Promotor : dr. ir. J. Sneep, emeritus hoogleraar in de leer van de plantenveredeling.

Co-promotor: dr. R. B. Austin, senior principal scientific officer, Plant Breeding Institute, Cambridge.

Variation in time of ear emergence of wheat (*Triticum aestivum* L.): physiology, genetics and consequences for yield

J. HOOGENDOORN

VARIATION IN TIME OF EAR EMERGENCE OF WHEAT (TRITICUM AESTIVUM L.): PHYSIOLOGY, GENETICS AND CONSEQUENCES FOR YIELD

Proefschrift
ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr. C. C. Oosterlee,
in het openbaar te verdedigen
op vrijdag 23 november 1984
des namiddags te vier uur in de aula
van de Landbouwhogeschool te Wageningen.

ISN=2155974-03

Aan mijn ouders

STELLINGEN

1. Vergelijking van fluctuaties in hormoongehaltes in onrijpe graankorrels gedurende vernalizatie in de aar en gedurende normale afrijping kan mogelijkerwijs licht werpen op de rol van hormonen in het vernalizatie proces.
   - Dit proefschrift

2. De resultaten van onderzoek naar de mogelijk grotere gevoeligheid van kortstro rassen voor sub-optimale teelt omstandigheden in vergelijking met traditionele langstro rassen suggereren dat de stabiliteit van beide typen rassen afhankelijk is van andere factoren, zoals korrelgrootte en bloeidatum, maar dat er tussen kortstro en langstro rassen verschillen bestaan in de wijze waarop door manipulatie van deze factoren de genotype x milieu interactie geminimaliseerd kan worden.
   - Gale, M.D. & S. Youssefian, 1984. In G.E. Russell (ed.) Plant Breed. Progr. Rev. Vol. 1, Butterworths: 1-36.
   - Bidinger, F.R. et al, 1984. J. Agr. Sci., Camb. (In the press)

3. Er zijn overtuigende aanwijzingen dat het endogene abscisinezuur-gehalte een rol speelt in de fysiologische processen die droogte resistentie bepalen, maar de correlatie tussen genetische verschillen in beide factoren is niet zodanig dat het gebruik van abscisinezuur-gehalte als selectiecriterium voor droogte resistentie te rechtvaardigen is.
   - Henson, I.E. et al, 1981. J. Expt. Bot. 32: 1211-1221
   - Quarrie, S.A. & P.G. Lister, 1983. J. Expt. Bot. 34: 1260-1270.

4. De bewering van Flood en Halloran dat bij een daglengte van 16 uur verschillen in gevoeligheid voor daglengte geen rol meer spelen bij de regulatie van het in de aar komen is onjuist. Het feit dat Chinese Spring(Thatcher 2B) later in de aar komt dan de analoge 2A en 2D substitutie lijnen is niet een gevolg van een genetisch bepaald verschil in temperatuurgevoeligheid maar van de substitutie van het $\underline{ppd}_2$ daglengte gevoeligheids allel op chromosoom 2B van Thatcher voor het $\underline{Ppd}_2$ daglengte gevoeligheids allel van Chinese Spring.
   - Flood, R.G. & G.M. Halloran, 1984. Euphytica 33: 91-98.

5. Het verkleuren van de pigment zone gedurende de korrelvulling valt samen met het moment waarop de tarwekorrel het maximale drooggewicht bereikt, en aangezien deze verkleuring eenvoudig waar te nemen is verdient dit kenmerk meer aandacht bij de bestudering van genotypische verschillen in afrijpingstijd.
   - Hanft, J.M. & R.D. Wynch, 1982. Crop Sci. 22: 584-588.

6. Alhoewel het toedienen van stikstof de bladduur fase in tarwe verlengt en leidt tot een hogere LAI en grotere biomassa, zijn er geen aanwijzingen dat stikstof daarnaast ook het moment van het in de aar komen vertraagt.
   - Pearman, I. et al, 1978. J. Agr. Sci., Camb. 91: 31-45.
   - Spiertz, J.H.J. & J. Ellen, 1978. Neth. J. Agr. Sci. 26: 210-231.

7. De analogie in moleculaire structuur tussen 'transposable elements' uit uiteenlopende gewassen zoals mais, Antirrhinum en soja, en de overeenkomst van hun activiteit met die van lysogene virussen, doet vermoeden dat 'transposable elements' bestaan uit virus-DNA dat de genen voor het mantel eiwit verloren heeft en daardoor ook het vermogen om zich te verplaatsen naar andere cellen en organismen.
   - Alberts, B. et al, 1983. Molecular biology of the cell. Garland Publ.: 232-247.
   - Freeling, M., 1984. Ann. Rev. Plant Phys. 35: 277-298.

8. Het is te betreuren dat triticale niet in grotere mate gebruikt wordt voor menselijke consumptie, aangezien triticale meer eiwitten en mineralen bevat dan tarwe en de smaak van het als het ware voorgemengde rogge-tarwe meel zeer aantrekkelijk is.
   - Gupta, P.K. & P.M. Priyadarshan, 1982. Adv. Gen. 21: 255-345.

9. De ervaring leert dat de introductie van kwekersrechten leidt tot de opbloei van de particuliere veredelings sector, maar niet tot een evenredige toename van het aandeel van particuliere bedrijven in het veredelings onderzoek.
   - Ruttan, V.W., 1982. Agricultural research policy. Univ. Minnesota Press: 181-214.

10. Gewassen die op arme gronden de hoogste opbrengsten geven, zoals sorghum en cassave, zijn het meest efficient in het ontrekken van voedingstoffen aan de bodem, en de teelt van deze gewassen put dientegevolge de grond alleen nog maar verder uit.
   - Geus, J.G. de, 1967. In: Fertilizer guide for tropical and subtropical farming. Centre d'Etude de l'Azote: 181-185.
   - Doggett, H., 1970. Sorghum. Longmans: 180-207.

11. Alleen in Taiwan en China is de groene revolutie gepaard gegaan met een verandering en verbetering van de sociale positie van de kleine boeren. Hieruit valt af te leiden dat de groene revolutie sociaal gezien een anti-revolutionair effect heeft gehad.
   - Pearse, A., 1980. Seeds of plenty, seeds of want. Oxford Univ. Press, 262 p.

12. Nederlanders in een engelse pub vallen liefst zo weinig mogelijk op, maar helaas klinkt hun 'one pint of ALE' duidelijk anders dan 'please luv, pint o BITTER', en dat is de schuld van de kruiswoordraadsels.

J. Hoogendoorn
Variation in time of ear emergence in wheat (Triticum aestivum L.): physiology, genetics and consequences for yield.
Wageningen, 23 November 1984.

PREFACE

Without the support of many - family, friends, colleagues and institutions, both in Great Britain and in the Netherlands - I would never have been able to start, let alone to complete the work for this dissertation.

Dr. R.B. Austin and Prof. dr. J. Sneep took on the difficult task to supervise this project (and me) and for their suggestions, criticism and continuous support I am deeply grateful.

I would like to thank all members of staff of the Physiology Department of the Plant Breeding Institute for being pleasant and helpful colleagues, but especially Peter Innes, Ray Blackwell and Margaret Ford who have been directly involved in this project, and to whom I owe much of my present understanding of the wheat plant. Many others at PBI, in particular in the Cytogenetics Department, allowed me to use their facilities and have given me highly appreciated advice. Leni Derks' assistance with the yield trials in 1983, both at Cambridge and The Murrays, is gratefully acknowledged.

To my family and friends I owe much for their support, patience, and never failing interest in the importance of early and late wheat varieties.

Without Klaartje Mulder's encouragement and very active involvement four years ago, it would never have been possible to overcome all the initial organizational problems connected with this project, and to her I am especially grateful.

The work was financially supported by

* Stichting Fonds Landbouw Export Bureau 1916 1918 (1980-1984)
* Fundatie van de Vrijvrouwe van Renswoude te 's Gravenhage (1980-1984)
* Stichting Landbouwhogeschoolfonds (1980-1984)
* Mej. H.J. Beck Fonds (1980-1981)

CONTENTS

1. INTRODUCTION

Wheat originates in the Fertile Crescent of the Middle East, where it was domesticated about 10000 years ago, as part of an agricultural system which included also barley, lentils, peas, flax, sheep, goats and pigs (Harlan, 1975). The genomes of three wild Gramineae species are present in the allopolyploid wheat plant. The genome from Triticum monococcum (AA) merged with a genome of which the origin is still not clear (BB), but it is likely to be related to Aegilops speltoides. The resulting allotetraploid, Triticum turgidum (AABB), hybridized with Aegilops squarrosa (DD), to give the allohexaploid Triticum aestivum (AABBDD). Aegilops squarrosa occupies a wider range of environments than do the other wheat progenitors, and as such is thought to have made it possible (Evans & Wardlaw, 1976) for the crop to spread to Central Europe (4500 BC), Ethiopia (3000 BC), India (3500 BC) and China (2500 BC), and much later to the Americas and Australia at the time of their colonization (Zeven, 1979; 1980). In comparison, the domesticated diploid and allotetraploid Triticum spp. are still grown successfully only in climates similar to the Mediterranean environment where they originated. At present wheat is the most important grain cereal in the world as regards both the total area sown and the annual production, although rice probably constitutes the staple diet of more people (Arnon, 1972). Wheat is grown in almost every country of the world (Figure 1), and because of the rising demand for wheat in the developing countries, it is expected that the wheat area will continue to expand into even colder, higher, wetter, drier and hotter regions (FAO, 1983).

Wheat has been able to become so important largely because of its great adaptability to a wide range of temperatures, to high and low input agricultural systems, and in particular because it displays enormous variation in the timing of its development. This has made it possible to sow and harvest a wheat crop within as little as 80 days in Canada (Aitken, 1974) and to extend the growing period to almost a full year in Northern Europe.

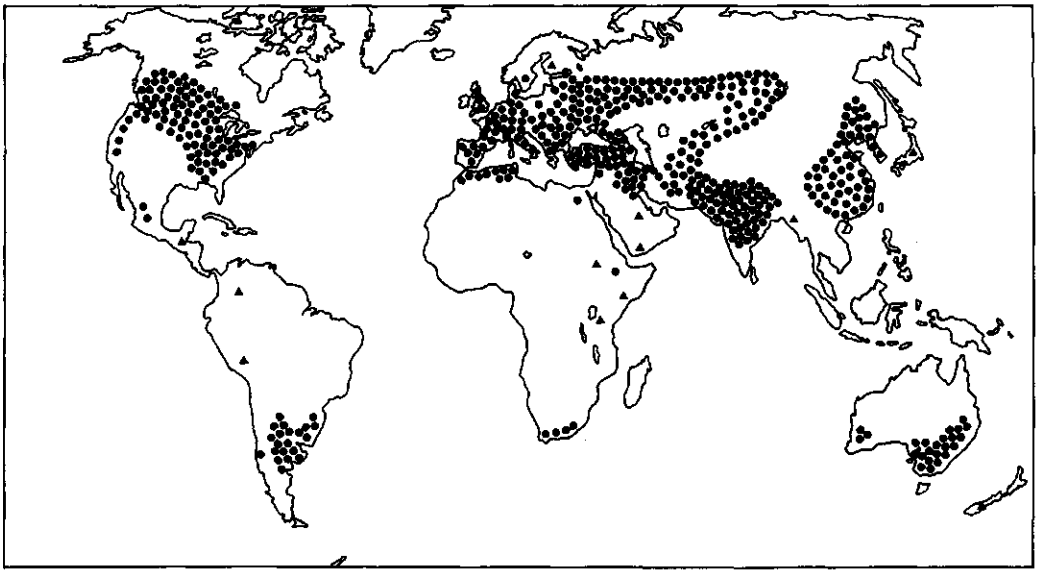

Figure 1. World wheat production in 1982 (FAO, 1983). ● - 500000 ha of wheat, ▲ - regions with more than 50000, but less than 500000 ha of wheat.

The growing cycle of wheat can be divided into three phases. In the vegetative phase, from sowing until ear initiation, numbers of leaves and potential number of tillers, and therefore carbohydrate source capacity, are determined. During the second phase, the reproductive period, from ear initiation to anthesis, the grain storage capacity of the crop is determined as the total number of ears, spikelets per ear and florets per spikelets. Conditions during the third phase in which grain filling takes place, determine to what extent the grain storage capacity is realized in final grain yield (Evans & Wardlaw, 1976). The three phases have to be completed within the growing period available. Environmental stress during the growing period, such as low light intensity, extreme high or low temperature, low nitrogen level and

Table 1. The effects of soil moisture stress at different stages of development, on yield components (Aspinall et al. 1964).

Stage of development when drought occurs	Effects
Before tillering	Tillering is supressed, but may be stimulated with renewed moisture supply
Prior to anthesis	Rate of elongation of the internodes is reduced Number of grains per ear is reduced
At, and shortly after anthesis	Grain size is reduced
Grain growth	Shrivelled grain is produced

moisture stress, determine the duration and the importance for final yield of each phase. Aspinall et al. (1964) describe the effects of soil moisture stress at different stages of development on barley (Table 1). These are considered to be similar for wheat (Arnon, 1972). An optimal balance between the duration of each development phase, so that stress on the fastest developing, and therefore most vulnerable plant parts is avoided, is a major breeding objective to achieve maximal yields.

Genotypic variation in the duration of each of the three phases is caused mainly by differences in sensitivity to photoperiod and vernalizing temperatures. Reduced daylength has been shown to delay ear initiation, and consequently to increase number of leaves and tillers and number of spikelets per ear, and to delay ear emergence and anthesis.

Many experiments (Marcellos & Single, 1971; Klaimi & Qualset, 1973; Hunt, 1979; Pugsley, 1983) have indicated a sharp distinction between those varieties which are only slightly delayed in ear initiation by short days, and those responding very strongly to reduced daylength.

Genotypic variation in response to vernalization, prolonged exposure to temperatures between 0 - 10°C, has been shown to be the other major factor in the determination of ear initiation. Some varieties have an almost absolute requirement for vernalization. Without vernalization these varieties might develop an ear eventually, but only after a very extended vegetative period. Other varieties respond to a period of low temperature, but will, although delayed, initiate and develop normal ears without vernalization. A third group of varieties is totally vernalization insensitive and reaches ear emergence equally early with or without a prior low temperature treatment.

Wheat varieties are often referred to as either winter, facultative or spring genotypes, a distinction based on the normal time of sowing for the varieties. Varieties with an absolute requirement for vernalization are winter wheats, while most vernalization insensitive wheats are used as spring wheats. Facultative wheats vary in response to vernalization. Several wheat varieties used as winter wheats, however, have been found to react to vernalization but not to have an absolute requirement, e.g. some Japanese winter wheat varieties (Gotoh, 1976), and similarly spring wheat varieties with a marked vernalization response have been identified (Levy & Peterson, 1972). Differences in sensitivity to temperature, growth rate and ear size, which are independent of photoperiod and vernalization, are thought to be a further source of genotypic variation in growth and development, and consequently in time of ear emergence (Calder, 1966). For example, Yasuda & Shimoyama (1965) showed that not only photoperiod and vernalization sensitivity, but also 'earliness in narrow sense', genetic factors independent of photoperiod and vernalization, determine the length of the pre-anthesis phase in wheat. Hunt (1979), and Ford et al. (1980) refer also to 'earliness' factors in the regulation of the life cycle of wheat. In the work described here the effects of these factors will be referred to as earliness *per se*.

Vernalization and photoperiod insensitivity were found to be controlled by relatively few genes, and to be dominantly, or at least partly dominantly inherited (Pugsley, 1970, 1971, Klaimi & Qualset, 1973, 1974). Experiments with aneuploid stocks and substitution lines have identified two major loci for photoperiod insensitivity on chromosome 2B and 2D, and one major and other minor loci for vernalization insensitivity on the group 5 chromosomes and on

chromosome 7B (Law & Scarth, 1984). Many other chromosomes have been shown to affect ear emergence, but often it is not clear if these are involved in differences in photoperiod or vernalization sensitivity, or in earliness *per se*.

The photoperiod and vernalization insensitivity genes have been manipulated, often unknowingly, by breeders to adjust the life cycle of the wheat crop to environmental conditions. For example, early Australian settlers found that wheat varieties brought from Great Britain did not develop normally in Australia. Introductions from India and Southern Africa proved to be better adapted (Macindoe, 1975). At that time the effects of daylength and low temperature were not known, and it was not realized that the strong vernalization and photoperiod sensitivity of the British varieties (van Dobben, 1965, Ledent, 1979) prevented normal development under Australian conditions.

The environmental conditions and the high input agricultural system of Great Britain do not present severe limitations to the growth and development of the wheat crop, although some stress in the form of a soil moisture deficit is likely to occur from April onwards on the lighter soils (Innes & Blackwell, 1981). The growing period of winter wheat, from sowing in September to harvesting in August, is amongst the longest in the world, and record yields of 13.5 t/ha (Austin, 1982) have been obtained. It was found, however, that present day British wheat varieties reached ear emergence earlier than varieties grown widely in the first part of the century (Austin et al. 1980), which suggested that variation in ear emergence time could have a significant influence on grain yield in Great Britain.

The work presented here decribes field experiments in which the effect of differences in the duration of the pre-ear emergence phase on grain yield under British winter wheat growing conditions is investigated. In experiments with monosomic lines, chromosomes were identified with loci controlling the response to photoperiod and vernalization and with loci affecting earliness *per se*. Controlled environment studies, in combination with field experiments, provided means of interpreting genotypic differences in ear initiation and ear emergence in terms of differences in photoperiod and vernalization sensitivity and earliness *per se*. Suggestions are presented on how to achieve

variation in the duration of the pre-ear emergence phase in Great Britain and also in other wheat growing environments.

REFERENCES

AITKEN, Y., 1974. Flowering time, climate and genotype. Melbourne University Press: 193 pp.

ARNON, I., 1972. Wheat. In: Crop production in dry regions. Vol. 2. Systematic treatment of the principal crops, Leonard Hill, London: 1-72.

ASPINALL, D., P.B. NICHOLLS & L.H. MAY, 1964. The effects of soil moisture stress on the growth of barley. I. Vegetative development and grain yield. Austr. J. Agric. Res. 15: 729-745.

AUSTIN, R.B., J. BINGHAM, R.D. BLACKWELL, L.T. EVANS, M.A. FORD, C.L. MORGAN & M. TAYLOR, 1980. Genetic improvements in winter wheat yields since 1900 and associated physiological changes. J. Agric. Sci., Camb. 94: 675-689.

AUSTIN, R.B, 1982. Crop characteristics and the potential yield of wheat. J. Agric. Sci., Camb. 98: 447-453.

CALDER, D.M., 1966. Inflorescense induction and initiation in the Gramineae. In F.L. MILTHORPE & J.D. IVINS (Eds) The growth of cereals and grasses, Butterworths, London: 59-73.

DOBBEN, W.H. VAN, 1965. The photoperiodical reaction of wheat in the Mediterranean region and in North Western Europe. Mediterranea 5: 54-59.

EVANS, L.T. & I.F. WARDLAW, 1976. Aspects of the comparative physiology of grain yield in cereals. Adv. Agron. 28: 301-359.

FAO, 1983. Production Yearbook 1982, Vol. 36, Rome: 320 pp.

FORD, M.A., R.B. AUSTIN, W.J. ANGUS & G.C.M. SAGE, 1981. Relationships between the responses of spring wheat genotypes to temperature and photoperiodic treatment and their performance in the field. J. Agric. Sci., Camb. 96: 623-634.

GOTOH, T., 1976. Studies on varietal differences in vernalization requirement in wheat. Jap. J. Breed. 26: 307-327 (Jap., Engl. summ.).

HARLAN, J.R., 1975. Crops and man. Am. Soc. Agron., Madison: 295 pp.

HUNT, L.A., 1979. Photoperiodic responses of winter wheats, from different climatic regions. J. Plant Breed. 82: 70-80.

INNES, P. & R.D. BLACKWELL, 1981. The effect of drought on the water use and yield of two spring wheat genotypes. J. Agric. Sci., Camb. 96: 603-610.

KLAIMI, Y.Y. & C.O. QUALSET, 1973. Genetics of heading time in wheat (Triticum aestivum L.). I The inheritance of photoperiodic response. Genetics 74: 139-156.

KLAIMI, Y.Y. & C.O. QUALSET, 1974. Genetics of heading time in wheat (Triticum aestivum L.). II The inheritance of vernalization response. Genetics 76 : 119-133.

LAW, C.N. & R. SCARTH, 1984. Genetics and its potential for understanding the action of light in flowering. In D. VINCE-PRUE (Ed.) Light and the flowering process, Academic Press, London (In the press).

LEDENT, J.F., 1979. Vernalization and anthesis in a collection of wheat

cultivars (Triticum aestivum L.), a quantitative study in controlled environments. Bull. Soc. R. Bot. Belg. 112: 186-192.

LEVY, J. & M.L. PETERSON, 1972. Responses of spring wheats to vernalization and photoperiod. Crop Sci. 21: 487-490.

MACINDOE, S.L., 1975. History of production of wheat in Australia. In A. LAZENBY & E.M. MATHESON (Eds) Australian field crops. Vol. 1. Wheat and other temperate cereals. Angus & Robertson, Sydney: 99-121.

MARCELLOS, H. & W.V. SINGLE, 1971. Quantitative responses of wheat to photoperiod and temperature in the field. Austr. J. Agric. Res. 22: 343-357.

PUGSLEY, A.T., 1971. A genetic analysis of the spring-winter habit of growth in wheat. Austr. J. Agric. Res. 22: 21-31.

PUGSLEY, A.T., 1972. Additional genes inhibiting winter habit in wheat. Euphytica 21: 547-552.

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

YASUDA, S. & H. SHIMOYAMA, 1965. Analysis of internal factors influencing the heading time of wheat varieties. Ber. Ohara Inst. Landw. Biol. Okayama Univ. 13: 28-38.

ZEVEN, A.C., 1979. The prehistoric spread of bread wheat into Asia. Proc. 5th Int. Wheat Genet. Symp. Vol. 1, New Delhi: 103-107.

ZEVEN, A.C., 1980. The spread of bread wheat over the Old World since the Neolithicum as indicated by its genotype for hybrid necrosis. J. d'Agric. Trad. et Bot. Appl. 27: 19-53.

2. A COMPARISON OF DIFFERENT VERNALIZATION TECHNIQUES IN WHEAT (*TRITICUM AESTIVUM* L.)

J.Hoogendoorn

Plant Breeding Institute, Trumpington, Cambridge CB2 2LQ, U.K.

Journal of Plant Physiology, 116: 11-20 (1984)

INDEX WORDS

Triticum aestivum L., vernalization technique.

SUMMARY

To measure the effect of vernalization on time to ear emergence allowance must be made for the growth which occurs during the vernalization treatment. In an experiment with eight contrasting wheat varieties it was shown that it is possible to express growth during vernalization in terms of days of growth at non-vernalizing temperatures, using linear regression of number of primordia on time after sowing. The use of linear regression of seedling height on time after sowing proved to be less accurate.

Seeds of the vernalization sensitive wheat variety Sage were vernalized while developing in the ear. These, and normal grains were subjected to a number of different vernalization treatments which varied in temperature, duration, and water availability. By vernalizing developing grains in the ear it was possible to obtain plants which had fewer leaves and were earlier in ear emergence than by using conventional vernalization techniques with normal seeds. Ear-vernalization proved to be an effective method of avoiding the complications caused by growth during vernalization of mature seed.

INTRODUCTION

While being vernalized, wheat seedlings increase in size and new primordia are initiated. These processes, described for convenience in this paper as growth during vernalization, are a function of the temperature and duration of the treatment, and vary with genotype. Independent of the vernalization effects, the amount of growth during the vernalization treatment will also influence time of ear emergence. Thus, if differences in ear emergence are to be attributed solely to the effect of vernalization itself, allowance must be made for growth which occurs during vernalization.

Syme (1968) and McKinney & Sando (1933) grew control plants at a non-vernalizing temperature to the same size as the vernalized seedlings. Vernalized and control plants were planted out at the same time, and they assumed that the differences in time to ear emergence observed could be attributed entirely to the effect of vernalization.

Others have tried to find methods of vernalization in which the growth during the treatment is reduced to a minimum without affecting the effectiveness of the vernalization process itself. Ridell & Gries (1958) and Pirasteh & Welsh (1980) vernalized wheat at 1°C, and hardly any growth occurred during vernalization. However, McKinney & Sando (1933) found that there are optimum temperatures for vernalization, 5°C and 2°C being most effective in accelerating ear emergence in wheat while higher and lower temperatures were less effective. A similar optimum was found by Chujo (1970).

Purvis & Gregory (1952), using winter rye, minimized growth by restricting the amount of water given to the seeds during the vernalization treatment. Vernalization under these conditions was slightly less effective than the vernalization of fully imbibed seeds, and ineffective when the water content of the seed fell below 55% of the dry weight.

Kostučenko & Zarubaĭlo (1937) compared wheat plants grown from seed that had been produced in a cold Northern region of the USSR with plants of the same variety grown from seed that had been produced in a more southerly and warmer climate. The seed from the North appeared to be partly vernalized, and it was postulated that some vernalization of the grain had taken place during its ripening on the parental plants. Gregory & Purvis (1936, 1938) showed that it

is possible to vernalize winter rye grains on the parental plants. The treatment was most effective in the early stages of embryo development. It was not clear from their work how effective vernalization on the parent plant was compared with other methods. Attempts to vernalize developing wheat grains in the ear failed (Gregory & Purvis, 1938), but successful attempts were reported by Pugsley & Warrington (1979).

The first experiment described here was set up to investigate whether it is possible to express growth during vernalization in terms of days of growth at higher, non-vernalizing temperatures, and to use this to make vernalized and unvernalized plants comparable for ear emergence. The second experiment compared the effectiveness of vernalization methods where growth had been reduced to a minimum by using lower temperatures, restricting water supply or vernalizing the developing grains in the ears of the parental plants.

MATERIALS AND METHODS

Experiment 1. Grains of eight wheat varieties of diverse origin (Table 1) were soaked for 24h at room temperature, then sown in hexagonal paper tubes (Paper Pot BA 213, Nippon Beet Sugar Manufacturing Co Ltd), diameter 1.8cm, in John Innes Compost No 2, and placed in a vernalization cabinet at 5°C, and illuminated with fluorescent lamps providing 18W/m^2 for 8h per day. Between 2 and 9 weeks after sowing four plants of each variety were taken out weekly, and height and number of primordia were measured to estimate growth during vernalization. Height was taken as the difference between the crown and the tip of the highest leaf. Number of primordia was counted by dissecting the seedling using the method described by Kirby & Appleyard (1981).

Another lot of grains of the eight varieties was sown in 9cm diameter pots in John Innes Compost No 2 and placed in a controlled environment cabinet at 12°C with a 12h photoperiod consisting of 10h of light from fluorescent and incandescent lamps, providing 118W/m^2, extended with 1h incandescent light at 30W/m^2 before and after the main light period. Pots were re-randomized weekly within the cabinet to minimize positional effects. Number of primordia and height were measured by dissecting and measuring seedlings at regular

intervals of 2 or 3 days between 4 and 25 days after sowing. Four plants of each variety were measured and dissected on each occasion. Regression equations were computed between days after sowing at 12°C, and height and number of primordia. Estimates of growth during vernalization, expressed as days of growth at 12°C, were obtained by substitution of the number of primordia or height recorded at the end of each vernalization treatment into the appropriate regression equation. The variance of these estimates was calculated as described by Snedecor & Cochran (1967):

$$\text{var} = (s_{xy}/b)^2 (1/m + 1/n + \hat{x}^2/\text{sum}(\bar{x}-x)^2)$$

In this formula s_{xy}, b, and n are the standard deviation, the regression coefficient and the number of values used, from the regression analysis. $\text{Sum}(\bar{x}-x)^2$ is the sum of the squared deviations of the independent variable, days after sowing; $\hat{x}$ is the difference between the mean days after sowing and the estimated days after sowing; and m is the number of measurements of number of primordia or height on which the estimate is based.

Experiment 2. Plants of the variety Sage were grown in a glasshouse. Previous experiments had shown that this variety is very responsive to vernalization. The temperature in the glasshouse was kept above 15°C, and daylength was never less than 16h. At flowering the plants were divided into two groups. One group was kept in the glasshouse to produce grain. The other group was moved to a vernalization cabinet 10 days after anthesis had occurred in the second and third ears. After 8 weeks (w) vernalization at 5°C in 8h photoperiod, as described for Expt 1, the plants were moved back to the glasshouse to allow the seed to ripen. Only seed from the second and third ears were used. The two different types of seed will be referred to as normal and ear-vernalized seed.

Both types of seed were then vernalized at different temperatures, for different times and in different moisture conditions in factorial combinations as follows. The two vernalization temperatures were 5°C and 2°C, which were given for 2, 4 or 8 weeks (light conditions as described for the vernalization treatment in Expt 1). Three different moisture conditions were used. All seeds were imbibed for 24h at room temperature, after which they had taken up water equivalent to approximately 55% of the dry weight of the grains. Nine seeds were then sown in compost in hexagonal paper tubes, and kept moist

throughout the vernalization treatment. For the other two treatments, nine seeds were put into 130 ml, 10cm high glass bottles, with a 4cm diameter circle of Whatman No 1 filter paper in the bottom of each. One bottle received extra water equal to 20% of the dry weight of the seeds, and the other bottle received no extra water. The bottles were sealed with 'Parafilm' and a screw top, and put into the vernalization cabinet. During the treatment, the bottles were weighed every two weeks, to check whether any loss of moisture had occurred. This proved not to be the case.

The experiment was scheduled so that all vernalization treatments were completed on the same day. After vernalization, six seedlings from each treatment were planted out, each in a 9cm diameter pot in John Innes No 2 Compost, and grown for 6 weeks in controlled environment cabinets in long days (20h). The pots were arranged in six randomized blocks. Unvernalized plants from ear-vernalized and normal Sage grains and unvernalized plants of Siete Cerros 66, a vernalization insensitive variety from Mexico, were included in each block. The temperature and light conditions were as described for Expt 1, except that the periods of incandescent light were 5h long. To minimize positional effects, the six blocks of pots were re-randomized weekly within and between cabinets. After 6 weeks, the plants were transplanted into 11cm diameter pots and moved to a glasshouse (minimum temperature 15^{o}C, daylength 16h) retaining the same arrangements of blocks. Days to ear emergence, and number of leaves on the main stem were recorded. The experiment was concluded 100 days after the end of the vernalization treatments.

To provide a measure of the growth which had taken place during the vernalization treatment without restrictions on water supply, two plants were dissected at the end of each vernalization period, and number of primordia was counted. The increase in number of primordia in non-vernalized plants from normal seed was measured by dissecting plants at regular intervals during the first weeks in the cabinet after sowing, as described for Expt 1. All dissections were done on two replicates on each occasion.

RESULTS

Experiment 1. All varieties had three visible primordia 4 days after sowing at 12°C, equal to the number found in the dry grain. Also the first root had appeared and the coleoptile had elongated. No new primordia could be distinguished until 7 days after sowing. In the vernalization treatment the first new primordia were found after 2 weeks.

The increase in number of primordia and height at 12°C and 5°C for the varieties Siete Cerros 66, Sage and Highbury are shown in Figs 1 and 2. The pattern of growth at the higher and lower temperature for these selected varieties was representative of all varieties. The correlation coefficients between number of primordia at 12°C and at 5°C, the vernalization temperature, and similarly between height at both temperatures, were positive and significant. For example, the correlation coefficient between number of primordia after 14 days at 12°C and 8w vernalization was 0.86 ($P<0.01$, D.F.6). The corresponding correlation coefficient for height was 0.92 ($P<0.01$, D.F.6). This indicates that varietal differences in growth at the non-vernalizing temperature were similar to those at the vernalizing temperature. Genotypic differences in height were not related to those in number of primordia, as indicated by the correlation coefficients between height and number of primordia, which were low and insignificant, both at 5°C and at 12°C.

The regression equations computed between days after sowing at 12°C and height and number of primordia are listed in Table 1. The data for the first dissection 4 days after sowing at 12°C were not used for the regression equations for number of primordia, because the initiation of new primordia had not begun. Data on number of primordia for those occasions where double ridges were visible, indicating the beginning of the initiation of the ear, were also excluded, since spikelet primordia are initiated at higher rates than leaf primordia (Kirby, 1974). The differences between the highest and the lowest regression coefficients for number of primordia and height were significant at the 10% and the 5% level, respectively.

Table 1 lists for all varieties the estimates of the days of growth at 12°C equivalent to 4w vernalization, and the corresponding variances. The mean estimate over all varieties and the mean variance of the estimates for

Table 1. Varieties used, their country of origin and growth habit (S-spring, W-winter), and the regression equations for the relation between number of primordia (PN) and height in cm, and days after sowing (DAS) at 12°C and 12h photoperiod. The last four columns are estimates and variances of the estimates of the growth, expressed in days at 12°C, 12h photoperiod to which growth during 4w vernalization at 5°C, 8h daylength is equivalent. These estimates have been derived using the regression equations.

Variety	Country of origin	Growth habit	Regression equations		Estimates of growth during 4 w vernalization (days)			
			PN=c+bDAS	Height=e+dDAS	PN	var	Height	var
Apu	Finland	S	2.17+0.40x	-6.29+1.57x	7.1	2.92	6.3	2.04
Bersee	France	W	1.08+0.41x	-7.28+1.43x	7.8	1.30	6.7	3.17
Gamset	Australia	S	1.01+0.43x	-6.59+1.51x	6.9	0.66	6.1	1.66
Highbury	UK	S	1.03+0.42x	-6.67+1.39x	8.2	0.74	6.4	3.03
Kitakomi Komugi	Japan	W	0.70+0.48x	-4.83+1.25x	7.9	0.90	6.2	1.96
Sage	USA	W	0.88+0.42x	-5.61+1.34x	8.0	1.14	6.2	2.16
Siete Cerros 66	Mexico	S	0.74+0.48x	-4.99+1.22x	7.4	0.53	6.5	2.25
Spica	Australia	S	0.94+0.38x	-8.62+1.71x	8.0	0.86	6.6	2.22

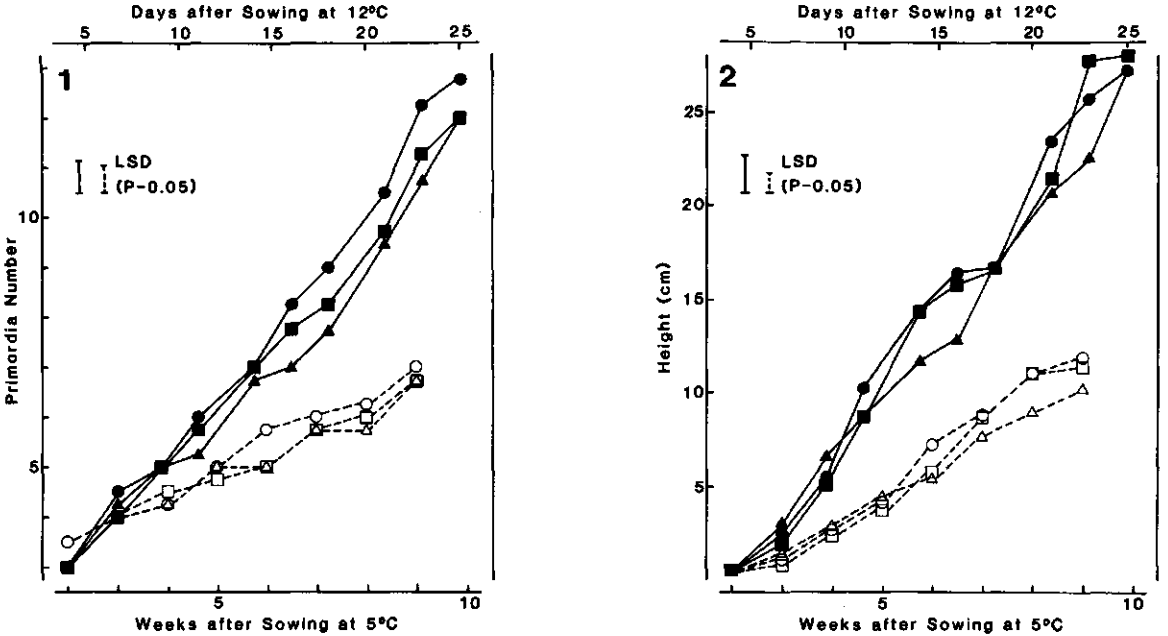

Figure 1. The increase in number of primordia at 12°C (closed symbols) and at 5°C (open symbols) for Siete Cerros 66 (◯), Sage (△) and Highbury (□).

Figure 2. The increase in height at 12°C (closed symbols) and at 5°C (open symbols) for Siete Cerros 66 (◯), Sage (△) and Highbury (□).

Table 2. The mean estimates, using number of primordia (PN) and height, of the growth during 2 to 9w vernalization at 5°C, 8h photoperiod, averaged over all eight varieties used, expressed in days after sowing at 12°C, 12h photoperiod (DAS), and the mean variance of the estimates.

	PN		Height	
Vernalization treatment	DAS 12°C	Mean var	DAS 12°C	Mean var
2 w	5.3	1.44	4.8	2.82
3 w	7.0	1.19	5.3	2.72
4 w	7.7	0.96	6.4	2.50
5 w	9.0	0.92	7.6	2.31
6 w	10.1	0.83	8.9	2.11
7 w	11.4	0.81	10.6	1.84
8 w	12.1	0.72	12.2	1.80
9 w	13.8	0.71	13.1	1.77

vernalization periods from 2 to 9w are listed in Table 2. The mean variance of the estimates using number of primordia is a weighted mean, because for some varieties regression equations were calculated from eight instead of nine values, due to the occurrence of double ridges.

Experiment 2. Vernalization of the grains while developing on the parent plant had a marked effect on grain weight. Mean grain weight of the ear-vernalized grains, 23.0mg, was only about half of that of the normal grains, which was 42.1mg. Despite this, there was no difference in rate of germination or percentage germination of the ear-vernalized and the normal grains.

All seedlings that had been vernalized under conditions of unrestricted water supply had grown into small plants at the end of the vernalization treatment. In the vernalization treatment with limited added water most seeds had germinated, and a small green coleoptile was visible, but no root development had occurred. The seeds which had been imbibed but had not recieved any additional water, showed no visible signs of germination.

Table 3. Days to ear emergence, adjusted for growth during vernalization, and number of leaves of Sage plants for vernalization treatments with no restrictions on water supply. Siete Cerros 66 was only included in the 0w vernalization treatment.

		w vern at 5°C			w vern at 2°C		
	0	2	4	8	2	4	8
Days to ear emergence							
Ear-vernalized grains	68.0	64.5	61.4	63.1	63.5	62.2	62.1
Normal grains	*	*	76.9	64.6	*	79.8	61.8
Siete Cerros 66	59.7	-	-	-	-	-	-
S.E.	1.0	1.3	1.2	1.1	1.2	1.2	1.1
Number of leaves							
Ear-vernalized grains	6.8	6.8	6.0	7.0	6.5	5.8	6.7
Normal grains	*	*	7.7	6.8	*	7.8	7.0
Siete Cerros 66	6.5	-	-	-	-	-	-
S.E.				0.2			

* - plants did not reach ear emergence

Under conditions of unrestricted water supply, seedlings were more advanced in the 5°C treatment than the comparable 2°C treatment. These differences were already detectable after 2 and 4w of vernalization, but were most obvious after 8w. After 8w at 5°C the seedlings were 10cm high and the second leaf had emerged. Those grown at 2°C were 6cm high and only the first leaf was visible.

There were no differences in number of primordia between the normal and the ear-vernalized seedlings at the end of similar vernalization treatments with unrestricted water supply. The mean numbers of primordia found after 8, 4 and 2w vernalization at 5°C, were 6.3, 4.3 and 3.5, and after 8, 4 and 2w vernalization at 2°C, 5.0, 4.0 and 3.8. The regression equation of number of

primordia on days after sowing at 12°C was PN=2.0+0.34days. This relationship was used to estimate growth during vernalization in terms of growth at 12°C, which for treatments at 5°C equalled 12.6, 6.6 and 4.3 days, and for 2°C 8.8, 5.8 and 5.1 days, respectively for the 8, 4 and 2w vernalization treatments. These estimates were added to the observed number of days to ear emergence for the plants vernalized under conditions of unrestricted water supply, to allow for growth during vernalization. Because growth during all vernalization treatments with restrictions on water supply was negligible, no adjustment of days to ear emergence was made for these treatments.

Table 3 shows the effect of the temperature and the duration of the vernalization treatments without restriction on water supply on days to ear emergence and number of leaves for ear-vernalized and normal plants, and lists the results for the unvernalized Siete Cerros 66 plants. Table 4 shows the effects of 8w vernalization at reduced moisture level and the effects of temperature. Standard error values for days to ear emergence for the treatments with no restrictions on water supply were computed after adding the variance of the adjustments, equal to 1.5, 2.1 and 3.3 for the 8, 4 and 2w treatments at 5°C, and 1.4, 2.4 and 2.8 for the 8, 4, 2w treatments at 2 °C, to the residual variance in the analysis of variance of days to ear emergence, where appropriate.

All ear-vernalized plants reached ear emergence, but the latest were those which were not vernalized again after sowing.

DISCUSSION

In Expt 1 there were differences between varieties in the rate at which number of primordia and height increased, both at vernalizing and non-vernalizing temperatures. This is reflected in the differences between the regression equations (Table 1). However, it did not result in differences between the estimates of growth during vernalization, expressed in terms of time at the higher non-vernalizing temperature, because growth at high temperature was strongly correlated with that at low temperature. Since the eight varieties in this experiment were deliberately chosen to represent a wide range in origin

Table 4. Days to ear emergence, adjusted for growth during vernalization, and number of leaves of Sage plants for 8w vernalization treatments differing in water supply. Full - unrestricted water supply. Restricted - 24h imbibition preceding vernalization, and water added equal to 20% of the dry weight of the grains. Zero - only 24h imbibition preceding vernalization, and no extra water added.

	Water supply during vernalization at 5°C			2°C		
	full	restricted	zero	full	restricted	zero
Days to ear emergence						
Ear-vernalized grains	63.1	62.2	60.8	62.1	60.8	63.8
Normal grains	64.6	62.8	*	61.8	*	*
S.E.	1.1	1.0	1.0	1.1	1.0	1.0
Number of leaves						
Ear-vernalized grains	7.0	6.2	6.0	6.7	5.8	6.3
Normal grains	6.8	7.2	*	7.0	*	*
S.E.			0.2			

* - plants did not reach ear emergence

and growth habit, these results suggest that growth during vernalization will be equal to a certain period of growth at non-vernalizing temperatures irrespective of the genotype. Data from Rahman & Wilson (1978, their Tables 2 and 5) also showed a significant correlation between rates of initiation of leaf primordia for eight wheat varieties, but at the higher temperatures of 16°C, 23°C, and 30°C.

From the formula for the variance of the estimates it can be seen that the variance can be reduced by measuring more plants at the end of each vernalization treatment. The variance will be small for the estimates which are close to the mean of the independent variable, days after sowing. This

caused the reduction in the mean variance between 2w and 9w shown in Table 2. Because there were no significant differences between varieties in the estimates, the mean of all varieties was be the most accurate estimate of the adjustment for growth during vernalization. The variance will be equal to 1/8 of the mean variance as listed in Table 2, and this should be added to the residual variance where appropriate for the calculation of the standard errors of the mean, as has been done in Expt 2.

The estimates of growth during vernalization using height had a higher variance than those using number of primordia, suggesting that they were less accurate. Also they were lower than those using number of primordia. This might have been a consequence of the reduced final leaf length at the lower temperature. Friend (1966) showed that the lamina length of the second leaf of wheat plants was reduced at low temperature, though increased at low light intensity. Similar effects were found by Terry (1968) for sugar beet leaves. The combined effect of the low temperature and the low light intensity during the vernalization treatments on final leaf length in this experiment cannot be estimated, but it is possible that it resulted not only in a lower rate of leaf expansion during the vernalization treatment, but also in a reduction of the final leaf length in comparison with the 12°C treatment. This would have the effect of underestimating growth during vernalization in terms of days after sowing at 12°C. The estimates using number of primordia are less likely to be influenced by such complicating effects. However, because the rate of primordia initiation will change significantly when spikelets are initiated, number of primordia can only be used as a measure of growth during vernalization when the regression equation is based upon the initiation rate of leaf primordia, restricting the use of this method to the vegetative phase of the development of the wheat plant.

The experiments with Sage showed that during vernalization treatments at 2°C, less growth had taken place than at 5°C, and also that vernalization treatments at a reduced moisture level restricted growth considerably. However, Table 4 shows that vernalization under conditions of limited water supply was less effective than vernalization with no restriction on water supply. The vernalization treatment in which the additional amount of water added to the imbibed seed was restricted to only 20% of its dry weight was

effective at 5°C but not at 2°C. This suggests an interaction between temperature and water availability on the vernalization process. All vernalization treatments following ear-vernalization resulted in days to ear emergence and numbers of leaves equal to those obtained with normal seed vernalized for 8w with unrestricted water supply. Vernalization in the ear was thus very effective, as was suggested by the results of Gregory & Purvis with rye (1936, 1938) and Pugsley & Warrington with wheat (1979). However, 8w ear-vernalization did not completely fulfill the vernalization requirement of Sage. The plants from ear-vernalized seeds which were not subsequently vernalized, were significantly later than those from all other treatments.

Both the ear-vernalized and the normal plants in the 8w treatments with unrestricted water supply had seven leaves, which is one leaf more than the six leaves found for the plants from ear-vernalized seed in the shorter vernalization treatments and in the treatments where water supply had been restricted, and for the unvernalized Siete Cerros 66 plants. In related work (data not presented), spring wheats grown under long day conditions without vernalization reached ear emergence with only six leaves on the main stem, and winter wheats, which had to be vernalized, always had at least seven or eight leaves. Similar results were obtained by Pugsley (1971), while Mckinney & Sando (1933) and Ridell et al. (1958) also found a minimum number of six leaves in spring wheat. It might be that the short day and low temperature conditions of the vernalization treatment allow only leaf primordia and not spikelet primordia to be initiated. However, Expt 2 showed that by using ear-vernalization, it is possible to obtain for the winter wheat variety Sage plants with only six leaves.

Essentially, ear-vernalization seems to transform vernalization-sensitive into vernalization-insensitive seeds. Thus this technique could be useful in studies where it is required to avoid the complications caused by growth during vernalization, for example when spring and winter wheats are to be compared independent of their different responses to vernalization. However, for ear-vernalization it is necessary to grow plants especially for seed production, which adds considerably to the duration of the experiments. If this is not feasible, vernalization of young seedlings without restrictions on water supply seems to be the most effective method. But in this case the

assessment of vernalization sensitivity will be complicated by the effects of growth during the vernalization treatment on the further development of the plants, and allowance for these effects has to be made. This can be done using the method based on number of primordia as described in this paper.

I thank R.B. Austin for the critical reading of the paper while in preparation.

REFERENCES

CHUJO, H., 1970. Some observations on the reversal of vernalization effect of wheat (Jap). Proc. Crop Sci. Soc. Jap. 39: 451-456.

FRIEND, D.J.C., 1966. The effects of light and temperature on the growth of cereals. In F.L. MILTHORPE & J.D. IVINS (Eds) The growth of cereals and grasses, Butterworths, London: 181-199.

GREGORY, F.G. & O.N. PURVIS, 1936. Vernalization of winter rye during ripening. Nature, 138: 973.

GREGORY, F.G. & O.N. PURVIS, 1938. Studies in the vernalization of cereals. II The vernalization of excised mature embryos, and of developing ears. Ann. Bot. N. S. 2: 237-251.

KIRBY, E.J.M., 1974. Ear development in spring wheat. J. Agric. Sci., Camb. 82: 437-447.

KIRBY, E.J.M. & M. APPLEYARD, 1981. Cereal Development Guide. Cereal Unit, National Agricultural Centre, Stoneleigh, 80 pp.

KOSTJUCENKO, I.A. & T.JA. ZARUBAILO, 1937. Vernalization of seed during ripening and its significance in practise. Herbage Rev. 5: 146-157.

MCKINNEY, H.H. & W.J. SANDO, 1933. Earliness and seasonal growth in wheat as influenced by temperature and photoperiodism. J. Hered. 24: 169-179.

PIRASTEH, B. & J.R. WELSH, 1980. Effect of temperature on the heading date of wheat cultivars under a lengthening photoperiod. Crop Sci. 20: 453-456.

PUGSLEY, A.T., 1971. A genetic analysis of the spring-winter habit of growth in wheat. Austr. J. Agric. Res. 22: 21-31.

PUGSLEY, A.T. & I.J. WARRINGTON, 1979. Developmental patterns in 'standard' and 'semi-dwarf' wheats. Australasian Pl. Gen. Nwsl. 29: 39-40.

PURVIS, O.N. & F.G. GREGORY, 1952. Studies in vernalization. XII The reversibility by high temperature of the vernalized condition in Petkus winter rye. Ann. Bot. N. S. 16: 1-21.

RAHMAN, M.S. & J.H. WILSON, 1978. Determination of spikelet number in wheat. III Effect of varying temperature on ear development. Austr. J. Agric. Res. 29: 459-467.

RIDDELL, J.A. & G.A. GRIES, 1958. Development of spring wheat. III Temperature of maturation and age of seed as factors influencing their response to vernalization. Agron. J. 50: 743-746.

RIDELL, J.A., G.A. GRIES & F. W. STEARNS, 1958. Development of spring wheat. I The effect of photoperiod. Agron. J. 50: 735-738.

SNEDECOR, G.W. & W.G. COCHRAN, 1967. Statistical methods, 6th edition, Iowa State University Press, Ames, Iowa, 159-160.

SYME, J.R., 1968. Ear emergence of Australian, Mexican and European wheat in relation to time of sowing and their response to vernalization and daylength. Austr. J. Exp. Agric. Anim. Husb. 68: 578-581.

TERRY, N., 1968. Developmental physiology of sugar beet. I The influence of light and temperature on growth. J. Exp. Bot. 19: 795-811.

3. A RECIPROCAL F1 MONOSOMIC ANALYSIS OF THE GENETIC CONTROL OF TIME OF EAR EMERGENCE, NUMBER OF LEAVES AND NUMBER OF SPIKELETS IN WHEAT (*TRITICUM AESTIVUM* L.)

J. Hoogendoorn

Plant Breeding Institute, Trumpington, Cambridge CB2 2LQ, U.K.

Submitted to Euphytica

INDEX WORDS

Triticum aestivum L., wheat, reciprocal F_1 monosomics, ear emergence, number of leaves, number of spikelets, photoperiod, vernalization, growth rate.

SUMMARY

A reciprocal F_1 monosomic analysis of chromosomal differences between Spica and Bersee was carried out under controlled environment conditions. Chromosomes associated with differences in days to ear emergence, number of leaves and number of spikelets were identified. The results indicate that chromosome 2B of Spica carries a photoperiod insensitivity allele at the Ppd_2 locus. Both Spica and Bersee appear to have a vernalization insensitivity allele at the Vrn_2 locus on chromosome 5B. On chromosome 3A, 4B, 4D and 6B factors were found with major effects on earliness *per se*, differences in ear emergence and number of spikelets which were independent of photoperiod and vernalization. The possibility that these factors influence growth rate is discussed.

INTRODUCTION

In wheat (*Triticum aestivum* L.) responses to photoperiod and vernalization regulate inflorescence initiation, which in turn affects the number of days to ear emergence, number of leaves and number of spikelets.

Loci controlling sensitivity to photoperiod, *Ppd*$_1$ and *Ppd*$_2$, are located on the long arm of chromosome 2D and the short arm of 2B (Scarth & Law, 1984); the dominant alleles confer insensitivity to photoperiod.

Several loci which are involved in the regulation of sensitivity to vernalization have been identified. The *Vrn*$_1$ locus, which is considered to have the greatest effect on sensitivity to vernalization, is located on the long arm of chromosome 5A. Less potent loci have been associated with the long arm of chromosome 5B (*Vrn*$_2$) and 5D (*Vrn*$_3$), and the short arm of 7B (*Vrn*$_5$). The dominant allele on the *Vrn*$_1$ locus has been shown to confer insensitivity to vernalization (Maystrenko, 1974; Law et al. 1976; Law & Scarth, 1984). Other chromosomes have been found to be involved in regulating sensitivity to photoperiod and vernalization, but their effects are not so well defined (Halloran & Boydell, 1967a; 1967b).

Not all varietal differences in development, however, are dependent on differences in sensitivity to photoperiod and vernalization. In field and in controlled environment experiments, variation has been found among varieties for earliness *per se*, differences in growth and development which can not be explained by differences in responses to photoperiod and vernalization (Hoogendoorn, 1984a, 1984b). The genetics of earliness *per se* has not yet been studied in great detail. Flood & Halloran (1983) showed that the substitution line Chinese Spring (Thatcher 7B) reached ear emergence earlier than Chinese Spring, both under fully vernalized and unvernalized conditions. Scarth & Law (1983) located the *Ppd*$_2$ locus on the short arm of chromosome 2B, but also found a factor on the long arm of the same chromosome which delayed ear development independently of photoperiod and vernalization.

Loci affecting inflorescence initiation have been identified on specific chromosomes using monosomic series or substitution lines. A disadvantage of experiments with monosomic lines is that differences between a line monosomic for the chromosome under study and other monosomic lines from the same series

or the euploid genotype, are unlikely to be due only to allelic variation on the hemizygous chromosome only. Effects of chromosome dosage or differences in the genetic background cannot be ruled out. Intervarietal substitution lines make it possible to study the effect of chromosomes in the disomic condition, but require more effort and time to develop. At least four backcross generations are needed to produce substitution lines which are expected to contain 95% of the recipient genotype. Interactions between the genetic background and the substituted chromosome can only be detected when chromosomes of a range of varieties are substituted into various backgrounds (Law et al, 1981; Law & Scarth, 1984).

McEwan & Kaltsikes (1970) suggested a more potent variation of the monosomic analysis where the effect of a chromosome is assessed by comparing reciprocal F_1 monosomics from crosses between two monosomic series. The method is illustrated in Fig. 1. Differences between reciprocal F_1 monosomic lines are due to allelic variation between the hemizygous chromosomes only, and are not confounded with differences in the genetic background, since both lines are the same for all chromosomes except the hemizygous chromosomes. Subsequently the development of intervarietal substitution lines can be restricted to only those chromosomes which were shown to influence the character under study. McEwan & Kaltsikes (1970) found that all chromosomes included in their field experiments (1B, 3A, 4B, 6B and 7D) were associated with differences in the timing of ear emergence.

Law et al. (1981) used an adaptation of this method to identify chromosomes involved in the regulation of ear emergence. They selfed reciprocal F_1 monosomic plants from a cross between Bersee and Cappelle Desprez, and produced reciprocal F_2 populations, which were mixtures of plants monosomic for the chromosome under study, and disomic plants, homozygous for this chromosome. Segregation for characters for which the F_1 is heterozygous occurs in the F_2, but on average the genetic background of each pair of reciprocal F_2 populations can be considered the same. In a field experiment sown late in spring, they found reciprocal differences in time of ear emergence associated with the chromosomes 1B, 1D, 3B, 4D, 5A, 5B, 7A and 7D.

The many chromosomal effects on ear emergence found by McEwan & Kaltsikes (1970) and Law et al. (1981) are thought to be caused by differences in, and

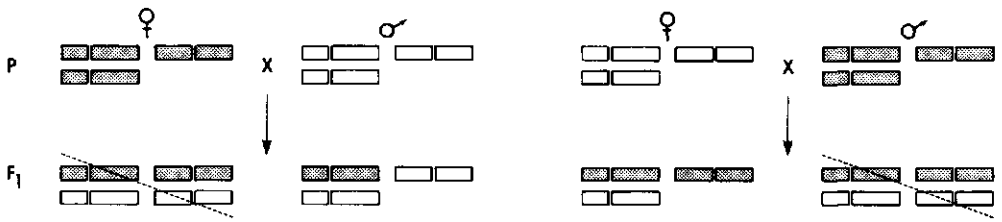

Figure 1. The development of reciprocal F_1 monosomic hybrids by crossing reciprocally homologous monosomics from two different varieties, shown as either dark or white. Only two pair of chromosomes are depicted instead of 21. The difference between the two reciprocal monosomic F_1's is due only to allelic differences between the monosomic chromosomes. Disomic lines are not used.

interactions between vernalization and photoperiod sensitivity and earliness per se. In the studies described here an attempt was made to separate earliness per se from sensitivity to photoperiod and vernalization by testing the genotypes in appropriate controlled environment conditions. Reciprocal F_1 monosomic lines from a cross between two semi-winter wheats, the early photoperiod insensitive variety Spica and the late photoperiod sensitive variety Bersee (Hoogendoorn, 1984a), were used.

MATERIALS AND METHODS

Production and selection of the experimental genotypes. The Bersee monosomic lines were developed at the Plant Breeding Institute in Cambridge by C.N. Law and A.J. Worland with the Cappelle Desprez monosomic series. The Spica monosomic lines were developed by R.A. McIntosh at the Plant Breeding Institute in Sydney with the Chinese Spring monosomic series.

For convenience the following terminology is used. Spica, Bersee and F_1 lines monosomic for chromosome 1A, will be referred to as Spica(1A), Bersee(1A) and F_1(1A), respectively. The F_1 line monosomic for chromosome 1A and carrying the Spica chromosome is referred to as F_1(S-1A). Similarly the corresponding Bersee 1A monosomic F_1 is F_1(B-1A). The euploid is described as F_1(42).

All Bersee monosomic lines had been backcrossed to Bersee more than six times. Bersee carries a translocation between chromosomes 5B and 7B (Law, 1971). The Bersee line monosomic for the two short arms of 5B and 7B was crossed reciprocally with Spica (5B), while the Bersee line monosomic for the two long arms of these chromosomes was crossed with Spica (7B). Most of the Spica monosomic lines had been backcrossed to Spica at least five times, except Spica (6B) which had only been backcrossed twice to Spica, and Spica (2B) which had not been backcrossed at all after the initial cross between Chinese Spring (2B) and Spica. The monosomic line Spica (2D) was not available. All the Spica monosomic lines had been selfed for several generations at Cambridge.

For the experiments described here reciprocal crosses between the homologous monosomic lines and between euploid Spica and Bersee plants were made in 1981 and 1982 in a glasshouse at the Plant Breeding Institute in Cambridge. When insufficient pollen was available from homologuos monosomic plants, euploid plants were used as pollen parent.

Monosomic Spica, Bersee and F_1 plants were selected by counting chromosomes of metaphase cells in squash preparations of seminal roots, taken from germinated grains and pre-treated with bromonaphthalene and stained with Feulgen reagent.

Controlled environment experiments. Because of limited availability of controlled environment facilities and because of the time needed for chromosome counting, a series of six experiments was undertaken to test the parental varieties, the reciprocal euploid F_1 and the reciprocal monosomic F_1 lines. Three vernalization treatments were factorially combined with two photoperiod treatments. Prior to vernalization the monosomic F_1 grains were placed in a incubator at 25°C for 2 to 3 days until seminal roots could be

taken for chromosome counting The vernalization treatments were 8, 2 and 0 weeks (w) at 5°C, in 8h photoperiods provided by fluorescent lamps at 18W/m^2. After vernalization, seedlings were transferred to 12°C and recieved 6 weeks with either a 12h or a 20h photoperiod. The main light period consisted of 10h fluorescent and incandescent light providing 118W/m^2, extended with 1h or 5h incandescent light at 30W/m^2 before and after the main light period. Each treatment was given to six plants of each genotype, and these were arranged in six randomized blocks. Blocks were re-randomized weekly between and within controlled environment cabinets, and plants were re-randomized within blocks, to minimize positional effects. After the photoperiod treatment, the plants were moved to a glasshouse where the temperature was kept above 15°C, and the natural daylength was extended to 16h. Number of days to ear emergence from the start of the photoperiod treatment, number of leaves and number of spikelets on the main stem were counted.

Spica, Bersee and the euploid F_1 were given all three vernalization treatments, but the reciprocal F_1 monosomic lines were only vernalized for 8 and 0w, because of the limited amount of seed available. In one experiment, involving the monosomic F_1 lines for the chromosomes 4A, 5A and 5D, the seed in the 0w vernalization treatments did not germinate. The apparent dormancy was broken by a 2w vernalization treatment in Petri dishes. The dormancy occurred for all monosomic lines in this experiment, but only in the unvernalized treatments. The cause of this dormancy is not known.

The number of reciprocal monosomic F_1 plants was limited for chromosomes 1D, 4D, 5A and 6B, and for these, the number of replicates per treatment was not 6 but only 4, 3, 2 and 3 plants respectively.

Complications in the determination of the response to vernalization expressed in days to ear emergence arose because of the growth occurring during the vernalization treatments. Adjustments were calculated as the number of days at 12°C that unvernalized seedlings required to reach the stage of growth of vernalized seedlings. These adjustments ranged from 13.2 to 16.2 days for the 8w, and from 4.8 to 7.7 days for the 2w vernalization treatment, and were added to days to ear emergence as measured from the start of the photoperiod treatment. The variance for the estimates, ranging from 0.24 to 1.22, and 0.37 to 1.59 days^2, was taken into account in all further calculations.

The method for deriving the adjustments has been fully described elsewhere (Hoogendoorn, 1984c).

Unvernalized plants of the spring wheat variety Siete Cerros 66 were included as repeated controls in all six experiments in order to estimate the effects of environmental variation between experiments. Mean days to ear emergence for Siete Cerros 66 in the six experiments was 60 days with a standard error of 3.3 days, and 75 days with a standard error of 3.3 days, for the 20h and 12h photoperiod treatment respectively. Days to ear emergence for each experiment were multiplied by factors calculated from days to ear emergence of Siete Cerros 66 as described elsewhere (Hoogendoorn, 1984a). Number of leaves and spikelets of Siete Cerros 66 did not vary significantly between the six experiments, and no adjustments for differences between experiments were made for these characters.

Analysis of the results. For each of the monosomic and euploid genotypes the effect of photoperiod and vernalization, and the interaction between photoperiod and vernalization, was calculated using the following model.

	Long days	Short days
Long vernalization	$\underline{m}-\underline{p}-\underline{v}+\underline{pv}$ (1)	$\underline{m}+\underline{p}-\underline{v}-\underline{pv}$ (2)
Short vernalization	$\underline{m}-\underline{p}+\underline{v}-\underline{pv}$ (3)	$\underline{m}+\underline{p}+\underline{v}+\underline{pv}$ (4)

The mean of all four treatments is estimated by $\underline{m}$, $\underline{2p}$ represents the mean difference between the long and the short photoperiod treatments and will be referred to as the photoperiod response. The mean difference between the long and the short vernalization treatment equals $\underline{2v}$, and will be referred to as the vernalization response. The interaction effect between photoperiod and vernalization is estimated by $\underline{pv}$.

Estimates of $\underline{p}$, $\underline{v}$ and $\underline{pv}$ can be calculated with a combination of these four treatments. The standard error of each of the estimates can be calculated from the sum of the within treatment variances (VARW) of all four treatments, each divided by the number of replicates used (n):

$$S.E. = 1/4 \left[\frac{VARW(1)}{n}+\frac{VARW(2)}{n}+\frac{VARW(3)}{n}+\frac{VARW(4)}{n}\right]^{1/2}$$

RESULTS

No significant differences in days to ear emergence, number of leaves or number of spikelets were found between reciprocal $F_1(42)$ plants. This indicates that cytoplasmic differences between Bersee and Spica did not influence infloresence initiation, consequently results for the reciprocal $F_1(42)$ plants will be presented as a single genotype.

The VARW's of the 0w vernalization and the 2w vernalization treatments were consistently greater than those of the 8w vernalization treatments, though not significantly so. Although there was much variation between genotypes, no genotype, monsomic or disomic, was consistently high or low in VARW. The differences in VARW between genotypes are therefore considered to be random and due to the small number of plants per genotype per treatment, and VARW has been estimated for each of the six treatments as a weighted mean of VARW of all genotypes.

The effects of photoperiod and vernalization on Spica, Bersee and $F_1(42)$ are shown in Table 1. Spica reached ear emergence significantly earlier ($P<0.01$) than Bersee with fewer leaves and spikelets in all treatments. $F_1(42)$ was similar to Spica in days to ear emergence, except for the 2w vernalization treatment, after which it reached ear emergence later than Spica, but was still earlier than Bersee both in the 20h and the 12h photoperiod treatment. In all treatments $F_1(42)$ had at least one leaf and three spikelets more than Spica.

Spica and $F_1(42)$ were relatively insensitive to photoperiod while Bersee reached ear emergence much later with more leaves and spikelets in all treatments (Table 1). For Bersee, but not for Spica and $F_1(42)$, the difference in days to ear emergence, number of leaves and number of spikelets between long and short photoperiods was much larger after 8w vernalization than after 2w or 0w vernalization. This significant interaction ($P<0.01$) shows that Bersee was not able to respond to photoperiod unless fully vernalized, and that sensitivity to photoperiod independent of vernalization could be estimated

Table 1. The effect of photoperiod and vernalization on days to ear emergence (DEE), number of leaves (LN) and number of spikelets (SN) of Spica and Bersee and $F_1(42)$. Means and standard errors (D.F. 180) of DEE have been adjusted for growth during the 8w and 2w vernalization treatments. Standard error of the means of $F_1(42)$ equal S.E./$\sqrt{2}$.

Photoperiod and vernalization treatment	Character	Spica	Bersee	$F_1(42)$	S.E.
20h - 8w	DEE	62.9	74.6	64.7	1.24
	LN	6.3	7.7	7.0	0.18
	SN	13.4	20.2	17.4	0.32
- 2w	DEE	64.2	85.7	73.5	1.14
	LN	7.0	9.2	8.0	0.22
	SN	16.5	22.7	19.2	0.42
- 0w	DEE	75.4	87.2	77.4	1.09
	LN	8.0	9.5	8.6	0.22
	SN	18.5	22.7	21.0	0.50
12h - 8w	DEE	70.5	102.8	76.0	1.13
	LN	7.0	10.0	8.0	0.15
	SN	16.6	24.2	21.7	0.33
- 2w	DEE	75.4	100.0	83.0	1.30
	LN	8.0	10.7	9.2	0.16
	SN	19.7	26.7	23.3	0.42
- 0w	DEE	82.0	97.1	83.6	1.14
	LN	9.0	11.2	9.4	0.19
	SN	20.7	27.2	24.3	0.49

only with fully vernalized Bersee plants. In addition, sensitivity to vernalization can be estimated only with plants grown under long day conditions.

All monosomics with Bersee (3D) as one of the parents died of hybrid necrosis. Spica is a carrier of the Ne-1 hybrid necrosis gene (Zeven, 1973). Bersee does not carry a hybrid necrosis gene, but Cappelle Desprez, which was used to develop the Bersee monosomic lines, carries the Ne-2 gene (Hermsen, 1963) which in combination with Ne-1 results in severe necrosis. Bersee (3D) must therefore have retained the Ne-2 gene from Cappelle Desprez in the background. Only F_1 plants from Spica(3D) x Bersee(42) survived.

Photoperiod and vernalization response. Response to photoperiod (2p) and vernalization (2v) are shown in Figs 2 and 3. Since the vernalization treatments used for F_1(4A), F_1(5A) and F_1(5D) were 8w and 2w, instead of the 8 and 0w as used for the other F_1 monosomic lines, the results for these are shown separately from the other F_1 monosomics, with the corresponding values for F_1(42), Spica and Bersee.

Only the results for days to ear emergence and number of spikelets are presented. The results for number of leaves showed a similar pattern as those for number of spikelets and therefore are not shown.

Because the interaction between the effect of photoperiod and vernalization was highly significant for Bersee and F_1(B-2B), photoperiod response for these two genotypes has been estimated using the 8w vernalization treatment only and vernalization response has been estimated using only the 20h photoperiod treatment.

Fig. 2 shows that only Bersee and F_1(B-2B) were significantly more sensitive to photoperiod than F_1(42). Fig. 3 shows that several chromosomes were associated with differences in vernalization response. For days to ear emergence F_1(B-2B) and F_1(S-7B) responded more strongly to vernalization than their reciprocal, as did F_1(S-3A). However, neither 3A monosomic line was significantly different from F_1(42). F_1(B-5BS,7BS) displayed a greater increase in number of spikelets when not vernalized than the reciprocal line F_1(S-5B), and F_1(S-1B) was significantly less sensitive to not being vernalized than the reciprocal line and F_1(42).

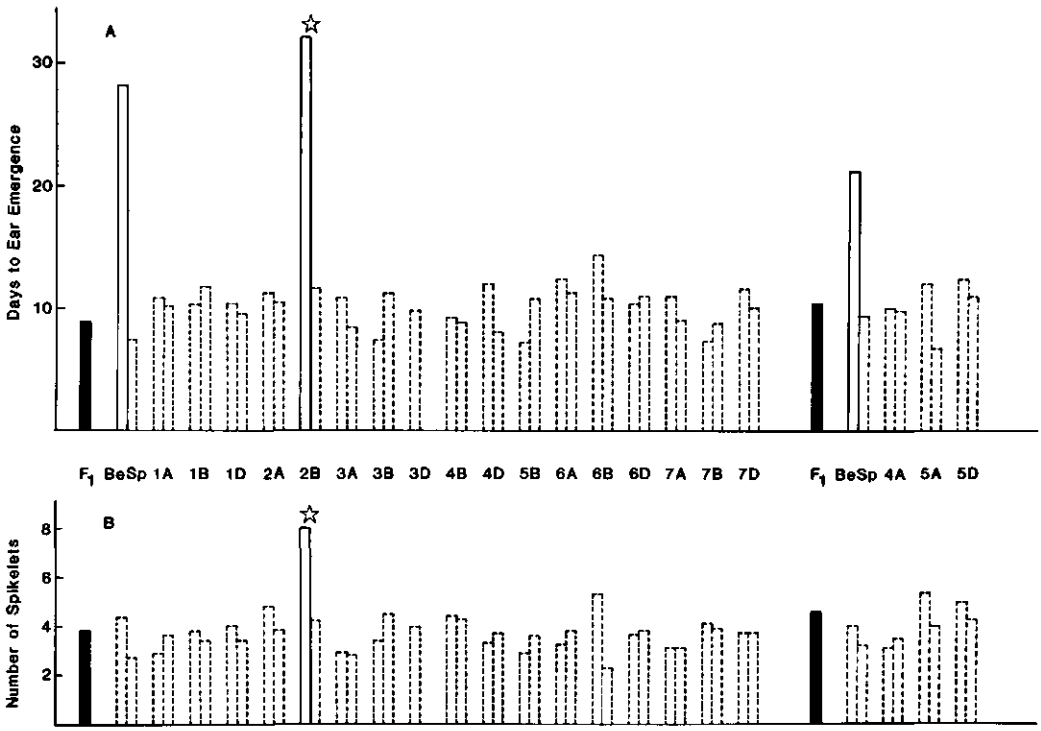

Figure 2. Response to photoperiod of $F_1(42)$ [F_1], Bersee [Be], Spica [Sp] and reciprocal F_1 monosomic lines, expressed in days to ear emergence (A) and number of spikelets (B). The F_1 monosomic line with the Bersee chromosome is shown on the left. For chromosome 4A, 5A and 5D different treatments were used to calculate photoperiod sensitivity (see text), and these are shown together with the corresponding values for $F_1(42)$, Bersee and Spica. Genotypes significantly different ($P<0.01$) from $F_1(42)$ are shown by bars with continuous lines, significant reciprocal differences ($P<0.01$) are marked with ☆.

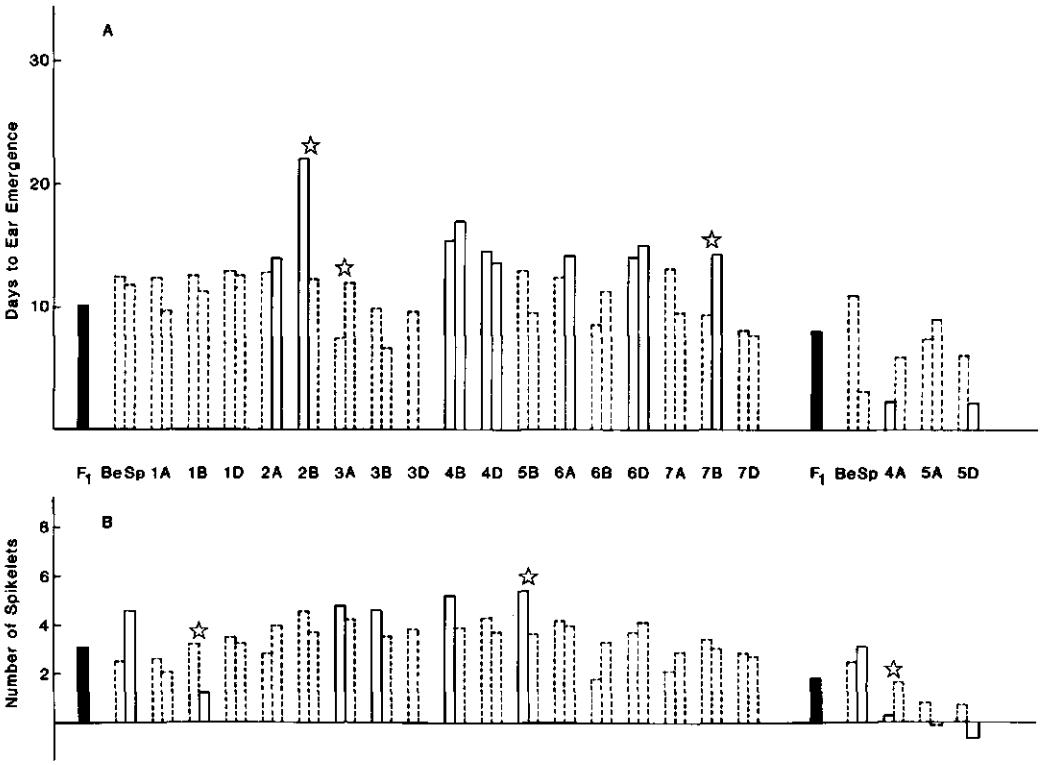

Figure 3. Response to vernalization of $F_1(42)$ [F_1], Bersee [Be], Spica [Sp] and reciprocal F_1 monosomic lines, expressed in days to ear emergence (A) and number of spikelets (B). The F_1 monosomic line with the Bersee chromosome is shown on the left. For chromosome 4A, 5A and 5D different treatments were used to calculate vernalization sensitivity (see text), and these are shown together with the corresponding values for $F_1(42)$, Bersee and Spica. Genotypes significantly different ($P<0.01$) from $F_1(42)$ are shown by bars with continuous lines, significant reciprocal differences ($P<0.01$) are marked with ☆.

Earliness per se. To identify differences in earliness per se it is necessary to compare genotypes under conditions where differences in development are least influenced by the effects of photoperiod and vernalization. There were significant differences in response to vernalization among the genotypes (Fig.3), and therefore only the data from the 8w vernalization treatments were used to estimate earliness per se. Except for Bersee and F_1(B-2B) there were no significant differences in response to photoperiod among the genotypes, and earliness per se was calculated as days to ear emergence, number of leaves and number of spikelets averaged over the 20h and the 12h photoperiod treatment. Earliness per se for F_1(B-2B) and Bersee were calculated using the 8w vernalization 20h photoperiod treatment only. The F_1 monosomic lines on average reached ear emergence 4.2 days later than F_1(42) ($P<0.01$). Since the mean of the F_1 monosomics for number of leaves and number of spikelets was not significantly different from that of F_1(42), this delay in ear emergence was considered not to be due to an effect of the monosomic condition on inflorescence initiation, but more likely to be caused by the fact that seminal roots had been taken from the monosomic plants to count chromosomes (see Materials and Methods). Therefore, the estimates of earliness per se expressed in days to ear emergence for the F_1 monosomic lines, but not for Spica and Bersee, have all been reduced by 4.2 days. Earliness per se is presented as the difference between F_1(42) and the F_1 monosomic lines, Bersee and Spica.

Earliness per se, expressed in days to ear emergence and number of spikelets, is shown in Fig. 4. The results for number of leaves followed the same pattern as those for number of spikelets and therefore are not presented. Significant differences in earliness per se between reciprocals expressed in days to ear emergence were found for chromosome 3A, 4B, 4D, 6B, and 7B. In all cases, except 4D, the F_1 with the Bersee chromosome was the late line. Significant differences in numbers of spikelets were found for chromosome 5D and 6B, and in both cases the F_1 with the Bersee chromosome had more spikelets.

Fig. 5 shows how earliness per se expressed in days to ear emergence and numbers of spikelets were related. F_1(4A) and F_1(S-4B) reached ear emergence earlier with fewer spikelets than F_1(42), while F_1(B-6B) reached ear emergence later with more spikelets ($P<0.01$). F_1(B-3A) and F_1(S-4D) were different

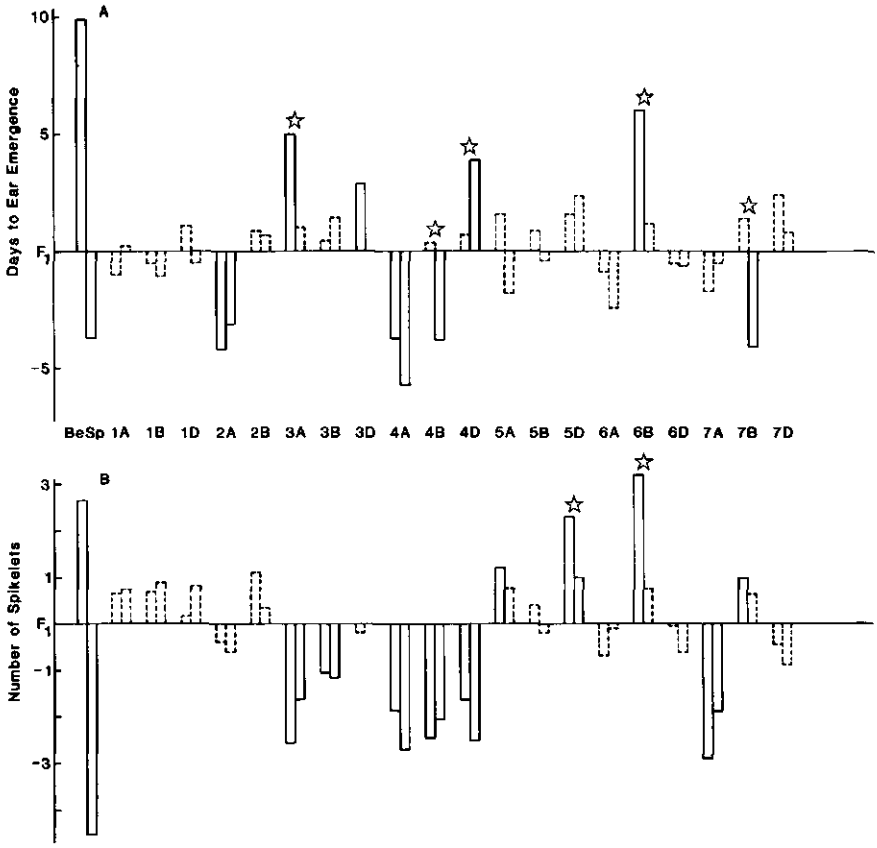

Figure 4. Earliness per se expressed in days to ear emergence (A) and (B) number of spikelets, and presented as the difference with F_1(42), for Bersee [Be], Spica [Sp] and reciprocal F_1 monosomic lines. The F_1 monosomic line with the Bersee chromosome is shown on the left. Genotypes significantly different from F_1(42) are shown by bars with continuous lines, significant differences between reciprocal F_1 monosomics are marked with ☆.

($P<0.10$) from the other F_1 monosomic lines (outlier test, Weisberg, 1980). These lines combined later ear emergence with a reduction in number of spikelets. The correlation between earliness *per se* expressed in days to ear emergence and earliness *per se* expressed in number of spikelets, excluding Spica, Bersee, F_1(B-3A) and F_1(S-4D), was significant ($r=0.50$, 35 D.F. $P<0.01$).

DISCUSSION

Under the controlled environment conditions used for the experiments reported here, it was possible to explain the effects of Bersee and Spica chromosomes on ear emergence as being due to either differences in photoperiod or vernalization response, or differences in earliness *per se*.

Significant differences between reciprocal F_1 monosomic lines are considered to be caused by allelic differences between Spica and Bersee only, while differences between F_1 monosomic lines and F_1(42) can be caused by allelic differences and chromosome dosage effects.

Only F_1(B-2B) was similar to Bersee in being very sensitive to photoperiod. All other F_1 monosomic lines and F_1(42) were insensitive to photoperiod, resembling Spica. Scarth & Law (1984) showed that the *Ppd*$_2$ photoperiod insensitivity locus is associated with the short arm of chromosome 2D, and it is likely that Spica carries an insensitivity allele on this locus, as was also suggested by Scarth (1982). There were no significant differences between Spica, Bersee, F_1(42) and F_1(S-2B) in response to photoperiod (Fig. 2), indicating that the effect of this insensitivity allele on chromosome 2B is dominant, and not influenced by dosage effects. Unfortunately it was not possible to test reciprocal F_1 monosomics for chromosome 2D, known to be associated with the very potent *Ppd*$_1$ locus (Scarth & Law, 1984), as the monosomic line Spica (2D) was not available.

There were no large differences in sensitivity to vernalization between Spica, Bersee and F_1(42). However, Fig. 3 suggests that there were reciprocal differences between Spica and Bersee in sensitivity to vernalization. Since Bersee carries a photoperiod sensitivity allele on chromosome 2B it cannot be established with confidence that the increased vernalization sensitivity

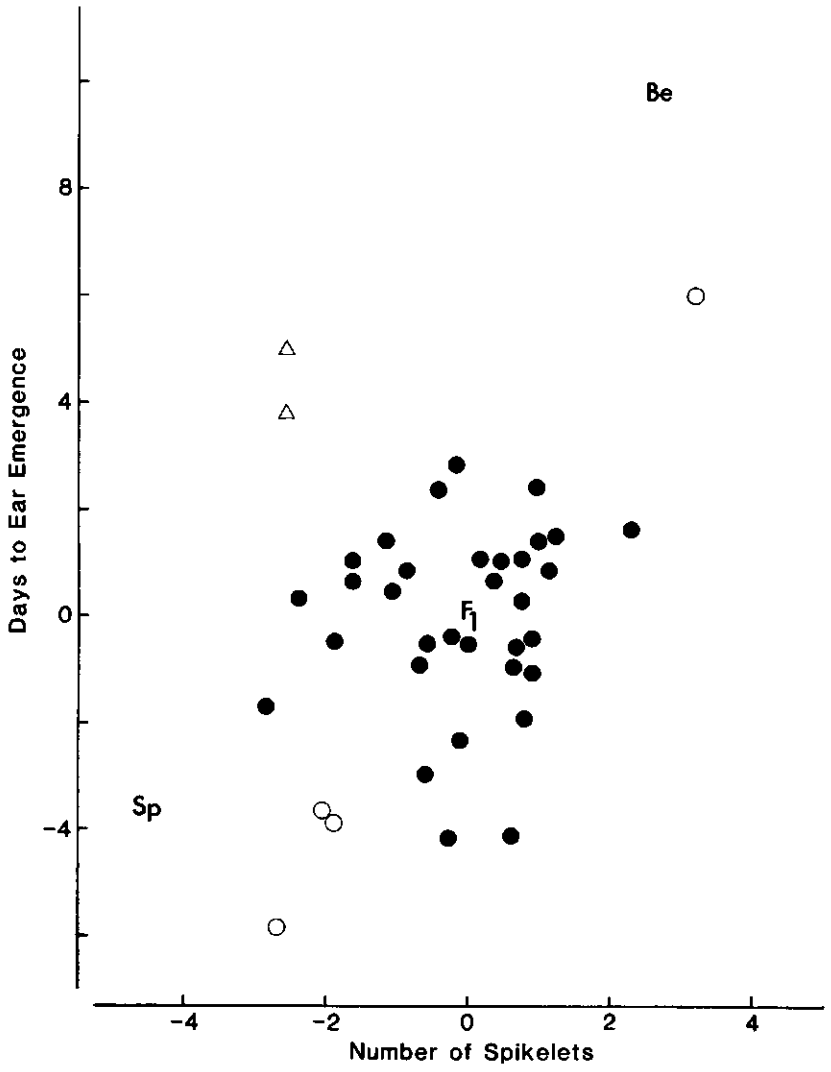

Figure 5. Relation between earliness per se expressed in days to ear emergence and number of spikelets, presented as the difference with F_1(42). ◯ - genotypes which are either positively or negatively different from F_1(42) in earliness per se, both for days to ear emergence and number of spikelets. △ - genotypes which are significantly different from F_1(42), but combine late ear emergence with a reduction in number of spikelets. Be - Bersee, Sp - Spica.

associated with this chromosome is independent of the interaction between the effects of photoperiod and vernalization, even although only the long day treatments have been used to estimate vernalization response.

The translocation in Bersee between chromosome 5B and 7B influences the comparisons between the F_1 monosomics for 5B and 7B. F_1(B-7BL,5BL), F_1(S-5B) and F_1(42) all carry both S-5BL and B-5BL. F_1(S-7B) lacks B-5BL and F_1(B-5BS,7BS) lacks S-5BL (Table 2). In the analysis of days to ear emergence, F_1(B-7BL,5BL) and F_1(S-5B) are similar to F_1(42) in vernalization sensitivity, but less sensitive than F_1(S-7B) and F_1(B-5BS,7BS). This suggests that both Bersee and Spica carry a vernalization insensitivity allele on 5BL, which has more effect in the disomic than in the monosomic condition. Since the $\underline{Vrn_2}$ locus is located on 5BL, it seems likely that both varieties carry an insensitivity allele on this locus. Similarly in the analysis of number of spikelets, F_1(B-5BS,7BS) was found to be significantly more sensitive to vernalization than F_1(S-5B), F_1(B-5BL,7BL) and F_1(42) (Table 2). However, no significant increase in vernalization sensitivity in comparison with F_1(S-5B), F_1(B-5BL,7BL) and F_1(42) was found for F_1(S-7B).

Number of spikelets of F_1(S-1B) and F_1(B-4A) was less sensitive to vernalization than that of their reciprocal F_1 lines and F_1(42). This suggests that a recessive allele on a locus for vernalization sensitivity might be associated with these chromosomes. Analogous reciprocal differences in vernalization sensitivity for days to ear emergence, however, were not found. It can be concluded therefore, that there were only small chromosomal differences between Spica and Bersee in the control of response to vernalization.

Law et al. (1978) found that as many as five chromosomes, 1D, 3D, 4D, 5A and 7A, were involved in the control of sensitivity to vernalization of Bersee. Fig. 3 shows that the F_1 monosomics lines for chromosome 4D were significantly more sensitive to vernalization than F_1(42), but no effects were found associated with 1D, 3D, 5A and 7A.

Scarth & Law (1984) suggested that a third photoperiod insensitivity locus might be located on chromosome 2A ($\underline{Ppd_3}$), homeologous to $\underline{Ppd_1}$ and $\underline{Ppd_2}$. In the present study no photoperiod insensitivity factor was found on chromosome 2A, but both F_1(2A) monosomic lines reached ear emergence earlier than F_1(42)

Table 2. Sensitivity to vernalization and chromosome arms of 5B and 7B present in F_1(42), F_1(5B) and F_1(7B). DEE - Days to ear emergence, SN- number of spikelets. ~ - significantly different from F_1(42) at P<0.10, ** - significantly different from F_1(42) at P<0.01.

	Chromosome arms present or absent				Vernalization sensitivity	
	Bersee		Spica			
Genotype	5BL,7BL	5BS,7BS	5BL,5BS	7BL,7BS	DEE	SN
F_1(42)	+	+	+	+	10.2	3.08
F_1(S-5B)	+	-	+	+	9.6	3.60
F_1(S-7B)	-	+	+	+	14.2**	3.00
F_1(B-5BS,7BS)	+	+	-	+	13.0~	5.42**
F_1(B-7BL,5BL)	+	+	+	-	9.4	3.40

after 8w vernalization (Fig. 4), which suggests that both Spica and Bersee might carry a lateness factor on this chromosome. Similar factors might be present on chromosome 4A.

Scarth & Law (1983) showed that a growth rate factor was located on chromosome 2B. No effect of this chromosome on earliness per se was found in this study. The significant reciprocal difference in earliness per se found for chromosome 7B supports the possibility of a factor on this chromosome as suggested by Flood & Halloran (1983), although because of the translocation between 5B and 7B in Bersee the possibility cannot be ruled out that the long arm of chromosome 5B might be involved.

The differences between Spica and Bersee in earliness per se were 13.5 days and 7.2 spikelets (Fig. 4). The total of all significant differences in earliness per se between reciprocal F_1 monosomic lines was 15.3 days and 3.8 spikelets. The agreement between the actual and the calculated differences between Spica and Bersee indicate that the differences between the chromosomes in the monosomic condition were similar to those in the euploid and that the

effects were largely additive.

Lateness combined with a reduction in number of spikelets, as shown by F_1(B-3A) and F_1(S-4D) is in contrast with the generally positive relation found between these two characters (Fig. 5). Both F_1 monosomic lines were similar to F_1(42) in number of leaves. The lateness caused by earliness *per se* factors on these chromosomes could represent a delay in normal ear development, resulting in later ear emergence but fewer spikelets.

The correlation between earliness *per se* expressed in days to ear emergence and in number of spikelets (Fig. 5) reflects the difference between Spica and Bersee after the 8w vernalization treatment followed by long days. In particular, lack of the Spica 6B chromosome seemed to convey lateness, combined with an increase in number of leaves and spikelets, while absence of either the Bersee or the Spica 4A chromosome or the Bersee 4B chromosome resulted in earliness, in combination with a reduction of number of leaves and spikelets. These factors might act by regulating growth rate. Although Bersee reached ear emergence later than Spica, seedlings of Bersee have been found to initiate primordia at a higher rate than Spica seedlings, both during the vernalization treatment at 5°C, and at a higher temperature, 12°C (Hoogendoorn, 1984c). If the processes by which photoperiod and vernalization influence the initiation of the reproductive phase occur independently of vegetative growth and the initiation of new primordia (Calder, 1966), then Bersee and F_1(B-6B) might enter the reproductive phase with more primordia than Spica, F_1(4A) and F_1(S-4B). Consequently, the latter genotypes would have fewer leaves and fewer spikelets, and are likely to reach ear emergence earlier, even although their growth rates are slow.

Earliness *per se* factors could be useful for adjusting time of ear emergence in plant breeding programmes. Because these factors are independent of photoperiod and vernalization sensitivity, they could be exploited to manipulate time of ear emergence in the production of varieties which require sensitivity to photoperiod or vernalization to avoid ear initiation under unfavourable conditions, such as North European varieties, and in genotypes which require insensitivity to photoperiod and vernalization, such as varieties grown in sub-tropical regions under short day conditions.

Further study is required to establish the way in which the earliness per se factors identified in monosomic lines influence time of ear emergence and number of leaves and spikelets in the euploid condition. In particular, effects on rate of primordia initiation and its interaction with time of ear initiation in young seedlings need to be studied, experiments which will require controlled environments. The reciprocal F_2 populations derived from selfed F_1 monosomic plants used in this study, are not very suitable for such experiments, because of segregation in the genetic background for all growth and development factors for which Spica and Bersee are different. Studies with substitution lines, especially with chromosome 3A, 4B, 4D and 6B of Spica and Bersee can be expected to give more information on the genetics and physiology of earliness per se.

I am grateful to C.N. Law and A.J. Worland for providing the Bersee and Spica monosomic lines and for their advice during the course of the experiments, and to R.B. Austin, prof. J. Sneep and J.W. Snape for the critical reading of the manuscript.

REFERENCES

CALDER, D.M., 1966. Inflorescence induction and initiation in the Graminae. In F.L. MILTHORPE & J.D. IVINS (Eds.), Butterworths, London: 59-73.

FLOOD, R.G. & G.M. HALLORAN, 1983. The influence of certain chromosomes of the hexaploid wheat cultivar Thatcher on time to ear emergence in Chinese Spring. Euphytica 32: 121-124.

HALLORAN, G.M. & C.W. BOYDELL, 1967a. Wheat chromosomes with genes for photoperiodic response. Canad. J. Genet. Cytol. 9: 394-398.

HALLORAN, G.M. & C.W. BOYDELL, 1967b. Wheat chromosomes with genes for vernalization response. Canad. J. Genet. Cytol. 9: 632-639.

HERMSEN, J.G.Th., 1963. Sources and distribution of complementary genes for hybrid necrosis in wheat. Euphytica 12: 147-160.

HOOGENDOORN, J., 1984a. The physiology of variation in the time of ear emergence among wheat varieties from different regions of the world. Euphytica (In the press).

HOOGENDOORN, J., 1984b. The basis of variation in date of ear emergence under field conditions among the progeny of a cross between two winter wheat varieties. J. Agric. Sci., Camb. (In the press).

HOOGENDOORN, J., 1984c. A comparison of different vernalization techniques in wheat (Triticum aestivum L.). J. Plant Phys. 116: 11-20.

LAW, C.N., 1971. Co-operative projects. EWAC Newsl. 3: 45-46.
LAW, C.N. & R. SCARTH, 1984. Genetics and its potential for understanding the action of light in flowering. In D. VINCE-PRUE (Ed.), Light and the flowering process, Academic Press, London (In the press).
LAW, C.N., J.W. SNAPE & A.J. WORLAND, 1981. Intra-specific chromosome manipulation. Phil. Trans. R. Soc. London B. 292: 509-518.
LAW, C.N., A.J. WORLAND & B. GIORGI, 1976. The genetic control of ear emergence time by chromosomes 5A and 5D of wheat. Heredity 36: 49-58.
LAW, C.N., A.J. WORLAND & C.F. YOUNG, 1978. Developmental studies in wheat using whole chromosome substitution lines. Proc. XIV Congress of Genetics, Moscow, 1978.
MAYSTRENKO, O.I., 1974. Identification of chromosomes carrying genes $\underline{Vrn_1}$ and $\underline{Vrn_3}$ inhibiting winter habit in wheat. Europ. Wheat Aneupl. Newsl. 4: 49-52.
MCEWAN, J.M. & P.J. KALTSIKES, 1970. Early generation testing as a means of predicting the value of specific chromosome substitutions into common wheat. Canad. J. Genet. Cytol. 12: 711-723.
SCARTH, R., 1982. The genetics of the daylength response in wheat and its effect on development. PhD Thesis, Cambridge.
SCARTH, R. & C.N. LAW, 1983. The location of the photoperiod gene, $\underline{Ppd_2}$ and an additional factor for ear emergence time on chromosome 2B of wheat. Heredity 51: 607-619.
SCARTH, R. & C.N. LAW, 1984. The control of the daylength response in wheat by the group 2 chromosomes. J. Plant Breed. 92: 140-150.
WEISBERG, S., 1980. Applied linear regression. Wiley, New York: 113-117.
ZEVEN, A.C., 1973. Sixth supplementary list of wheat varieties classified according to their genotype for hybrid necrosis and geographical distribution of $\underline{Ne}$-genes. Euphytica 22: 618-632.

4. THE PHYSIOLOGY OF VARIATION IN THE TIME OF EAR EMERGENCE AMONG WHEAT VARIETIES FROM DIFFERENT REGIONS OF THE WORLD

J. Hoogendoorn

Plant Breeding Institute, Trumpington, Cambridge CB2 2LQ, U.K.

Submitted to Euphytica

INDEX WORDS

Triticum aestivum L., wheat, ear emergence, number of leaves, number of spikelets, photoperiod, vernalization, geographical distribution.

SUMMARY

Differences in response to photoperiod and vernalization and genetic variability independent of photoperiod and vernalization (earliness *per se*), affecting time of ear emergence of wheat, were identified in controlled environment experiments with 33 varieties of diverse geographical origin. The results were compared with an analysis of time of ear emergence of 10409 *Triticum aestivum* accessions from the USDA Small Grain Collection grown from autumn sowings in Pendleton, Oregon, and spring sowings in Fargo, North Dakota. The effect of differences in photoperiod and vernalization sensitivity on time of ear emergence was similar to the effect of earliness *per se*, both under controlled environment conditions and in the field. Most of the accessions from low latitude regions reached ear emergence early due to their insensitivity to photoperiod and vernalization and having 'positive' earliness *per se* factors. Lateness was common among accessions from Northern Europe, Afghanistan and Turkey, which was due to sensitivity to photoperiod and vernalization, and to having 'negative' earliness *per se* factors. The physiological basis of earliness *per se* is discussed.

INTRODUCTION

Photoperiod and vernalization are important factors in the control of the timing of ear emergence in wheat. Large differences between varieties in sensitivity to these factors have been found. Hunt (1979), in a study of 26 winter wheat varieties of diverse geographical origin, showed that sensitivity to photoperiod and vernalization was linked to the pattern of daylength and temperature of the wheat growing season in the regions of origin of the varieties. Wall & Cartwright (1974) and Ford et al. (1981) also found associations between geographical origin and differences in sensitivity to vernalization and photoperiod. Halse & Weir (1970) found large differences between varieties in sensitivity to vernalization and photoperiod, in a study restricted to wheat varieties from Australia. Qualset & Puri (1973) showed that there were large differences in response to photoperiod and vernalization within a collection of 3300 durum wheats. Varieties sensitive to photoperiod and vernalization came from Pakistan, Ethiopia and Israel; photoperiod sensitivity was found in genotypes from Poland, the USSR and the USA, and vernalization sensitive varieties came from the Balkans and Afghanistan.

Sensitivity to photoperiod and vernalization has been shown to be controlled by major genes. Two loci have been identified with major effects on the response to photoperiod, $\underline{Ppd_1}$ and $\underline{Ppd_2}$. Sensitivity to vernalization is thought to be controlled by the presence or absence of insensitivity alleles on the major $\underline{Vrn_1}$ locus, determining the difference between spring and winter wheats, and insensitivity alleles with much smaller effects on at least four other Vrn loci, which have been found in winter wheats with a weak response to vernalization (Law & Scarth, 1984). There is evidence that different insensitivity alleles occur in varieties from different wheat growing areas. Most of the photoperiod insensitive wheat varieties from the Mediterranean and those bred by CIMMYT in Mexico carry an insensitivity allele at the $\underline{Ppd_2}$ locus, which was probably introduced from India (Law & Scarth, 1984). Gotoh (1979) found that the vernalization insensitivity allele $\underline{Vrn_3}$ is present in Japanese varieties while $\underline{Vrn_2}$ prevails in Mediterranean winter wheat varieties (C.N. Law, personal communication).

The genetic differences in sensitivity to photoperiod and vernalization are thought to be the primary factors controlling differences in ear emergence between genotypes. However, differences which cannot be explained by photoperiod and vernalization sensitivity have also been found. Yasuda & Shimoyama (1965) reported differences in 'earliness in narrow sense' between varieties, but did not consider these differences to be as important as differences in sensitivity to photoperiod and vernalization. Hunt (1979) and Ford et al. (1981) also described varietal differences in timing of ear emergence which were independent of sensitivity of photoperiod and vernalization. These genetic differences, hereafter referred to as earliness per se, could be used in breeding programmes to manipulate the life cycle of the crop, irrespective of the prevailing daylength and temperature conditions. As yet, however, little is known about earliness per se, and how its effects compare with those of sensitivity to photoperiod and vernalization.

The experiments described in this paper were done to assess the contributions made by vernalization and photoperiod sensitivity and differences in earliness per se to the regulation of time of ear emergence under controlled environment conditions. In addition, an analysis of relevant data for a much larger number of genotypes available from the USDA Small Grain Collection was carried out to determine in which parts of the world early and late genotypes are likely to be found.

MATERIALS AND METHODS

Controlled environment experiments. From the wheat collection at the Plant Breeding Institute 33 varieties were chosen, representative of the major wheat growing areas in the world (Table 1). Both spring and winter types were included. The parentage of the varieties chosen was checked as far as was possible by reference to Zeven & Zeven-Hissink (1975), to ensure that they were bred in the region they were thought to represent, and that they were not closely related to each other.

The responses of the varieties to vernalization and photoperiod were determined using all combinations of three vernalization and two photoperiod

treatments. All varieties were vernalized for 8, 2 and 0 weeks (w). Seeds were soaked for 24h at room temperature, then sown in hexagonal paper tubes (Paper Pot BA 213, Nippon Beet Sugar Manufacturing Co Ltd), diameter 1.8cm, in John Innes Compost No 2, and placed in a vernalization cabinet at 5°C, illuminated with fluorescent lamps providing 18W/m^2 for 8h per day. After the vernalization treatments, which were scheduled in such a way that all treatments ended on the same day, seedlings were transplanted into 9cm diameter pots, and placed in controlled environment cabinets for six weeks of photoperiod treatment. Temperature in the cabinets was 12°C, and the relative humidity 85%. The main light period consisted of 10h fluorescent and incandescent light, at 118W/m^2, and was extended with 1h and 5h incandescent light, at 30W/m^2, before and after the main light period, providing photoperiods of 12h and 20h. Each treatment was given to six plants of each variety, which were arranged in six randomized blocks. To minimize positional effects blocks were re-randomized weekly between and within the cabinets, and plants were re-randomized within blocks. After the photoperiod treatment, the plants were transplanted into 11cm diameter pots, and moved to a glasshouse. The temperature in the glasshouse was kept above 15°C, and natural daylength was extended to 16h.

Space in the controlled environments was limited and the 33 varieties were therefore grown in six identical experiments, which were carried out from 1981 to 1983, each with five or six varieties and, as a repeated standard variety, the Mexican spring wheat Siete Cerros 66. The experiments were ended 100 days after the start of the photoperiod treatment, and number of days to ear emergence from the start of the photoperiod treatment and number of leaves and spikelets on the main stem were counted. Complications in the determination of the response to vernalization arose as a consequence of growth during the vernalization treatments, and adjustments to days to ear emergence were determined as follows, using additional plants included in the experiments for this purpose (Hoogendoorn, 1984a). At the end of each vernalization treatment two seedlings of each variety were dissected and the number of primordia on the main shoot was counted. The rate at which number of primordia increased in non-vernalized seedlings during the first three weeks of the photoperiod treatment was determined by dissecting twice a week three seedlings of each

variety. Growth during vernalization was expressed in terms of days of growth at 12°C, and these adjustments were added to the observed days to ear emergence of the vernalized plants.

Analysis of data from the USDA Small Grain Collection. A data file with information on 10409 accessions of Triticum aestivum was kindly provided by W.M. Porter of the Beltsville Agricultural Research Center in Maryland, USA. The file contained data for the following descriptors: species code, name or designation, source, origin, growth habit, and days to ear emergence. Growth habit of the accessions was described as either winter, spring or facultative. For those accessions for which the region of origin was not known, the region from where the seed had been acquired (source), was taken as the region of origin. Some changes were made to the origin descriptor. Origins for which only few accessions were available and which were thought to be very similar in climate were combined, e.g. Belgium and the Netherlands, and Morocco, Algeria and Tunisia. For the USA, 38 states were coded individually as regions of origin, but for the present analysis these were combined into six origins, North West, North Centre, North East, South West, South Centre and South East.
For each accession number of days to ear emergence from 1 January had been recorded either in one of six spring sowings in Fargo, North Dakota (47°N, 97°W) carried out in 1970-4 and 1978, or in one of two autumn sowings in Pendleton, Oregon (46°N, 119°W) carried out in 1952 and 1953. Both in the spring and in the autumn sowings on average 95% of all accessions reached ear emergence within a period of 3.5 weeks. The mean date of ear emergence from the autumn sowings was 1 June, and from the spring sowings 9 July.
Means and variances for days to ear emergence were determined for each of the six spring sowings and the two autumn sowings. There were no significant differences between sowings in variance of days to ear emergence, and the variance averaged 29.2 days^2. The mean of the autumn sowings and the 1970 and 1972 spring sowings were significantly different from each other and the means of the remaining four spring sowings, which were not different from each other ($P<0.01$). For further analysis these four spring sowings were treated as one sowing.

The following procedure, adapted from Seidewitz (1974), was used to make the data comparable for the five sowings amongst which mean days to ear emergence differed significantly. For each sowing the mean and the variance was used to calculate an interval covering 95% of the variation in days to ear emergence. This interval was divided into 17 equal parts, numbered 2 to 18. Days to ear emergence of each accession was converted into a scoring on this scale. Accessions reaching ear emergence outside the 95% interval were scored as 1 or 19. The ear emergence score was analyzed as a new descriptor. Two separate analyses were carried out, one for the combined spring sowings and the other for combined autumn sowings. For each of 59 regions of origin the mean ear emergence score, the number of accessions, and the number of accessions that had not reached ear emergence, were determined separately for winter wheats, spring wheats and facultative wheats.

RESULTS

Controlled environment experiments. The mean estimates of growth during vernalization for the six experiments expressed as days of growth at 12 ^{o}C, ranged from 13.2 to 16.2 days for the 8w vernalization treatment, and from 4.8 to 7.7 days for the 2w vernalization treatment. Within experiments no significant differences were found between the estimates for different varieties, as was found previously (Hoogendoorn, 1984a). Therefore, for each experiment, the mean estimates of growth during the 8w and 2w vernalization treatments were added to the days to ear emergence from the start of the photoperiod treatment as appropriate. The variances of these estimates, ranging from 0.24 to 1.22 and 0.37 to 1.59 days^2 for the 8w and the 2w estimates respectively, were taken into account in all further calculations.

Days to ear emergence for unvernalized plants of the standard variety Siete Cerros 66 varied between 56.3 and 62.0 and 71.2 and 77.7 days for the long and the short photoperiod treatments respectively. To allow for this environmental variation in days to ear emergence between experiments, correction factors for each experiment were calculated as days to ear emergence of Siete Cerros 66 divided by the mean for this variety of all six experiments. To enable

Table 1. Effect of photoperiod and vernalization on days to ear emergence (DEE), number of leaves (LN) and number of spikelets (SN) of winter wheat varieties. Response to photoperiod [8w vern, 12h phot - 8w vern, 20h phot], response to vernalization [0w vern, 20h phot - 8w vern, 20h phot]. DEE of the 8w vernalization treatment were adjusted for growth during vernalization.

Phenotype class	Variety	Origin	8 w vern 20 h phot treatment			Response to photoperiod			Response to vernalization		
			DEE	LN	SN	DEE	LN	SN	DEE	LN	SN
extra-winter	Holdfast	UK	78.3	8.7	20.3	28.9	2.8	3.3	-*	-	-
	Solid	Sweden	81.9	9.5	22.8	30.4	1.9	6.7	-	-	-
winter, photoperiod sensitive	Sage	USA	67.7	7.8	14.2	25.6	2.4	8.8	-	-	-
	Mentana	Italy	71.1	7.5	13.7	24.8	3.2	8.5	-	-	-
	Sundance	Canada	73.0	7.7	16.3	27.0	2.7	7.7	-	-	-
	Norman	UK	75.9	7.8	19.8	27.7	2.5	3.8	-	-	-
	mean		71.9	7.7	16.0	26.3	2.7	7.2	-	-	-
winter, photoperiod insensitive	Kitakomi Komugi	Japan	63.0	7.7	18.8	10.8	0.7	4.5	-	-	-
	Biserka	Yugoslavia	64.1	7.7	15.8	9.0	1.5	5.0	-	-	-
semi-winter, photoperiod sensitive	Bersee	France	74.6	7.7	20.2	28.2	2.3	4.0	12.7	1.8	2.5
semi-winter, photoperiod insensitive	Short Stalk	China	55.8	6.3	15.7	9.2	0.8	3.8	21.5	3.3	9.5
	Shirasi Komugi	Japan	57.2	7.8	16.4	9.3	-0.2	3.6	5.0	0.3	2.8
	Ke Dung 81	China	61.8	7.8	17.5	7.5	1.0	3.8	25.8	4.5	9.3
	Spica	Australia	62.9	6.3	13.2	7.6	0.7	3.4	12.5	1.7	5.2
	Campodora	Italy	63.9	7.7	16.7	9.6	0.3	3.3	8.3	0.8	3.8
	Flaminio	Italy	64.3	7.8	16.2	9.5	0.2	3.7	15.3	1.9	6.8
	San Pastore	Italy	64.7	7.7	15.8	6.6	1.6	2.8	8.8	1.0	4.0
	Talent	France	66.7	7.5	17.8	10.2	1.3	3.7	36.1	4.5	8.8
	mean		62.2	7.4	16.2	8.7	0.7	3.5	16.7	2.3	6.3
	S.E. (Var. mean)		1.10	0.22	0.42	1.54	0.31	0.59	1.51	0.31	0.59

*- varieties did not reach ear emergence without vernalization

Table 2. Effect of photoperiod and vernalization on days to ear emergence (DEE), number of leaves (LN) and number of spikelets (SN) of spring wheat varieties. Response to photoperiod [0w vern, 12h phot - 0w vern, 20h phot], response to vernalization [0w vern, 20h phot - 8w vern, 20h phot]. DEE of the 8w vernalization treatment was adjusted for growth during vernalization.

Phenotype class	Variety	Origin	0w vern 20h phot treatment			Response to photoperiod			Response to vernalization		
			DEE	LN	SN	DEE	LN	SN	DEE	LN	SN
photoperiod sensitive	Dimitrovka	USSR	54.3	6.0	16.0	29.4	3.2	6.8	-8.1	-0.9	0.0
	Apu	Finland	56.7	6.0	16.2	27.7	3.0	11.7	-9.3	-1.0	-0.7
	Trym	Norway	57.2	6.0	19.0	28.2	3.3	6.0	-9.1	-0.6	0.5
	Krasnodar 93	USSR	58.9	6.5	15.8	25.2	3.5	7.9	-6.0	-1.3	-2.1
	Highbury	UK	60.5	6.2	17.3	29.1	3.0	10.2	-7.2	-0.5	0.0
	Neepawa	Canada	61.5	6.7	14.0	23.7	2.8	7.3	-2.6	-0.2	0.8
	Era	USA	61.9	6.2	16.0	26.5	3.2	9.3	-4.3	-0.5	0.5
	Sicco	Holland	67.7	7.0	18.7	24.4	3.2	12.0	-1.9	-1.5	-0.2
	mean		59.8	6.3	16.6	26.8	3.1	8.9	-6.1	-0.8	-0.1
photoperiod insensitive	Ciano 67	Mexico	52.9	5.8	15.3	13.3	1.6	3.9	-7.9	-1.0	-0.7
	Gamset	Australia	54.1	6.0	12.8	7.3	0.5	2.0	-4.1	0.0	-0.2
	Janak	India	55.4	6.2	16.2	12.4	0.7	3.5	-2.5	0.0	-0.2
	Shera	India	56.1	6.0	14.5	9.1	1.0	3.3	-3.2	-0.5	0.2
	K 65	India	56.5	6.5	15.0	16.7	1.7	5.0	-0.9	-0.3	-1.8
	Gatcher	Australia	57.7	6.3	15.0	16.7	1.7	5.0	1.2	-0.7	0.7
	Siete Cerros 66	Mexico	58.9	6.4	16.6	15.4	1.5	4.4	-5.4	-0.8	-0.1
	C 306	India	59.0	7.3	15.2	15.8	1.5	4.7	-0.1	0.7	1.0
	mean		56.3	6.3	15.1	13.2	1.3	3.9	-2.9	-0.3	-0.1
	S.E.(Var. mean)		1.06	0.22	0.42	1.49	0.31	0.59	1.51	0.31	0.59

comparisons to be made among all 33 varieties, the data on days to ear emergence, adjusted for growth during vernalization, has been divided by these correction factors. Number of leaves and spikelets of Siete Cerros 66 did not vary significantly between experiments, and no adjustments were made for these characters.

Table 1 and 2 show the response to photoperiod and vernalization for all 33 varieties in terms of days to ear emergence and number of leaves and spikelets on the main stem. Some of the varieties failed to reach ear emergence within the experimental period when not vernalized or vernalized only for 2 weeks. These varieties will be referred to as winter wheats. Another group of varieties reached ear emergence after 2w vernalization and also without vernalization, but considerably later than after 8w vernalization. These varieties will be referred to as semi-winter wheats. Most varieties reached ear emergence after 8 w vernalization with six or seven leaves, but two varieties, Holdfast and Solid, had more than eight leaves and were significantly later than the other winter varieties ($P<0.01$). For these two varieties 8w vernalization had apparently been less effective than for the other winter varieties, and they will be referred to as extra-winter wheats. Those varieties which reached ear emergence equally early after vernalization and when not vernalized will be referred to as spring wheats. In the 20h photoperiod treatments these varieties were often later after vernalization than when not vernalized. Although the vernalization treatment was followed by long days it seems likely that the short days during the low temperature treatment prevented spikelet initiation in these varieties until the end of vernalization, while in the long day treatment without vernalization ear initiation was not inhibited.

For the vernalization sensitive wheats (Table 1) days to ear emergence, number of leaves and number of spikelets presented are those from the 8w, 20h treatment. For the spring wheats (Table 2) the results from the 0w, 20h treatment are shown. The response to vernalization has been calculated as the difference between the 8w and the 0w vernalization treatment in long days. The results for the 2w vernalization treatment are not presented because they were not different from those of the 0w vernalization treatment, except for one variety, Short Stalk. This Chinese variety was equally early after 8 or 2w

vernalization, but was delayed by the 0w treatment, which indicates that it was fully vernalized within 2w of exposure to the vernalization conditions used.

The response to photoperiod of each variety is expressed as the difference between the 20h and the 12h treatment after 8w vernalization for the vernalization sensitive wheats (Table 1), and for the 0w vernalization treatment for the spring wheats (Table 2). Some varieties responded very strongly to photoperiod. These varieties will be referred to as sensitive to photoperiod. Another group of varieties responded only weakly to photoperiod. These will be referred to as insensitive to photoperiod.

Table 1 and 2 present the varieties in groups with similar sensitivity to vernalization and photoperiod. The means for days to ear emergence differ significantly between groups ($P<0.01$), but there are also significant differences between varieties within each group, and since this variation in days to ear emergence, as measured in the 20h photoperiod treatments, was not significantly correlated with response to photoperiod or vernalization it will be referred to as variation in earliness *per se*.

Correlation coefficients were calculated between days to ear emergence and number of leaves and spikelets within the long day treatment. Days to ear emergence and number of leaves were correlated, but number of spikelets did not seem to be related to number of leaves or days to ear emergence (Table 3).

Analysis of data from the USDA Small Grain Collection. The field experiments with the USDA Small Grain Collection were carried out over several years, and differences between spring and autumn sowings were confounded with the effects of differences in climate between the sites, Fargo and Pendleton. Regions of origin differed greatly in area. Although the growing environment for wheat is likely not to vary much within a region such as France or Japan, considerable differences in photoperiod and temperature occur within the USSR and China, each treated as a single region of origin in the analysis presented here. The weaknesses in the dataset, however, are likely to be outweighed by the fact that the analyses were carried out on as many as 10409 accessions.

Table 4 shows for winter, spring and facultative wheats the mean ear emergence score and the number of accessions that did or did not reach ear emergence from the autumn and the spring sowings. Fig. 1 and Fig. 2 show which wheat

Table 3. Correlation between days to ear emergence (DEE), number of leaves (LN) and number of spikelets (SN) as measured in the 20h photoperiod treatment. DEE of the 8w vernalization treatments were adjusted for growth during vernalization.

	Spring varieties (not vernalized)		Semi-winter varieties (vernalized)
	photoperiod insensitive	photoperiod sensitive	photoperiod insensitive
DEE & LN	0.77*	0.84**	0.36
DEE & SN	0.42	0.22	0.18
LN & SN	0.20	-0.03	0.71*

*) significant at P<0.05, **) significant at P<0.01, 6 D.F.

Table 4. Results for the USDA Small Grain collection from autumn sowings (Pendleton, Oregon) and spring sowings (Fargo, North Dakota).

Type of accessions	Mean score	No. reaching ear emergence	No. not reaching ear emergence
autumn sowings			
winter	10.78	1672	0
spring	9.23	2527	0
facultative	11.09	544	0
spring sowings			
winter	10.60	221	2742
spring	9.82	2142	504
facultative	13.30	10	47

growing regions had contributed predominantly early or late genotypes to the collection. Early spring and winter wheats had come from China and Japan, India and Pakistan, Ethiopia, Southern Africa, Argentina, Mexico and the South West of the USA, while late accessions had been collected from Northern Europe, the USSR and Afghanistan.

More than 40% of the accessions classified as winter wheats from Argentina, Brazil, Canada, Ethiopia and Portugal reached ear emergence in a spring sowing, indicating that the accessions which are apparently normally used for autumn sowings in these areas were not very sensitive to vernalization. At least 20% of the accessions classified as spring wheats from Afghanistan, Austria, Chile, Turkey and Yugoslavia did not reach ear emergence in a spring sowing, which suggests that vernalization sensitive wheats can be used for spring sowings in these regions, probably because vernalizing temperatures occur during the early phase of crop growth.

Many spring accessions were grown from a winter sowing (Table 4). Spring wheats from a spring sowing were slightly earlier in ear emergence score than spring wheats from a winter sowing (Table 4). However, the mean score of spring wheats from Brazil, Ethiopia, Spain and Italy was much lower from a winter sowing than from a spring sowing, suggesting that spring wheats from these regions could be sensitive to vernalization.

There were relatively few facultative accessions in the collection. Most, 14 from India, 122 from Spain, 346 from Turkey and 32 from Australia, were tested in a winter sowing, and gave mean ear emergence scores of 8, 10, 12 and 12 respectively.

Comparison of the controlled environment experiment with the analysis of the USDA Small Grain Collection. A variety classified as a semi-winter wheat in the controlled environment experiment would not necessarily have been listed as a facultative accession in the USDA Small Grain Collection. Thus, of the three semi-winter wheats common between the controlled environment experiments and the USDA collection, two, Shirasi Komugi and Spica, were classified as spring wheats, and one, San Pastore, was classified as a winter wheat in the USDA collection.

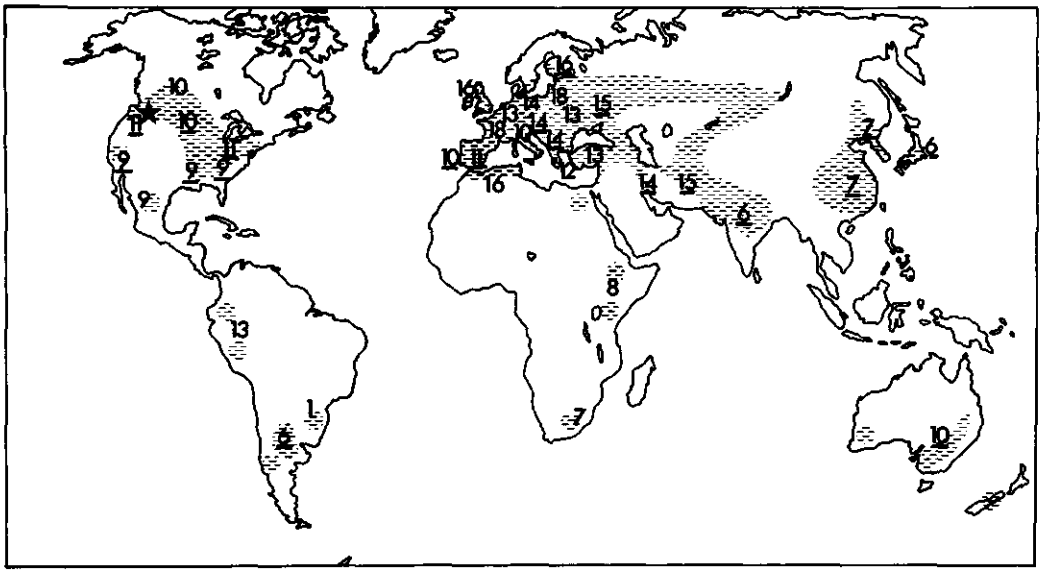

Figure 1. Relation between region of origin and mean ear emergence score in Pendleton, Oregon (★) for winter accessions in autumn sowings. Underlined numbers represent regions of origin for which more than 10 accessions reaching ear emergence were available. Dashed area outlines major wheat growing areas in the world.

Of the 33 varieties tested in controlled environments 13 were also represented in the USDA collection. The ear emergence score for these varieties can be compared with the results of the controlled environment tests. The extra-winter wheat Holdfast and the winter wheat Mentana were grown from an autumn sowing. Ear emergence score of Mentana was 7, considerably earlier than the score of Holdfast, which was 15. Two other winter wheats, Sage and Sundance, were only tested in a spring planting, and as expected, did not reach ear emergence. The semi-winter wheat Spica reached ear emergence from a

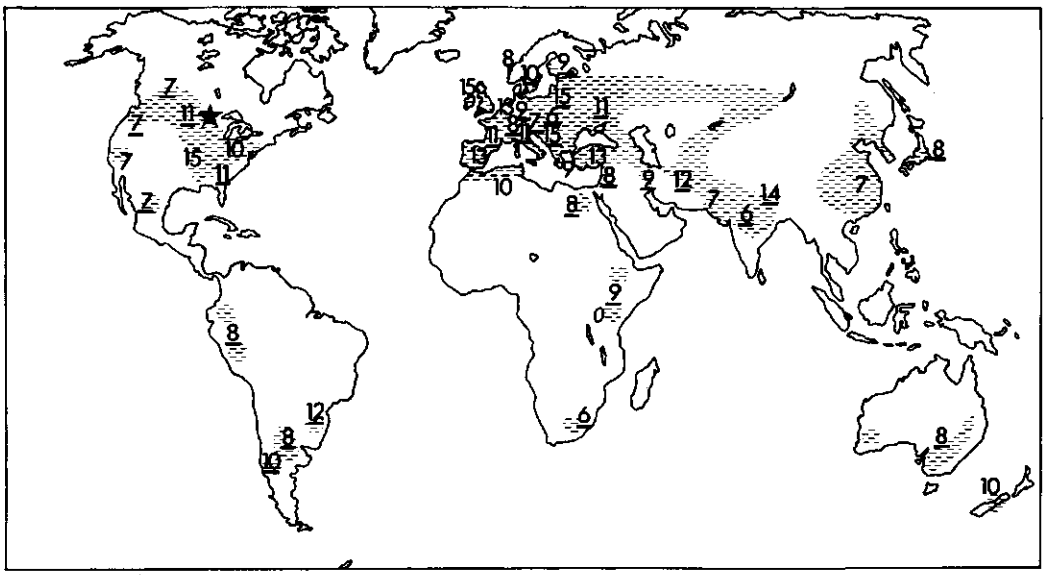

Figure 2. Relation between region of origin and mean ear emergence score in Fargo, North Dakota (★) for spring accessions in spring sowings. Underlined numbers represent regions of origin for which more than 10 accessions reaching ear emergence were available. Dashed area outlines major wheat growing areas in the world.

spring sowing, but the two other semi-winter wheats, Shirasi Komugi and San Pastore, did not reach ear emergence from a spring sowing. Ear emergence score of the photoperiod sensitive spring variety Neepawa was 8 and the scores of the insensitive varieties Ciano 67, Gamset, Gatcher and Siete Cerros 66 were 3, 4, 6 and 6 respectively, showing a similar ranking to that found in the controlled environment experiments.

The mean ear emergence scores for regions of origin from the USDA collection can also be compared with the results of the controlled environment experiment. From autumn sowings, winter accessions from China and Japan were

earlier than those from Italy, which in their turn were earlier than those from France. Table 1 shows an identical ranking for the semi-winter wheats. In spring sowings, spring accessions from India, Mexico and Australia, many of which are thought to be insensitive to photoperiod, were early (scores 6, 7, and 8 respectively). Accessions from the Balkans (score 7), Scandinavia (9), North America (7-15), the Netherlands and Belgium (13) and Great Britain (14), many of which are likely to be sensitive to photoperiod, were later. In the controlled environment experiments the photoperiod insensitive spring varieties were also found to be earlier than the sensitive varieties (Table 2). These results suggest that the ranking for days to ear emergence in the long day controlled environment treatment, within the group of photoperiod sensitive and within the insensitive varieties, was related to differences between means of regions of origin found in the field experiments with the USDA collection.

DISCUSSION

The major differences in response to photoperiod and vernalization between the groups of varieties as presented in Table 1 and 2 are likely to reflect effects of different photoperiod and vernalization genes. Photoperiod sensitivity and insensitivity is thought to be controlled by the $\underline{Ppd_1}$ and $\underline{Ppd_2}$ loci. An insensitivity allele at the $\underline{Ppd_1}$ locus has been found in Ciano 67 (Scarth & Law, 1984) and Talent (J.W. Snape, personal communication), and at $\underline{Ppd_2}$ in Spica (Hoogendoorn, 1984b). The difference between the vernalization sensitive wheats and the spring wheats is thought to be due to a strong vernalization insensitivity allele at the $\underline{Vrn_1}$ locus, and further variation is probably caused by alleles with smaller effects. An insensitivity allele at the $\underline{Vrn_3}$ locus has been found in Shirasi Komugi (Gotoh, 1979), and at the $\underline{Vrn_2}$ locus in Campodora (C.N. Law, personal communication), and Spica and Bersee (Hoogendoorn, 1984b). Bersee is also thought to have a weak insensitivity allele at the $\underline{Vrn_1}$ locus (Law et al. 1981). Within each group as presented in Table 1 and 2 several genes are thus considered to control sensitivity to photoperiod and vernalization, and this indicates that

different genes can have similar effects on ear emergence, number of leaves and number of spikelets.

The variation in days to ear emergence, number of leaves and number of spikelets within groups was shown to be independent of photoperiod and vernalization, and was regarded as earliness *per se*. It is not clear what causes this variation in earliness *per se*. Number of leaves was shown to be correlated with variation in days to ear emergence due to earliness *per se* factors, but no relation was found for number of spikelets (Table 3). Differences in growth rate associated with varietal differences in response to temperature might be important. Gotoh (1977) showed that earliness under field conditions in Japan was found in photoperiod insensitive varieties which were the earliest to reach ear emergence under low temperature conditions in controlled environment experiments. Plants grown at high temperatures have often been shown to have more leaves than those grown at lower temperatures in the same photoperiod (Ridell & Gries, 1958; Rahman & Wilson, 1978). Therefore they tend to reach ear emergence later, and this is so even though high temperature accelerates further growth and development after ear initiation. Genotypic differences in primordium initiation rate could have similar effects on days to ear emergence, the genotypes initiating primordia at a slower rate paradoxically reaching ear emergence first with fewer leaves. Evidence for such genetic factors has been found in monosomic F_1 lines from a cross between Spica and Bersee (Hoogendoorn, 1984b).

In the 8w vernalization and 20h photoperiod treatment the photoperiod sensitive winter wheats were 6 days later than the photoperiod sensitive spring wheats, the photoperiod insensitive semi-winter wheats were 3.0 days later than the photoperiod insensitive spring wheats, and the photoperiod sensitive spring wheats were 6 days later than the photoperiod insensitive spring wheats, differences significant at $P<0.01$. The range in days to ear emergence within these four groups, due to earliness *per se*, averaged 8.5 days. The effect of earliness *per se* genes under controlled environment conditions after vernalization and in long days was thus similar to that of photoperiod and vernalization sensitivity genes.

Although in the field daylength changes continuously and temperature fluctuates, in contrast with the controlled environments where photoperiod and

temperature are kept constant, it was found that the differences between varieties in ear emergence in the controlled environments were similar to those found in the field in Pendleton and Fargo. The results of these field experiments with the USDA collection show in which parts of the world genotypes are likely to be found which will be early or late at Fargo and Pendleton, but cannot disclose whether the variation in time of ear emergence observed is caused by differences in sensitivity to photoperiod or vernalization or in earliness per se. The conclusions from the controlled environment experiments can be used to interprete the differences in ear emergence found within the USDA collection.

The difference between the spring and the winter accessions in the winter sowings was 1.6 units, equal to a difference of approximately 2.5 days. Tables 1 and 2 showed that photoperiod insensitive genotypes came from China and Japan, Australia, Mexico and India. Photoperiod sensitive accessions were found in the USA and Canada, The USSR, Scandinavia, and Great Britain, the Netherlands and Belgium. The average ear emergence score for these two sets of countries were calculated for winter and spring wheats from the autumn sowings, and for spring wheats from the spring sowings. In the spring sowings and in the autumn sowings the difference in ear emergence score between the origins which were thought to be represented by mainly photoperiod insensitive and sensitive genotypes was 3.5 units, equal to a difference of approximately 5 days in ear emergence. Within each of the two sets of regions, differences in ear emergence score, which in analogy with the controlled environment experiments is taken to be due to earliness per se, varied between 2.3 to 6.8 units, equal to differences of approximately 3 to 10 days. The magnitude of these effects in photoperiod and vernalization sensitivity and earliness per se in Fargo and Pendleton, where daylength reaches a maximum of 17h, were thus similar to those found after 8w vernalization in 20h days in the controlled environment experiments in Cambridge.

At similar locations in the USA, Bush & Chamberlain (1981) found a comparable difference of 4 days in date of ear emergence under field conditions between photoperiod sensitive and insensitive spring selections from a cross between Ciano 67 and the photoperiod sensitive variety Justin. Under field conditions in Great Britain an average difference of 7 days in ear

emergence has been observed between photoperiod sensitive and insensitive winter selections from a cross between Norman and Talent. A difference of 5 days in ear emergence was found between photoperiod sensitive winter and semi-winter lines selected from this cross while earliness per se factors were responsible for 5 days variation (Hoogendoorn, 1984c). Syme (1968), however, reported a difference in ear emergence of approximately 100 days between photoperiod sensitive and insensitive spring varieties and between photoperiod insensitive semi-winter and spring wheats when sown under a shortening photoperiod in March in Australia, which was reduced to only 7 days when sown in July. This shows that the effect of photoperiod and vernalization sensitivity on ear emergence under field conditions can vary considerably with prevailing daylength and temperature conditions.

The analysis of the field experiments with the USDA collection, in combination with the information on photoperiod and vernalization sensitivity and earliness per se factors from the controlled environment experiments, suggests that the early ear emergence score found for low latitude regions is caused by both photoperiod insensitivity and earliness per se factors. Similar results were obtained by Qualset & Puri (1973) for durum wheat. In these regions wheat is often grown during the winter period in short days (Arnon, 1972). Earliness due to earliness per se factors in photoperiod sensitive genotypes was found for spring wheat varieties from Scandinavia, Canada and Central Europe (Table 2, Fig. 2). This might be a consequence of the short growing period in these areas. Lateness found for accessions from Poland and Scandinavia and Afghanistan are thought to be caused by strong vernalization sensitivity and earliness per se factors. This might be a requirement for wheat varieties in these regions, because frosts occur frequently till late in the spring, to prevent early ear initiation and consequent severe frost damage. In many parts of the world therefore, photoperiod or vernalization sensitivity or insensitivity will be a requirement for wheat varieties to avoid adverse conditions and to prevent crop failure.

By combining controlled environment experiments and field experiments it has been possible to explain the variation in ear emergence in the field in terms of differences in photoperiod and vernalization sensitivity and earliness per se, and to show that the effects of earliness per se on time of

ear emergence can be equal to the effects of photoperiod and vernalization sensitivity, both under controlled environment conditions and in the field. The results presented should be of particular value in wheat breeding programmes enabling genotypes to be identified which could be exploited as sources of variation in time of ear emergence within the limitations of photoperiod and vernalization sensitivity needed for the prevailing climatic conditions.

I am grateful to W. M. Porter from the Beltsville Agricultural Research Center in Maryland, USA, for providing the data file and all further information needed on the USDA Small Grain Collection, C. W. Howes for his technical advice on the computer analysis of the datafile, and R.B. Austin and Prof. J. Sneep for their critical reading of the manuscript.

REFERENCES

ARNON, I., 1972. Wheat. In: Crop production in dry regions. Vol. 2. Systematic treatment of the principal crops, Leonard Hill, London: 1-72.

BUSCH, R.H. & D.D. CHAMBERLAIN, 1981. Effects of daylength response and semi-dwarfism on agronomic performance of spring wheat. Crop Sci. 21: 57-60.

FORD, M.A., R.B. AUSTIN, W.J. ANGUS & G.C.M. SAGE, 1981. Relationships between the responses of spring wheat genotypes to temperature and photoperiodic treatment and their performance in the field. J. Agric. Sci., Camb. 96: 623-634.

GOTOH, T., 1977. Varietal differences in photoperiodic and thermal responses of wheat. Jap. J. Breed. 27: 57-69 (Jap., E. summ.).

GOTOH, T., 1979. Factors determining varietal differences of heading behaviour of wheats. Jap. Agric. Res. Q. 13: 222-225.

HALSE, N.J. & R.N. WEIR, 1970. Effects of vernalization, photoperiod and temperature on phenological development and spikelet number of Australian wheat. Austr. J. Agric. Res. 21: 383-393.

HOOGENDOORN, J., 1984a. A Comparison of different vernalization techniques in wheat (Triticum aestivum L.). J. Plant Phys. 116: 11-20.

HOOGENDOORN, J., 1984b. A reciprocal F_1 monosomic analysis of the genetic control of time of ear emergence, number of leaves and number of spikelets in wheat (Triticum aestivum L.). Euphytica (In the press).

HOOGENDOORN, J. 1984c. The basis of variation in date of ear emergence under field conditions among the progeny of a cross between two winter wheats. J. Agric. Sci., Camb. (In the press).

HUNT, L.A., 1979. Photoperiodic responses of winter wheats, from different

climatic regions. J. Plant Breed. 82: 70-80.

LAW, C.N. & R. SCARTH, 1984. Genetics and its potential for understanding the action of light in flowering. In D. VINCE-PRUE (Ed.) Light and the flowering process, Academic Press, London (In the press).

LAW, C.N., J.W. SNAPE & A.J. WORLAND, 1981. Intra-specific chromosome manipulation. Phil. Trans. R. Soc. London B.292: 509-518.

QUALSET, C.O. & Y.P. PURI, 1973. Heading time in a world collection of durum wheat: photo- and thermal-sensitivity related to latitudinal responses and geographic origins. In G.T. SCARIASCIA-MUGNOZZA (Ed.) Genetics and breeding of durum wheat. Univ. Bari, Italy : 165-178.

RAHMAN, M.S. & J.H. WILSON, 1978. Determination of spikelet number in wheat. III Effect of varying temperature on ear development. Austr. J. Agric. Res. 29: 459-467.

RIDDELL, J.A. & G.A. GRIES, 1958. Development of spring wheat. II The effect of temperature on responses to photoperiod. Agron. J. 50: 739-742.

SCARTH, R. & C.N. LAW, 1984. The control of the daylength response in wheat by the group 2 chromosomes. J. Plant Breed. 92: 140-150.

SEIDEWITZ, L., 1974. Thesaurus for the international standardization of genebank documentation, Vol. 1 (2nd edition). Inst. Pflanzenbau und Saatgutforschung, Braunschweig: 113 pp.

SYME, J.R., 1968. Ear emergence of Australian, Mexican and European wheats in relation to time of sowing and their response to vernalization and daylength. Austr. J. Exp. Agric. Anim. Husb. 8: 578-581.

WALL, P.C. & P.M. CARTWRIGHT, 1974. Effects of photoperiod, temperature and vernalization on the phenology and spikelet numbers of spring wheats. Ann. Appl. Biol. 76: 299-309.

YASUDA, S. & H. SHIMOYAMA, 1965. Analysis of internal factors influencing the heading time of wheat varieties. Ber. Ohara Inst. Landw. Biol., Okayama Univ. 13: 23-38.

ZEVEN, A.C. & N.CH. ZEVEN-HISSINK, 1975. Genealogies of 14000 wheat varieties. Netherlands Cereals Centre (NGC), Wageningen, & CIMMYT, Mexico: 121 pp.

5. THE BASIS OF VARIATION IN DATE OF EAR EMERGENCE UNDER FIELD CONDITIONS AMONG THE PROGENY OF A CROSS BETWEEN TWO WINTER WHEAT VARIETIES

J. Hoogendoorn

Plant Breeding Institute, Trumpington, Cambridge, CB2 2LQ, U.K.

Submitted to Journal of Agricultural Science, Cambridge

SUMMARY

From the progeny of a cross between the winter wheat varieties Norman and Talent early and late F_5 lines were selected in the field. These selections and the two parental varieties were grown in controlled environment cabinets to assess their sensitivity to photoperiod and vernalization.

The F_5 selections and Norman and Talent were also grown in field trials, at the Plant Breeding Institute in Trumpington, and at The Murrays Experimental Farm of the Scottish Crop Research Institute, near Edinburgh.

Norman was more sensitive to photoperiod and vernalization than Talent. The early F_5 lines were relatively insensitive to photoperiod and/or vernalization. The late lines were sensitive to both photoperiod and vernalization. Differences in date of ear emergence among the selections were found which were independent of photoperiod and vernalization sensitivity. This variation in ear emergence, described as earliness *per se*, was similar under controlled environment conditions and in the field, and was also shown to be comparable in magnitude to that due to differences in sensitivity to photoperiod and vernalization.

INTRODUCTION

A major objective in wheat breeding is to select for appropriate life cycle timing to ensure that the effects of adverse environmental conditions, such as frost damage and drought, are minimized. It has long been known that photoperiod and vernalizing temperatures are important environmental factors controlling ear emergence in wheat, and that there are genetic differences in

sensitivity to photoperiod and vernalization, controlled by a relatively small number of loci. Scarth & Law (1984) have described the effects of two major loci, $\underline{Ppd_1}$ and $\underline{Ppd_2}$, which are considered to control the difference between the strong response to photoperiod shown by many North European varieties, hereafter referred to as the sensitive response, and the weak response to photoperiod found in many low latitude varieties, hereafter referred to as the insensitive response. At least five loci involved in the control of the response to vernalization have been identified. Allelic variation at one of these loci, $\underline{Vrn_1}$, is considered to control the major difference between spring and winter wheat, while the other loci are thought to control smaller differences in sensitivity to vernalization (Pugsley, 1971; 1972; Law & Scarth, 1984), causing the considerable range in vernalization sensitivity within winter wheats and within spring wheats found by Levy & Peterson (1972) and Syme (1968). In general, insensitivity to photoperiod and vernalization is dominant over sensitivity. (Klaimi & Qualset, 1973; 1974).

Sensitivity to photoperiod and vernalization can only be determined accurately in controlled environments, where temperature, photoperiod and light intensity can be kept constant. Ford et al. (1981) showed that genotypic differences in photoperiod and vernalization sensitivity determined in controlled environment studies were correlated with differences in the time of ear emergence under field conditions in Great Britain. Halse & Weir (1970) obtained similar results in field experiments in Western Australia. Hunt (1979), however, found that differences in photoperiod sensitivity between winter wheats were only weakly related to differences in apical development in the field in an autumn sowing in Ontario, Canada.

Yasuda & Shimoyama (1965) found that not only was sensitivity to photoperiod and vernalization related to date of ear emergence in the field in Japan, but also 'earliness in a narrow sense', as assesed by time of ear emergence in long days after vernalization. Ford et al. (1981) also suggested that factors independent of photoperiod and vernalization were important in the regulation of time of ear emergence.

The experiments reported in this paper were undertaken to ascertain whether genotypes which were early or late in the field were insensitive or sensitive, respectively, to photoperiod and vernalization, and whether other genetic

factors, independent of photoperiod and vernalization, also contributed to the control of ear emergence in the field.

MATERIALS AND METHODS

Development of experimental genotypes. In 1978, a cross was made between the two winter wheat varieties Norman and Talent. Norman is a mid season semi-dwarf (Rht_2) variety bred at the Plant Breeding Institute, which was added to the recommended list for England and Wales in 1981. Talent was bred by Benoist in France, and has been on the French national list since 1973. It has not been grown commercially in Great Britain. It is comparable to the semi-dwarf varieties in height although it does not carry either of the Norin 10 (Rht_1 or Rht_2) dwarfing alleles (M. D. Gale, personal communication). In field trials in Trumpington, Talent, previously known as Benoist 10483, reached ear emergence 6 days earlier than modern British varieties. (Austin et al. 1980). In 1980 selections were made from the F_2 population to produce a range of genotypes differing in date of ear emergence. Although initially it was hoped to produce genotypes representing a continuous range in ear emergence, it became apparent by the F_3 generation that the selections segregated into two groups, early and late. After selection for homogeneity of date of ear emergence and height within the F_3 and F_4 lines grown in the field, early and late F_5 lines were available in 1982, each derived from a single F_3 plant. These two groups were further subdivided into tall and short lines. All short lines had the Rht_2 dwarfing allele present in Norman, while it was absent from all tall lines (Hoogendoorn, Innes & Blackwell, 1984). The presence or absence of the dwarfing allele did not affect date of ear emergence and will not be discussed further in relation to the results presented here.

Controlled environment experiments. Two controlled environment experiments were carried out to investigate the sensitivity to photoperiod and vernalization of Norman and Talent and of 17 early and 18 late F_5 selections.

In the first experiment, with Norman and Talent, four vernalization treatments were factorially combined with four photoperiods, giving 16

treatment combinations. Seeds were soaked for 24h at room temperature, then sown in hexagonal paper tubes (Paper Pot BA 213, Nippon Beet Sugar Manufacturing Co Ltd), diameter 1.8cm, in John Innes compost No. 2, and placed in a vernalization cabinet at 5°C, illuminated with fluorescent lamps providing 18W/m^2 for 8h per day. Seedlings were vernalized for 8, 4, 2 and 0 weeks (w). After the vernalization treatments, which were scheduled in such a way that they all ended on the same day, seedlings were transplanted into 9cm diameter pots and placed in controlled environment cabinets for 6 weeks for the photoperiod treatments. The temperature in the cabinets was 12°C, and the relative humidity 85%. Ten hours of light from fluorescent and incandescent lamps, at 118W/m^2, were extended with 0, 1, 2 and 5h of incandescent light at 30W/m^2, before and after the main light period, providing photoperiods of 10, 12, 14 and 20h respectively. Plants were re-randomized weekly between and within cabinets to minimize positional effects. After 6 weeks the plants were transplanted into 11cm diameter pots and moved to a glasshouse. The temperature in the glasshouse was kept above 15°C, and natural daylength was extended to 16h.

Each vernalization-photoperiod treatment was given to six plants of the two varieties. The experiment was ended 120 days after the start of the photoperiod treatment. For each plant, number of leaves and spikelets on the main stem was counted. Days to ear emergence was counted from the end of the vernalization treatment to the day at which the top of the ear emerged above the ligule of the flag leaf.

The assesment of the effect of vernalization treatments on days to ear emergence is influenced by the the amount of growth which occurs during the vernalization treatment. To make allowance for this the following procedure, fully described elsewhere, was used (Hoogendoorn, 1984), with additional plants included in the experiment for this purpose. Number of primordia at the shoot apex of two seedlings of both varieties at the end of each vernalization period was counted, and the rate at which number of primordia increased in unvernalized seedlings during the first three weeks of the photoperiod treatments was estimated by dissecting three seedlings of each variety twice a week. From these data, growth during vernalization was estimated in terms of days of growth in the controlled environment cabinets at 12°C. These

corrections were added to the observed days to ear emergence of the appropriate vernalization treatment.

In the second experiment the sensitivity to photoperiod and vernalization of the 35 F_5 lines was tested. Because of limited space in the controlled environments, only two vernalization treatments, 8 and 4w, and two photoperiod treatments, 20 and 12h, were used. All other controlled environment conditions were as described for the experiment with Norman and Talent, except that instead of six plants per genotype for each treatment the available space permitted only four plants per genotype to be used for each 8w, and five plants for each 4w vernalization treatment. Since the selections were derived from a cross between two winter wheat varieties, it seemed unlikely that any F_5 line would reach ear emergence without any vernalization treatment. This was tested by including three unvernalized plants of each selection in the long photoperiod treatment. On 26 May 1983, after the photoperiod treatment, the plants were moved to a sheltered outdoor area. Natural daylength exceeded 16h. The experiment was ended 100 days after the start of the photoperiod treatment. Corrections for growth during vernalization were estimated as described for the first experiment, but only for four early and four late selections.

In both experiments six unvernalized plants of the spring wheat Siete Cerros 66 were included in the 20h photoperiod treatment to enable variation between experiments to be measured.

Field experiments. Date of ear emergence of the F_5 lines and Norman and Talent was recorded in two field experiments which were part of a larger study on the effects of differences in date of ear emergence and height on yield (Hoogendoorn et al. 1984). In brief, a trial comparing each selection at two sowing dates was carried out at Trumpington in 1982-1983. A split plot design was used with three replicates and with sowing date as the main treatment. The early sowing was drilled on 27 September 1982 and the late sowing on 29 October 1982.

The other trial, with one sowing date but in all other aspects similar to the experiment at Trumpington, was carried out at The Murrays Experimental Farm of the Scottish Crop Research Institute at Pathhead, near Edinburgh. The trial

was sown on 2 October 1982.

All plots were observed on a daily basis at Trumpington and at The Murrays, and the date at which an estimated 50% of the ears had emerged was recorded. At Trumpington only, numbers of leaves and spikelets on the main stem were measured on 10 plants of each plot in one of the three replicates.

RESULTS

Controlled environment experiments. Growth during vernalization was estimated to be equivalent to 16.1, 9.3 and 6.2 days at 12°C for the 8, 4 and 2 weeks vernalization treatments in the first experiment, and to 16.3 and 9.2 days at 12°C for the 8 and 4 weeks vernalization treatment in the second experiment. As previously found, there were no differences among genotypes in the estimates of growth during vernalization treatments (Hoogendoorn, 1984). These estimates were added to days to ear emergence, calculated from the completion of the vernalization treatments, and the variance of the estimates, 0.52 days^2, was added to the residual variance for the calculation of standard errors of means.

Siete Cerros 66 in the experiment with Norman and Talent reached ear emergence in 59.0 days and in the second experiment in 63.3 days. This was considered to imply that progress towards ear emergence was 63.3/59.0=1.07 fold more rapid in the experiment with Norman and Talent than in the second experiment. To make the two experiments comparable, days to ear emergence in the experiment with Norman and Talent were multiplied by 1.07. For number of leaves and spikelets there were no significant differences between experiments for Siete Cerros 66.

After 8, 4 and 2w vernalization Talent reached ear emergence earlier in long than in short days (Fig. 1A). Unvernalized Talent plants did reach ear emergence, but there was no difference between the photoperiod treatments. Frequently, in contrast to the vernalized plants, it was not the ear of the main stem that emerged first. For Norman (Fig. 1B), the difference between the short and the long photoperiod was considerable after 8w vernalization but the effect of photoperiod was less after the shorter vernalization treatments.

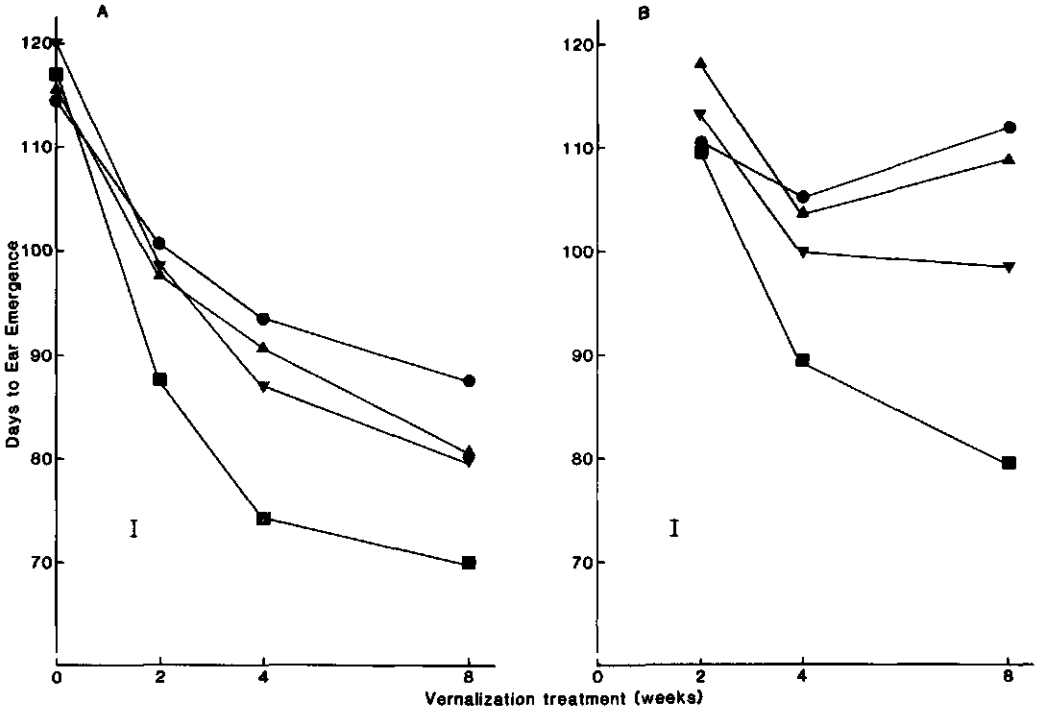

Figure 1. The effect of photoperiod and vernalization on days to ear emergence (DEE) in Norman (A) and Talent (B), under controlled environment conditions. Days to ear emergence has been adjusted for growth during vernalization. ●- 10h, ▲- 12h, ▼- 14h, ■- 20h photoperiod treatment. Bars indicate standard error of treatment means.

When vernalized for only 2 weeks, Norman plants reached ear emergence earlier in the 10h than in the 12h and the 14h photoperiod treatments, although the difference between the 10h and the 14h photoperiod treatment was not significant. A similar vernalizing effect of short days has been observed for other winter cereals (Bernier, Kinet & Sachs, 1981). Unvernalized plants of Norman failed to reach ear emergence within the experimental period.

As expected, all F_5 selections required vernalization to reach ear emergence within the experimental period. Pronounced differences between genotypes in sensitivity to photoperiod and vernalization were found listed in Table 1. A significant interaction between the effect of photoperiod and vernalization, as found for Norman (Fig. 1B), was found for 16 F_5 selections. Therefore, sensitivity to photoperiod has been estimated using the 8w vernalization treatments only, and sensitivity to vernalization has been calculated with the 20h photoperiod treatments only. Six different phenotype classes (Table 1) differing in response to photoperiod and vernalization were identified, but three of these phenotype classes were represented by only one selection.

Most early selections were classified as phenotype A, most late selections as B. Phenotypes A and B appeared to have the vernalization sensitivity of Norman, but A was insensitive to photoperiod, like Talent, while B resembled Norman in being sensitive. The 16 selections forming the B phenotype class were those for which a significant interaction between the effect of photoperiod and vernalization was found. Phenotype C, although early, resembled the late phenotype B and Norman in being sensitive to photoperiod, but, like Talent, was less sensitive to vernalization. Phenotype D was similar to Talent, being relatively insensitive to both photoperiod and relatively insensitive to vernalization. After 8w vernalization the two selections described in Table 1 as E and F, were similar in days to ear emergence, number of leaves and number of spikelets to the A and the B phenotype classes after 4w vernalization, suggesting that both E and F might require more vernalization than Norman. Phenotype E, like Talent, was insensitive to photoperiod, while F appeared to posses a photoperiod response similar to that of Norman. The vernalization response of F could not be determined because it did not reach ear emergence within the experimental period after the 4w vernalization and 20h photoperiod treatment, indicating that after 4w its threshold vernalization requirement had not been fulfilled. However, F did reach ear emergence after 4w vernalization followed by the 12h photoperiod treatment. This may have been due to the vernalizing effect of short days.

Table 1 also shows that the selections in late phenotype class B had more spikelets than those of early phenotype class A. However, within the A and within the B phenotype class the correlation between days to ear emergence and

Table 1. The effect of photoperiod and vernalization on days to ear emergence (DEE), number of leaves (LN) and number of spikelets (SN) on the main stem, of Norman and Talent and the F_5 selections. Effect of vernalization = [4w vern, 20h phot - 8w vern, 20h phot], effect of photoperiod = [8w vern, 12h phot - 8w vern, 20h phot]. DEE has been adjusted for growth during vernalization. For explanation of A - F, see text. S.E. - standard errors for single genotype means.
*(n)-number of lines in phenotype class, when greater than 1.

Phenotype class/ variety	Phenotype in the field	8w vern + 20h phot treatment			4w vern + 12h phot treatment			Effect of vernalization			Effect of photoperiod		
		DEE	LN	SN	DEE	LN	SN	DEE	LN	SN	DEE	LN	SN
Talent	early	70.2	7.5	17.8	91.0	9.8	21.5	4.2	0.8	1.8	10.7	1.3	3.7
Norman	late	79.8	7.8	19.8	104.2	10.8	25.8	10.1	1.6	0.5	29.3	2.5	3.9
A(13)*	early	73.2	7.9	18.2	91.1	10.3	24.0	9.6	1.2	2.8	11.0	1.3	3.9
B(16)	late	79.2	8.1	20.6	96.5	10.9	27.0	8.6	1.4	2.2	19.0	2.3	6.8
C(3)	early	74.3	8.1	19.3	92.8	10.5	25.7	5.6	1.0	3.2	17.5	1.6	6.2
D	early	79.8	8.3	22.3	90.2	10.0	26.2	2.7	0.7	0.7	12.0	1.0	4.0
E	late	78.3	8.5	20.0	97.2	11.0	24.7	14.3	1.7	2.6	10.1	1.3	3.5
F	late	89.8	9.0	22.0	101.1	10.7	26.0	-	-	-	12.5	1.8	5.8
S.E.		1.83	023	0.56	1.67	0.22	0.65	2.47	0.31	0.76	2.59	0.38	0.85

number of spikelets was not significant in any of the treatments.

Field experiments. Fig. 2 shows the mean date of ear emergence of the six different phenotype classes in the field experiments, and the variation in ear emergence among the A and B selections. Ear emergence occurred over a shorter period at The Murrays than from either sowing at Trumpington, where the range in ear emergence was more compressed in the late sowing than in the early sowing. Table 2 lists number of leaves and number of spikelets for the experiment at Trumpington. Talent was not different from Norman in the early sowing, but had fewer leaves and spikelets in the late sowing, although these differences were not significant. In both sowings the selections in the late phenotype class B had more spikelets than those in the early phenotype class A ($P<0.01$), but date of ear emergence and number of spikelets were not significantly correlated within the A and within the B phenotype class.

Table 2. Number of leaves and number of spikelets on the main stem of Talent and Norman and the F_5 lines in the early (ES) and the late sowing (LS) of the field trial at Trumpington. For explanation of A - F, see text. S.E. - standard errors for single genotype means.
*(n)-number of lines in class, when greater than 1.

Phenotype class/ variety	Phenotype in the field	No. of leaves ES	No. of leaves LS	No. of spikelets ES	No. of spikelets LS
Talent	early	12.5	10.0	20.0	18.4
Norman	late	12.3	10.8	20.0	19.4
A(13)*	early	12.4	10.2	19.2	18.2
B(16)	late	12.5	10.7	20.3	19.4
C(3)	early	13.0	10.4	20.0	18.6
D	early	12.4	10.2	19.3	18.7
E	late	12.3	10.3	18.3	17.0
F	late	13.8	11.2	19.8	19.2
S.E.		0.21		1.26	

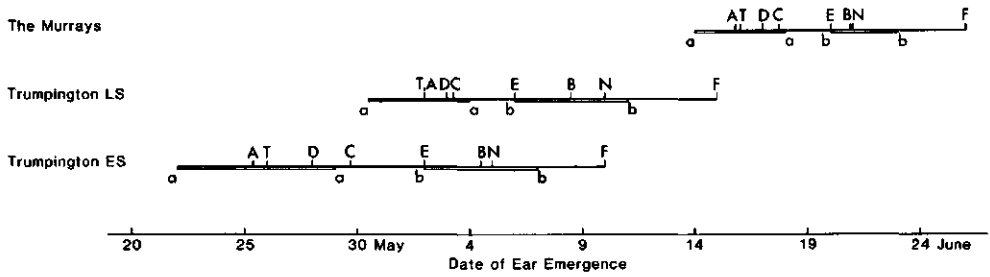

Figure 2. Date of ear emergence for Norman and Talent and the F_5 selections derived from the cross between Norman and Talent in May and June 1983 at The Murrays and in an early (ES) and a late sowing (LS) at Trumpington. T - Talent, N - Norman, for explanation of A - F, see text. The underlined areas represent the range in date of ear emergence of the selections within the A and the B phenotype class. Standard errors of means of single genotypes are 0.48 days for Trumpington and 0.30 days for The Murrays.

Date of ear emergence and number of spikelets in the field experiments was significantly correlated with days to ear emergence as measured in the controlled environment experiments. Both in the field and in the cabinets the A selections reached ear emergence earlier and with fewer spikelets than the C selections, which in their turn were earlier than the B selections. Not only between, but also within the A and the B phenotype classes significant correlations were found between date of ear emergence in the field and in the controlled environment experiments. The correlation coefficient between date of ear emergence, averaged over the field experiments, and days to ear emergence, averaged over the four controlled environment treatments, was 0.75 for the A phenotype class ($P<0.01$, 11 D.F.) and 0.75 for the B group ($P<0.01$, 14 D.F.). For mean number of spikelets this correlation coefficient was 0.58 for the A selections ($P<0.05$, 11 D.F.) and 0.70 for the B selections ($P<0.01$, 14 D.F.). The relation between days to ear emergence as measured after 8w vernalization followed by the 12h photoperiod treatment, and date of ear emergence from the late sowing at Trumpington is shown in Fig. 3.

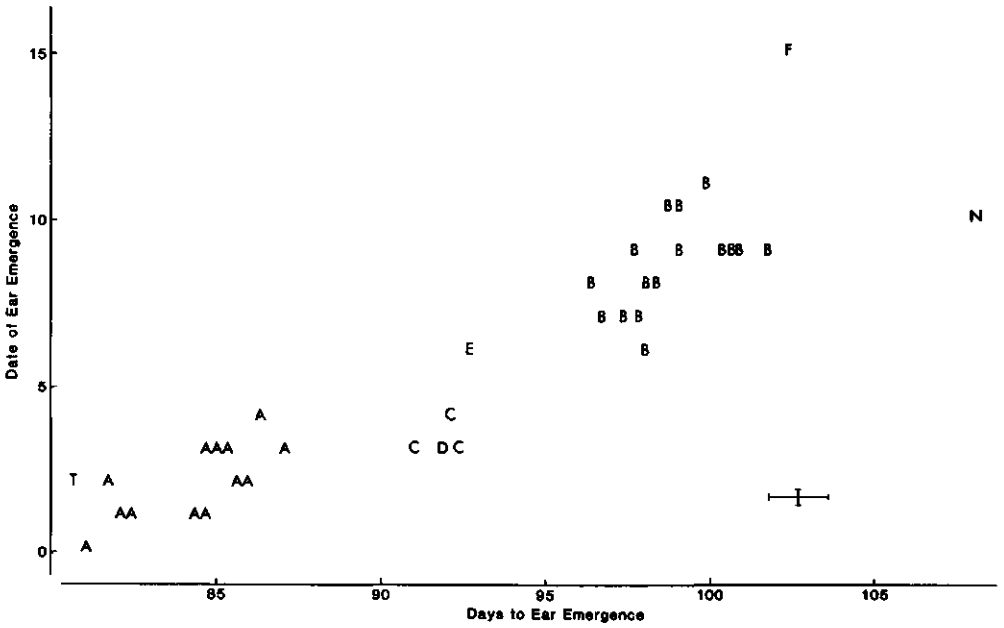

Figure 3. The relation between days to ear emergence (DEE) after the 8w vernalization and 12h photoperiod controlled environment treatment and date of ear emergence in the late sowing in Trumpington in June 1983 for Norman and Talent and the F_5 selections. T - Talent, N - Norman, for explanation of A - F, see text. Bars indicate standard error of genotype means.

DISCUSSION

Most of the 35 selections were similar to Talent or Norman or were recombinant types in terms of their sensitivity to photoperiod and vernalization. Table 1 shows that Talent and the A, D and E selections were insensitive to

photoperiod. It has been found recently that Talent carries a photoperiod insensitivity allele on the $\underline{Ppd_1}$ locus (J.W. Snape, personal communication). For two selections the vernalization sensitivity appeared to transgress that of the parents. This suggest that Norman and Talent both carry an allele for vernalization insensitivity, but on a different locus, the allele present in Norman being weaker than that in Talent. The strong sensitivity to vernalization of phenotype E and F could be explained by the absence of both insensitivity alleles. No selections less sensitive to vernalization than Talent were found. Either the genotype with both vernalization insensitivity alleles could not be recognized as being different from Talent, at least not with the controlled environment treatments used, or it was not represented amongst the selections, due to the restricted number of F_5 lines tested. Hunt (1979) showed that Talent was less sensitive to vernalization than Maris Templar and Maris Huntsman, winter varieties which, like Norman, were bred at the Plant Breeding Institute. Several varieties, mainly from Central Europe, were shown to be more sensitive to vernalization than Maris Templar and Maris Huntsman, suggesting that weak vernalization insensitivity alleles might be present in English winter wheat varieties such as Norman. It is not known which loci control the vernalization insensitivity of Norman and Talent.

In the field the A selections were earlier than those of the B phenotype class. The C selections were later than those from the A phenotype class, and phenotype E was earlier than the B selections. Phenotype F, which is thought to combine a very strong sensitivity to vernalization with sensitivity to photoperiod, was by far the latest to reach ear emergence in all field experiments. In this material, therefore, it seems that sensitivity to photoperiod was the main determinant of the genetic variation in date of ear emergence in the field, but differences in response to vernalization also appeared to be important. Ford et al. (1981) obtained similar results. They found a difference of 4 days in ear emergence between photoperiod sensitive and insensitive spring genotypes, and a difference of only 2 days between genotypes partially sensitive to vernalization and insensitive lines, following an early spring sowing.

Syme (1968) showed that under Australian conditions the effect of differences in photoperiod or vernalization sensitivity on date of ear

emergence could vary considerably, depending on the date of sowing. Similarly in the field experiments described here it was found that the difference between the mean date of ear emergence of the photoperiod insensitive A and the photoperiod sensitive B phenotype classes was smaller at The Murrays and in the late sowing at Trumpington, than in the early sowing at Trumpington (Fig. 2). This reduction of the difference between A and B is likely to be due both to the higher temperature and the longer daylength in the period preceding ear emergence in the late sowing at Trumpington and at The Murrays, as shown by Baker & Gallagher (1983) in experiments with the winter wheat variety Maris Huntsman. By expressing the differences between the A and the B phenotype classes in degree days instead of in days to ear emergence it is possible to separate the effect of temperature from that of daylength. Differences of 150, 111 and 80 degree days, calculated from daily mean temperatures, were found for the early sowing and the late sowing at Trumpington and at The Murrays, respectively. It is likely that the shorter days at the time of ear initiation in the early sowing at Trumpington compared with the late sowing and at The Murrays, delayed ear emergence of the photoperiod sensitive lines more than that of the insensitive genotypes.

Date of ear emergence in the field was correlated with days to ear emergence in the controlled environments, both for phenotype class means and within phenotype classes. The variation in time of ear emergence within the A and within the B phenotype classes is taken to represent 'earliness *per se*', and to be due to factors independent of photoperiod and vernalization, such as sensitivity to temperature, growth rate and ear size. For example, Talent was similar to the selection representing phenotype D in its sensitivity to photoperiod and vernalization (Table 1), but Talent reached ear emergence earlier, both under controlled environment conditions and in the field. Talent had smaller ears than selection D, and the greater time taken by D in comparison with Talent for ear initiation and ear growth may explain the observed difference in earliness *per se*. Differences in ear size, however, cannot be the main factor responsible for the variation in date of ear emergence among the A and amongst the B selections, because the correlation between number of spikelets and days to ear emergence within these groups was shown to be not significant. Further investigation is required to establish

whether genotypic differences in growth rate, response to temperature, or other factors determine earliness per se.

The variation in earliness per se within the A and the B group was estimated as the difference in time of ear emergence between the earliest and the latest genotype within each phenotype class, and averaged 6 days under controlled environment conditions, and 5 days in the field experiments. This is comparable to the average differences of 7 days in the field experiments between the mean of the photoperiod insensitive A selections and the photoperiod sensitive B selections, and the average difference of 5 days between the relatively vernalization insensitive C selections and the vernalization sensitive B selections (Fig. 1). Elsewhere it has been shown that the variation in ear emergence under field conditions discussed here is likely to influence yield and yield components (Hoogendoorn et al. 1984; Innes, Blackwell & Hoogendoorn, 1984; Bidinger, Blackwell & Innes, 1984). The results presented here show that time of ear emergence of winter wheat under field conditions in Great Britain could be varied by exploiting variation in earliness per se as well as variation in sensitivity to photoperiod and vernalization.

I am grateful to H.H.W.M. Derks for assistance with the controlled environment experiments, and R. B. Austin and Prof. J. Sneep for their critical reading of the manuscript.

REFERENCES

AUSTIN, R.B., J. BINGHAM, R.D. BLACKWELL, L.T. EVANS, M.A. FORD, C.L. MORGAN & M. TAYLOR, 1980. Genetic improvements in winter wheat yields since 1900 and associated physiological changes. J. Agric. Sci., Camb. 94: 675-689.

BAKER, C.K. & J.N. GALLAGHER, 1983. The development of winter wheat in the field. 2. The control of primordium initiation rate by temperature and photoperiod. J. Agric. Sci., Camb. 101: 337-344.

BERNIER, G., J. KINET & R.M. SACHS, 1981. The physiology of flowering, Vol. I, CRC Press, Florida, 149 pp.

BIDINGER, F.R., R.D. BLACKWELL & P. INNES, 1984. Effects of differences in ear emergence and height on yield of winter wheat. 3. Individual tiller yield and yield components. J. of Agric. Sci., Camb. (In the press).

FORD, M.A., R.B. AUSTIN, W.J. ANGUS & G.C.M. SAGE, 1981. Relationships between the responses of spring wheat genotypes to temperature and photoperiodic

treatment and their performance in the field. J. Agric. Sci., Camb. 96: 623-634.

HAISE, N.J. & R.N. WEIR, 1970. Effects of vernalization, photoperiod and temperature on phenological development and spikelet number of Australian wheat. Austr. J. Agric. Res. 21: 383-393.

HOOGENDOORN, J., 1984. A comparison of different vernalization techniques in wheat (Triticum aestivum L.). J. Plant Phys. 116: 11-20.

HOOGENDOORN, J., P. INNES & R.D. BLACKWELL, 1984. Effects of dices in ear emergence and height on yield of winter wheat. 1. Interactions with year, location and sowing date. J. Agric. Sci., Camb. (In the press).

HUNT, L.A., 1979. Photoperiodic responses of winter wheats from different climatic regions. J. Plant Breed. 82: 70-80.

INNES, P., R.D. BLACKWELL & J. HOOGENDOORN, 1984. Effects of differences in ear emergence and height on yield of winter wheat. 2. Effects of drought on water use and yield. J. Agric. Sci., Camb. (In the press).

KLAIMI, Y.Y. & C.O. QUALSET, 1973. Genetics of heading time in wheat (Triticum aestivum L.). I The inheritance of photoperiodic response. Genetics 74: 139-156.

KLAIMI, Y.Y. & C.O. QUALSET, 1974. Genetics of heading time in wheat (Triticum aestivum L.). II The inheritance of vernalization response. Genetics 76: 119-133.

LAW, C.N. & R. SCARTH, 1984. Genetics and its potential for understanding the action of light in flowering. In D. VINCE-PRUE (Ed.) Light and the Flowering Process. Academic Press London, (In the Press).

LEVY, J. & M.L. PETERSON, 1972. Responses of spring wheat to vernalization and photoperiod. Crop Sci. 21: 487-490.

PUGSLEY, A.T., 1971. A genetic analysis of the spring-winter habit of growth in wheat. Austr. J. Agric. Res. 22: 21-31.

PUGSLEY, A.T., 1972. Additional genes inhibiting winter habit in wheat. Euphytica 21: 547-552.

SCARTH, R. & C.N. LAW, 1984. The control of the daylength response in wheat by the group 2 chromosomes. J. Plant Breed. 92: 140-150.

SYME, J.R., 1968. Ear emergence of Australian, Mexican and European wheats in relation to time of sowing and their response to vernalization and daylength. Austr. J. Exp. Agric. Anim. Husb. 8: 578-581.

YASUDA, S. & H. SHIMOYAMA, 1965. Analysis of internal factors influencing the heading time of wheat varieties. Ber. Ohara Inst. Landw. Biol., Okayama Univ. 13: 23-38.

6. EFFECTS OF DIFFERENCES IN DATE OF EAR EMERGENCE AND HEIGHT ON YIELD OF WINTER WHEAT

1. INTERACTIONS WITH YEAR, LOCATION AND SOWING DATE

J. Hoogendoorn, P. Innes and R.D. Blackwell

Plant Breeding Institute, Trumpington, Cambridge CB2 2LQ, U.K.

Submitted to Journal of Agricultural Science, Cambridge

SUMMARY

Early and late and short and tall lines were selected from a cross between the winter wheat varieties Norman and Talent. All short selections carried the $\underline{Rht}_2$ dwarfing gene, in contrast with the tall selections. These selections were compared in three field experiments, two at the Plant Breeding Institute in Trumpington and one at The Murrays Experimental Farm of the Scottish Crop Research Institute near Pathhead.

In all trials the early selections gave yields equal to or greater than the late selections. There were no differences in mean number of ears/m^2 or in mean number of grains per ear between the early and the late selections. Mean weight per grain of the early selections was higher than that of the late selections.

In all trials the short selections gave yields equal to or greater than the tall selections. There were no differences in mean number of ears/m^2 between the short and the tall selections. Mean number of grains per ear was higher and mean weight per grain was lower for the short selections than that for the tall selections.

It is concluded that new varieties for Great Britain should be semi-dwarf with large grains, and earlier than those currently grown. Such genotypes are thought to have a high potential yield and to be able to avoid or tolerate high temperatures and drought around and after ear emergence and anthesis.

INTRODUCTION

The timing of ear emergence in wheat is determined by genes conferring sensitivity to photoperiod and vernalization, and by environmental factors such as daylength, temperature, and available water. Woodruff (1983) showed that hastening development with different photoperiod treatments or by exploiting genetic differences in sensitivity to photoperiod decreased number of spikelets per ear and total plant dry weight at anthesis, and resulted in a reduction in potential grain yield. Environmental conditions at anthesis determined whether this resulted in a difference in actual grain yield.

Wheat is particulary sensitive to environmental stress in the immediate pre-anthesis period (Woodruff & Tonks, 1983; Bingham, 1967). Fischer & Maurer (1978) showed that in Mexico when drought was created by witholding irrigation, earlier flowering had adaptive advantages in wheat and other temperate cereals through drought escape, resulting in higher yields. Similar effects have been demonstrated for sorghum (Seetharama et al. 1982).

In Great Britain high yields are obtained with autumn sown wheat, when full advantage is taken of the long growing season. The climate of the British Isles is mild, and in comparison with the very hot and dry summers in some of the major wheat growing areas in the world, does not impose great constraints on the realization of potential yield. However, although severe drought and very high temperatures are not common in Great Britain, evaporation exceeds rainfall from April onwards, and except on heavy soils, crops can experience levels of water stress between May and maturity which reduce yield (Innes & Blackwell, 1981). The intensity of this stress varies from year to year and site to site. In Scotland water stress is less likely to occur around anthesis, but cold and wet weather is often detrimental at harvest time.

Modern British winter wheat varieties reach ear emergence earlier and are shorter than those grown in the early part of this century. The height reduction, which has been associated with an increase in harvest index (Austin et al. 1980), is partly attributable to the introduction of the Norin 10 dwarfing genes; in 1983 10 out of the 15 winter wheat varieties on the Recommended List for England and Wales carried the $\underline{Rht_2}$ dwarfing gene (M. D. Gale, personal communication). This dwarfing gene has been shown not only to

reduce height, but also in general to be associated with an increase in mean number of grains per ear, and a reduction in mean weight per grain (Pinthus & Millet, 1978; Gale, 1978). Woodruff & Tonks (1983) showed that semi-dwarf genotypes might be more sensitive to drought and high temperatures than tall genotypes.

The work reported here formed part of a series of experiments studying the effects of differences in ear emergence on yield and yield components under British environmental conditions (Innes, Blackwell & Hoogendoorn, 1984; Bidinger, Innes & Blackwell, 1984). To minimize genotypic differences in yield potential other than those caused by differences in date of ear emergence, the experimental genotypes used were selected from a single cross between two modern winter wheat varieties. The late parent was the semi-dwarf ($\underline{Rht_2}$) variety Norman, characterized by low tillering, mid season flowering, and, for a semi-dwarf variety, large grains. Norman has been on the Recommended List for England and Wales since 1981. The early parent was the French variety Talent, comparable in height with semi-dwarf varieties, but without the $\underline{Rht_2}$ dwarfing gene. The dwarfing gene(s) in Talent have not yet been identified. Talent is characterized by high tillering, low mean grain weight and earliness of flowering, and has been on the French list of approved varieties since 1973. It has not been grown commercially in Great Britain.

The effects of genotypic differences in date of ear emergence and height on yield and yield components were evaluated in three experiments, in which site, season and sowing date were varied.

MATERIALS AND METHODS

Production of the experimental genotypes. The varieties Norman and Talent were crossed in 1978 as part of the winter wheat breeding programme at the Plant Breeding Institute. Selection started from the F_2 population in 1980 to produce lines covering a continuous range in date of ear emergence under field conditions. F_3 rows from selected F_2 plants were grown in 1980-1, and date of ear emergence and height were measured; 56 F_3 rows were selected. In the F_3 generation it became apparent that the population segregated into early and

late and into short and tall phenotype classes. F_4 grains from a representative plant from each selected F_3 row were sown in multiplication plots in 1981-2 to produce F_5 seed, while at the same time the remaining F_4 grains from each F_3 row were used for an unreplicated yield experiment (Expt 1). In the F_4 multiplication plots, date of ear emergence and height were measured. Four phenotype classes, each represented by ten lines, short-early, short-late, tall-early and tall-late, were selected using homogeneity for date of ear emergence and height within the F_4 multiplication plots as selection criteria. All 40 selections were used in the experiments reported by Innes et al. (1984). For the F_5 yield experiments described here, nine selections for each phenotype class were used.

All selections were tested for the presence of the $\underline{Rht_2}$ dwarfing gene using the method described by Gale, Law & Worland (1975). It was not possible to test for the presence of the Talent dwarfing gene(s) as no test is available. All short selections carried the $\underline{Rht_2}$ dwarfing gene, and all tall selections lacked the $\underline{Rht_2}$ dwarfing gene.

Controlled environment experiments, described elsewhere (Hoogendoorn, 1984), showed that most selections had a pronounced sensitivity to vernalization, similar to Norman. Most of the early selections were relatively insensitive to photoperiod like Talent, while the late selections resembled Norman in being sensitive to photoperiod.

Experiment 1: F_4 yield experiment at Trumpington, 1981-2. The experiment was sown on 22 October 1981, using F_4 seed of all 56 selected F_3 lines together with Norman and Talent. A split-plot design was used. The experimental area, on a sandy clay loam soil, was divided into two main plots, one with the tall selections, the other with the short selections. Subplots with early and late selections were randomized within each main plot. Guard plots were sown around each main plot to minimize edge and neighbour effects. The experiment was unreplicated, except for the parent varieties Norman and Talent, since only a limited amount of seed was available from each selected F_3 line. Norman and Talent were each replicated three times in each main plot and provided estimates of the variation between and within main plots.

Each subplot was 4m long with seed drilled in 7 rows, 17cm apart at an average density of ca. 300 seeds/m^2. No fertilizer was applied to the seed bed, as the wheat followed a radish crop which had been ploughed in. Early in April, 75kg N/ha was applied. The experiment was kept free from diseases and weeds by spraying with appropriate chemicals throughout the season, and was covered with netting just after anthesis to prevent bird damage.

Date of ear emergence was recorded as the date on which the tips of the ears had emerged on an estimated 50% of the stems in each plot. The number of leaves on the main stem and the number of spikelets on the main ear were counted on 10 plants of Norman and Talent and three selections from each phenotype class. Plant height to the base of the ears was measured, and number of ears was counted in a 30cm wide strip across each subplot just before harvest. Harvest index, calculated as the ratio of grain yield to total above-ground dry matter, was determined for all selections from a 10cm wide sample taken across each subplot.

The experiment was harvested on 29 July 1982. Grain yields (t/ha, 15% moisture content) were calculated to allow for the influence of edge effects (Austin & Blackwell, 1980). Mean weight per grain was determined on two samples of 200 grains from each subplot.

Experiment 2: F_5 yield experiment at Trumpington, 1982-3. In this experiment, two sowing dates were used to study the effects of time of sowing and genotypic differences in date of ear emergence on grain yield. The early sowing was carried out on 27 September 1982, the late sowing on 29 October 1982, using nine selections of each of the four phenotype classes together with Norman and Talent. A double split-plot design with three replicates was used. The experimental area was divided into three blocks, each of two main plots corresponding to the early and late sowing. Each main plot was subdivided into two subplots, one with the tall selections, the other with the short selections. Sub-subplots with early and late selections and Norman and Talent were fully randomized within each height subplot. Guard plots were sown around each height subplot to minimize neighbour effects.

The experimental site was adjacent to that used in 1981-2, and plot size, sowing density and crop protection measures were similar to those used in

Expt 1. The wheat again followed a radish crop which had been ploughed in, and no fertilizer was applied to the seed bed. At the end of April 100kg N/ha was applied. All variates measured in Expt 1 were also recorded in this experiment. The number of leaves and spikelets on the main stem were determined on all selections and on Norman and Talent in one replicate. As harvest approached, random samples of 30 spikelets were taken twice weekly from each sub-subplot of two replicates, and grain moisture content was measured. The date on which the moisture content of the grain had fallen to 25% was determined by interpolation. Preliminary experiments had indicated that this moisture content was attained just after the grains had ceased to increase in dry weight. The length of the post-ear emergence period was determined as the difference between the date of ear emergence and the date on which grain moisture content had fallen to 25%. The experiment was harvested on 16 August 1983.

Experiment 3: F_5 yield experiment at The Murrays, 1982-3. This experiment was sown on 4 October 1982, using the same nine selections for each phenotype class as in Expt 2 together with Norman and Talent, at The Murrays Experimental Farm of the Scottish Crop Research Institute at Pathhead near Edinburgh. The soil at The Murrays was a heavy loam. A split-plot design with three replicates was used. Each replicate consisted of two main plots, one with the tall, the other with the short selections. Subplots with early and late selections and Norman and Talent were fully randomized within each main plot, and guard plots were sown around each main plot.

Each subplot was 4.75m long and seed was drilled in 8 rows, 13cm apart, at an average density of ca. 300 seeds/m^2. The wheat crop followed a 2 year grass ley. Crop protection measures and applied nitrogen fertilizer dressings were similar to those used in Expt 2. Date of ear emergence, plant height, number of ears/m^2 and grain yield were measured as described for Expt 1. The experiment was harvested on 4 September 1983.

Meteorological data. The estimated soil moisture deficits for a winter cereal crop, supplied by the MAFF Meteorological Office in Cambridge from the Meteorological Office Rainfall and Evaporation Calculation System (MORECS),

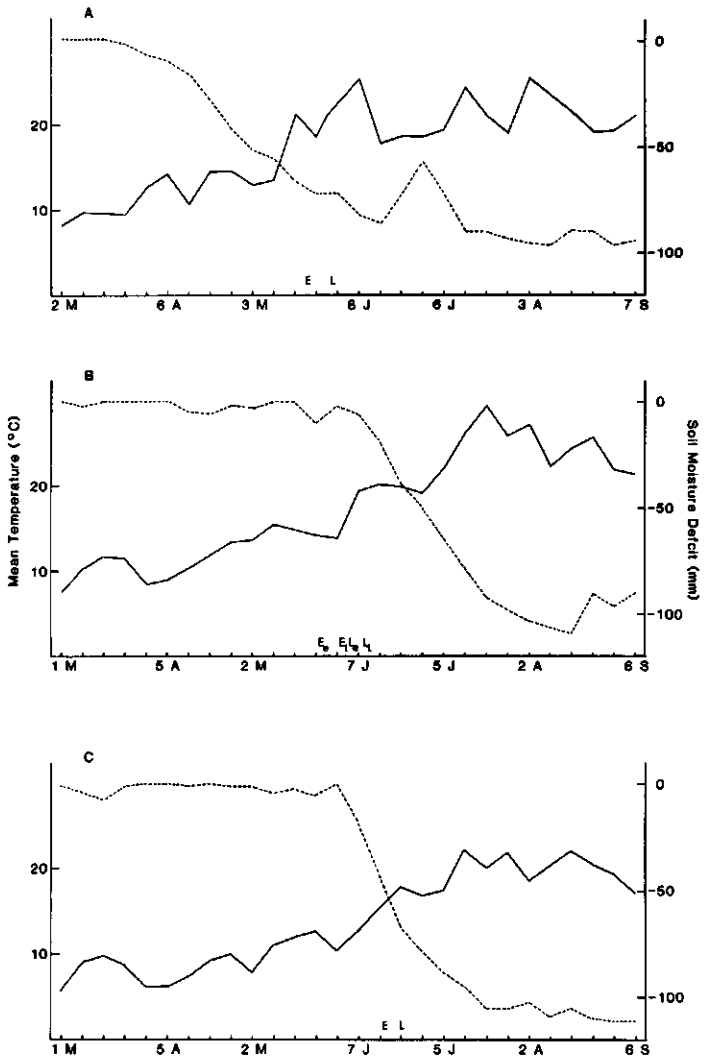

Figure 1. Maximum screen temperature in ^{o}C (———) and calculated soil moisture deficit for a winter cereal crop in mm (------) for Trumpington 1982 (A), Trumpington 1983 (B) and The Murrays (C). E - mean date of ear emergence for the early selections, L - mean date of ear emergence for the late selections, e - early sowing, l - late sowing.

and the maximum daily temperature as measured on site at Trumpington and at The Murrays are shown in Fig. 1 for all three experiments. Actual evaporation normally falls below potential evaporation when 50% of the available water in a soil profile has been used (cf. Day et al. 1978). If the amount of available water in the soil profile falls below this limiting deficit grain yield is likely to be reduced. On both fields at Trumpington and at The Murrays this limiting deficit was estimated to be 50 mm (P. Innes, unpublished results).

RESULTS

Experiment 1: F_4 yield experiment at Trumpington, 1981-2. Table 1 summarizes the results from Expt 1. Although 56 selections were used, only the results for the 36 F_5 lines used in Expts 2 and 3 are presented to enable a direct comparison to be made with the results from these other experiments. Means and standard errors calculated for the 56 selections did not differ significantly from those presented in Table 1.

The early selections measured had an average of 11 leaves and 20 spikelets, the late selections 12 leaves and 23 spikelets on the main stem. There were no significant differences in number of leaves or spikelets between the short and the tall selections. Both Norman and Talent had 12 leaves and 22 spikelets.

Because this was an unreplicated experiment, environmental differences between and within main plots could only be estimated using the data for Norman and Talent. These indicated that there were no significant differences between or within main plots for any of the variates measured. Therefore it was assumed that fertility differences within the experimental area did not bias the comparison between selections.

No significant differences in yield between the early and the late selections, or between the short and the tall selections were found, when tested against the variation between selections within phenotype classes. The early selections had heavier grains than the late selections. The short selections had lighter grains and a greater harvest index than the tall selections. There were no significant differences between the means of the four phenotype classes in number of ears/m^2. Number of ears/m^2 was

Table 1. Yield and yield components for Expt 1. S.E. - standard error of phenotype class mean, C.V. - mean coefficient of variation within phenotype classes. S.E. for Norman and Talent is 2.1 times the S.E. for phenotype class means.

Phenotype class/ variety	Grain yield (t/ha)*	Harvest index (%)	Plant height (cm)	Days to ear emergence after 30 April	No. of ears/m^2	Mean weight/ grain (mg)*
short-early	7.37	53.3	71	22	356	48.7
short-late	6.69	51.8	66	28	309	47.5
tall-early	7.21	50.5	85	22	341	53.9
tall-late	7.14	46.3	86	31	374	48.6
Mean	7.10	50.5	77	26	345	49.6
S.E.	0.242	0.77	2.3	0.5	13.2	1.24
C.V.(%)	10.2	4.3	8.3	5.4	11.1	6.4
Norman	8.03	53.0	73	30	313	53.5
Talent	6.48	55.0	74	21	367	44.0

* at 15 % moisture content

significantly correlated with yield ($r=0.45$, $P<0.01$, 34 D.F.), as shown in Fig. 2A. Within a phenotype class, neither date of ear emergence nor height were correlated with grain yield. Mean weight per grain was significantly correlated with yield among the tall selections when averaged over the early and the late phenotype classes using the z-transformation (Snedecor & Cochran, 1967) ($r=0.63$, $P<0.01$, 13 D.F.).

Experiment 2: F_5 yield experiment at Trumpington, 1982-3. Table 2 summarizes the results from Expt 2. A hail storm caused some lodging in mid July, both in the tall and the short selections, but no significant effect on grain yield was found, probably because the remainder of the summer was warm and dry.

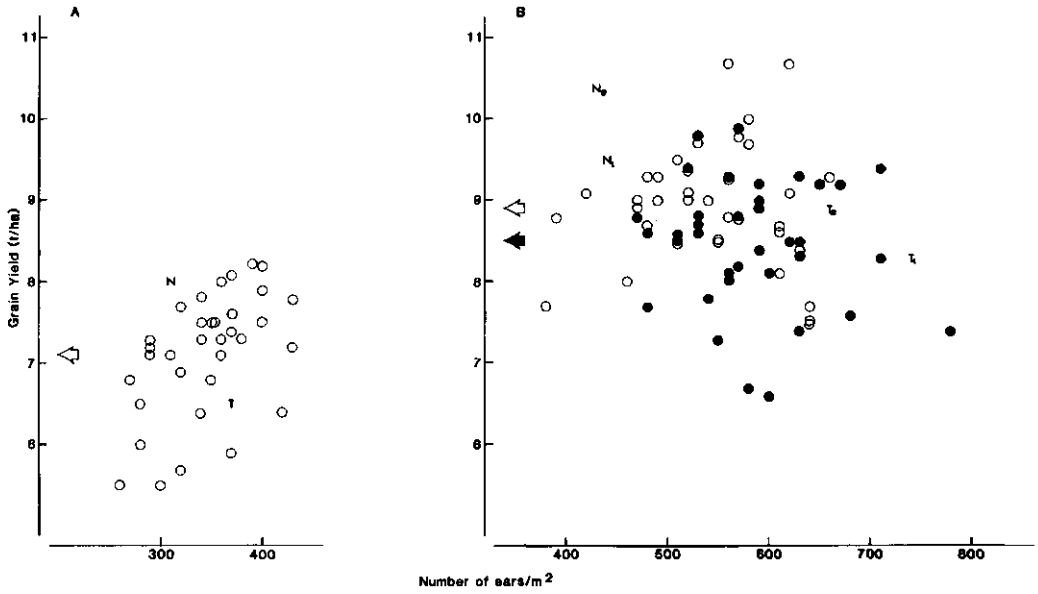

Figure 2. The relationship between grain yield and mean number of ears/m^2 in Expt 1 (A) and in Expt 2 (B), ○ early sowing, ● late sowing. N - Norman, T - Talent, in e - early sowing and l - late sowing. Arrows indicate mean grain yields.

Grain yields were greater from the early than from the late sowing for all phenotype classes and Norman and Talent. Sowing date x phenotype class interactions were not significant. The higher yield of the selections in the early sowing (0.44 t/ha) is thought to be due to the longer growing period.

The early selections yielded significantly more than the late selections, had a longer post ear emergence period and a greater mean weight per grain. The short selections were higher yielding than the tall selections, and had smaller grains but a greater harvest index. There were no significant

Table 2. Yield and yield components for Expt 2. S.E. - standard error of phenotype class mean, C.V. - mean coefficient of variation within phenotype classes. S.E. for Norman and Talent is 2.1 times the S.E. for phenotype class means.

Phenotype class/ variety	Grain yield (t/ha)*	Harvest index (%)	Plant height (cm)	Days to ear emergence after 30 April	Post ear emergence period (days)	No. of ears/m^2	Mean weight/ grain (mg)*
Early sowing							
short-early	9.67	51.1	77	28	58	563	48.9
short-late	9.11	49.6	76	35	53	521	47.5
tall-early	8.71	47.0	91	25	63	533	52.1
tall-late	8.12	44.6	96	37	53	558	50.7
Mean	8.90	48.1	85	31	57	544	49.8
Norman	10.41	50.9	82	36	53	429	57.8
Talent	8.88	47.5	81	26	61	662	44.5
Late sowing							
short-early	9.22	51.7	72	34	53	603	48.3
short-late	8.61	50.4	73	39	50	584	46.2.
tall-early	8.43	48.0	88	33	56	570	52.4
tall-late	7.57	44.3	93	40	51	583	49.6
Mean	8.46	48.6	82	37	53	585	49.2
Norman	9.52	50.9	76	41	51	473	56.6
Talent	8.27	48.4	77	33	55	668	44.7
S.E.	0.158	0.57	1.0	0.3	0.5	19.2	0.74
C.V.(%)	6.7	2.9	4.0	2.2	1.9	15.1	2.3

* at 15 % moisture content

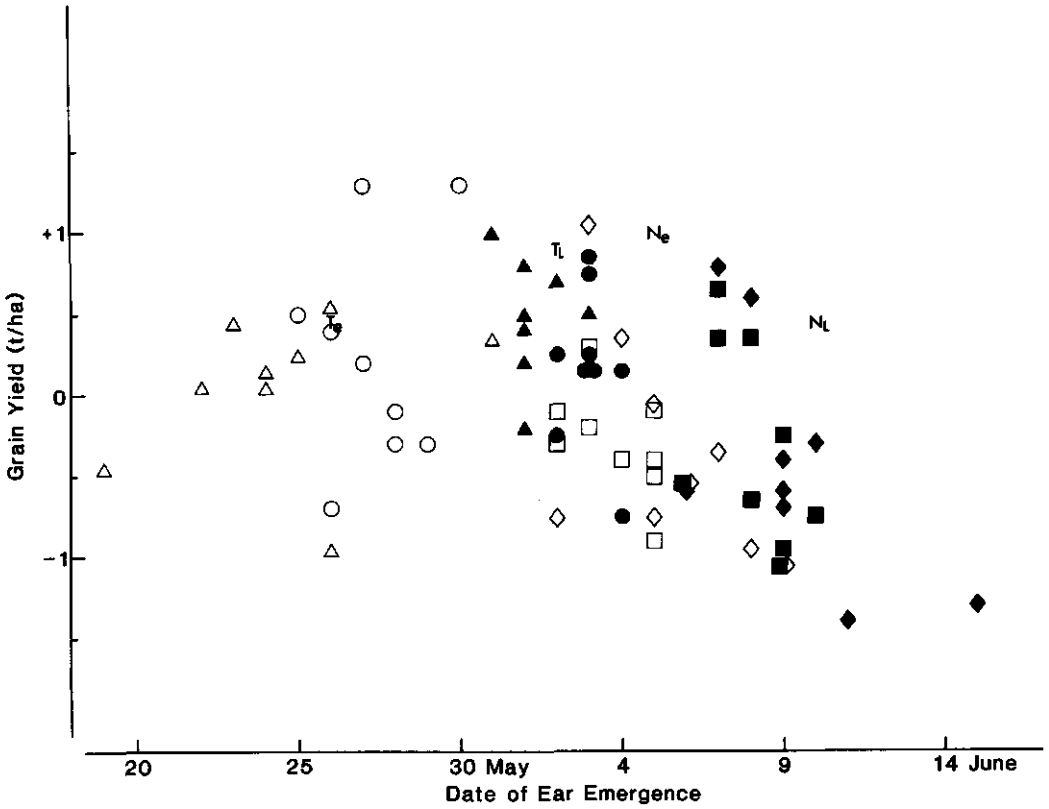

Figure 3. The relationship between grain yield and date of ear emergence in Expt 2. Grain yield is expressed as the difference between actual yield and the mean yield of the height classes in each sowing. Open symbols - early sowing, closed symbols - late sowing. ○● - short-early, □■ - short-late, △▲ - tall-early, ◇◆ - tall-late, N - Norman, T - Talent, in e - early sowing, l - late sowing.

differences between the four phenotype classes in number of ears/m^2, and there was no relationship between yield and number of ears/m^2 (Fig. 2B).

In the early sowing there were no significant differences between the phenotype classes and Norman and Talent in number of leaves and spikelets on the main stem, which averaged 12.5 and 20, respectively. In the late sowing the late selections had on average 11 leaves and 19 spikelets, one leaf and one spikelet more than the early selections. A similar difference was found between Norman and Talent. There were no significant differences in number of leaves and number of spikelets between the short and the tall phenotype classes for either sowing date.

Within each of the four phenotype classes neither plant height nor post-ear emergence period were correlated with grain yield.

For the early selections in the early sowing, the correlation coefficient between grain yield and date of ear emergence, averaged over the short and the tall selections using the z-transformation was significant and positive ($r=0.54$, $P<0.05$, 13 D.F.), but for the late selections in the early sowing and for both early and late selections in the late sowing, date of ear emergence was negatively correlated with grain yield ($r=-0.35$, $P<0.05$, 37 D.F.). Fig. 3 shows the relationship between date of ear emergence and yield. Because the early sowing was higher yielding than the late sowing and the short selections were higher yielding than the tall selections, yields in Fig. 3 have been expressed as the difference between actual yield and the mean yield of the height class in each sowing. Mean weight per grain was not correlated with yield in the early sowing, but in the late sowing the correlation between yield and mean weight per grain was significant and positive within all phenotype classes, the average correlation coefficient being 0.56 ($P<0.01$, 25 D.F.). No significant effect of number of ears/m^2 on grain yield was found (Fig. 2B).

Experiment 3: F_5 yield experiment at The Murrays, 1982-3. Table 3 summarizes the results for Expt 3. There was no significant difference in yield between the early and the late selections. The short selections yielded more than the tall selections, and had significantly fewer ears/m^2 than the tall selections.

Within the four phenotype classes neither height, date of ear emergence or number of ears/m^2 were correlated with grain yield.

Table 3. Yield and yield components for Expt 3. S.E. - standard error of phenotype class mean, C.V. - mean coefficient of variation within phenotype classes. S.E. for Norman and Talent is 2.1 times the S.E. for phenotype class means.

Phenotype class/ variety	Grain yield (t/ha)*	Plant height (cm)	Days to ear emergence after 31 May	No. of ears/m^2
short-early	8.81	78	17	581
short-late	8.72	78	21	576
tall-early	8.12	95	16	629
tall-late	8.01	96	22	646
Mean	8.41	87	19	608
S.E.	0.113	0.9	0.3	15.8
C.V.(%)	3.7	2.6	1.2	9.4
Norman	9.65	83	21	440
Talent	7.24	83	16	739

* at 15 % moisture content

Correlations between experiments. The distributions of date of ear emergence, height, mean weight per grain and harvest index were not continuous, but were different for phenotype classes. Therefore correlation coefficients between experiments were calculated separately for each phenotype class. Table 4 lists the correlation coefficients between experiments, averaged over the four classes using the z-transformation, and shows that the variation between selections within phenotype classes in Expt 1 was significantly correlated with that in Expts 2 and 3, except for grain yield, while within-phenotype class correlations between Expts 2 and 3 were significant for all variates, including yield.

Table 4. Average correlation coefficients between experiments for yield and yield components, calculated with the z-transformation. T82 - Trumpington 1981-2 (Expt 1), T83ES - Trumpington 1982-3, early sowing, T83LS - Trumpington 1982-3, late sowing (Expt 2), M83 - The Murrays 1982-3 (Expt 3).
For 25 D.F. $P<0.05$, $r=0.39$.

	Grain yield	Harvest index	Plant height	Days to ear emergence	No. of ears/m^2	Mean weight/ grain	No. of spikelets	Post ear emergence period
T82,T83ES	0.15	0.29	0.42	0.59	0.61	0.75	-	-
T82,T83LS	0.05	0.49	0.49	0.57	0.45	0.74	-	-
T82,M83	0.10	-	0.66	0.47	0.62	-	-	-
T83ES,T83LS	0.54	0.64	0.87	0.79	0.54	0.97	0.66	0.86
T83ES,M83	0.39	-	0.76	0.67	0.64	-	-	-
T83LS,M83	0.45	-	0.86	0.81	0.49	-	-	-

Table 5. Mean number of grains per ear for Expt 1 and Expt 2. S.E. - standard error of phenotype class mean, C.V. - mean coefficient of variation within phenotype classes. S.E. for Norman and Talent is 2.1 times the S.E. of phenotype class means.

Phenotype class/ variety	Expt 1	Expt 2	
		early sowing	late sowing
short-early	43.2	35.6	32.1
short-late	45.7	37.5	32.8
tall-early	39.6	32.2	28.7
tall-late	39.5	30.0	27.2
Mean	42.0	33.8	30.2
S.E.	1.22	0.86	0.86
C.V.(%)	8.4	11.4	11.4
Norman	47.9	42.2	36.4
Talent	40.1	31.8	27.7

Mean number of grains per ear. Mean number of grains per ear was not measured but was estimated by dividing grain yield by the product of mean number of ears/m^2 and mean weight per grain (Table 5). The short selections combined a smaller mean grain weight with a higher number of grains per ear. This is in agreement with the difference commonly found between genotypes carrying the Rht_2 dwarfing gene and non-semi-dwarf genotypes (Pinthus & Millet, 1978; Gale, 1978). The late lines had smaller grains than the early lines, but there were no differences in number of grains per ear between early and late lines. Bidinger et al. (1984) found similar differences between the short and tall and the early and late selections, and also showed that the higher number of grains per ear of the short selections was due to an increased number of grains per spikelet.

DISCUSSION

In a fully irrigated experiment Innes et al. (1984) found that the four phenotype classes had similar grain yields although they differed in date of ear emergence, height and yield component structure. In the experiments described here significant differences in grain yield between and within the four phenotype classes were found which were not consistent over the experiments. In contrast, the genotypic differences within and between phenotype classes in date of ear emergence, height and other variates were shown to be stable over years and sites, and were similar to those described by Innes et al. (1984) for their fully irrigated treatment. The weather conditions varied considerably for the three experiments reported here, suggesting that interactions of date of ear emergence, height and yield components with climatic factors were responsible for the variation in yield. The two growing seasons contrasted in temperature and in the occurrence of soil moisture deficits. In 1982 a dry spring was followed by a wet summer. In 1983, at both sites, a dry and hot summer followed a wet spring (Fig. 1). In both years, soil water deficits exceeded 50mm and probably reduced yields.

In Expt 1, when drought occurred early, 3 weeks before ear emergence (Fig. 1A), number of ears/m^2 was low compared with Expts 2 and 3. Innes et al. (1984) reported also a significant reduction of number of ears/m^2 for the selections at Trumpington under conditions of pre-anthesis water stress, but not to such low levels as those found in Expt 1. In their experiments, however, nitrogen fertilizer was applied at a higher rate, 150kg/ha compared with 75kg/ha in Expt 1. It is likely that the combination of an early drought and low nitrogen in this experiment reduced ear density to such a low level that it became the limiting factor for grain yield (Fig. 2A).

Although the early selections yielded more grain than the late selections in all three experiments, the difference was significant only for the two sowing dates of Expt 2. In this experiment soil moisture stress began to develop to critical levels in mid June, when the selections were flowering, and continued to build up throughout the post ear emergence period (Fig. 1). It is likely that the yield advantage of the early selections under these circumstances was due to their greater degree of drought escape compared with the late

selections. A similar result was reported by Innes et al. (1984), who showed that the grain yield of the late selections was more reduced than that of the early selections by a post-anthesis drought.

In general, late selections produced more leaves and spikelets than early selections, and it could thus be anticipated that late selections would have an increased potential for grain yield compared with early ones. The expected benefits of lateness, however, seem to be offset by the fact that the grain filling occurs later for late selections when rising temperatures, and hence accelerated ontogenesis, outweigh the potential advantage of increased leaf area and increased ear size. The results of Expt 2 support this interpretation. For early selections in the early sowing there was a positive correlation between yield and date of ear emergence (Fig. 3). For late selections in the early sowing and for all selections in the late sowing the correlation was negative. In addition, early selections had longer post ear emergence periods and larger grains than late selections in both sowings.

In Scotland a significant soil moisture deficit was established just before the earliest selections reached ear emergence (Fig. 1C). Also, the difference in mean date of ear emergence between early and late selections was reduced to approximately 5 days in comparison with 10 days in the early sowing of Expt 2, and consequently the opportunity for early selections to escape drought was less. This could explain why there were no differences between early and late selections in grain yield at The Murrays. Also the benefits of early ear emergence in terms of drought escape are likely, on average, to be less of an advantage in Scotland where water shortage is less common than in the South and East of England. However, Table 3 shows that the early selections reached maturity earlier than the late selections, and this may be advantageous in Scotland where an earlier harvest is more likely to coincide with favourable weather.

Differences in date of ear emergence are thought to confer drought escape (Fischer & Maurer, 1978). Innes et al. (1984) reported that the short and the tall selections were different in drought susceptibility: a late drought from anthesis onwards, in particular affecting mean weight per grain, reduced yield more for the short than for the tall selections, and Bidinger et al. (1984) showed that within the short selections those genotypes with the largest

grains were least affected. A similar susceptibility of short selections to late drought is also evident from the results of Woodruff & Tonks (1983) under Australian conditions, but not in the experiments reported here, where the short selections gave greater yields than the tall selections, with the exception of the unreplicated yield trial in 1981-2 (Expt 1). Post-anthesis drought in 1982-3 at Trumpington and at The Murrays (Expts 2 and 3), however, were less severe than the late drought treatment of Innes et al. (1984) and in the experiments of Woodruff & Tonks (1983). This suggests that the short genotypes in general will have a yield advantage over the tall selections, except in environments with severe post anthesis water shortage, conditions found in semi-arid regions (Arnon, 1972), but not commonly encountered in the U.K.

In all trials Norman yielded more than Talent. Talent had more ears/m^2 than Norman, but smaller and fewer grains per ear. Norman is not a typical $\underline{Rht_2}$ semi-dwarf variety because it is high in mean weight per grain, well above the mean of the short selections used here. Talent is not typical for the non-$\underline{Rht_2}$ varieties, because it has a very low mean grain weight compared with the average of the tall selections. This may explain why Norman yielded more than the mean of the comparable short-late phenotype class, while Talent was equal or lower in yield than the tall-early selections.

The late selections were similar to Norman in date of ear emergence. Most of the winter wheat varieties currently grown in the U.K. reach ear emergence at more or less the same time as Norman. In our experiments, genotypes earlier than Norman, though not selected for high yield, were shown to be as high yielding as Norman and to suffer less from a soil moisture deficit in the summer. The average yield advantage of the short selections compared with the tall ones was estimated as 0.50 t/ha, and the yield advantage of the early selections compared with the late ones was 0.42 t/ha in a combined analysis of all experiments carried out with these selections (Innes et al. 1984). Variation between years and sites clearly influenced grain yield and further work covering more seasons and sites is needed, to verify that the results presented here are of general applicability. However, it seems likely that in Great Britain semi-dwarf genotypes which flower earlier than Norman, but which like this variety have large grains, would have a high potential yield and

would suffer less from high temperatures and drought at anthesis and grain filling.

We are grateful to F.J.W. England and A. Young for organizing the trial at The Murrays, to H.H.W.M. Derks for assistance with the field trials in 1983, to J.W. Snape for help with the screening of the selections for the $\underline{Rht}_2$ dwarfing gene, and to R.B. Austin and Prof. J. Sneep for their critical reading of the manuscript. The F_2 populations from which the lines used in these experiments were selected were grown by J. Bingham FRS and J.A. Blackman, and we are grateful for their permission to take these selections.

REFERENCES

ARNON, I., 1972. Wheat. In: Crop production in dry regions. Vol. 2. Systematic treatment of the principal crops. Leonard Hill, London: 1-72.

AUSTIN, R.B. & R.D. BLACKWELL, 1980. Edge and neighbour effects in cereal yield trials. J. Agric. Sci., Camb. 94: 731-773.

AUSTIN, R.B., J. BINGHAM, R.D. BLACKWELL, L.T. EVANS, M.A. FORD, C.L. MORGAN & M. TAYLOR, 1980. Genetic improvements in winter wheat yields since 1900 and associated physiological changes. J. Agric. Sci., Camb. 94: 675-689.

BIDINGER, F.R., R.D. BLACKWELL, & P. INNES, 1984. Effects of differences in date of ear emergence and height on yield of winter wheat. 3. Individual tiller yield and yield components. J. Agric. Sci., Camb. (In the press).

BINGHAM, J., 1967. The physiology of yield in winter wheat. J. Agric. Sci., Camb. 68: 411-422.

DAY, W., B.J. LEGG, B.K. FRENCH, A.E. JOHNSTON, D.W. LAWLOR, & W. de C. JEFFERS, 1978. A drought experiment using mobile shelters: the effect of drought on barley yield, water use and nutrient uptake. J. Agric. Sci., Camb. 91: 599-623.

FISCHER, R.A. & R. MAURER, 1978. Drought resistance in spring wheat cultivars. 1. Grain yield responses. Austr. J. Agric. Res. 29: 897-912.

GALE, M.D., 1978. The effects of Norin 10 dwarfing genes on yield. In Proc. 5th Int. Wheat Gen. Symp., Indian Soc. Gen. Plant Breed., New Delhi: 978-987.

GALE, M.D., C.N. LAW, & A.J. WORLAND, 1975. The chromosomal location of a major dwarfing gene from Norin 10 in new British semi-dwarf wheats. Heredity 35: 417-421.

HOOGENDOORN, J., 1984. The basis of variation in date of ear emergence under field conditions among the progeny of a cross between two winter wheats. J. Agric. Sci., Camb. (In the press).

INNES, P. & R.D. BLACKWELL, 1981. The effect of drought on the water use of two spring wheat genotypes. J. Agric. Sci., Camb. 96: 603-610.

INNES, P., R.D. BLACKWELL & J. HOOGENDOORN, 1984. Effects of differences in date

of ear emergence and height on yield of winter wheat. 2. Effects of drought on water use and yield. J. Agric. Sci., Camb. (In the press).

PINTHUS, M.J. & E. MILLET, 1978. Interactions among numbers of spikelets, number of grains and grain weight in the spikes of wheat, Triticum aestivum L.. Ann. Bot. 42: 839-848.

SEETHARAMA, N., B.V. SUBBA REDDY, J.M. PEACOCK, & F.R. BIDINGER, 1982. Sorghum improvement for drought resistance. In: Drought resistance in crops with emphasis on rice, IRRI: 317-338.

SNEDECOR, G.W. & W.G. COCHRAN, 1967. Statistical methods, 6th edition. Iowa State University Press, Ames, Iowa, USA: 185-188.

WOODRUFF, D.R., 1983. The effect of a common date of either anthesis or planting on the rate of development and grain yield of wheat. Austr. J. Agric. Res. 34: 13-22.

WOODRUFF, D.R. & J. TONKS, 1983. Relationship between time of anthesis and grain yield of wheat genotypes with differing developmental patterns. Austr. J. Agric. Res. 34: 1-11.

7. DISCUSSION

The work presented in this thesis describes aspects of the regulation of the life cycle of wheat. The effects of daylength and low temperature on genotypes with and without photoperiod and vernalization sensitivity, and genotypic variation independent of these environmental factors, described as earliness per se, have been investigated under controlled environment conditions and in the field. Genotypic variation in the time of ear emergence and its interaction with environmental stress factors, such as soil moisture deficits and high temperature, and interaction with other genetic factors such as dwarfing genes, was shown to influence yield and yield components under British growing conditions. In the following the results and their implications for wheat breeding programmes will be discussed and suggestions for further experiments are presented.

The interactions between the effects of daylength and vernalization. Short days delay ear emergence in genotypes sensitive to photoperiod in a similar way, but not necessarily to a similar extent, as insufficient low temperature treatment affects the development of genotypes sensitive to vernalization, both under controlled environment conditions and in the field. The following theory on how photoperiod and vernalization insensitivity genes, and daylength and low temperature treatments might regulate development is based on two further observations. Firstly genotypes classified as 'photoperiod insensitive' are not totally insensitive to daylength. Insensitive genotypes were delayed in ear emergence in short days, but only slightly in comparison with photoperiod sensitive genotypes. No totally photoperiod insensitive variety was present among the varieties tested (chapter 4), and no report of such a genotype was found, suggesting that totally insensitive varieties might not exist (cf. Hunt, 1979). Secondly it was noticed that the effect of daylength on ear emergence in genotypes sensitive to both photoperiod and vernalization was dependent on the vernalization treatment. Without a sufficiently long vernalization treatment these genotypes appeared not to be

able to respond fully to long days (chapter 3 & 5; Evans & Wardlaw, 1976). Under such conditions these genotypes reacted to long days as genotypes insensitive to photoperiod, although ear emergence, both under long and short days, was much delayed in comparison with a longer vernalization treatment (Fig. 1A). Table 1 shows the effects of photoperiod and vernalization on days to ear emergence under controlled environment conditions of some of the genotypes used in the experiments. The diagram presented in Fig. 1B is an attempt to explain these observations on ear emergence in terms of interactions between daylength and low temperature treatments and the presence or absence of photoperiod and vernalization insensitivity alleles. The diagram is based on the model for rye as presented by Gott et al. (1955).

The duration of the pre-ear emergence phase is represented as a straight line between germination and ear emergence, which at certain points may be 'blocked', thus causing delay in the developmental processes leading to ear emergence. The blocks can be overcome by either the presence or absence of photoperiod and vernalization insensitivity alleles (Ppd, Vrn), or long days (LD) and short or long low temperature treatments (LT_S, LT_1).

Vernalization and photoperiod insensitive genotypes (Siete Cerros 66) grown in long days, will be able to pass all 'blocks' and proceed to ear emergence along the straight line (1). In short days such a genotype will not be able to pass the last block (LD), and will show the 'genotype independent' response (2). Vernalization insensitive but photoperiod sensitive genotypes (Highbury) grown in long days will similarly pass all blocks and proceed to ear emergence along the straight line (1). In short days, however, such a genotype will not be able to pass the Ppd/LD, and the LD block, and will show both the 'genotype dependent' and the 'genotype independent' response to short days (4).

For vernalization sensitive genotypes the Vrn/LT blocks will be crucial. To be able to pass the first, the Vrn_x/LT_S block, either the major vernalization insensitivity allele Vrn_1 or one of the minor Vrn insensitivity alleles, or a short low temperature treatment is needed. Without this, ear emergence will not occur normally. A long low temperature treatment or the Vrn_1 insensitvity allele is needed to pass the Vrn_1/LT_1 block. Genotypes will then react to short days like spring genotypes, only regulated by the presence (e.g. Talent, PPvv) or absence (e.g. Norman, Bersee, ppvv) of photoperiod insensitivity

Table 1. Response to photoperiod and vernalization, expressed as a percentage of days to ear emergence after 8w vernalization at 5°C, and subsequent 20h photoperiod treatment. a. Means of photoperiod sensitive (ppvv) and means of photoperiod insensitive (PPvv), vernalization sensitive F_5 selections from the cross between Norman and Talent (chapter 5). b. Vernalization sensitive varieties (chapter 4). c. Vernalization insensitive varieties (chapter 4). Standard error of mean ear emergence dates was 1.8 day, standard errors of percentages was 2.5%.
(-) Treatment not grown, (*) Plants failed to reach ear emergence. Treatments are described by [weeks vernalization, hours photoperiod].

Genotype	Days to ear emergence for [8,20]	Days to ear emergence as % of [8,20]				
		[8,12]	[4,20]	[4,12]	[0,20]	[0,12]
a.						
ppvv	75.2	124	111	122	*	*
PPvv	69.5	115	113	124	*	*
b.						
Norman	75.9	137	112	131	*	*
Bersee	74.6	138	99	133	117	130
Talent	66.7	115	106	130	154	165
c.						
Highbury	67.8	144	-	-	90	131
Siete Cerros 66	65.3	116	-	-	90	113

alleles. If the effect of the low temperature treatment or the vernalization insensitivity alleles is sufficient to pass the $\underline{Vrn_x}/LT_s$ block, but insufficient to pass the the $\underline{Vrn_1}/LT_1$ block, the genotype dependent response will be shown, independent of the daylength and the presence or absence of photoperiod insensitivity alleles. The occurrence of the genotype independent response will still be dependent on the daylength (3)(4).

The effect of a minor vernalization insensitivity allele combined with a short low temperature treatment (Talent, Bersee) is equivalent to the presence of the $\underline{Vrn_1}$ allele (spring wheats) in being able to pass the $\underline{Vrn_1}/LT_1$ block. This can explain why in the case of Bersee there was no difference in response

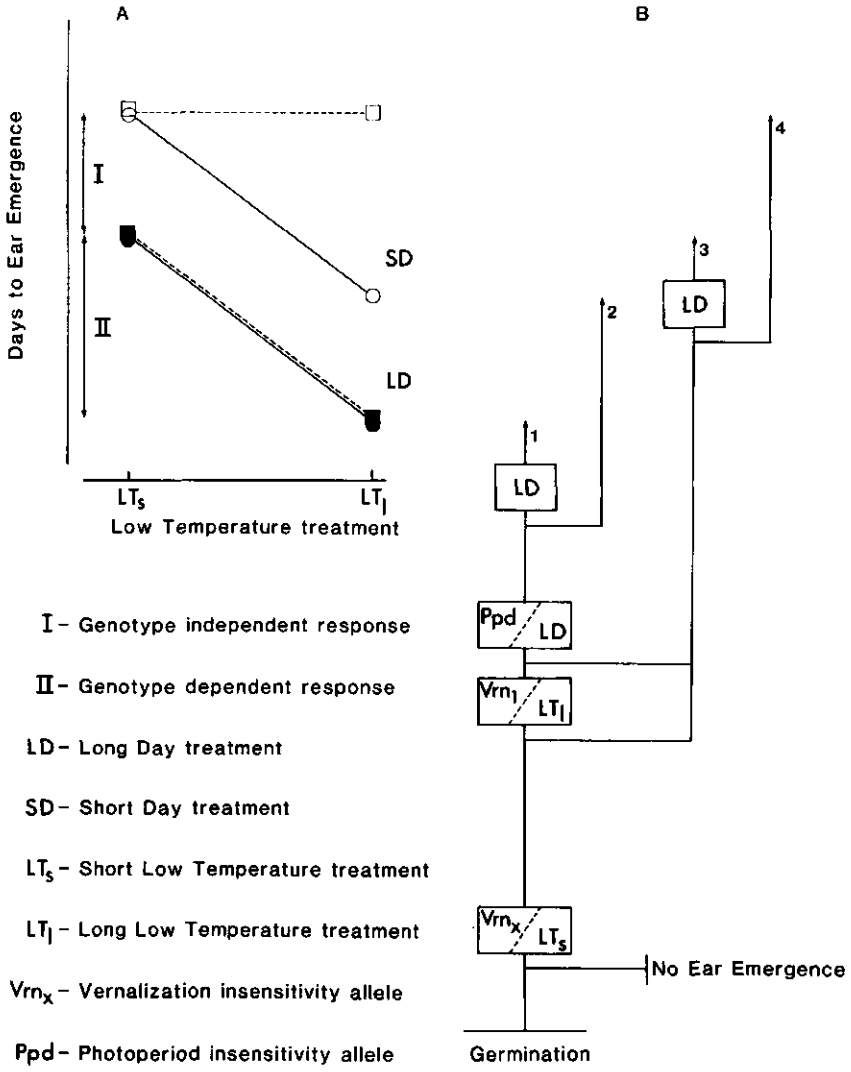

Figure 1. A) Schematic representation of the effect of daylength and vernalization treatment on date of ear emergence of vernalization sensitive and photoperiod sensitive (- - - -) or photoperiod insensitive (———) varieties. Open symbols - short daylength treatment, closed symbols - long daylength treatment. B) Theoretical representation of the effects of the daylength and low temperature in interaction with photoperiod and vernalization insensitivity alleles on the length of the pre-ear emergence period.

to daylength between the 8 and 4w vernalization treatment, while unvernalized plants were less sensitive (Table 1).

For reasons of simplification it has been assumed that the insensitivity alleles on all Vrn loci other than Vrn_1 require a similar amount of additional low temperature treatment to be completely vernalized, but it is highly likely that there are differences between the effects of these alleles. The results presented in this thesis, on which the model is based, suggest that a spring wheat can be regarded as a genetically vernalized winter wheat and that there is an interaction between the effects of photoperiod and vernalization sensitivity on time of ear emergence.

Gott et al. (1955) did not use an intermediate vernalization treatment, and therefore it cannot be deduced from their data whether there was a difference in response to photoperiod between partly vernalized and completely vernalized rye plants. The use of factorial combinations of a range of vernalization and photoperiod treatments is crucial to detect the interaction between photoperiod and vernalization sensitivity and will be needed to investigate this model further.

The genetics of the regulation of development. The discovery of the effects of photoperiod and vernalization made it possible to recognize insensitivity genes and to study their inheritance (Klaimi & Qualset, 1973; 1974; Pugsley, 1971; 1972). Experiments where the inheritance of earliness per se genes has been studied have not been reported, however. Fig. 2 shows results of an experiment with plants derived from a cross between the vernalization insensitive varieties Highbury and Gamset (Hoogendoorn, internal report PBI, 1984). Gamset is insensitive, Highbury is sensitive to photoperiod (chapter 4). Parents, F_1 and F_2 plants were grown in long and short days. Insensitivity to photoperiod was dominant and apparently controlled by one gene in this cross.

Under long day conditions Highbury reached ear emergence 8 days after Gamset with 5 more spikelets, a difference considered to be controlled by the photoperiod sensitivity gene as well as by earliness per se genes (chapter 4). The F_1 was intermediate between the parents. In short days the photoperiod insensitive genotypes in the F_2 were on the average later and had more spikelets than Gamset. Photoperiod sensitive genotypes were on the average

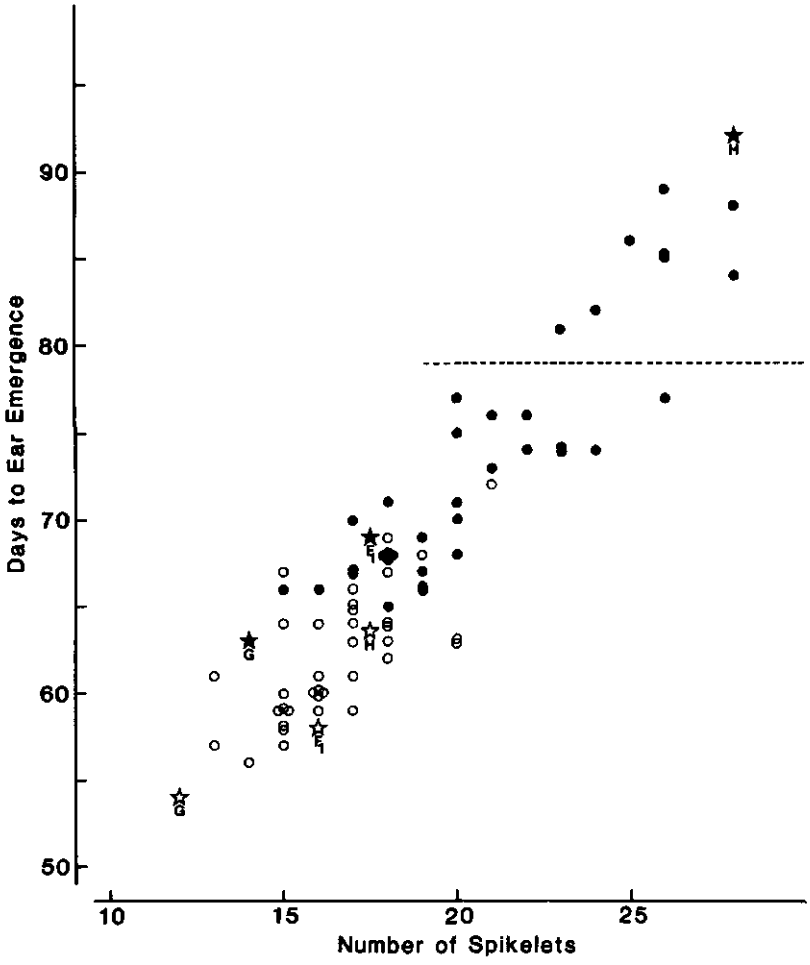

Figure 2. The correlation between days to ear emergence and number of spikelets in the F_1 and the F_2 from a cross between Highbury (H) and Gamset (G), grown in 20h daylength (open symbols) or 12h daylength (closed symbols). Line (----) marks difference between photoperiod sensitive and insensitive F_2 plants.

earlier and had fewer spikelets than Highbury. The variation in days to ear emergence and in number of spikelets of F_2 plants was highly correlated both under long days ($r=0.69$, $P<0.01$) and in short days ($r=0.78$, $P<0.01$, using only the photoperiod insensitive genotypes). The difference in earliness *per se* between Highbury and Gamset appears to be related to a difference in ear size, which was inherited quantitatively and was independent of photoperiod insensitivity.

The availability of aneuploid stocks in wheat and the use of controlled environment experiments has made it possible to locate the photoperiod insensitivity genes on chromosome 2B and 2D, and the vernalization insensitivity genes on the group 5 chromosomes and on chromosome 7B (Law & Scarth, 1984). Mork work is needed to compare the effects of allelic variation on the *Ppd*$_1$ and the *Ppd*$_2$ photoperiod insensitivity loci, and to study the effects of allelic variation at the vernalization insensitivity loci. Earliness *per se* genes have been located on 2B (Scarth & Law, 1983), 7B (Flood & Halloran, 1983) and 3A, 4B, 4D and 6B (chapter 3). Scarth & Law (1983) were able to separate the effect of a gene affecting growth rate on chromosome 2B from that of the major photoperiod insensitivity gene by studying primordia initiation and using marker genes. Similar methods will be needed to study the effects of the earliness *per se* factors reported in this thesis. It has been argued that substitution lines carrying the Bersee and Spica chromosomes would be the most appropriate genotypes for such experiments. To avoid complications caused by sensitivity to photoperiod and vernalization, monosomic series providing an insensitive background should be used to develop these substitution lines. From the monosomic series listed by Law et al. (1981), Kalyansona, an Indian variety closely related to Siete Cerros 66, or Federation, an old Australian variety, are most likely to offer such an insensitive background.

Although the number of identified genes controlling growth and development of wheat is still increasing, very little is known about how these genes control the biochemical processes in the plant which determine photoperiod and vernalization insensitivity, and differences in earliness *per se*. Phytochrome is likely to be involved in the regulation of photoperiod insensitivity (Vince-Prue, 1975). No clear indication that any hormone or pigment is involved

in vernalization insensitivity has been found (Chouard, 1960; Bernier et al. 1981). Thus conventional biochemical approaches are failing to make much progress towards the identification of the active agents formed under the influence of long days and low temperature or by the photoperiod and vernalization insensitivity genes. Developments in DNA biology might in the future open new approaches to the study of the structure and the effects of proteins coded for by the photoperiod and vernalization insensitivity alleles. Law & Scarth (1984) suggest that mobile DNA elements could be used to produce clones of insensitivity genes. Subsequently DNA sequencing would give information on the structure of the proteins coded by the genes. The cloned DNA could also be used as a probe to determine when and where in the plant the gene is activated. Ultimately it might be possible to introduce the gene into bacteria and higher plants, and to bring it to expression. However, mobile elements, such as those discovered in Drosophila, Zea mays and Antirrhinum, have not yet been found in wheat. Until then molecular techniques will not be available to study the effects of developmental genes in wheat, but it seems that molecular studies will be more likely to add to the understanding of the biochemical pathways regulating the development of the wheat plant than conventional biochemical studies.

The implications for wheat breeding programmes. The increased understanding of how the low temperature, the daylength, and developmental genes interact in the regulation of the length of the pre-anthesis and the grain filling period under field conditions, should enable plant breeders to 'design' a ideotype for development optimally adjusted to the environmental conditions, and to introduce the appropriate combinations of photoperiod, vernalization and earliness per se genes into breeding programmes.

Austin et al. (1980) showed that modern British winter wheat varieties reach ear emergence earlier than varieties widely grown in the earlier part of this century. Most British wheat varieties are sensitive to photoperiod and vernalization. There are some indications that the earlier ear emergence might be due to a reduction of vernalization sensitivity (Holdfast versus Norman, chapter 4). Between 1900 and 1960 the average length of the growing season in England, as measured by the number of days with a temperature above 6^{o}C, has

increased by 2 to 3 weeks, a change in climate which is comparable to the present difference between the Netherlands and Ireland (Lamb, 1965). A reduced vernalization sensitivity is likely to have beneficial effects on grain yield because of a higher assimilation rate during the winter months resulting in increased pre-anthesis biomass.

It has been argued that for British conditions, because of the frequent occurrence of a soil moisture deficit in the later part of the growing season, genotypes earlier than the present highest yielding varieties might enable high yields to be combined with increased yield stability, and that this would be especially the case for varieties with dwarfing genes (chapter 6; Innes et al. 1984). Photoperiod insensitivity, vernalization insensitivity, and earliness per se all are likely to result in earlier ear emergence when introduced into British wheat varieties. An optimum date for ear emergence was found in field trials in 1982-3, suggesting that extremely early ear emergence will have negative effects on yield. The effect of photoperiod insensitivity alleles in advancing ear emergence and reducing number of spikelets per ear, was much larger than the effect of the vernalization insensitivity alleles (chapter 5). Therefore introduction of photoperiod insensitivity alleles without simultaneous selection for later ear emergence using earliness per se, might be less suitable than changing the degree of vernalization sensitivity as a means of achieving earlier ear emergence. Recently, semi-winter varieties less sensitive to vernalization have been accepted for the Recommended List for England and Wales, which reach ear emergence slightly earlier than the common vernalization sensitive varieties (J. Bingham, personal communication).

Photoperiod and vernalization genes are easier to identify than earliness per se genes, and offer therefore a simpler way of achieving earlier ear emergence. Earliness per se, however, will be the only possible source of variation in ear emergence which can be exploited in Continental climates with severe winters where the photoperiod and vernalization sensitivity cannot be altered because this will in general be accompanied by a decrease in winter hardiness. The international wheat breeding programme of CIMMYT in Mexico, which has supplied material for many national breeding programmes in the tropics and sub-tropics, produces varieties which are mostly insensitive to photoperiod and vernalization. Earlier ear initiation and ear emergence in

these genotypes can only be achieved by using earliness per se genes, which might be required for double and triple cropping systems (Hanson et al. 1982). For those tropical areas where a longer growing period is available, photoperiod or vernalization sensitivity can be introduced. Since, however, wheat in the tropics in general is grown in the 'winter', when the daylength is equal to or less than 12h, the introduction of alleles for sensitivity to photoperiod might extend the growing cycle too far, and the replacement of the Vrn_1 insensitivity allele with minor vernalization insensitivity genes could be more appropriate.

The analysis of the data on the USDA Small Grain Collection has shown where genotypes can be found with either photoperiod and vernalization sensitivity or insensitivity, and positive or negative earliness per se factors. Sensitivity or insensitivity and earliness per se in individual genotypes selected to be used in breeding programmes has to be checked. Minor vernalization genes are easily identified by growing plants under extended daylength conditions without vernalization. Genotypes reaching ear emergence late, with nine or more leaves, are likely to have minor vernalization genes. Early genotypes with six or seven leaves probably are vernalization insensitive genotypes, and those that do not reach ear emergence at all will be true vernalization sensitive 'winter' genotypes. Selecting genotypes with photoperiod insensitivity genes requires a long vernalization treatment followed by a short day treatment. Earliness per se genes can only be accurately recognized in controlled environment conditions, and only when the photoperiod and vernalization sensitivity of the studied genotypes is known.

The length of the pre-ear emergence phase in wheat is correlated with number of leaves, tillers and spikelets per ear, and hence with potential yield. It is not suprising, therefore, that the regulation of ear emergence has been widely studied. The control of ear emergence was found to be largely due to just two environmental factors, photoperiod and vernalizing temperatures. Subsequently it has become clear that sensitivity to photoperiod and vernalization is regulated by relatively few genes with major effects. It would thus be expected that our understanding of ear emergence would be clear and complete by now. However, this is certainly not the case. Interactions between the major

genes have led to complicated patterns of ear emergence in which it is difficult to identify the effects of individual genes. Characters such as ear size, growth rate and sensitivity to temperature influence grain yield directly, but also indirectly, since these factors cause variation in earliness *per se*, modifying the effects of photoperiod and vernalizing temperatures on time of ear emergence.

Much of the work on the control of ear emergence has been focussed on either the genetics, or the physiology, or the effects of time of ear emergence on yield and yield components. In the work presented here these three approaches were combined to try to achieve an integrated study of time of ear emergence. The results have left many problems unsolved, and raised several new questions. However, the integrated approach used here has been able to demonstrate that both genes and environmental factors controlling ear emergence can have similar effects on ear emergence and subsequently on grain yield, and that there are sources of variation in ear emergence which can be exploited in any part of the world where wheat is grown. The results also imply that the possibilities of varying time of ear emergence have not yet been exhausted, and that it should be feasible to grow wheat in climates now still considered to be too extreme, by manipulating sensitivity to photoperiod, sensitivity to vernalization or earliness *per se*.

REFERENCES

AUSTIN, R.B., J. BINGHAM, R.D. BLACKWELL, L.T. EVANS, M.A. FORD, C.L. MORGAN & M. TAYLOR, 1980. Genetic improvements in winter wheat yields since 1900 and associated physiological changes. J. Agric. Sci., Camb. 94: 675-689.

BERNIER, G., J. KINET & R.M. SACHS, 1981. The physiology of flowering. Vol. I, CRC Press, Florida, 149 pp.

CHOUARD, P., 1960. Vernalization and its relations to dormancy. Ann. Rev. Plant Phys. 11: 191-238.

EVANS, L.T. & I.F. WARDLAW, 1976. Aspects of the comparative physiology of grain yield in cereals. Adv. Agron. 28: 301-359.

FLOOD, R.G. & G.M. HALLORAN, 1983. The influence of certain chromosomes of the hexaploid wheat cultivar Thatcher on time to ear emergence in Chinese Spring. Euphytica 32: 121-124.

GOTT, M.B., F.G. GREGORY & O.N. PURVIS, 1955. Studies on vernalization of cereals. XIII Photoperiodic control of stages in flowering between initiation and ear formation in vernalized and unvernalized Petkus winter rye. Ann. Bot.

19: 87-126.

HANSON, H., N.E. BORLAUG & R.G. ANDERSON, 1982. Wheat in the third world. Westview Press Inc. Colorado, 174 pp.

HUNT. L.A., 1979. Photoperiodic responses of winter wheats, from different climatic conditions. J. Plant Breed. 82: 70-80.

INNES, P., R.D. BLACKWELL & J. HOOGENDOORN, 1984. Effects of differences in date of ear emergence and height on yield of winter wheat. 2. Effects of drought on water use and yield. J. Agric. Sci., Camb. (In the press).

KLAIMI, Y.Y. & C.O. QUALSET, 1973. Genetics of heading time in wheat (Triticum aestivum L.). I The inheritance of photoperiodic response. Genetics 74: 139-156.

KLAIMI, Y.Y. & C.O. QUALSET, 1974. Genetics of heading time in wheat (Triticum aestivum L.). II The inheritance of vernalization response. Genetics 76: 119-133.

LAMB, H.H, 1965. Britain's changing climate. In C.G. JOHNSON & L.P. SMITH (Eds) The biological significance of climatic changes in Britain, Academic Press, London: 3-33.

LAW, C.N., J.W. SNAPE & A.J. WORLAND, 1981. Intra-specific chromosome manipulation. Phil. Trans. R. Soc. London, B.292: 509-518.

LAW, C.N. & R. SCARTH, 1984. Genetics and its potential for understanding the action of light in flowering. In D. VINCE-PRUE (Ed.) Light and the flowering process, Academic Press, London (In the press).

PUGSLEY, A.T., 1971. A genetic analysis of the spring-winter habit of growth in wheat. Austr. J. Agric. Res. 22: 21-31.

PUGSLEY, A.T., 1972. Additional genes inhibiting winter habit in wheat. Euphytica, 21: 547-552.

SCARTH, R. & C.N. LAW, 1983. The location of the photoperiod genes $\underline{Ppd_2}$ and an additional factor for ear emergence time on chromosome 2B of wheat. Heredity 51: 607-619.

VINCE-PRUE, D., 1975. Photoperiodism in plants. McGraw Hill, London, 444 pp.

SUMMARY

The timing of ear emergence in wheat is largely controlled by photoperiod and vernalization. Large genotypic differences in sensitivity to photoperiod and vernalization exist.

Studies on the response to vernalization are complicated by growth and development during the vernalization treatment. It was shown that this growth and development could be adequately equated to time at higher non-vernalizing temperatures by comparing the increase in number of primordia during a vernalization treatment with that under non-vernalizing conditions. Alternatively the vernalization treatment could be given to developing grains in the ear, transforming vernalization sensitive into insensitive grains (chapter 2).

Controlled environment experiments with reciprocal crosses between monosomic lines of two vernalization sensitive wheats, the early variety Spica from Australia and the late variety Bersee from France, showed that a photoperiod insensitivity allele was present on the $\underline{Ppd}_2$ locus in Spica, and that both varieties carried a vernalization insensitivity allele on chromosome 5B. Factors independent of photoperiod and vernalization, the effects of which are described as earliness *per se* and in this experiment were thought to influence rate of development and number of spikelets, were found on chromosomes 4B, 4D, 3A and 6B (chapter 3).

Experiments in controlled environments showed that even after vernalization and in long days, genotypes sensitive to photoperiod and vernalization reached ear emergence later than insensitive genotypes. The variation in ear emergence within phenotype classes, however, was shown to be large, and this was considered to be due to earliness *per se*. The results of the controlled environment studies were compared with data on the wheat accessions in the USDA Small Grain Collection, and a close correlation between the two sets of data was found, both for differences in sensitivity to photoperiod and vernalization and for differences in ear emergence independent of photoperiod and vernalization. This indicates that the results of controlled environment

experiments can be used to predict the timing of ear emergence under field conditions (chapter 4).

The effects of differences in ear emergence on yield were tested with F_5 lines selected from a cross between Norman, a late semi-dwarf winter variety from Great Britain, and Talent, an early winter variety from France. The selections represented early and late, and short and tall genotypes in equal numbers. Earliness was shown to be linked with photoperiod and/or vernalization insensitivity (chapter 5), and short stature with the presence of the $\underline{Rht_2}$ dwarfing allele. In field trials in 1981-2 and 1982-3 at PBI in Cambridge, and in 1982-3 at The Murrays experimental farm of the Scottish Crop Research Institute near Edinburgh, the short selections gave yields greater or equal to the tall selections, and the early selections gave yields greater or equal to the late selections. Earliness was thought minimize yield loss by enabling the crop to escape drought stress around and after ear emergence, and this was considered to be especially important for the short selections (chapter 6).

It has been shown that both genes and climatic factors such as daylength and winter temperatures can have similar effects on ear emergence and subsequently on yield. When it is considered beneficial to alter time of ear emergence, either vernalization sensitivity, photoperiod sensitivity or earliness *per se* factors could be varied. Changing photoperiod or vernalization sensitivity will be relatively easy because the effects of the genes involved can be recognized. However, the climate might not allow a change in photoperiod or vernalization sensitivity. Variation for earliness *per se* will affect time of ear emergence independently of vernalizing temperatures and daylength but is difficult to identify and as yet little is known about the underlying physiology and genetics.

SAMENVATTING

Het gewas tarwe wordt gekenmerkt door een wijde verspreiding over de wereld en grote variatie in groeiduur. De overgang van de vegetatieve naar de generatieve groeifase, en daarmee voor een groot gedeelte ook de lengte van de totale groeiperiode, wordt voornamelijk bepaald door twee klimaatsfactoren, daglengte en temperatuur; korte dagen en het ontbreken van een periode van lage temperaturen tussen 0 en 10°C (vernalizatie), vertragen het in de aar komen van vele tarwe rassen. Dit heeft bijvoorbeeld tot gevolg dat tarwe gezaaid in de herfst in gematigde streken gedurende de wintermaanden vegetatief blijft en pas in het voorjaar in de aar komt. Er bestaat grote genetische variatie voor daglengte en vernalizatie gevoeligheid. Zo worden de meeste zomer tarwe rassen in het geheel niet in de ontwikkeling geremd door het achterwege blijven van vernalizatie. Het in de aar komen van sub-tropische tarwe rassen wordt nauwlijks vertraagd door korte dagen. Dit maakt het mogelijk tarwe in de sub-tropen in de wintermaanden te telen om zo de droogte en hoge temperaturen van de zomer te vermijden. Naast gevoeligheid voor daglengte en vernalizatie zijn er ook andere factoren die het in de aar komen van tarwe beïnvloeden, zoals bijvoorbeeld groeisnelheid en aargrootte. Het gezamelijk effect van factoren onafhankelijk van daglengte en vernalizatie kan worden beschreven als vroegheid *per se*. De regulatie van het in de aar komen van de tarweplant en de consequenties van variatie hierin voor opbrengst vormen het onderwerp van dit proefschrift.

Gevoeligheid voor daglengte en vernalizatie kunnen nauwkeurig worden onderzocht in een fytotron. De bestudering van het effect van vernalizatie op het in de aar komen wordt evenwel bemoeilijkt door het optreden van vegetatieve groei gedurende de vernalizatie behandeling. Door de ontwikkeling te volgen van het hoofdstengel meristeem van zaailingen in vernalizerende en niet vernalizerende omstandigheden, bleek het mogelijk te zijn de groei die optreedt gedurende vernalizatie behandelingen uit te drukken in dagen groei in niet vernalizerende omstandigheden. Daarnaast bleek het mogelijk te zijn om onrijpe korrels op de moederplant te vernalizeren, en zo konden verschillende

vernalizatie behandelingen vergeleken worden zonder de complicaties veroorzaakt door vegetatieve groei gedurende vernalizatie (hoofdstuk 2).

F_1 planten van reciproke kruisingen tussen monosome lijnen van twee vernalizatie gevoelige tarwe rassen, het vroege ras Spica en het late ras Bersee uit Frankrijk, werden vergeleken voor vernalizatie en daglengte gevoeligheid in het fytotron. Spica bleek een allel voor daglengte ongevoeligheid te bezitten op het $\underline{Ppd_2}$ locus op chromosoom 2B. Een zwak vernalizatie ongevoeligheids allel op het $\underline{Vrn_2}$ locus kon worden aangetoond op chromosoom 5B in zowel Spica als Bersee. Aanwijzingen voor vroegheid *per se* genen werden gevonden voor de chromosomen 4B, 4D, 3A en 6B (hoofdstuk 3).

De grote verschillen in vernalizatie en daglengte gevoeligheid tussen tarwe rassen van zeer uiteenlopende herkomsten, aangetoond in fytotron proeven, vormden de basis voor een indeling in extra-winter, winter, semi-winter en zomer tarwes, en in daglengte gevoelige en ongevoelige rassen. Zelfs na vernalizatie en onder lange dag condities bleken de daglengte gevoelige en de vernalizatie gevoelige rassen (winter types) later in de aar te komen dan ongevoelige rassen. Aangetoond werd dat het gezamelijk effect van vroegheid *per se* factoren in belangrijke mate bijdraagt tot de regulatie van het in de aar komen. Resultaten van fytotron proeven kwamen overeen met de resultaten van veldproeven met de tarwe collectie van de USDA Small Grain Collection, bestaande uit 10.409 nummers. Dit geeft aan dat daglengte gevoeligheid, vernalizatie gevoeligheid, en vroegheid *per se* niet alleen in het fytotron, maar op vergelijkbare wijze ook onder veldomstandigheden het in de aar komen bepalen (hoofdstuk 4).

De relatie tussen opbrengst en het moment waarop tarwe in de aar komt is onderzocht met F_5 lijnen geselecteerd uit de nakomelingschap van een kruising tussen Norman, een kortstro winter tarwe ras uit Groot Brittannie, en Talent, een winter tarwe ras uit Frankrijk dat in Cambridge vroeger dan Engelse rassen in de aar komt. Vroege en late, en kortstro en langstro genotypes werden in gelijke aantallen geselecteerd. Het verschil in strolengte bleek gecorreleerd te zijn met de aanwezigheid van het $\underline{Rht_2}$ kortstro allel. De vroege selecties en Talent bleken daglengte ongevoelig te zijn en/of minder gevoelig voor vernalizatie, in vergelijking met de late selecties en Norman (hoofdstuk 5). Opbrengst proeven werden in 1981-2 en in 1982-3 uitgevoerd op het Plant

Breeding Institute in Cambridge en in 1982-3 op The Murrays, de proefboerderij van het Scottish Crop Research Institute, vlakbij Edinburgh. In alle proeven waren de kortstro en de vroege selecties tenminste gelijk en meestal hoger in opbrengst dan respectievelijk de langstro en de late selecties. Vroegheid bleek opbrengst reductie ten gevolge van het in Engeland regelmatig voorkomende watertekort gedurende de vroege korrelvullingsfase te kunnen beperken (hoofdstuk 6).

Uit de gegevens gepresenteerd in dit proefschrift blijkt dat genen en klimaat het in de aar komen van het tarwe gewas bepalen, en tezamen daardoor zowel de potentiele als de gerealiseerde opbrengst beinvloeden. Variatie in het in de aar komen kan worden gecreeerd door daglengte gevoeligheid, vernalizatie gevoeligheid en vroegheid per se te veranderen. Verschillen in daglengte en vernalizatie gevoeligheid zijn relatief eenvoudig te identificeren, maar het effect is sterk afhankelijk van het klimaat. Vroegheid per se is niet zo eenvoudig te herkennen, maar het effect is onafhankelijk van daglengte en vernalizerende temperaturen, en kan daardoor gebruikt worden om het moment van het in de aar komen te optimaliseren wanneer het klimaat het niet toelaat om daglengte en vernalizatie gevoeligheid te veranderen.

CURRICULUM VITAE

Coosje Hoogendoorn was born on 3 July 1955 in Amsterdam. Both grandfathers were farmers; her father is a chief gardener in Amsterdam. Therfore it should not be surprising that after passing the university entrance exams (Gymnasium β , oude stijl) at the Hervormd Lyceum West in Amsterdam in 1973, she choose to do a degree at the Agricultural University in Wageningen. She completed the 'Kandidaats' degree (BSc) in plant breeding in 1977, and the 'Ingenieurs' degree (MSc) in 1980.

The work for this thesis was done between October 1980 and June 1984 in the Physiology Department of the Plant Breeding Institute in Cambridge. Presently she is working in the Cytogenetics Department of this institute on the genetics of dwarfing genes and their pleiotropic effects on wheat yield and yield components under tropical and sub-tropical conditions, a joint project of CIMMYT (Mexico) and the Plant Breeding Institute, financed by the British Overseas Development Administration.