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PHASIC DEVELOPMENT IN BARLEY

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ABSTRACT

The short days and mild winter temperatures of the Australian growing season elicit the expression of inherent variation in the phasic development of certain barley genotypes that does not correspond with their developmental behaviour from either winter or spring plantings at higher latitudes.

Results from the screening of a range of genotypes exhibit considerable variation for a basic vegetative period and for response to photoperiod. Floral initiation must occur at photoperiods of less than 10.5 hours for ear emergence to occur at a time appropriate for commercial barley production in southern Australia.

Differential genotype response to vernalisation can be demonstrated from summer plantings but not, other than in extreme cases, from commercial seeding dates, in late autumn/early winter.

KEYWORDS

Vernalisation, photoperiod, vegetative phase, reproductive phase, phenotypic variation, ear emergence, anthesis.

INTRODUCTION

The life cycle of a typical Gramineae is punctuated by a sequence of irreversible developmental events, commencing with germination and leading through floral initiation to ear emergence/anthesis and then to maturity. Floral initiation separates an initial *vegetative* phase from the *reproductive* phase that follows, with ear emergence/anthesis subdividing the latter into pre and post anthesis stages. The vegetative phase is divisible into three stages defined by Calder (1965) as juvenile, induction, and initiation, with progress from one to the next depending on the completion of the proceeding stage.

Temporal variation in the duration of the life cycle and that of its component phases/stages provides the basis for differences in developmental behaviour contrastingly described for agronomic purposes as 'winter' v. 'spring' and/or as 'early' v. 'late' (Reid and Wiebe, 1979). Such differences arise primarily from variation in the duration of the *vegetative* phase, because the day-degree requirements covering the duration of the period from floral initiation to ear emergence/anthesis are similar in most genotypes (Yasuda, 1981; Inagaki and Masuda, 1984).

The time to floral initiation, and indirectly, to ear emergence, is a function of four variables — three of which involve inherent independent differences in genotype response to the environment. The role of vernalisation (in respect of the induction stage) and photoperiod (in respect of the initiation stage), have been well documented. Numerous authors have contributed to this literature, notably Takahashi, Yasuda and their co-workers (see Takahashi and Yasuda, 1957 and 1970; Yaduda, 1981).

These authors have also identified a 'third physiological factor' affecting residual variation which is expressed under conditions of non-limiting photoperiod once requirements for vernalisation have been provided for. This third factor corresponds to the concept of juvenility discussed by Calder (1965) for sugar cane, bamboo, and *Hordeum spontaneum*, and variously described for *H. vulgare* as 'earliness in the narrow sense' by Takahashi and Yasuda (1957 and 1970), 'sensitivity to long photoperiod' (Inagaki and Masuda, 1984) and, a 'minimum growth requirement' (Yasuda, 1981).

A fouth variable, or complex of variables normally associated with growth and quantitative developmental variation, such as nutrient supply, light intensity, spectral composition, and crop density has been reported to modify relative durations separating phasic developmental events (Ormrod, 1965; Aitken, 1965; Kirby and Faris, 1970; Briggs, 1978).

PHENOTYPIC VARIATION AND GENETIC INTERPRETATION

Inherent differences in response to vernalisation and photoperiod, and for a basic vegetative period, have been reported. Studies on the duration of exposure to vernalisation temperatures required to effect conversion from winter to spring have led Takahashi and Yasuda (1970) to recognise six 'grades of spring habit' ranging from Grade I (= zero requirement = extreme spring) to Grade VI (= obligate exposure for more than 40 days during the Japanese winter = extreme winter).

This qualitative difference in vernalisation requirement has been explained on the basis of three gene loci; Sh/sh, Sh2/sh2, and Sh3/sh3 located on Chromosomes 4, 7, and 5, respectively. Alleles sh Sh2 Sh3 code for extreme spring

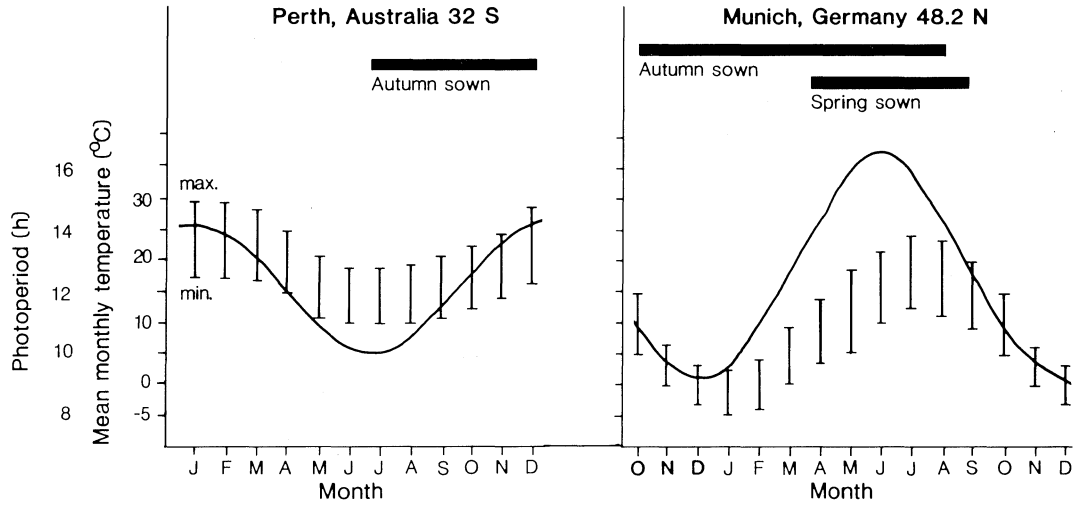

Figure 1. Seasonal trends for photoperiod (h) and temperature range (°C) for Perth and Munich. Growing season duration for autmn and spring-sown crops shown by horizontal bars.

(Grade 1) and their alternative alleles for extreme winter habit (Grade VI). The combination of multiple factors, dominant epistasis of Sh and sh over their respective alleles at the other two loci, and a multiple allelic series at the Sh2 locus accounts for the intermediate grades of spring habit recognised.

Likewise, genotypes differ in respect of the critical photoperiod required for floral initiation to proceed. They range from day neutral in which reproductive development proceeds under either short or long photoperiods. Those genotypes that remain vegetative under short days but develop reproductively as photoperiod increases are referring to as being 'sensitive to short photoperiod'.

Genetic control of earliness under short days has been explained by Takahashi and Yasuda (1970) on the basis of a two gene model involving a minor deviation due to dominance or, to the action of a single recessive located on Chromosome 5 and designated ea_k. This gene is considered allelic to ea_a reported by Gustaffson *et al.* (1960) but not to other recessive ea genes reported by Ramage and Suneson (1958) or, to a number of genes for early maturity designated Ea, Ea2, ea4, Ea5, ea7 (Soggaard *et al.*, 1984).

Precise details of the concept of juvenility in the Gramineae have not been examined. From the study of segregating populations of barley Takahashi and Yasuda (1970) suggest the character they define as 'earliness in the narrow sense' is either quantitatively inherited (heritability of 76%) or, as shown in some crosses, governed by a simple recessive for earliness. In either event the duration is reported to be of low magnitude (0-10 days) in Japan and in Canada (Major, 1980).

PHASIC DEVELOPMENTAL VARIATION APPROPRIATE TO BARLEY-PRODUCING AREAS IN AUSTRALIA

Barley production in Australia takes place between latitudes 26 and 35°S and over the course of a growing season that spans the winter months. In contrast, much of the barley production in the northern hemisphere occurs at higher latitudes and under growing season conditions very different from those experienced in Australia (Fig. 1). This distinction is important because much of the terminology, findings of studies on phasic development, and introductions of improved barley germplasm into Australia, derive from those higher latitudes.

The present study was initiated when it became apparent that the developmental behaviour of introduced genotypes did not correspond with their reported classification or predicted behaviour. This has complicated selecting genotypes for the development of cultivars for extending barley production into regions and to seeding dates not commercially considered, and attempts to transfer genes for desirable characters (disease resistance and straw strength) from unadapted introductions. The results presented below refer to the screening of a diverse range of genotypes which was undertaken to define the nature of phasic developmental variation occurring under Australian conditions. Subsequent studies will concentrate on genetic control of the variation observed and on the prospects of its judicious manipulations.

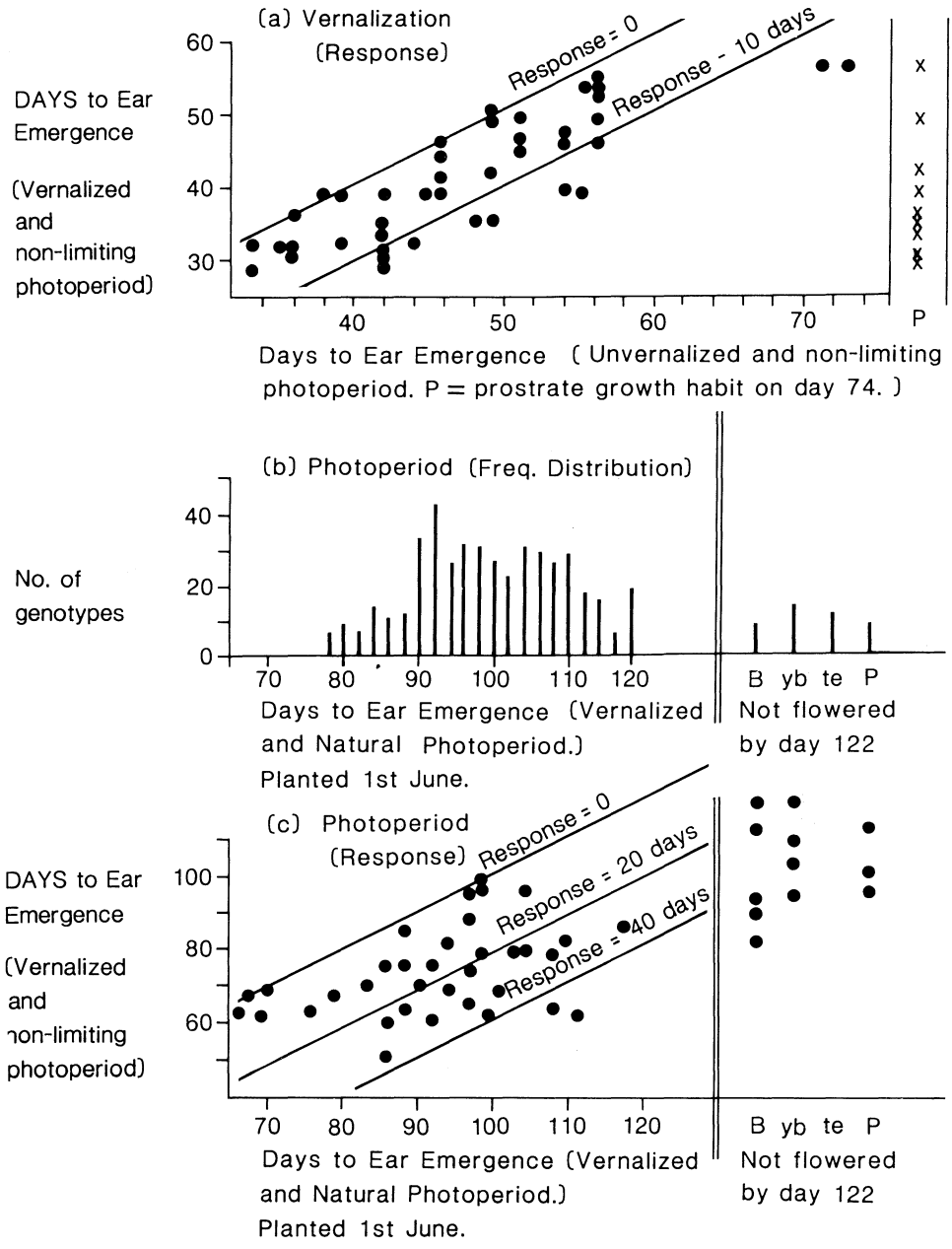

Figure 2. Distribution of responses amongst selected genotypes to vernalisation (a) and photoperiod (c). Frequency distribution of date to ear emergence amongst 500 genotypes studied for response to photoperiod (b). B = boot, yb = young boot, te = tiller elongation, P = prostrate.

Response to vernalisation

Response to vernalisation has been evaluated by comparing vernalised with unvernalised treatments under non-limiting photoperiods following the transplanting of seedlings on 1 November when the likelihood of naturally vernalising temperatures (taken as less than 10°C) is remote. Vernalisation was carried out by exposing germinating seed to temperatures fluctuating between 3 and 6°C for eight weeks. Non-limiting photoperiod was achieved by interrupting the dark period for two hours using incandescent lamps.

The results for a sample of 50 genotypes selected to represent the range observed in an earlier screening of 400 genotypes (Boyd, 1983) are presented in Fig. 2(a). Eight weeks vernalisation advanced ear emergence from 0 to 14 days, amongst those that flowered without vernalisation. Nine genotypes remained vegetative amongst the unvernalised controls and, without evidence of tiller elongation, were considered to have an obligate vernalisation requirement. With few exceptions the responses observed differed little from exposure to vernalisation for four weeks (range 0-11 days), and were similar to those in which vernalisation was continued for 12 weeks. Repeating the study from a 1 June planting date indicated that natural vernalisation is approximately equivalent to that provided artificially for four weeks.

Response to photoperiod

Response to photoperiod has been evaluated by comparing advance to ear emergence for natural and non-limiting photoperiods following the transplanting on 1 June of seedlings vernalised for eight weeks. Natural photoperiods range from 10.1 hours at the time of planting and remain at or about that duration until mid-July, increasing thereafter to 10.5 (1 Aug.), 11.5 (1 Sep.), 12.5 hours (1 Oct.). The distribution of the period to ear emergence for 500 genotypes under natural photoperiod is presented in Fig. 2(b). The continuous nature of this distribution combines variation in the duration of a basic vegetative period with differences between genotypes in the particular photoperiod at which floral initiation occurs. It is not possible, from field studies, to specify the critical photoperiods involved. However, it can be extrapolated that floral initiation in commercially available cultivars must occur at photoperiods of less than 10.5 hours, based on tiller elongation commencing before 1 August.

Data presented in Fig. 2(c) represent the developmental behaviour of a sample of 50 genotypes selected to represent the range of responses observed. The range varies from those considered day neutral to those in which ear emergence was advanced by 52 days amongst the genotypes that did flower. A number of genotypes which had not flowered by the time the study was concluded ranged in their development from the boot stage to those in which floral initiation had yet to occur. This indicates that the critical photoperiod for those that remained prostrate would exceed 13.5 hours.

Variation in basic vegetative period

In the absence of any physiological/morphological details of the mechanisms contributing to variation in ear emergence under non-limiting photoperiods after the vernalisation has been provided for (eight weeks exposure), the term 'basic vegetative period' has been used following Veraga and Chan (1976). This is appropriate as the word period refers to time, and hence units, in which variation is measured. Measurements expressed in days can only be interpreted in relative terms due to increase in day degrees as the season progresses, particularly from winter plantings.

Figs. 2(a) and 2(c) provide information on the duration to ear emergence under non-limiting photoperiods of fully vernalised material. The durations range from 30 to 54 days following transplanting on 1 November (summer — Fig. 2(a)) and, from 51 to 118 days following transplanting on 1 June (winter — Fig. 2(c)). Clearly, the duration of the basic vegetative period is influenced by the environment, presumably by ambient temperature. In either case there is an approximate two-fold difference which greatly exceeds the measured response to vernalisation. In a further study involving 111 genotypes including all entries to interstate variety trials plus additional introductions, the basic vegetative period ranged from 32 to 60 days (1 Nov. planting) and 65 to 132 days (1 June planting) with a correlation of 0.5053.

It is significant from the point of view of future phenological and genetic studies, that the range in basic vegetative period recorded for the November planting applied to genotypes that did not respond to vernalisation and to those for which it was an obligate requirement (Fig. 2(a)). Similarly, the range recorded from the 1 June planting applied to genotypes that were day neutral and to those in which floral initiation had yet to occur under natural photoperiods when the study was terminated (Fig. 2(c).

DISCUSSION

According to Calder (1965), the juvenile stage represents a prerequisite requirement before competence to respond either to vernalisation or to photoperiod is achieved. From the results of this study it appears that variation in the duration of a basic vegetative period is greater than has been reported previously and is an important variable determining differences in the phasic development of barley under Australian conditions.

The ecological consequences of major variation in the duration of a basic vegetative period for barley grown over a winter growing season characterised by mild temperatures, low radiation, and short photoperiods are numerous. They include an inability to extrapolate the classifications of winter, spring, early, or late at higher latitudes to local conditions. Late flowering introductions may be late for various reasons, or combinations of them, and only a small proportion of F_2 recombinants develop as rapidly as their locally-adapted parent.

Inherent differences in response to vernalisation have little impact, other than in extreme cases, due to naturally vernalising temperatures occurring for an extended period following normal commerical planting. Such differences could be exploited to delay premature flowering from early (autumn) seeding. Inherent and major differences in response to photoperiod have been recorded. These would be important to the breeder in his selection of parents and in the complications that arise when selecting progeny in which floral initiation has to occur at photoperiods of less than 10.5 hours to be considered commercially viable.

REFERENCES

Aitken, Y. 1965. Flower initiation in relation to maturity in crop plants. *Australian Journal of Agricultural Research 17:* 1-15.

Boyd, W.J.R. 1983. Evaluation of barley germplasm. Australian Plant Breeding Conference, Adelaide.

Briggs, D.E. 1978. Barley, Chapman and Hall, London.

Calder, D.M. 1965. *Proceedings 12th Easter School Agricultural Science.* Nottingham, Butterworths, London pp. 59-73.

Gustaffsson, A., Hagberg, A., Lundquist, U. 1960. The induction of early mutants in bonus barley. *Hereditas 46:* 675-699.

Inagaki, M., Masuda, S. 1984. Heading responses to temperature and day length in barley varieties. *Japan Journal of Breeding 34:* 423-430.

Kirby, E.J.M., Ferris D.G. 1970. Plant population induced growth correlations in the barley plant main shoot and possible hormonal mechanisms. *Journal of Experimental Botany 21:* 787-798.

Major, D.J. 1980. Photoperiod response charactristics controlling flowering of nine crop species. *Canadian Journal of Plant Science 10:* 777-784.

Ormrod, D.P. 1963. Photoperiod sensitivity of head differentiation, culm elongation and heading in some spring wheat and spring barley varieties. *Canadian Journal of Plant Science 43:* 323-329.

Ramage, R.T., Suneson, L.A. 1958. A gene marker for the g chromosome of barley. *Agronomy Journal 50:* 114.

Reid, D.A., Wiebe, G.A. 1979. Barley, Agricultural Handbook, U.S.D.A. Washington.

Soggaard, B., Nilan, R.A., von Wettstein, E. 1984. Masterlist of barley genes. *Barley Genetics Newsletter 14:* 140-172.

Takashashi, R., Yasuda, S. 1957. Genetic studies of time of heading in barley. *Proceedings of the International Genetic Symposium 1956:* 498-501.

Takashashi, R., Yasuda, S. 1970. Genetics of earliness and growth habit in barley. *Proceedings of the 2nd International Barley Genetics Symposium Pullman, 1969.*

Veraga, B.S., Chang, T.T. 1976. The flowering response of the rice plant to photoperiod. *International Rice Research Institute Technical Bulletin (8).*

Yasuda, S. 1981. The physiology of earliness in barley. *Proceedings of the 4th International Barley Genetics Symposium Edinburgh, 1981.*