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<u>Accessory Publication</u> to accompany manuscript by Boyd *et al.* (2003). "Conventional and Molecular analysis of factors contributing to variation in the timing of heading among spring barley genotypes (*Hordeum vulgare L.*) grown over a mild winter growing season". *Australian Journal of Agricultural Research* pp. 1277 – 1301.

Background

A summary of the molecular results has been included in the above paper, but the details were omitted as their interpretation was complicated by some missing data, considerable variation in the contribution of the numerous QTLs identified, and unexpected complexities arising from apparent contradictions and possible confounding with ambient temperature. Presentation proved cumbersome – requiring repetition (with the same few QTLs dominant for most traits), up to 12 pages of text and a number of large tables to illustrate the results obtained.

Introduction

This accessory publication presents the detailed results of the molecular analyses for each of the 4 traits described under "Data organisation for QTL analyses" on page 24 in the above paper.

Results

Segregation for response to vernalisation was observed in only one population (Halcyon/Sloop) and not, as was expected, in the Dicktoo (winter) /Morex (spring) population. For that reason the influence of vernalisation is not considered in the results presented, and the analysis of the Halcyon/Sloop population was limited to those lines considered homozygous for no response to vernalisation.

Based on the consensus markers selected, a total of 22 QTLs distributed over all chromosome arms except 4HL and 4HS were identified. Sixteen (16) of those contributed > 10% of the variation recorded; with 6 to 9 for each analysed trait (Table 1). Only those contributing > 10% are included in the trait-specific results illustrated in Tables 2 to 5. Details of individual traits are presented below.

MDH-GR-18 h and MDH-Summer-18 h. With ambient temperatures in the ranges of 15 to 25°C (Growth Room) and 13 to 30°C in late October (Summer) field plantings, the duration to heading among vernalised materials exposed to an 18h photoperiod would be considered a minimum (MDH) under those warm ambient temperature conditions. It was hypothesised that; "variation in MDH would be for reasons other than the influences of vernalisation and photoperiod, and presumably due to the action of *"eps"* or "*development rate* genes" proposed by Laurie et al. (1995) and Hay and Ellis (1998), respectively.

- Progeny distributions in most populations mimicked a classical model for a quantitatively inherited trait; being normal about the mid-parent value, or skewed toward the early heading parent (Table 2), and characterised by considerable, including transgressive, segregation. This provisional inference is supported by the identification of eight (8) QTLs (Tables 1 and 2).
- The QTL identified on 2HS (marker BCD221) was the dominant contributor (39 to 65%) of the variation in heading date recorded in all populations, including those in which both parents are characterised by a long MDH-GR-18 h's (= late heading). The major contribution of this QTL to calculated response to increased photoperiod mitigates against acceptance of the proposed hypothesis. This is discussed later..
- Other major contributions were identified in some populations due to a locus on 2HC (marker Bmy2) and another on 5HL (marker CDO400). The QTL on 2HC was limited to the three populations involving two Australian parents (Chebec and Sloop) and characterised by a short MDH-GR-18 h's (= early heading), and that on 5HL limited to two populations involving a "winter parent" (Halcyon and Dicktoo). QTLs on 3HS, 6HL, 7HL, 7HS and another (unassigned) were either limited to a single population or of minor influence.
- Historical genetic studies located a gene for early maturity under long days (*Eam1*) on 2HS. That locus is considered by Lundquist *et al.* (1997) to be synonymous with a QTL for photoperiod response (Ppd-H1) identified by (Laurie *et al.*1995) who, in addition, reported *"eps"* loci on 2HS, 5HL, 6HL(x2) and 7HS. In this study the QTL assigned to 2HC (marker Bmy2) could be synonymous with the "*eps"* locus Laurie *et al*. (1995) assigned to 2HS. Significantly, its identification was limited to three populations involving Australian parents exhibiting a short MDH-GR-18 h (Chebec

and Sloop, Table 2). Based on the low to minor contributions of the remaining and prospective *"eps"* loci, and the few populations they involved, it would appear unlikely their role is anything more than that of a modifying influence. Further discussion will be deferred until results of the analyses of the remaining traits have been presented.

- The QTL identified on 5HL (marker CDO400) was confined to populations in which one parent is classified as a winter type. Segregation for response to vernalisation was not observed in the Dicktoo/Morex population, or among the progeny selections analysed for the Sloop/Halcyon population. Both parents and many of their progeny, however, were characterised by a prostrate / semi-prostrate seedling growth habit. As a gene for growth habit (Sh_2) has been located on 5HL, this result could indicate a pleiotrophic influence of that gene on variation in heading date. This will be discussed further. The alternative would be to implicate the "*eps5L*" gene located by Laurie *et al*. (1995).
- The QTL on 3HS was unique to the Tallon/Kaputar population. Tallon was developed for early planting under the warmer Queensland environment and, together with Franklin, is characterised by a long MDH. There is no report of a gene influencing heading date on 3HS, and this QTL was not identified in the Arapiles/Franklin population.
- It is noted that a high proportion of the progeny among the two N. American populations heading earlier than those involving an Australian parent, despite the introduced parents heading later than those of Australian origin.

<u>MDH-June-18 h.</u> With ambient temperatures in the range of 5 to 18°C from a mid-June (winter) field planting, the duration to heading among vernalised materials exposed to an 18 h photoperiod would be considered a minimum under those cooler ambient temperature conditions. It was again hypothesised that: "variation in the minimum duration to heading (MDH) would be for reasons other than the influences of vernalisation or photoperiod", and presumably due to the action of "*eps"* or "*development rate* genes".

- Duration's to heading were longer than for the same materials grown under an 18h photoperiod at higher temperatures (MDH-GR-18 h / MDH-Summer 18 h, above), where population means ranged narrowly from 34.3 to 40.9 days (Table 2). In this treatment (MDH-June-18 h) that range increased to 76.4 to 100.5 days (Table 3). This

response to growing conditions (presumably ambient temperature), calculated as the difference between populations means in Table 2 and 3, was expressed more strongly in the two N. American populations (61.7 to 65.3 days) and involving parents adapted to summer growing conditions, than among populations involving an Australian parent adapted to under winter growing conditions (38.1 to 49.9 days). Population means across growing conditions were not correlated. Although the generalised influence of growing conditions, and ambient temperature, is well recognised and widely documented, this factor(s) has not been specifically investigated under conditions in which the influences of vernalisation and photoperiod have been experimentally negated. The implication of this finding includes the confounding effect that differential genotype response to growing conditions (ambient temperature) could have on the study of developmental variation in barley.

- Other differences associated with growing conditions included a wider range of segregation in this winter planting (particularly in the Sloop populations), and variation in progeny distribution patterns ranging from near normal in some, to being skewed toward either the early or late parent (Table 3) in others. These distribution patterns suggest a quantitative mode of inheritance and this inference is supported by the identification of six (6) QTL's distributed over all chromosomes except 4 and 7 (Tables 1 and 3).
- The QTL on 2HS (marker BCD221) was again the dominant contributor in all populations other than Dicktoo / Morex. The QTL on 2HC (marker Bmy2) was again a major contributor in all populations involving an Australian parent characterised by a short MDH. These coincidences with variation in MDH under warm growing conditions implicate the identified loci with the influence of an 18h photoperiod. For that reason the proposed hypothesis must again be rejected.
- The remaining QTLs identified differed from those reported in the MDH-GR-18 h treatment. They included one on 1HL (marker abg55) that was limited to the N. American populations, with another on 5HL but associated with a different marker (ABG3) from that reported under MDH-GR-18 h / MDH-Summer-18 h above. The populations to which these QTLs apply involved vernalised parents and progeny characterised by, or segregating for, prostrate seedling growth habits. Historical genetic studies have identified genes for growth habit (Sgh_3 and Sgh_2) on chromosomes 5HL

and 1HL, respectively. This association questions whether genes for vernalisation are synonymous with those for growth habit as proposed by Takahashi and Yasuda (1970).

- QTLs on 1HL, 5HL and 6HL were important contributors to variation in heading date in the Dicktoo / Morex population. A number of genes on these chromosomes have been reported to effect heading date. These include "eps" loci on 5HL and 6HL and, in addition, *eam8* and *Ppd-H2* on 1HL.
- Previous studies have identified loci on 1HL (*eam8* and *Ppd-H2*) specifically associated with variation in heading date under short photoperiods. In this study a QTL on 1HL is identified under an 18h photoperiod from a winter (June) planting, but not under the higher temperature regime in MDH-GR-18 h / MDH-Summer-18 h above. This finding applied only to the two populations involving parents of N. Hemisphere origin and adapted to summer growing conditions. The implication that this could provide evidence of an interaction between photoperiod and temperature is supported by the observation that most of the DH progeny in the N. American populations headed earlier than Australian parents / populations under warm conditions (Table 2), but later under cooler conditions (Table 3).

<u>(c). DH-June-10.2 h.</u> Under the same cool ambient temperatures from a mid June (winter) field planting, variation in the duration to heading (DH) among vernalised materials would be subject to differential genotype sensitivity to the developmental influences of photoperiod. Planting dates were selected to ensure that coleoptile emergence occurred on or about, the shortest day of the year (June 21st when photoperiod = 10.2h), and this increased minimally (to 10.5h) over the following 6 weeks.). Data presented in Table 4 are specific for a shorter photoperiod than those presented in Table 3, when the same materials were planted on the same day but under an 18 h photoperiod.

- Duration to heading increased from population means of 64.7 to 100.5 days under MDH-June-18h, to 87.2 to 118.5 days in this treatment. This increase would have to be ascribed to the mean response to extended photoperiod which, it may be noted is lower (18.0 to 26.1 days, Table 4) than were responses to growing conditions (Table 3).
- In most populations DH progeny were normally or near normally distributed about the mid-parent point, with considerable transgressive segregation in populations involving an Australian parent characterised by a short MDH and shown above to be more

responsive to the influence of extended photoperiod (Table 4). Distributions were skewed toward the earlier flowering parent in the Sloop / Halcyon population, and toward the later flowering parent in the Arapiles / Franklin population. Date of heading in the N. American populations was generally delayed relative to those involving an Australian parent.

- Variation in this trait was inherited in a quantitative manner, and that inference is supported by the identification of 7 QTL's (Tables 1 and 4); only two of which (on 2HC and 5HL) coincided with those identified under either of the 18h photoperiod treatments reported above.
- The QTL on 2HC (marker Bmy2) was again of major effect in all populations involving an Australian parent. Its identification under both long (MDH-GR-18h and MDH-June-18h) and short (DH-June-10.2h) photoperiods, irrespective of growing conditions, suggests the locus influences heading date for reasons other photoperiod. This would constitute evidence that the locus involved codes for MDH.
- In contrast, the QTL (marker BCD221) on 2HS that dominated variation in heading date in both 18h treatments was conspicuous in its absence in this analysis of variation in heading date under a natural (short) photoperiod. This suggests the locus involved is sensitive to the influence of extended photoperiod. This is discussed more fully in the next section.
- The other significant difference from the traits discussed above was the identification of QTL's on 1HL, 2HS, 3HL, 6HL and 7HS – none of which were identified under the 18h treatments. These QTL's, together with one on 5HL and identified previously, were associated with parents exhibiting a prostrate seedling growth habit. Of them, those on 1HL (marker Bmag382) and 3HL (marker ABG4) were represented in 3 or more populations and could be synonymous with the previously designated genes *eam8 or Ppd-H2* and *eam10*, respectively, which are reported to contribute to variation in heading date under a short, but not long photoperiods. Laurie *et al*. (1995) located *eps3L* and the *sdw (denso)* gene on 3HL, both of which are reported to modify heading date.

(d). Response to Extended Photoperiod. The difference in durations to heading between DH-June 10.2h (Table 4) and MDH-June-18h (Table 3), for vernalised materials planted on the same day, has been calculated to provide a measure of response to

extended photoperiod under winter growing season conditions. The calculated response to photoperiod would, therefore, be strongly influenced by variation in the treatments used in its calculation. The results are presented in Table 5.

- The range of calculated responses among individual progeny ranged from 0 to > 61days and among parents from 0 to > 30 days (excluding Halcyon which did not head in the short natural photoperiod treatment. Progeny distributions exhibited considerable transgressive segregation and, with one exception, near normally distributed about their mid parent points. The exception was found in the Arapiles / Franklin population in which the distribution was skewed toward the Franklin parent. The implied qualitative mode of inheritance is supported by the identification of 9 QTL's located on all but chromosome 4.
- QTL's on 1HL, 1HS, 2HL, 3HL, 5HS and 7HS were not identified in any of the photoperiod treatments and are therefore ignored. Their individual contributions to variation in this calculated response were minor and applied to only single populations.
- In marked contrast the QTL on 2HS (marker BCD221) was of dominant influence in all populations for which this response was calculated. As this locus did not contribute to variation under the short day treatment (DH-June-10.2h), the calculated response recorded can only reflect on the dominant influence of this QTL on variation to heading under the 18 h treatment. That variation or as it now appears, response to, extended photoperiod was not expected based on the evidence of Major (1980) and Roberts et al. (1988) that 18 h exceeds the upper critical threshold for floral induction to proceed among vernalised genotypes. That evidence supports the rejection of the hypotheses proposed for the two MDH treatments. However, in this study, where durations to heading were used as a surrogate for the timing of floral initiation, it could be assumed that variation in heading date under an 18 h photoperiod reflects variation in the timing of floral initiation for reasons other than photoperiod, plus variation in the rate at which developmental events unfold. The former would include variation in the duration of the "*photoperiod insensitive period*" proposed by Roberts et al. (1988) or its equivalent defined as a "*basic vegetative period*" by Major (1980). The latter would include variation in the rates of leaf initiation and appearance, the timing of the commencement of stem extension relative to the status of apex differentiation and the rate of stem internode elongation. In either event, acceptance of these assumptions would contradict the conclusion that the proposed hypotheses should be rejected.

- One significant finding was the absence of a QTL on 2HC. The marker Bmy2 , identified a locus for variation to heading under both long and short photoperiods, in most populations. That its influence did not extend to variation for response to photoperiod confirms that the locus is not influenced by photoperiod.

Generalised Summary of the analyses of individual traits

- A locus on 2HS (marker BCD221) was the dominant contributor to variation in heading date in most populations grown under 18h photoperiods in both warm and cool ambient temperature conditions, and for the calculated response to extended photoperiod. Its influence was conspicuously absent when the same populations were grown under a natural (short) photoperiod.
- A second locus on chromosome 2 (marker Bmy2) was a major contributor to variation in heading date in populations involving an Australian parent characterised by a short MDH, under both long (18h) and short (10.2h) photoperiods, and irrespective of ambient temperature conditions. Its influence was conspicuously absent for the calculated response to extended photoperiod. The proximity of Bmy2 to the centromere on chromosome 2 questions its location, hence the designation 2HC.
- Other QTL's of major effect were located 1HL, 3HL and 5HL. Their influence was limited to some traits and to those populations in which one of the parents, and many of its progeny, exhibited a prostrate seedling growth habit. Depending on analysed trait the identity of markers on those chromosome arms varied.
- The comparison of mean population durations to heading, between warm and cool ambient temperature conditions, for vernalised materials under 18h photoperiods, indicated major and differential genotype response to growing conditions (presumably reflecting the influence of ambient temperature). The magnitude of that mean population response was greater than the equivalent mean response to extended photoperiod, calculated from the comparison between long and short photoperiod treatments under cool ambient temperature conditions.
- A characteristic of all traits analysed, and common to most populations, was evidence of considerable, including transgressive, segregation.

Table 1. Chromosome arms carrying previously identified genes for development, and the markers on those arms identifying QTLs for developmental variation for each of 4 traits in one or other of the 7 DH populations examined. ? = a QTL on the arm indicated but uncertain if it is the same locus identified by the marker shown.

DH Populations	**DH Populations**	**% contributions**
1=Steptoe/Morex	5=Halcyon/Sloop	<10%
2=Dicktoo/Morex	6=Tallon/Kaputar	11 to 24%
3=Chebec/Harrington	7=Arapiles/Franklin	**26 to 50%**
4=Alexis/Sloop		**> 50%**

Chromo -some	Desig[n] genes	Marker	MDH-GR-18h	MDH-June-18h [A]	DH-June 10.2h	Response to Photoperiod [A]
1HL	Sh_3 eam8 PpdH-2	abg55		1?, 2 ?		
		Bmag382			1, **2**, **5**	
		CMWG706A				1,2.
1HS		Bmac213				4
2HC 2HL		Bmy2 [B]	3, 4, 5	3, **4**, 5, 7	**3**, 4, 5, 6?, 7	
		ABG14				4
2HS	Eam 1 PpdH-1 eps2S	BCD221	**1**, **2**, **3**, **4**, **5**, **6**	1, **3**, **4**, **5**, **7**		1, 2, **3**, **4**, **5**, **7**
		ABG2			1,2	
3HL	eam10 eps3L denso	ABG4			**4**, 5, 6, 7	
		HVM62				1
3HS		p12m47KT118	6			
4HL	eam9 Sh eps4L					
4HS						
5HL	Sh_2 eps5L	CDO400	2?, 5			
		ABG3		**2?**,5, 7	2, 5	3,5, 7
5HS		Rm2				1
6HL	eps6L-1 eps6L-2	MR	2,6?	**2**, 3?		2
		BCD269			3, *4*, 6	
6HS	eam7					
7HL	eps7L	ABR303		1		
		Bmac156	2?, *3*			
7HS	eps7S	HVWAXYG	3		2, 3, 6*?*	
		ABC158				2
???		E36M36F462	2			

[A] Population 6 was not included in these traits.
[B] Bmy2 located close to the centromere. Hence the designation 2HC

Table 2. Distribution (in days) for MDH-GR-18h or MDH-Summer-18h of parents and progeny for each of 7 populations, and the chromosome location of markers contributing >10% of the variation recorded. The percentage contibution of the parental allele responsible for delayed heading is indicated eg. 44% (M) where M indicates the contributing parent. 20> indicates class interval from 20 - 24 days. ? = a QTL on the chromosome arm indicated but unsure if the same locus identified by the marker. S, M, D, C, Hr, Al, H, and T identify the parent contributing the major allele and the class interval in which they are included.

				Minimum duration (days) to Heading										
Popln.	**Chrom**	**Marker**		**20>**	**25>**	**30>**	**35>**	**40>**	**45>**	**50>**	**55>**	**60>**	**>65**	**Mean**
Steptoe /	2HS	BCD221	44% (**M**)	1	40	37	28	34	8					35.2
Morex							**S,M**							
Dicktoo /	2HS	BCD221	57% (**M**)	4	31	16	19	12	8	5	2			35.5
Morex	5HL	CDO400	14% (**D**)?				**D,M**							
	?	E36M36F462	13% (**D**)											
Chebec /	2HC	Bmy2	14% (**Hr**)			22	55	16	7	12	7			39.8
Harrington	2HS	BCD221	69% (**Hr**)		**C**			**Hr**						
Alexis /	2HC	Bmy2	21% (**Al**)		13	37	12	9	11	3	2			34.3
Sloop [A]	2HS	BCD221	65% (**Al**)		**Sl**					**Al**				
Halcyon /	2HC	Bmy2	12% (**H**)		5	33	9	6	6	8	2	0	0	53	37.4 [B]
Sloop [A]	2HS	BCD221	39% (**H**)		**Sl**									**H>**	
	5HL	CDO400	20% (**H**)												
Tallon /	2HS	BCD221	40% (**T**)			4	32	32	12	6	2				37.1
Kaputar	3HS	p12m47KT118	25% (**T**)			**K**		**T**							
	6HL	MR	22% (**T**)?												
Arapiles /	2HC	Bmy2	n/a			8	14	27	4						40.9
Franklin	2HS	BCD221	n/a												

[A] refers to population grown over summer, under an 18 h photoperiod

[B] refers to the mean of 59 progeny homozygous for no response to vernalisation.The remaining 53, and Halcyon were responsive.

Table 3. Distribution (in days) for MDH-June-18h of parents and progeny for each of 6 populations, together with the chromosome location of the markers contributing >10% of the variation recorded, The percentage contribution of individual markers is shown together with the identity of the parent allele responsible for delaying heading is indicated eg. 20%(S) where S indicates the contributing parent. 50> indicates class interval from 50 - 54 days. ? = a QTL on the chromosome arm indicated but unsure if the locus identified by the marker shown. The influence of growing conditions (GC), preumably ambient temperature, and shown as Mean diff. GC, was calculated as the difference between population means shown in Table 2 and this Table. S, M, D, C, Hr, Sl, Al, H, F and Ar identify the parent contributing the major allele and the class interval in which they are included.

				Minimum duration (days) to Heading																Mean diff.
Popln.	**Chrom**	**Marker**		**50>**	**55>**	**60>**	**65>**	**70>**	**75>**	**80>**	**85>**	**90>**	**95>**	**100>**	**105>**	**110>**	**115>**	**120>**	**125>**	**Mean**	**GC**
Steptoe /	1HL	ABG55	20%(**S**) ?								3	4	22	57	30	30	2			100.5	63.5
Morex	2HS	BCD221	15%(**S**)							**M**					**S**						
Dicktoo /	1HL	ABG55	14%(**D**) ?							5	16	23	26	11	10	6				97.2	61.7
Morex	5HL	ABG3	36%(**D**) ?							**M**							**D**				
	6HL	MR	40%(**D**)																		
Chebec /	2HC	Bmy2	19%(**Hr**)				5	23	25	9	22	4	8							75.9	36.1
Harrington	2HS	BCD221	53%(**Hr**)						**C**		**Hr**										
Alexis /	2HC	Bmy2	33%(**Al**)	2	4	9	6	5	8	5	7	9	8	5	3	0	0	1		76.4	40.1
Sloop	2HS	BCD221	34%(**Al**)					**Sl**					**Al**								
Halcyon /	2HC	Bmy2	21%(**H**)			1	4	6	5	11	23	15	14	9	3	1	0	1		83.9	46.5
Sloop	2HS	BCD221	34%(**H**)					**Sl**											**H>**		
	5HL	ABG3	17%(**H**)																		
Tallon /				population not sown																	
Kaputar																					
Arapiles /	2HS	BCD221	33%(**F**)					4	10	22	20	16	20	25	31	6				90.8	49.9
Franklin	5HL	ABG3	13%(**F**)										**Ar**			**F**					

Table 4. Distribution (in days) for DH-June-10.2h of parents and progeny for each of 7 populations, together with the chromosome location of the markers contributing >10% of the variation recorded. The percentage contribution of individual markers is shown together with the identity of the parental allele responsible for delaying heading is indicated eg. 18%(S) where S identifies the contributing parent. 80> indicates a class interval of 80 - 84 days. ? = a QTL on the chromosome arm indicated but unsure if the locus identified by the marker shown. The mean influence of photoperiod, shown as Mean diff. Ppd, was calculated as the difference between population means shown in Table 3 and this Table. S, M, D, C, Hr, Sl, Al, H, Ar, and F identify the parent contributing the major allele and the class interval in which they are included.

				Duration (days to Heading															Mean diff.
Popln.	**Chrom**	**Marker**		**80>**	**85>**	**90>**	**95>**	**00>**	**105>**	**110>**	**115>**	**120>**	**125>**	**130>**	**135>**	**140>**	**145>**	**Mean**	**Ppd**
Steptoe /	1HL	Bmag382	18%(**S**)				1	3	10	18	22	36	19	17	15	6	1	118.5	18
Morex	2HS	ABG2	20%(**S**)				**M**								**S**				
Dicktoo /	1HL	Bmag382	27%(**D**)				3	6	10	14	21	13	12	3	7	5	3	115.7	18.5
Morex	5HL	ABG3	20%(**D**)				**M**										**D**		
	7HS	ABG380	11%(**D**)																
Chebec /	2HC	Bmy2	48%(**Hr**)		12	34	33	14	3									90.8	24.9
Harrington	6HL	BCD269	12%(**C**)				**C,Hr**												
	7HS	ABG380	13%(**C**)																
Alexis /	2HC	Bmy2	18%(**Al**)	1	0	2	6	18	28	13	3	1						102.5	26.1
Sloop	3HL	ABG4	31%(**Al**)					**Sl**	**Al**										
Halcyon /	1HL	Bmag382	30%(**H**)					9	34	24	14	13	1					108.6	24.7
Sloop	2HC	Bmy2	16%(**H**)					**Sl**									**H>**		
	5HL	ABG3	20%(**H**)																
Tallon /	2HC	Bmy2	14%(**T**)?		4	29	39	9	2	5								92.8	n/a
Kaputar	3HL	ABG4	19%(**K**)				**T,K**												
Aralipes /	2HC	Bmy2	17%(**F**)			2	23	59	38	33								109.8	18
Franklin	3HL	ABG4	17%(**F**)			**Ar**		**F**											

Table 5. Distribution of parents and progeny (in days) for response to photoperiod for each of 6 populations, together with the chromosome location of the markers contributing >10% of the variation recorded. The percentage contribution of individual markers is shown, together with the identity of the parental allele eliciting the greater response eg. 22%(S) where S identifies the contributing parent. 0> indicates a class interval of 0 - 4 days. ?= a QTL on the chromosome arm but uncertain if the same locus identified by the marker shown. M, S, D, Hr, C, Al, Sl, F, and Ar identify the parent contibuting the major allele and the class interval in which they are included. Halcyon (H) failed to head in DH-June 10.2 h, hence no response could be calculated for that parent.

				Response to Photoperiod (days)														
Popln.	**Chrom**	**Marker**		**0>**	**5>**	**10>**	**15>**	**20>**	**25>**	**30>**	**35>**	**40>**	**45>**	**50>**	**55>**	**60>**	**65>**	**Mean**
Steptoe /	2HS	BCD221	22%(**S**)	0	4	9	39	45	29	18	4							18.1
Morex						**M**			**S**									
Dicktoo /	1HL	CMWG706A	24%(**D**)	0	1	11	19	28	25	9	3	1						18.6
Morex	2HS	BCD221	20%(**D**)			**M**				**D**								
Chebec /	2HS	BCD221	59%(**C**)	3	11	11	14	37	15	5								15.3
Harrington	5HL	ABG3	10%(**C**) ?			**Hr**	**C**											
Alexis /	2HL	ABG14	22%(**Sl**)	3	1	6	10	8	8	6	10	2	10	7	1			26.1
Sloop	2HS	BCD221	39%(**Sl**)			**Al**				**Sl**								
Halcyon /	2HS	BCD221	32%(**H**)	2	1	6	16	6	18	12	19	8	5	1	0	1		24.7
Sloop										**Sl**							**H>**	
Arapiles /	2HS	BCD221	37%(**Ar**)	13	41	27	12	19	27	11	4	0	1					12.3
Franklin	5HL	ABG3	12%(**Ar**)	**F**			**Ar**											