYES, J.D. (1977). The breeding implications of studies on yield and its components in contrasting genotypes of spring barley. Cereal Res. Comm., 5: 113-118.

YAP, T.C. and HARVEY, B.L. (1972). Relation between grain yield and photosynthetic parts above the flag-leaf node in barley. Can.J.Pl.Sci., 52: 241-246.

YOSHIDA, S. (1972). Physiological aspects of grain yield. Ann.Rev.Pl.Physiol., 23: 437-464.

ZEEVART, J.A.D. (1971). Effects of photoperiod on growth rate and endogenous gibberellins in the long day rossette plant, spinach. Pl.Physiol., 47: 821-827.

PERSONAL COMMUNICATIONS

I wish to express my thanks to the following for their contributions to this thesis via personal communications.

GILES, R.G.J., Scottish Plant Breeding Station, Pentlandfield, Edinburgh.

HUBBARD, F.R., Ministry of Agriculture, Fisheries and Food, Cambridge.

RICHARDSON, M.R., Official Seed Testing Station, East Craigs, Edinburgh.

WILLIAMS, R.H., Department of Biology, University of Reading, Reading.

APPENDIX - TABLE I

Environmental conditions during apical development

Weeks after sowing:	1	2	3	4	5	6	7	8	9	10	11	12	13
a. 1976													
S.1 (27 March)													
Daylength (h)	12.9	13.3	13.8	14.1	14.8	15.5	16.0	16.6	16.9	17.1	17.4		
Air temp. (max.)(°C)	2.5	10.1	10.6	12.8	9.9	13.1	14.3	14.5	16.5	13.9	20.4		
Air temp. (min.)(°C)	2.2	2.1	3.8	4.6	3.9	4.1	5.9	6.8	8.8	7.7	10.9		
Grass temp. (°C)	2.4	3.7	3.4	5.0	4.4	2.9	3.6	4.7	7.8	7.0	9.3		
Rainfall (mm)	5.0	0.2	3.2	0.5	0.1	0.7	1.1	2.6	12.3	12.2	0.6		
S.2 (20 April)													
Daylength (h)	14.5	15.3	15.8	16.3	16.8	17.0	17.3	17.5	17.7				
Air temp. (max.)(°C)	10.2	11.6	15.0	13.8	15.6	14.2	16.8	19.1	16.1				
Air temp. (min.)(°C)	2.9	3.9	5.3	6.0	7.8	8.0	9.3	10.6	8.3				
Grass temp. (°C)	3.1	3.9	3.6	4.0	6.0	7.2	8.0	9.4	7.3				
Rainfall (mm)	0.1	0.7	0.2	1.1	3.1	4.6	0.3	0.6	1.7				
S.3 (17 May)													
Daylength (h)	16.7	17.0	17.2	17.5	17.7	17.7	17.5						
Air temp. (max.)(°C)	14.9	14.9	15.9	20.1	15.3	12.7	25.3						
Air temp. (min.)(°C)	7.7	8.3	9.2	10.3	8.7	11.8	12.5						
Grass temp. (°C)	5.9	7.5	8.2	8.9	7.9	10.0	11.2						
Rainfall (mm)	2.4	4.7	0.9	0.6	1.7	0.0	0.3						

(contd.)

APPENDIX - TABLE I (contd.)

Weeks after sowing	1	2	3	4	5	6	7	8	9	10	11	12	13
b. 1977													
S.1 (15 March)													
Daylength (h)	12.0	12.5	13.1	13.5	13.8	14.4	15.1	15.7	16.2	16.7	17.0	17.2	17.5
Air temp. (max.)(^{o}C)	8.1	6.0	7.8	7.8	8.9	12.1	9.8	10.5	10.8	15.3	16.4	17.6	12.1
Air temp. (min.)(^{o}C)	3.9	2.2	1.9	1.5	2.5	5.8	3.9	4.8	3.7	3.4	6.1	7.3	5.6
Grass temp. (^{o}C)	2.6	2.0	2.3	2.1	2.4	4.6	2.6	3.2	3.3	2.8	4.6	5.8	4.7
Rainfall (mm)	3.6	1.5	1.5	0.9	0.9	1.1	2.5	1.8	0.7	0.0	0.0	4.8	9.7
S.2 (20 May)													
Daylength (h)	16.8	17.1	17.3	17.6	17.8	17.8	17.4						
Air temp. (max.)(^{o}C)	16.3	18.4	14.4	11.8	15.8	17.7	23.0						
Air temp. (min.)(^{o}C)	5.5	5.1	7.5	6.1	6.6	9.4	11.8						
Grass temp. (^{o}C)	4.0	3.2	6.3	5.3	5.7	8.1	9.3						
Rainfall (mm)	0.1	0.0	7.0	7.7	0.0	1.0	0.0						

APPENDIX - TABLE II

Influence of sowing date on plant number per plot for 15 barley cultivars in the field in 1977. A negative value denotes an increase in S.2.

Cultivar	Plant no.		per plot	% reduction in S.2
Clipper	19.0	*	30.3	-59.6
Spartan	16.0	*	28.7	-79.2
CI 5791	18.3	*	28.7	-56.4
Ingrid	16.7	*	27.0	-62.0
Chevallier	17.7	*	28.3	-60.3
Bohmervald	16.0	*	29.7	-85.4
Lami	21.3	*	30.7	-43.8
Domen	16.0	*	29.3	-83.3
Afghan R668	15.7	*	22.3	-42.5
Maris Mink	19.3	*	30.0	-55.2
Golden Promise	16.3	*	27.0	-65.3
Spratt	15.0	*	27.7	-84.5
Hillmarsh	17.3	*	28.3	-63.5
Uzu	17.3	*	29.2	-69.2
Ymer	23.7	*	30.7	-29.6

APPENDIX - TABLE IIIa

Influence of sowing date on components of grain yield per plant. Sowing 1.

Cultivar	Ear no./ plant [a]	Grain no./ main ear [b]	Grain no./ tiller ear [c]	Grain no./ ear [d]	1000 Grain wt./ main ear [e]	1000 Grain wt./ tiller ear [e]	1000 Grain wt./ ear [e]
Early 12A Bonus	5.5	22.6	18.1	18.9	48.5	43.1	44.1
Clipper	7.2	14.7	12.7	13.0	51.8	45.6	46.4
Spartan	4.6	11.8	11.4	11.5	51.4	46.9	47.9
Turkish	3.0	18.5	16.0	16.5	61.3	51.7	53.6
CI 5691	5.7	18.2	14.8	15.4	48.7	44.6	45.3
Ingrid	6.1	23.5	19.1	19.8	49.8	42.1	43.3
Banba	5.0	25.5	20.7	21.6	45.9	39.9	41.1
Chevallier	5.7	19.9	17.2	17.7	53.5	47.2	48.3
Midas	5.2	26.7	22.9	23.7	41.2	34.8	36.0
Bohmerwald	4.6	25.9	19.9	21.2	48.5	41.2	42.8
Heils Franken	4.4	24.7	20.8	21.7	53.3	49.8	50.6
Lami	6.3	23.6	20.8	21.2	49.8	44.6	45.5
Mimi	6.1	25.8	21.6	22.4	35.4	30.0	30.9
Charlottetown 80	4.4	26.3	21.7	22.7	45.3	40.1	41.3
Domen	4.4	24.1	19.1	20.3	49.3	40.1	42.2
Scotch Common	4.7	26.5	20.1	21.5	45.9	37.7	39.5
Tyra	6.9	26.0	16.5	17.1	52.4	44.4	45.5
Proctor	5.4	25.9	20.1	21.2	44.9	38.1	39.4
Ark Royal	6.4	24.3	20.7	21.2	46.5	40.5	41.4
Afghan R668	5.5	22.3	18.3	19.0	50.1	42.9	44.2
Zephyr	5.2	26.0	20.5	21.5	48.6	39.5	41.3
Maris Mink	5.5	24.2	20.2	20.9	42.4	38.2	39.0
Ariel	4.6	26.2	21.5	22.5	49.7	44.4	45.6
Golden Promise	5.7	25.4	20.5	21.3	36.0	30.5	31.5
Abacus	4.7	26.2	22.5	23.3	54.7	47.6	49.1
Spratt	4.7	27.8	26.5	26.7	48.1	42.0	43.3
Hillmarsh	4.6	26.2	21.2	22.3	50.4	44.5	45.8
Uzu	6.0	24.5	18.5	19.5	44.8	38.4	39.5
Ymer	6.2	26.7	20.2	21.3	52.9	44.9	46.2

a = Values based on a mean of between 24 and 92 plants.
b = Values based on a mean of between 24 and 92 main ears.
c = Values based on a mean of between 109 and 150 tiller ears.
d = Values computed from previous columns.
e = Values for 1000 grain weight in g (computed from sub-samples of 250 grain).

APPENDIX - TABLE IIIb

Influence of sowing date on components of grain yield per plant. Sowing 2.

Cultivar	Ear no./ plant [a]	Grain no./ main ear [b]	Grain no./ tiller ear [c]	Grain no./ ear [d]	1000 Grain wt./ main ear [e]	1000 Grain wt./ tiller ear [e]	1000 Grain wt./ ear [e]
Early 12a Bonus	4.7	21.3	19.4	19.8	49.6	37.8	40.3
Clipper	5.0	15.9	13.4	13.9	51.3	40.1	42.4
Spartan	4.0	13.3	12.0	12.3	49.0	43.4	44.8
Turkish 1106	3.9	17.7	15.5	16.0	63.1	45.1	49.7
CI 5791	4.5	14.7	9.9	11.0	49.5	43.9	45.2
Ingrid	4.5	24.0	20.4	21.2	45.5	34.3	36.7
Banba	4.1	24.1	18.0	20.0	46.5	36.0	38.6
Chevallier	4.4	20.1	17.0	17.7	49.2	40.6	42.5
Midas	4.8	27.2	22.1	23.2	45.4	34.9	37.1
Bohmervald	4.2	26.1	19.5	21.0	49.6	39.4	41.8
Heils Franken	4.1	22.0	17.6	18.7	50.8	40.0	42.6
Lami	4.9	22.5	19.3	20.0	51.2	44.3	45.7
Mimi	4.3	26.5	21.2	22.4	39.0	28.1	30.7
Charlottetown 80	3.3	25.0	19.7	21.3	38.2	32.2	34.0
Domen	4.3	21.1	18.0	18.7	52.0	38.7	41.8
Scotch Common	4.6	23.8	20.1	20.9	46.4	34.0	36.7
Tyra	4.7	21.8	19.0	19.6	59.0	43.8	47.1
Proctor	4.3	26.4	21.3	22.5	49.6	37.2	40.0
Ark Royal	5.2	27.6	22.7	23.6	45.1	32.7	35.1
Afghan R668	5.4	18.1	13.7	14.5	45.3	32.5	34.9
Zephyr	4.2	23.4	20.7	21.3	45.4	39.2	40.7
Maris Mink	4.6	25.8	20.6	21.7	46.4	33.9	36.6
Ariel	4.0	27.2	22.0	23.3	49.3	37.8	40.6
Golden Promise	3.9	25.9	21.7	22.7	39.9	29.3	32.0
Abacus	3.3	24.4	22.4	23.0	51.7	41.1	44.3
Spratt	3.4	26.4	21.7	23.1	47.5	36.3	39.6
Hillmarsh	4.6	25.5	19.1	20.7	51.1	40.4	42.7
Uzu	4.4	16.2	12.8	13.6	46.5	34.8	37.5
Ymer	4.3	26.2	19.9	21.4	50.3	40.9	43.1

a = Values based on a mean of between 34 and 83 plants.
b = Values based on a mean of between 26 and 83 main ears.
c = Values based on a mean of between 86 and 150 tiller ears.
d = Values computed from previous columns.
e = Values for 1000 grain weight in g (computed from sub-samples of 250 grain).

APPENDIX - TABLE IV

Percentage reduction of components of grain yield per plant in S.2 compared with S.1. A negative value indicates an increase in S.2.

Cultivar	Ear no./ plant	Grain no./ main ear	Grain no./ tiller ear	Grain no./ ear	1000 Grain wt./ main ear	1000 Grain wt./ tiller ear	1000 Grain wt./ ear
Early 12A Bonus	14.8	5.9	-6.8	-4.3	-2.2	12.4	8.7
Clipper	31.4	-7.9	-5.7	-7.2	0.9	11.9	8.7
Spartan	12.0	-15.4	-5.5	-7.7	4.8	7.4	6.5
Turkish 166	22.8	4.4	3.5	2.9	-2.9	12.8	7.2
CI 5791	22.0	19.3	33.2	28.8	1.8	1.6	0.3
Ingrid	25.7	-2.0	-6.8	-6.7	8.6	18.6	15.2
Banba	18.1	-2.4	13.1	7.8	4.9	9.8	6.2
Chevallier	22.0	-1.3	1.2	-0.1	8.0	14.1	12.0
Midas	6.9	-2.0	3.6	2.1	-10.1	-0.2	-2.8
Bohmerwald	8.5	-0.5	2.2	0.9	-2.3	4.6	2.4
Heils Franken	6.4	10.9	15.1	13.7	4.9	19.8	15.9
Lami	22.6	4.8	6.8	5.8	-2.8	0.8	-0.6
Mimi	29.4	-2.6	1.8	-0.4	-10.2	6.5	0.9
Charlottetown 80	25.5	5.1	9.2	6.3	15.7	19.7	17.5
Domen	3.0	12.7	6.0	7.6	-5.3	3.8	0.8
Scotch Common	2.8	10.4	-0.3	2.4	-1.1	9.9	7.1
Tyra	32.6	-3.6	-15.3	-14.4	-12.7	1.2	-3.4
Proctor	19.8	-1.9	-6.2	-6.3	-10.3	2.4	-1.7
Ark Royal	19.0	-13.5	-9.5	-11.1	3.1	19.3	15.3
Afghan R668	2.2	18.6	25.2	23.7	9.5	24.1	21.0
Zephyr	20.0	9.9	-1.1	0.8	6.7	0.8	1.4
Maris Mink	13.9	-6.9	-2.0	-3.8	-9.4	11.5	6.3
Ariel	13.4	-4.1	-2.3	-3.5	-0.8	15.0	10.8
Golden Promise	31.4	-1.8	-5.9	-6.6	-10.8	3.9	-1.8
Abacus	30.4	6.8	0.4	1.1	5.4	13.7	9.8
Spratt	27.5	5.0	18.1	13.7	1.3	13.6	8.6
Hillmarsh	0.9	2.9	10.0	8.1	-1.4	9.3	6.8
Uzu	26.1	34.0	30.8	30.4	-3.7	9.4	5.1
Ymer	31.1	1.6	1.8	-0.4	4.8	8.9	6.7