The nature and agronomic implications of a juvenile stage in barley

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Summary. Barley varieties differ in duration to anthesis in the absence of vernalization and photoperiod influences. Such variation is expressed to a greater extent under winter (Australia) than summer (Canada) growing season conditions, and arises from the consequences of differences among varieties in the minimum number of main stem leaves at which plants respond to the inductive effects of light. This trait is inherited as a simple Mendelian recessive, but more than one locus may be involved. The consequences of a low minimum leaf number include pleiotrophic relationships with a short duration to floral initiation, and shorter durations with faster rates of development after that event. There is a negative relationship with the development of yield potential.

Introduction

Variation in the duration from planting to anthesis, for reasons other than differences among varieties in responses to vemalisation and photoperiod, has been reported in barley, wheat, oats, rice and maize (7).

Most studies reporting on this source of variation have been carried out under actual or simulated summer growing conditions. With the exception of rice (11) minor agronomic importance with little difference among varieties has been ascribed to this variable (6, 10, 12). That opinion is not supported for barley grown under winter growing season conditions in Western Australia (I, 8). Authors also differ in their definitions of the variation observed and their interpretations of the reasons for it. The terms "juvenile stage" (3), "basic vegetative period" (6), and "pre-inductive period" (10) propose a period following planting during which plants are insensitive to the effects of those factors (vemalisation and photoperiod) that later promote floral initiation. "Basic development rate" (4) proposes variation among varieties in the rate at which development proceeds to anthesis due to differences in the response of varieties to ambient temperature.

In this paper we report the results of studies carried out to investigate the nature, variation and genetic control of variation in the duration to anthesis for reasons other than vernalization and photoperiod influences.

Methods

Two closely related barley varieties, Mona (early) and Bonus (late), which do not respond to vernalization or photoperiod, but differ in their durations to anthesis, were grown in field plots from April, June and October sowing dates with and without extended photoperiods at Perth. A further five sowing dates, from May 10 to July 5, were undertaken under natural photoperiods (15.6 to 16.5 h) over the summer at Saskatoon (Canada). Details of mean temperature, photoperiod and radiation at the time of planting, and the direction of seasonal change over the following 10 week period, are given in Table I. Plots were maintained in a weed-free condition with soil moisture and nutrient supply considered non-limiting. Five plants were sampled every 50? Cd (2-4 days) with the median 3 dissected to determine total and visible leaf numbers, and thermal times to floral initiation (FL, maximum primordia number (Max. P) and anthesis (A). Rates of primordia initiation and leaf appearance were calculated from linear regressions against thermal time.

Emphasis has been given to major biological trends rather than statistically significant differences which. with low variance are numerous but of negligible biological consequence within seeding date/location combinat ions.

Results

Over all treatments Mona flowered consistently earlier (mean = 829?Cd than Bonus (mean = 1234? Cd) and at a lower main stem leaf number (Mona. mean = 7.8, Bonus, mean = 11.2) (Table I).

Table I. Mean temperature, photoperiod, radiation at different planting dates at Perth and Saskatoon with direction of seasonal changes over the following 10 weeks, and leaf numbers and thermal times to anthesis for Mona and bonus. NP = natural photoperiod as indicated in parenthesis.

Site	Plant Date	Temperature °C	Photo period (h)	Radition $MJ/m^2/d$	Leaf Number		Anthesis °Cd	
					Mona	Bonus	Mona	Bonus
Perth	24.4	17.2→14.5	NP (11.1→10.2)	16.1→9.4	7.7	12.0	897	1644
	24.4	17.2→14.5	NP + 8	16.1→9.4	7.7	12.0	879	1630
	Mean				7.7	12.0	888	1637
Perth	6.6	14.5→10.1	NP (10.2→12.3)	9.4→14.0	7.7	12	990	1488
	6.6	14.5→10.1	NP + 2	9.4→14.0	7.7	12	1016	1444
	6.6	14.5→10.1	NP + 4	9.4→14.0	7.7	11.7	1011	1469
	6.6	14.5→10.1	NP + 6	9.4→14.0	8.0	11.7	999	1379
	6.6	14.5→10.1	NP + 8	9.4→14.0	8.0	12.0	995	1388
	Mean	14.5→10.1		9.4→14.0	7.8	11.9	1002	1434
Perth	3.10	15.0→18.1	NP(12.3→14.3)	18.8→25.0	7.7	11	791	1361
	3.10	15.0→18.1	NP + 8	18.8→25.0	7.7	10.7	791	1227
	Mean				7.7	10.9	791	1294
Sask	10.5	6.0→15.0	15.0→16.0	14.0→24.0	8.0	10.2	581	750
	24.5	10.0→18.0	15.7→ 16.3	14.0→24.0	7.7	10.8	640	840
	7.6	15.5→22.2	16.3→16.5	16.0→25.0	8.1	10.4	638	802
	20.6	15.5→22.2	16.5→16.2	25.0→22.0	7.6	10.7	677	859
	5.7	22.2→15.9	16.2→15.5	24.0→15.0	7.8	10	696	851
Perth	Mean				7.76	11.7	929.9	1448.1
Sask	Mean				7.84	10.4	646.1	820.4
Grand	Mean				7.79	11.2	828.6	1223.7
c.v.%					1.93	6.52	18.67	25.95

Although leaf numbers remained relatively constant in Mona (7.6 to 8.1) and marginally lower in Bonus at Saskatoon (10.4) than at Perth (11.7), thermal times to anthesis varied substantially with location and among, but not within, seeding dates. There was no effect of extended photoperiod treatments at Perth. Varieties differed in their response to location and seeding date (Perth), with differences in thermal times to flowering being greater at Perth (518?Cd) than at Saskatoon (174 ?Cd). and more so for Bonus than Mona (Table 1).

The shorter durations in Mona for component intervals in the period from planting to anthesis, were associated with faster rates of leaf initiation, leaf appearance, spikelet initiation and, by extrapolation, stem intemode elongation. Tiller numbers (not shown) and spikelet numbers (maximum and fertile) were lower (Table 2).

Table 2. Mean developmental details for Mona (M) and Bonus (B) from different seeding dates at Perth and over seeding dates at Saskatoon for (a) thermal times to floral initiation, for ear

formation. for ear/stem growth and rates of leaf initiation (plastocron), and (h) rates of leaf appearance (phyllocron) rates of spikelet initiation (plastocron) and for maximum and fertile spikelet number.

(a)

Site	Plant Date	Floral Initiation (°Cd)		Ear Formation (°Cd)		Ear/Stem Growth (°Cd)		Leaf Plastocron (°Cd/leaf)	
		M	B	M	B	M	B	M	B
Perth									
	AprilL	309	509	200	424	380	705	18.6	22.7
	June	316	485	279	496	408	455	25.9	29.3
	Oct	266	442	186	378	339	474	10.5	16.5
Sask	May/June	275	362	166	183	205	275	N/A	N/A

(b)

Site	Plant Date	Leaf Phyllocron °Cd/leaf		Spikelet Plastocron (°Cd/spikelet)		Maximum Number Spikelets		Fertile Number Spiklets	
		M	B	M	B	M	B	M	B
Perth									
	April	86	118	9.6	17.0	26.9	44.2	23.5	31.5
	June	95	100	11.5	14.8	33.8	43.7	22.1	32.7
	Oct	71	108	10.7	15.2	24.7	32.4	19.2	20.4
	May/June	65	63	n.a.	n.a.	26.4	28.3	18.7	23.5

Conclusion

Mona and Bonus differed in their duration to anthesis for reasons other than influences of vernalization and photoperiod. They did not differ in embryonic leaf number (3-4), in the duration from planting to colcoptile emergence (about 100?Cd from 5 ems), and only minimally in their leaf plastocrons (5). On that basis it can be calculated that both varieties would have had 7-8 initiated leaves at the time of coleoptile emergence. Mona proceeded to floral initiation at that number but in Bonus this event was delayed until a further 2-3 leaves had been initiated. As this was repeatable over a wide range of environments, including photoperiods up to 18h, varieties must differ in the minimum number of main stem leaves initiated before they responded to the inductive effects of light (as distinct from photoperiod). The latter finding supports the concept of a pre-inductive period (10) and the inference of variation in the duration to floral initiation (= vegetative phase) implicit in the terms "juvenile stage" (3) and "basic vegetative period" (6).

The concept of a minimum number of leaves at which floral initiation can occur was first reported by Purvis (9), and in barley ranges from 6 to > 10 (2). Genetic studies based on the cross Mona x Bonus, and involving F_2 and selected F_2-derived F_3. F_4 and F_5 progeny, have demonstrated a pleiotrophic relationship between minimum leaf number (MLN) and duration of the juvenile stage (JS) due to the action of a single recessive gene (5). This pleiotrophism extends to include positive associations with duration and rate of development after floral initiation, but a negative association with the development of yield potential. The characteristic of high MLN/long juvenile stage in Bonus was also associated with a greater response to environmental conditions favouring ear and stem growth. This explains why variation to anthesis, for reasons other than influences of vernalization and photoperiod, was expressed to a greater extent under winter than summer growing conditions.

Variation in the pleiotrophic trait (MLN/JS) occurs in combination with high and low responses to either vernalization or photoperiod. Commercially released spring cultivars for the southern Australian wheatbelt do not respond to vemalisation. have a short juvenile stage but are responsive to increasing photoperiod. Unconscious selection for this combination suggests that photoperiod determines the timing of floral initiation, with the effect of a short juvenile stage ensuring rapid progress from floral initiation to anthesis. This would be of adaptive advantage under circumstances where growing conditions improve rapidly from a low in winter to a high in spring ahead of impending moisture stress. Varieties from Queensland and Tasmania have a longer juvenile phase and reduced response to photoperiod (ie. similar to Bonus). This is thought to reflect on better growing conditions from early (April) plantings in Queensland, and extended growing seasons in Tasmania. Genetic studies based on the cross Mona x Clipper, indicate different recessive genes for a low MLN/short juvenile stage which are epistatic to dominant alleles at other loci.

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