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Dual Floral Induction Requirements in *Phleum alpinum*

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ABSTRACT

Flowering requirements of four Norwegian populations of *Phleum alpinum* were studied in controlled environments. A dual induction requirement was demonstrated in all populations. Inflorescence initiation had an obligatory requirement for short days (SD) and/or low temperature, while culm elongation and heading were enhanced by long days (LD) and higher temperatures. At 3 and 6 °C primary induction was almost independent of photoperiod, whereas SD was more effective than LD at higher temperatures. The critical temperature for primary induction was about 15 °C in SD and 12 °C in LD. Saturation of induction required 12 weeks of exposure to inductive conditions, although some heading and flowering took place with 6 weeks exposure to optimal conditions (9 °C/SD). Inflorescence development also took place in 8 h SD although it was delayed and culm elongation was strongly inhibited compared with LD conditions. Only small differences in flowering response were found between the populations.

Key words: *Phleum alpinum* L., alpine timothy, dual floral induction, flowering, photoperiod, temperature.

INTRODUCTION

The cultivated hexaploid timothy (*Phleum pratense* L.) is firmly documented as a long day plant (Evans and Allard, 1934; Ryle and Langer, 1963; Heide, 1982). Unlike most other temperate perennial grasses such as *Alopecurus pratensis*, *Bromus inermis*, *Dactylis glomerata*, *Festuca* spp., *Lolium perenne* and *Poa pratensis* (for references see Cooper and Calder, 1964; Evans, 1964; Heide, 1988b), it has no winter requirements for flowering. First-year seedlings readily initiate inflorescences in long days (LD) without any preceding chilling (vernalization) or short-day (SD) treatment (Langer, 1955; Cooper, 1958; Heide, 1982; Junttila, 1985).

However, the closely related diploid *P. pratense* subsp. *bertolonii* (DC.) Bornm. (syn. *P. nodosum* L.) did not flower in a heated glasshouse without preceding outdoor overwintering or SD treatment (Cooper and Calder, 1964). Low temperature (2–4 °C) for 6 or 12 weeks did not cause floral initiation in subsequent LD.

Field observations of heading and flowering of the tetraploid alpine or mountain timothy (*P. alpinum* L.) revealed very early heading after snowmelt in the spring. This suggested that

primary floral induction had already taken place during the SD and low temperature of autumn and winter, and possibly, that inflorescence primordia were initiated in the autumn before overwintering, which is a common strategy in arctic alpine perennial grasses (Hodgson, 1966; Håbjörg, 1979; Heide, 1980, 1986a, 1989a). With this background and since *Phleum alpinum* depends strongly upon sexual reproduction (Callaghan, 1974; Callaghan and Collins, 1981), a study of its flowering physiology was undertaken.

The floral induction requirements have been studied in controlled environments with four Norwegian populations of *P. alpinum* from different latitudes and altitudes.

MATERIALS AND METHODS

Seeds of *Phleum alpinum* L. were collected from natural populations at the following localities in Norway: Rondane, Ringebu, 61° 42' N, 10° 02' E, 970 m above sea level (asl); Grytøy, Harstad, 68° 53' N, 16° 28' E, 30 m asl; Iselvdal, Målselv, 68° 54' N, 18° 53' E, 390 m asl; Berlevåg, 70° 50' N, 29° 00' E, 30 m asl.

After germination at 21 °C the plants were raised at 18 °C in continuous light (10 h summer

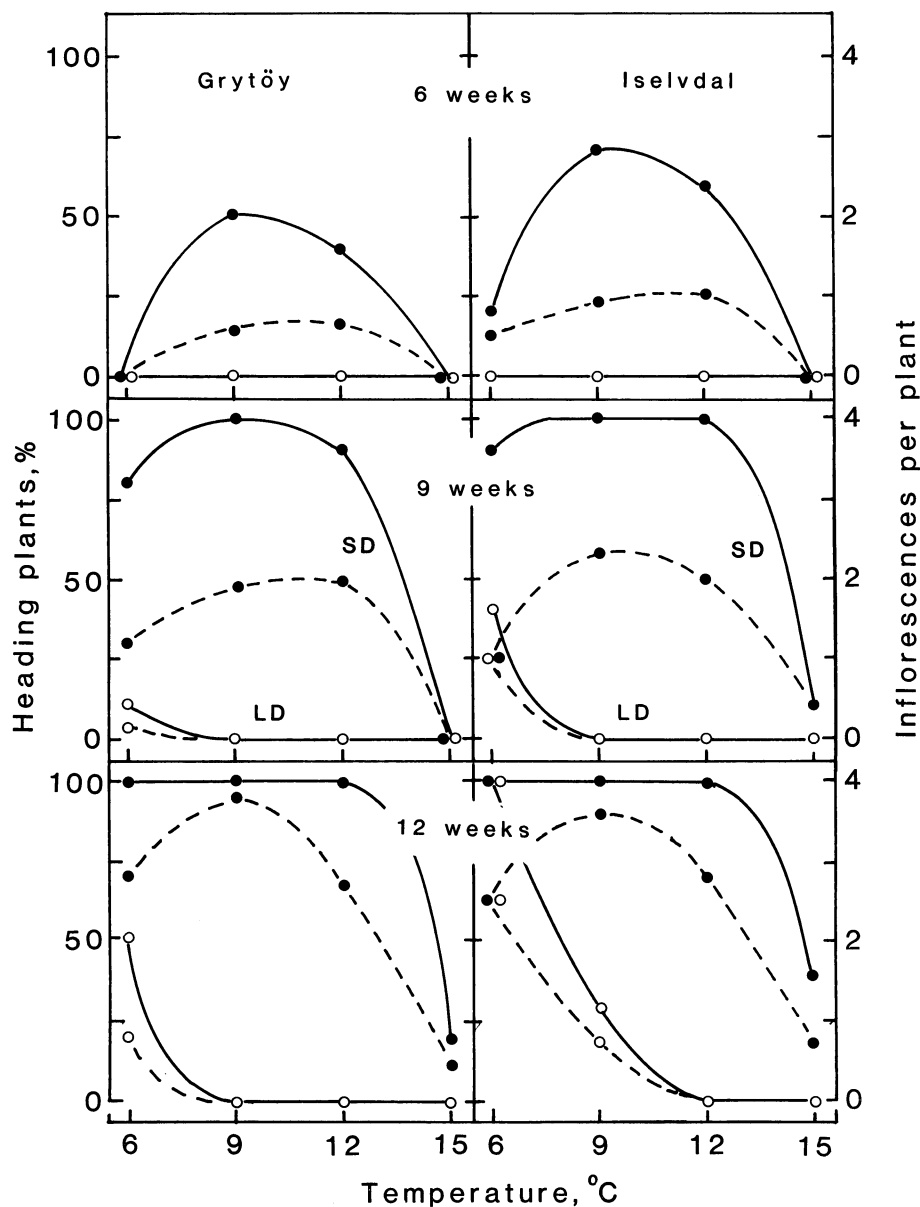


FIG. 1. Effects of 6, 9 and 12 weeks exposure to various temperatures in SD and LD on subsequent flowering of two populations of *Phleum alpinum* at 15 °C/24 h photoperiod. (—) percentage of heading plants; (----) number of inflorescences per plant. (●) 8-h photoperiods; (○) 24-h photoperiods.

daylight plus 14 h low-intensity incandescent light) as described by Heide (1988b). Treatments were started when the plants had five visible leaves.

The experiments were conducted in the Ås phytotron (59° 39' N) in naturally lit compartments with adjacent growth rooms for photoperiodic control or, in the case of 3 and 6 °C, in

artificially lit growthrooms. Summer daylight or light from Philips TL 32 fluorescent tubes (90 W m⁻², PAR) for 8 h was combined with 16 h of darkness or low-intensity incandescent light (approx. 1.5 W m⁻²) to establish 8-h (SD) or 24-h (LD) photoperiods, respectively. All plants thus received nearly the same amount of daily light

TABLE 1. *Culm height at anthesis and days to inflorescence appearance (heading) in two populations of Phleum alpinum at 15 °C/24 h photoperiod following varying primary induction treatments as indicated. Figures in brackets refer to a single heading plant*

Exposure time (weeks)	Temperature (°C)	Photoperiod (h)	Culm height (cm)		Days to heading*	
			Grytøy	Iselvdal	Grytøy	Iselvdal
6	6	8	—	51.2 ± 4.6	> 100	32.5 ± 4.5
		24	—	—	> 100	> 100
		8	46.8 ± 3.7	47.2 ± 1.5	35.5 ± 5.8	39.9 ± 2.8
		24	—	—	> 100	> 100
	12	8	53.7 ± 3.8	56.2 ± 1.9	41.9 ± 5.3	51.3 ± 4.0
		24	—	—	> 100	> 100
		8	—	—	> 100	> 100
		24	—	—	> 100	> 100
9	6	8	61.5 ± 3.5	59.4 ± 2.2	28.9 ± 2.8	26.1 ± 3.6
		24	(45)	58.2 ± 2.9	(43)	23.3 ± 3.9
		8	51.6 ± 2.7	50.2 ± 5.6	26.0 ± 2.4	24.4 ± 3.2
		24	—	—	> 100	> 100
	12	8	52.8 ± 3.6	56.9 ± 2.3	36.6 ± 2.9	40.9 ± 2.7
		24	—	—	> 100	> 100
		8	—	(43)	> 100	(55)
		24	—	—	> 100	> 100
12	6	8	62.7 ± 1.9	63.5 ± 1.1	20.1 ± 2.0	21.8 ± 1.2
		24	61.3 ± 4.0	61.0 ± 1.4	24.8 ± 2.7	23.3 ± 1.2
		8	59.6 ± 1.4	58.1 ± 2.5	23.1 ± 1.4	23.3 ± 2.3
		24	—	48.2 ± 8.3	> 100	30.7 ± 2.8
	12	8	56.8 ± 2.4	54.6 ± 3.1	27.9 ± 2.5	22.7 ± 1.9
		24	—	—	> 100	> 100
		8	50.3 ± 4.3	44.3 ± 5.2	63.0 ± 1.2	57.3 ± 3.8
		24	—	—	> 100	> 100

* From end of primary induction treatments.

energy in both photoperiods. Temperatures were controlled to ± 0.5 °C and a water vapour pressure deficit of 530 Pa was maintained at all temperatures at or above 9 °C.

Experiments were of the factorial split-plot design with temperatures as main plots and photoperiods and populations as sub-plots. Ten plants were used in each treatment.

The percentage of flowering plants and the number of inflorescences per plant were used as the main criteria of flowering, while culm height at anthesis (tallest culm in each plant) and rate of flower development (days to heading) were used as additional criteria. Analyses of variance were done according to standard methods (Snedecor and Cochran, 1967).

RESULTS

Primary induction

A preliminary experiment with the Rondane population demonstrated dual induction require-

ments for flowering. Heading in subsequent LD occurred in plants exposed to 3–12 °C for 10 weeks; at 3 and 6 °C, SD and LD were about equally effective, at 9 °C, LD was only partly inductive, and at 12 °C, SD only was inductive. No heading occurred in plants grown at 15 °C regardless of daylength conditions (data not shown).

The results of a factorial (temperature \times photoperiod \times exposure time) experiment with the Grytøy and Iselvdal populations are presented in Fig. 1 and Table 1. With 6 weeks exposure heading occurred in subsequent LD at 15 °C in plants that had been grown in SD at 6–12 °C only (9–12 °C in Grytøy). However, induction was only partial with such short exposure (maximum 70 % heading). By extending the exposure to 9 and 12 weeks complete heading was obtained with SD at 6–12 °C and with partial heading at 15 °C. With such extended exposure, induction took place also in LD but only at 6 and 9 °C (6 °C only in Grytøy). Although the two populations responded rather similarly, the Iselvdalen population clearly required less induction than the Grytøy population.

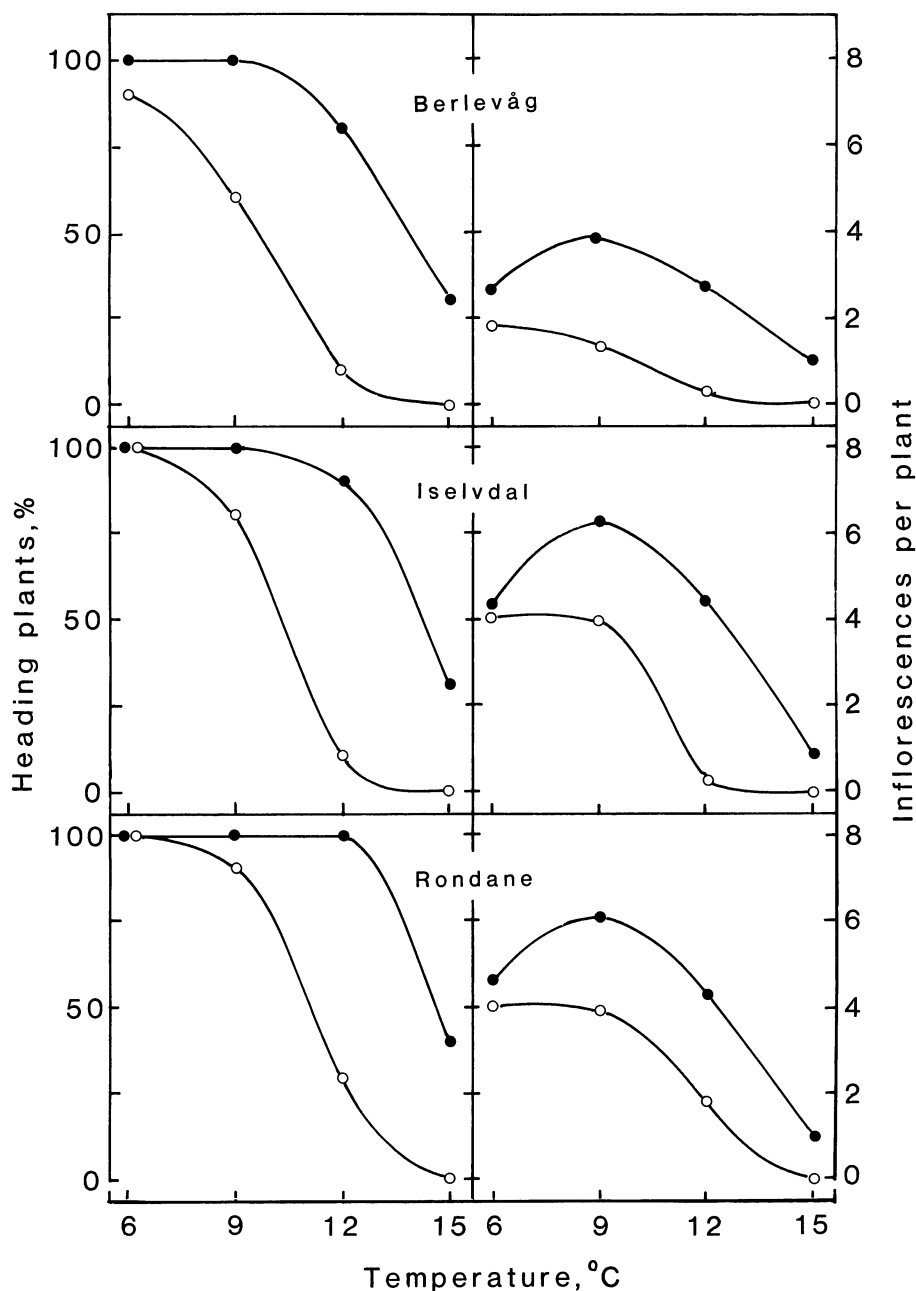


FIG. 2. Effects of 12 weeks exposure to various temperatures in SD and LD on subsequent flowering of three populations of *Phleum alpinum* at 15 °C/24 h photoperiod. (●) 8-h photoperiods; (○) 24-h photoperiods.

An analysis of variance of the inflorescence number data, using the three exposure time groups as replications, revealed highly significant main effects of photoperiod and temperature ($P < 0.001$) and population ($P < 0.01$), as well as their two- and three-factor interactions ($P < 0.001$).

Culm height increased and time to heading decreased with the degree of induction, with similar trends and values in both populations (Table 1).

In a second experiment plants of populations Berlevåg, Iselvdal and Rondane were exposed to the same temperatures and daylengths for 12

weeks before transfer to 15 °C/24 h photoperiod for flower development. As with 12 weeks exposure in the previous experiment, 100% heading was obtained in all populations with SD at 6 and 9 °C, and in a high proportion (80–100%) at 12 °C, but only 30–40% at 15 °C (Fig. 2). In the LD series full induction (90% in Berlevåg) was again obtained at 6 °C, but in contrast to the previous experiment, a high proportion of heading and flowering was also obtained at 9 °C and with marginal induction at 12 °C. No heading was observed with LD at 15 °C. Similar responses are reflected in the inflorescence number results (Fig. 2). A higher number of inflorescences than in the previous experiment was probably due to the fact that the plants were 1 week older and had on average 1.2 more leaves at the start of the treatments.

The two inland and higher elevation populations Iselvdal and Rondane had a stronger flowering response than the coastal Berlevåg population. This was especially pronounced in the inflorescence number data. In all populations the highest number of inflorescences was found in the 9 °C/SD treatment. An analysis of variance of the inflorescence number data, using the ten parallel plants in each treatment as replications, revealed highly significant ($P < 0.001$) main effects of temperature, photoperiod and population, as well as of all the two-factor interactions.

Culm height at anthesis increased and days to heading decreased in parallel with the degree of induction in all populations. At the lower temperatures there was little effect of photoperiod on these parameters.

Secondary induction

Plants of populations Berlevåg, Iselvdal and Rondane which had been exposed to 6 °C/SD for 12 weeks were transferred to 9, 15 or 21 °C and photoperiods of 8 and 24 h in order to determine the effects on inflorescence development.

Although heading took place in nearly all plants under all conditions (data not shown), SD significantly ($P < 0.01$) reduced the number of inflorescences (Table 2), delayed their appearance (Table 3), and strongly reduced culm height at anthesis (Table 4). Low temperature significantly increased inflorescence number ($P < 0.01$) and strongly delayed their appearance, but had little effect on culm height (interaction with photoperiod).

Although the three populations showed similar trends in these responses, there was a significant ($P < 0.01$) difference in inflorescence number among populations, Iselvdal having the highest

TABLE 2. *Effects of temperature and daylength during flower development of Phleum alpinum on number of inflorescences per plant. Means \pm s.e. for the populations Berlevåg, Iselvdal and Rondane*

Temperature (°C)	Photoperiod (h)		Mean
	8	24	
9	4.0 \pm 0.2	5.1 \pm 0.4	4.5 \pm 0.2
15	3.1 \pm 0.3	4.2 \pm 0.3	3.7 \pm 0.2
21	3.3 \pm 0.3	3.7 \pm 0.3	3.5 \pm 0.2
Mean	3.5 \pm 0.1	4.3 \pm 0.2	

TABLE 3. *Effects of temperature and daylength during flower development on days to inflorescence appearance in Phleum alpinum. Means \pm s.e. for the populations Berlevåg, Iselvdal and Rondane*

Temperature (°C)	Photoperiod (h)		Mean
	8	24	
9	59.3 \pm 1.2	45.9 \pm 1.3	52.6 \pm 1.2
15	30.0 \pm 1.6	22.7 \pm 0.6	27.0 \pm 0.8
21	22.6 \pm 0.6	15.6 \pm 0.4	19.1 \pm 0.6
Mean	37.7 \pm 1.7	26.1 \pm 1.5	

TABLE 4. *Effects of temperature and daylength during flower development on culm height at anthesis (cm) of Phleum alpinum. Means \pm s.e. for the populations Berlevåg, Iselvdal and Rondane*

Temperature (°C)	Photoperiod (h)		Mean
	8	24	
9	22.9 \pm 0.7	39.4 \pm 1.3	31.1 \pm 1.3
15	19.4 \pm 0.4	46.7 \pm 0.7	32.7 \pm 1.9
21	17.1 \pm 0.8	44.7 \pm 0.7	31.1 \pm 1.8
Mean	19.6 \pm 0.5	43.6 \pm 0.6	

number with an average of 4.3 and Berlevåg the lowest number with 3.1. Rondane was intermediate with 4.0. There were only small differences among the populations in the other parameters.

SD during heading and flower development also resulted in a plagiotropic growth orientation, causing the heading shoots to grow at an angle of about 30° to the horizontal. Occasionally, viviparous proliferations were observed in inflorescences developing in SD at 21 °C, especially in the Rondane population.

TABLE 5. *Effects of increasing numbers of LD cycles during flower development at 15 °C on number of inflorescences per plant in three Phleum alpinum populations. Values are means \pm s.e.*

Population	No. of LD cycles					Mean
	0	4	8	12	16	
Berlevåg	2.3 \pm 0.4	2.4 \pm 0.4	2.4 \pm 0.4	2.6 \pm 0.4	3.0 \pm 0.4	2.6 \pm 0.2
Iselvdal	3.6 \pm 0.5	3.6 \pm 0.5	3.9 \pm 0.2	4.0 \pm 0.6	4.8 \pm 0.4	3.9 \pm 0.2
Rondane	3.3 \pm 0.4	3.4 \pm 0.6	3.9 \pm 0.1	3.9 \pm 0.5	3.9 \pm 0.4	3.7 \pm 0.2
Mean	3.0 \pm 0.3	3.2 \pm 0.3	3.4 \pm 0.2	3.5 \pm 0.3	3.9 \pm 0.2	

TABLE 6. *Effects of increasing numbers of LD cycles during flower development at 15 °C on days to inflorescence appearance in three populations of Phleum alpinum. Values are means \pm s.e.*

Population	No. of LD cycles					Mean
	0	4	8	12	16	
Berlevåg	29.0 \pm 1.9	28.6 \pm 1.8	26.3 \pm 1.0	25.3 \pm 2.2	22.1 \pm 1.0	25.7 \pm 0.8
Iselvdal	28.2 \pm 1.8	26.4 \pm 1.8	25.6 \pm 1.2	22.4 \pm 1.3	19.8 \pm 1.0	24.5 \pm 0.7
Rondane	31.0 \pm 0.8	28.7 \pm 1.9	25.6 \pm 1.3	23.3 \pm 1.4	24.0 \pm 1.1	26.5 \pm 0.7
Mean	29.4 \pm 0.8	27.9 \pm 1.0	25.8 \pm 0.8	23.6 \pm 0.8	22.0 \pm 0.6	

TABLE 7. *Effects of increasing numbers of LD cycles during flower development at 15 °C on culm height (cm) in three populations of Phleum alpinum. Values are means \pm s.e.*

Population	No. of LD cycles					Mean
	0	4	8	12	16	
Berlevåg	19.0 \pm 0.8	19.9 \pm 1.1	22.4 \pm 0.7	26.6 \pm 2.1	30.4 \pm 1.3	22.9 \pm 0.7
Iselvdal	20.2 \pm 0.5	21.6 \pm 1.5	21.1 \pm 0.7	28.0 \pm 0.8	33.0 \pm 0.9	24.0 \pm 0.8
Rondane	18.4 \pm 0.9	19.3 \pm 1.0	22.8 \pm 0.4	25.7 \pm 1.1	30.7 \pm 1.4	22.0 \pm 0.8
Mean	19.2 \pm 0.4	20.3 \pm 0.2	22.1 \pm 0.3	26.8 \pm 0.6	31.4 \pm 0.7	

In another experiment, plants of the same populations given the same primary induction treatments (12 weeks at 6 °C/SD), were exposed to 0, 4, 8, 12 or 16 LD cycles (24 h) at 15 °C.

Again nearly all plants headed in continuous SD (data not shown), but the number of inflorescences significantly ($P < 0.01$) increased with increasing number of LD cycles (Table 5). This increase was similar in all three populations, but again the Iselvdal population had the highest and Berlevåg the lowest number of inflorescences (significant at $P < 0.05$). Days to inflorescence appearance decreased (Table 6) and culm height at anthesis increased with increasing number of LD cycles (Table 7). With 16 LD cycles the time of inflorescence appearance was about the same as in

continuous LD (cf. Table 3), while inflorescence number and culm height was still reduced compared with continuous LD (cf. Tables 2 and 4). These trends were very similar in all populations. Occasionally, viviparous proliferation of inflorescences was observed in the various treatments, especially in the Rondane and Berlevåg populations. The plagiotropic growth orientation was gradually reduced with increasing number of LD cycles, but was still very marked with 16 cycles.

DISCUSSION

The results in Figs 1 and 2 demonstrate an obligatory winter requirement for induction of flowering in *Phleum alpinum*. This is in contrast to

the single LD induction requirement of the hexaploid *P. pratense* (Langer, 1955; Cooper, 1958; Heide, 1982; Junttila, 1985), but parallels the winter requirement found in the diploid *P. pratense* subsp. *bertolonii* by Cooper and Calder (1964). This is a demonstration of the distinct differences in floral induction requirement that can exist among species and even subspecies within the same genus.

The dual floral induction system which predominates among temperate and high-altitude grasses [*Phleum pratense* (Heide, 1982) and *Poa nemoralis* (Heide, 1986*b*) being the only single LD induction exceptions (Heide, 1980–1990); cf. also Cooper and Calder (1964)] is a very versatile and well-adapted system for perennial plants native to the temperate region. Primary induction requirements are met by the decreasing photoperiod and temperature of autumn and winter, and secondary induction by the increasing temperature and photoperiod of spring and summer. Through genecological modifications of critical photoperiods, temperatures and exposure times for both of these floral induction events, there are almost unlimited possibilities for ecotypic differentiation leading to optimum reproductive success in the various environments. However, only moderate population differences in primary and secondary induction requirements of *Phleum alpinum* are indicated by the present results. This parallels the limited genecological variation found among arctic *P. alpinum* populations from Disko Island in Greenland in contrast to the marked variation among subantarctic populations from South Georgia (Callaghan, 1974).

The SD substitution for low temperature (vernalization) in primary induction (Figs 1 and 2) is also found in a whole range of temperate grasses such as *Lolium perenne* (Cooper, 1960; Evans, 1960), *Dactylis glomerata* (Blondon, 1972; Heide, 1987), *Alopecurus pratensis* (Heide, 1986*a*), several *Poa* (Heide, 1980, 1989*a, b*), and *Festuca* species (Heide, 1988*a, b*, 1990), in winter rye (Purvis and Gregory, 1937), in certain types of winter wheat (Evans, 1987), and even in some dicot species such as *Campanula medium*, *Scabiosa succisa* (Chouard, 1961), and the high-arctic *Cerastium regelii* (Heide, Pedersen and Dahl, 1990). Although primary induction by SD and low temperature produces the same result, both allowing flowering in subsequent LD, there are several lines of evidence indicating that their effects are distinct in nature (cf. Evans, 1987).

The absence of an obligatory LD requirement for heading and flowering (secondary induction) may seem rather odd for a high-latitude species such as *Phleum alpinum* (Table 2–7). However, a

similar situation has been demonstrated in arctic and sub-arctic *Poa* species (Heide, 1980, 1989*a*) and may represent an adaptation to arctic alpine environments in which LD and even continuous light prevail even before snowmelt in the spring. Under such conditions there is no need for a strong SD barrier to prevent precocious heading during winter and early spring. Nevertheless, the enhancement effect of LD on culm elongation and heading (Tables 2–7) may still be of great adaptive value in such a marginal environment. According to Callaghan (1974), the length of the growing season is the most critical factor limiting growth and development of *P. alpinum*. Since floral initiation took place even in a late snowbed site at Disko Island where no internode elongation occurred (Callaghan, 1974), flower development and seed maturation become the real limiting reproductive events in such conditions. Vivipary, which was shown to occur, although not regularly, represents a reproductive advantage under such marginal conditions (Heide, 1988*a*, 1989*a*), by reducing the critical length of the growing season.

Dissection of plants collected in the field in mid-September (Rondane population) showed that no inflorescence primordia had been initiated by that time. Likewise, when such plants were transferred to LD (24 h) at 18 °C no heading or flowering took place. These results indicate that in the natural environment *Phleum alpinum* does not initiate inflorescence primordia before overwintering, but that this takes place early in the spring.

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LITERATURE CITED

- BLONDON, F., 1972. Facteurs externes et déterminisme floral d'un clone de *Dactylis glomerata* L., pp. 135–81. In *Phytotronique et Prospective Horticole*, eds P. Chouard and N. de Bilderling, 390 pp. Gauthier-Villards, Paris.
- CALLAGHAN, T. V., 1974. Intra-specific variation in *Phleum alpinum* L. with specific reference to polar populations. *Arctic and Alpine Research* **6**, 361–401.
- and COLLINS, N. J., 1981. Life cycles, population dynamics and the growth of tundra plants, pp. 257–83. In *Tundra Ecosystems: A Comparative Analysis*, eds L. C. Bliss, O. W. Heal and J. J. More, 813 pp. Cambridge University Press, Cambridge.
- CHOUARD, P., 1961. Vernalization and its relation to dormancy. *Annual Review of Plant Physiology* **11**, 191–238.
- COOPER, J. P., 1958. The effect of temperature and photoperiod on inflorescence development in strains of timothy (*Phleum* spp.). *Journal of the British Grassland Society* **13**, 81–91.

- 1960. Short day and low-temperature induction in *Lolium*. *Annals of Botany* **24**, 232–46.
- and CALDER, D. M., 1964. The inductive requirements for flowering in some temperate grasses. *Journal of the British Grassland Society* **19**, 6–14.
- EVANS, L. T., 1960. The influence of temperature in species of *Lolium* and in *Poa pratensis*. *Journal of Agricultural Science, Cambridge* **54**, 410–16.
- 1964. Reproduction, pp. 126–153. In *Grasses and Grasslands*, ed. C. Barnard, 269 pp. Macmillan and Co, London.
- 1987. Short day induction of inflorescence initiation in some winter wheat varieties. *Australian Journal of Plant Physiology* **14**, 277–86.
- EVANS, M. W. and ALLARD, H. A., 1934. Relation of length of day to growth of timothy. *Journal of Agricultural Research* **48**, 571–86.
- HÅBJÖRG, A., 1979. Floral differentiation and development of selected ecotypes of *Poa pratensis* L. cultivated at six localities in Norway. *Meldinger fra Norges Landbrukshøgskole* **58** (4), 1–19.
- HEIDE, O. M., 1980. Studies on flowering in *Poa pratensis* L. ecotypes and cultivars. *Meldinger fra Norges Landbrukshøgskole* **59** (14), 1–27.
- 1982. Effects of photoperiod and temperature on growth and flowering in Norwegian and British timothy cultivars (*Phleum pratense* L.). *Acta Agriculturae Scandinavica* **32**, 241–52.
- 1984. Flowering requirements in *Bromus inermis*, a short-long-day plant. *Physiologia Plantarum* **62**, 59–64.
- 1986a. Primary and secondary induction requirements for flowering in *Alopecurus pratensis*. *Physiologia Plantarum* **66**, 251–6.
- 1986b. Long day control of flowering in *Poa nemoralis* in controlled and natural environments. *New Phytologist* **104**, 225–32.
- 1987. Photoperiodic control of flowering in *Dactylis glomerata*, a true short-long-day plant. *Physiologia Plantarum* **70**, 523–9.
- 1988a. Environmental modification of flowering and viviparous proliferation in *Festuca vivipara* and *F. ovina*. *Oikos* **51**, 171–8.
- 1988b. Flowering requirements in Scandinavian *Festuca pratensis*. *Physiologia Plantarum* **74**, 487–92.
- 1989a. Environmental control of flowering and viviparous proliferation in seminiferous and viviparous arctic populations of two *Poa* species. *Arctic and Alpine Research* **21**, 305–15.
- 1989b. *Poa*, pp. 538–45. In *Handbook of Flowering*. Vol. 6, ed. A. H. Halevy, 753 pp. CRC Press, Boca Raton, FL.
- 1990. Primary and secondary induction requirements for flowering in *Festuca rubra*. *Physiologia Plantarum* **79**, 51–6.
- PEDERSEN, K. and DAHL, E., 1990. Environmental control of flowering and morphology in the high-arctic *Cerastium regelii*, and the taxonomic status of *C. jenisejense*. *Nordic Journal of Botany* **10**, 141–7.
- HODGSON, H. J., 1966. Floral initiation in Alaskan gramineae. *Botanical Gazette* **127**, 64–70.
- JUNTILA, O., 1985. Experimental control of flowering and vivipary in timothy (*Phleum pratense*). *Physiologia Plantarum* **63**, 35–42.
- LANGER, R. H. M., 1955. Ear formation in timothy grass (*Phleum pratense*) following vernalization and short-day treatment. *Nature* **176**, 263.
- PURVIS, O. N. and GREGORY, F. G., 1937. Studies in vernalisation of cereals. I. A comparative study of vernalisation of winter rye by low temperature and by short days. *Annals of Botany* **1**, 569–92.
- RYLE, G. J. A. and LANGER, R. H. M., 1963. Studies on the physiology of flowering of timothy (*Phleum pratense* L.). I. Influence of day-length and temperature on initiation and differentiation of the inflorescence. *Annals of Botany* **27**, 213–31.
- SNEDECOR, G. W. and COCHRAN, W. G., 1967. *Statistical Methods*, 6th edn. 593 pp. The Iowa State University Press, Ames, IA.