# Do Low, Non-freezing Night Temperatures During Anthesis Affect Seed Set in *Bromus inermis* Leyss. and *Poa pratensis* L. ?

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## ABSTRACT

**In Norway, seed yields of *Bromus inermis* Leyss. and *Poa pratensis* L. are often low despite a reasonable panicle number. This research was initiated to examine the effect of low, non-freezing temperatures on seed set. In the first experiment artificially induced plants of *Bromus inermis* cv. Løfar and Manchar and *Poa pratensis* cv. Lavang and Leikra were exposed to day/night temperatures of 20/5, 20/10 or 20/15°C from heading or first anthesis until harvest. The same treatments were also imposed on detached panicles/spikelets placed on tap water. In a second experiment plants of *Bromus inermis* were kept at 20/5°C for an increasing number of days before transfer to 20/15°C. In a third experiment sods from commercial seed crops were placed overnight in growth chambers with temperatures of 2, 6 or 10°C during their flowering periods. Percent seed set was never affected by night temperature, the mean values being 62% in *Bromus inermis* and 64% in *Poa pratensis*. Although empty florets occurred throughout the panicles of both species, seed set generally decreased in the one or two most terminal florets in each spikelet. Percentage seed set and seed weight were much lower in detached than in intact panicles. It is concluded that low seed set in *Bromus inermis* and *Poa pratensis* is mostly of genetic origin.**

***Additional index words:*** **detached spikelets, floret position, floret site utilsation, germination, seed yield, thousand seed weight.**

## INTRODUCTION

In Norway, seed yields of *Bromus inermis* Leyss. and *Poa pratensis* L. are often low despite a reasonable panicle number. This may be attributed to several causes, such as non-viable egg cells or pollen grains, poor pollination, lack of fertilization, abortion of embryos or developing seeds, seed shedding before harvest and seed losses during harvesting and cleaning. Anthesis and pollination are pre-requisites for seed production in open-pollinated grasses. The largely apomictic *Poa pratensis* requires pollination for endosperm and thus seed development (Nilsson, 1937; Tinney, 1940). In *Bromus inermis* anthesis is usually at its maximum between 3 and 10 p.m. (Lowe, 1950; Vough, 1975), but *Poa pratensis* flowers most profusely between 3 and 8 a.m. ( Maun, Canode and Teare, 1969).

Few investigations have dealt with the effect of meteorological conditions on anthesis. Temperatures below 14°C inhibit or increase the duration of anthesis in *Lolium perenne* L. (Hill, 1980). Anthesis in *Bromus inermis* was inhibited by rain during pollen release and on cloudy days following nights with temperatures below 13°C (Vough, 1975). Little or no flowering in *Bromus inermis* occurred on cloudy days with temperatures below 15.5°C (Evans and Wilsie, 1946). Jones and Brown (1951) stated that pollen shedding in *Bromus inermis* was reduced by cool weather, the optimum temperature for pollen release being as high as 30°C.

High or low temperature stress during anthesis may damage both the male and female parts of the grass flower (Hill, 1980). Night temperatures above 20°C arrested normal anther development in *Poa annua* L. without injuring the female organs (Hovin, 1958). As opposed to 21 and 27°C, 8 h exposure to 32°C for two consecutive days reduced pollen germination and seed set in *Poa pratensis* (Maun *et al.* 1969). In *Bromus inermis* high temperatures often reduce pollen longevity because of desiccation (Jones and Brown, 1951).

In an attempt to destroy only the male part of the *Bromus inermis* flower, Domingo (1944) treated inflorescences with hot water (37-51°C), hot air (37-51°C) or cold air (approximately 0°C) at various growth stages between heading and anthesis. While emasculation with hot air and, in particular, hot water was quite successful, cold air for up to 20 minutes had no effect on pollination or fertilization, even when applied just prior to anthesis (Domingo, 1944).

Detailed studies into the effect of temperature on pollen performance in *Lolium perenne* were conducted by Elgersma, Stephenson and den Nijs (1989). Increasing temperature in the range 14-26°C enhanced pollen tube length when measured 0.5 - 5.0 h after the pollen grain had reached the stigma. In a later experiment with detached spikelets, plants were kept in an identical environment until anthesis, and the temperature treatments commenced only after pollination. In this case no difference in percentage seed set between day/night temperatures of 14/14, 17/12 or 20/15°C could be detected seven days after pollination, but the average caryopsis length increased with higher temperature (Elgersma, Nieboer and Keizer, 1993).

An examination of seed yields of *Lolium perenne* over a ten year period indicated that minimum screen temperature during the week of anthesis or the week after anthesis accounted for 70 % of the variation in seed number (Hampton and Hebblethwaite, 1983). Hebblethwaite (1985) later assumed that low average temperatures (below 8°C) during anthesis were likely to decrease seed set and thus seed yield.

Detailed studies of seed set and seed development in grasses are often complicated by great differences in the

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timing of anthesis and seed maturation, even within a single plant or inflorescence. If such investigations are to be conducted with intact plants, they also require a lot of valuable space in growth chambers. An early attempt to study seed production of *Bromus inermis* panicles detached prior to pollination and inserted into glass jars in immediate proximity to the field crop was undertaken by Keller (1943), who found that this technique reduced seed weight and germination by 55-75 % as compared with intact plants. Wiesner and Grabe (1972) later found detached culms to be useful for the study of seed dormancy and germination in *Lolium perenne*, although they also reported lower seed weights from detached than from intact panicles.

While the previous authors worked with undivided inflorescences, Elgersma and van Hateren (1991) examined seed set and development in individual spikelets of *Lolium perenne* obtained by cutting the the rachis between spikelets and floating them on water in a petri dish. In this case a weak, but positive correlation between seed set in detached and intact spikelets was obtained, and the seeds seemed to elongate normally during the first week after pollination. Elgersma *et al.* (1993) later used this technique in their experiments with various temperatures after pollination.

The objective of the present study was to clarify whether low, non-freezing temperatures during anthesis have an adverse effect on seed yields of *Bromus inermis* and *Poa pratensis*. The experiments were initatated during the author's sabbatical to the USDA-ARS National Forage Seed Production Research Center, Oregon, USA, in 1991, and were completed in 1993 after his return to Apelsvoll Reseach Centre, Division Landvik, Norway.

## MATERIAL AND METHODS

### Experiments with single plants, Oregon 1991

Seed of *Bromus inermis* cv. Manchar (of Idaho origin) was obtained from the US National Seed Storage Laboratory, Colorado, while seed of the Norwegain cultivars Løfar (*Bromus inermis*) and Lavang and Leikra (*Poa pratensis*) was provided by the Norwegian Basic Seed Centre, Hellerud. Shortly after germination, seedlings were transplanted to plastic cones containing 450 $cm^3$ of standard potting soil and raised in a greenhouse with the minimum and maximum temperatures set to 15 and 20°C, respectively. Daylength was extended to 16 h using high pressure sodium vapour lamps (PPFD ≈ 400 $\mu E\ m^{-2}\ s^{-1}$). Plants were fertilised with a complete nutrient solution (Peters 20:20:20) every week.

Six to nine weeks after sowing, plants were transferred to artifically lit growth chambers (PPFD ≈ 400 $\mu E\ m^{-2}\ s^{-1}$) for flower induction. For the first sets of plants, primary induction comprised six weeks at 15°C and an 8 h photoperiod for *Bromus inermis* (Heide, 1984) and eight weeks at 8°C and a 10 h photoperiod for *Poa pratensis* (Heide, 1980). After primary induction, plants were brought back to the greenhouse for secondary induction at a 24 h photoperiod and 15-25°C (both species). These treatments induced heading in 58 and 75 % of all plants of *Bromus inermis* cv. Manchar and Løfar, and 80 and 30 % of *Poa pratensis* cv. Lavang and Leikra. Heading of *Bromus inermis* was later improved by cutting plants back at the beginning of primary induction and prolonging the short day treatment to 10 weeks. In *Poa pratensis* ten weeks primary induction at 5°C and an 8 h photoperiod later resulted in 86% heading in cv. Leikra, but only 34% in cv. Lavang.

Treatments with various night temperatures were either started just after heading or immediately before anthesis. Intact plants, detached panicles and detached spikelets were transferred to growth chambers with a flux density (fluorescent tubes plus incandescent light) at panicle level corresponding to 300 $\mu E\ m^{-2}\ s^{-1}$ for tall plants of *Bromus inermis* and 200 $\mu E\ m^{-2}\ s^{-1}$ for short plants of *Poa pratensis*. A day temperature of 20°C was always maintained for 9 hours per day, and the three night temperatures, 5, 10 or 15°C, also lasted 9 hours. Lights gradually came on and went out during the 3 hour changeover periods every morning and evening. Most experiments were replicated in time.

### *Bromus inermis* expt. 1: Detached and intact panicles at three day/night temperatures until harvest.

On the day of complete emergence of the primary panicle, ten individual plants of each cultivar were transferred to each of the temperatures 20/5, 20/10 and 20/15°C. The primary panicle of each plant was tagged and the number of days to anthesis recorded.

In the same experiment, 60 plants of cv. Løfar and 46 plants of cv. Manchar remained in the greenhouse for about two more weeks. Just before expected anthesis, a total of 12 large panicles of each cultivar were detached by cutting the peduncle 5 cm below the lowest node in the inflorescence. The entire panicles were arranged in three similar groups and inserted four by four into holes in styrofoam pieces which were then floated in bowls filled with tap water. The bowls were placed at 20/5, 20/10 and 20/15°C with the detached panicles at the same height as those of intact plants.

In cv. Løfar, six more inflorescences representing different clones were detached from the culms and divided into segments by cutting the rachis 1 cm below the inflorescence nodes. These segments, each consisting of three to nine spikelets, were put on water as for the entire panicles. Temperature treatments were restricted to 20/5 and 20/15°C.

The plants which had not been used for detachment were divided into twelve groups, each group containing an average of 10 panicles of each cultivar. Four groups (replicates) were allocated to each of the three growth chambers at the beginning of anthesis.

Detached as well as intact panicles were harvested individually 28 days after anthesis. For each combination of temperature and cultivar, the number of spikelets was counted in three primary panicles, and percentage seed set was determined by examining all floret positions in one spikelet per node. Rudimentary florets at the end of each spikelet were discarded from analysis. Some secondary panicles were also examined in order to see if any relationship existed between seed set in different panicles on the same plant. The moisture content of seed from these panicles was determined after drying at 120°C for two hours.

For intact panicles estimates for seed yield per panicle and thousand seed weight were obtained after drying, hand threshing, cleaning on a seed blower and purity analyses. Seed number per panicle was calculated from seed yield per pani-

cle and thousand seed weight. Germination was determined after 7 and 21 days at 30/20°C.

### *Bromus inermis* expt. 2: Increasing number of days at 20/5°C before transfer to 20/15°C.

A total of 180 plants of cv. Løfar were divided into eighteen groups, each consisting of approximately 30 panicles. Three groups were transferred directly to 20/15°C on the day of first anthesis. Remaining plants were placed at 20/5°C for 2, 4, 8, 12 or 16 days after anthesis, three groups being transferred to 20/15°C on each of these days. Panicles were harvested on day 35. Recordings were as in expt. 1, except that seed moisture content at harvest, spikelet number, floret number and percent seed set were not determined.

### *Poa pratensis* expt.: Intact panicles at 20/5, 20/10 and 20/15°C from anthesis until harvest.

Intact plants of cv. Lavang and cv. Leikra were grouped and transferred to 20/5, 20/10 and 20/15°C at the first sign of anthesis, three groups of each cultivar per treatment. With the exception of cv. Leikra in time replicate I, all groups consisted of at least 10 panicles. Panicles were harvested 35, 31 and 28 days after anthesis for temperatures of 20/5, 20/10 and 20/15°C, respectively. Percent seed set was determined by counting empty and filled florets in approximately 60 spikelets in one panicle per group, but the total number of spikelets per panicle was not recorded. Remaining panicles were hand threshed and the seed cleaned and analyzed for purity before determination of seed yield per panicle, seed number per panicle, thousand seed weight and germination after 10 and 28 days at 25/15°C.

### Experiments with sods from established seed crops, Norway 1993

On 26-28 May 1993, 35 x 74 cm sods of *Bromus inermis* cv. Løfar and Leif (a newly released Norwegian cultivar) and *Poa pratensis* cv. Lavang and Leikra were dug from established swards and placed into twelve open containers. Plants were kept outside until the beginning of anthesis. During their flowering periods (cv. Lavang: 28 May - 15 June; cv. Leikra: 4-19 June; cv. Løfar and cv. Leif: 25 June - 11 July), three containers (replicates) of each cultivar were moved to each of three growth chambers with constant temperatures of 2, 6 or 10°C during the nights (9 p.m. - 8 a.m.). In order to simulate outdoor daylength, the growth chambers were furnished with weak fluorescent light (approximately 35 $\mu E\ m^{-2}\ s^{-1}$) which came on in the periods 9 - 10.30 p.m. and 4 - 8 a.m. One control treatment (3 containers of each cultivar) remained outdoor during the nights. Hourly temperature data are provided in Fig. 1 for *Poa pratensis* cv. Lavang and the *Bromus inermis* cultivars. Temperature data for *Poa pratensis* cv. Leikra closely resembled those for cv. Lavang and are therefore not shown.

Throughout the experiments, plants were watered with pure water or a complete fertilizer solution on alternate days. At normal time for harvest (cv. Lavang: 1 July; cv. Leikra: 4 July; cv. Løfar and cv. Leif: 13 August) all inflorescences were cut and dried in paper bags at ambient temperature. Recordings followed the same pattern as in the Oregon experiments.

## RESULTS

### Experiments with single plants, Oregon 1991

### *Bromus inermis* expt. 1.

At the highest temperature combination, anthesis in cv. Løfar started only five days after complete head emergence (Fig. 2). Day/night temperatures of 20/10 and 20/5°C delayed flowering by an average of 5 and 11 days as compared with 20/15°C. Lowering the night temperature from 15 to 10°C also deferred anthesis in cv. Manchar, but a further decrease to 5°C had less effect in the American cultivar (data not shown).

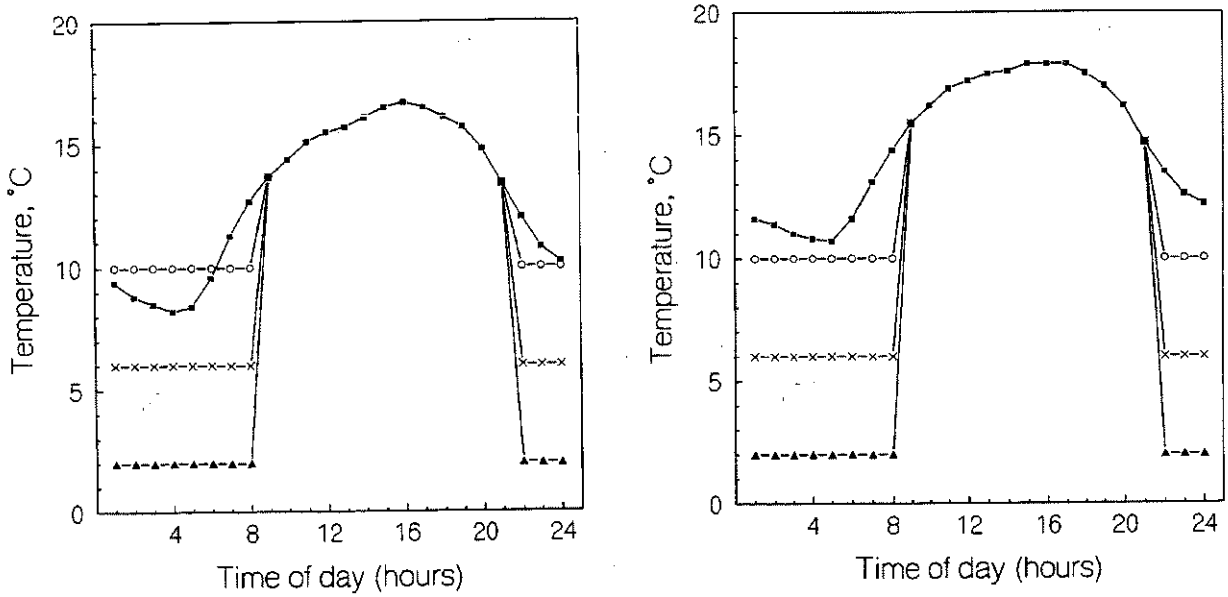


**Figure 1. Average hourly temperature during the treatment period in (a) *Poa pratensis* cv. Lavang (b) and *Bromus inermis* cv. Løfar and Leif. Experiments in Norway. (■—■ = outdoor control, o—o = 10°C night, x—x = 6°C night, ▲—▲ = 2°C night).**

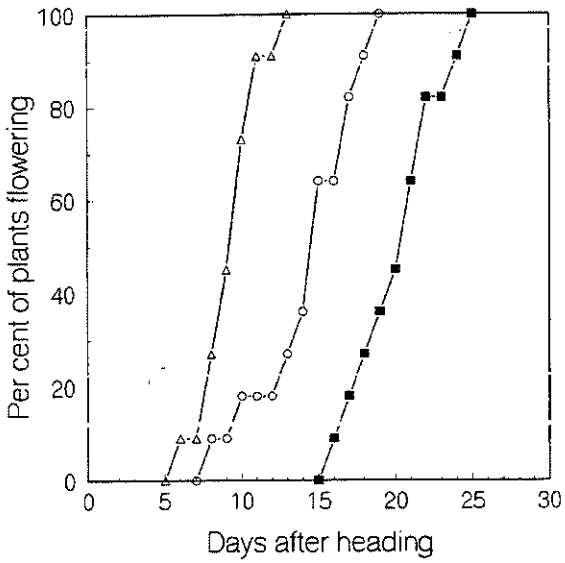


**Figure 2. Time course of flowering in *Bromus inermis* cv. Løfar. Experiments in Oregon. (■—■ = 20/5°C, o—o = 20/10°C, △—△ = 20/15°C)**

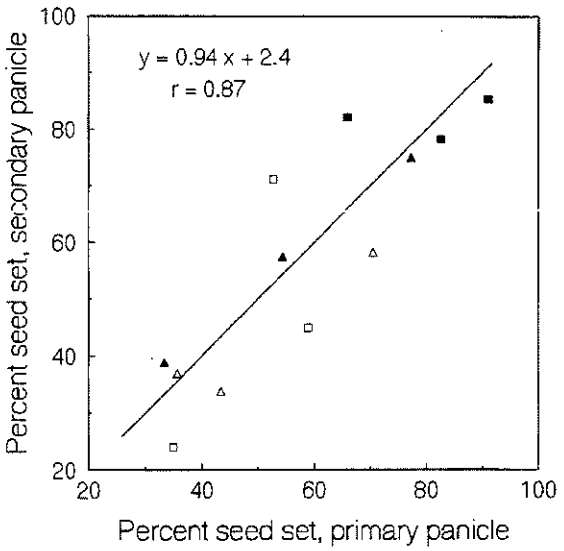


**Figure 3. Relationship between seed set in primary and secondary panicles on the same plant of *Bromus inermis*. Experiments in Oregon. (□= cv. Manchar, 20/5°C; ■ = cv. Manchar, 20/15°C; △ = cv. Løfar, 20/5°C; ▲ = cv. Løfar, 20/15°C)**

Spikelet number per panicle or floret number per spikelet were not significantly different in cv. Løfar and Manchar, the averages across cultivars being 31.6 and 6.9, respectively. There was also little or no difference between the two cultivars with regard to percent seed set, seed moisture content at harvest, seed yield per panicle, seed number per panicle, thousand seed weight or germination (data not shown in tables).

Increasing night temperature resulted in lower seed moisture content, higher thousand seed weight and better germination in seeds harvested 28 days after anthesis (Table 1). Seed yield per panicle was significantly lower at 20/5 than at 20/10 and 20/15°C. The calculated seed number per panicle tended to increase linearly with night temperature (P=0.08), but spikelet examinations revealed no effect of night temperature on percent seed set.

A significant correlation (r=0.87) was obtained between percent seed set in primary and secondary panicles on the same plant (Fig. 3).

The average percent seed set was more than twice as high in intact as in whole, detached panicles (Table 2). When harvested after 28 days, seeds from detached panicles were drier and lighter as compared to intact ones.

The low fertility in detached panicles could mainly be attributed to a strong reduction in seed set from the basal to the terminal floret in each spikelet (Fig. 4). Seed set also tended to be higher in spikelets positioned at upper than at intermediate and lower nodes of detached panicles, the respective numbers being 35, 29 and 30 %. Contrary to this, seed set in spikelets from intact panicles was not reduced until positions 6 (cv. Løfar) or 7 (cv. Manchar, Fig. 4), and the average seed set at upper nodes was 60 % as compared to 67 and 71 % for intermediate and lower nodes.

**Table 1. Effect of night temperature on percent seed set, seed moisture content at harvest 28 days after first anthesis, seed yield per panicle, seed number per panicle, thousand seed weight and germination after 7 and 21 days in intact panicles of *Bromus inermis*. Data are means of cv. Løfar and Manchar.**

| | Night temperature,°C | | | LSD |
|---|---|---|---|---|
| | 5 | 10 | 15 | (P<0.05) |
| Seed set (%) | 60 | 70 | 60 | ns |
| Seed moisture content at harvest (%) | 65 | 62 | 47 | 10 |
| Seed yield[1] per panicle (mg) | 201 | 290 | 314 | 76 |
| Seed number per panicle (calc.) | 62 | 74 | 84 | ns(P=0.08) |
| Thousand seed weight[2] (mg) | 3248 | 3750 | 3928 | 261 |
| Germination, 7 days | 40 | 48 | 55 | 4 |
| Germination, 21 days | 58 | 67 | 77 | 7 |

[1] *100% purity, 14% moisture content*
[2] *14% moisture content*

**Table 2. Percent seed set, seed moisture content at harvest 28 days after first anthesis and thousand seed weight in intact and detached panicles of *Bromus inermis*. Data are means for two cultivars and three night temperatures.**

| | Intact | Detached | LSD P<0.05 |
|---|---|---|---|
| Seed set (%) | 63 | 29 | 9 |
| Seed moisture content at harvest (%) | 58 | 48 | 5 |
| Thousand seed weight (mg) | 3642 | 2491 | 413 |

Division of detached panicles into segments revealed no difference in seed set between night temperatures of 5 and 15°C, the average value being only 22%. The difference between clones was almost significant (P=0.08, data not shown).

### *Bromus inermis* expt. 2

An increasing number of days at 20/5°C before transfer to 20/15°C had no effect on seed yield per panicle, the calculated seed number per panicle, thousand seed weight or germination. The average values were, seed yield per panicle, (234 mg); seed number per panicle, calc. (54); thousand seed weight, (4193 mg); germination, 7 days, (43); germination, 21 days, (80).

### *Poa pratensis* expt.

Despite a lower percentage seed set, seed yield and seed number per panicle were higher in cv. Leikra than in cv. Lavang (Table 3). To a certain extent this could be explained by more florets per panicle in the former cultivar. Germination after 10 days was higher in cv. Lavang than in cv. Leikra, but no difference could be detected with regard to thousand seed weight or final germination.

None of the investigated characters was significantly influenced by night temperature, but thousand seed weight tended to be higher at 5°C than at 10 and 15°C (Table 4).

Spikelet position had no significant effect on percentage seed set in any of the cultivars. Seed set in cv. Lavang was significantly lower at floret position 3 than at positions 1 and 2, and a similar tendency was recorded for terminal florets in cv. Leikra (Fig. 5).

## Experiments with sods from established seed crops, Norway 1993

### *Bromus inermis*

Cultivar Løfar had more florets per spikelet and tended to produce heavier panicles than cv. Leif. On the other hand, cv. Leif had greater germination than cv. Løfar (Table 5).

None of the examined characters was significantly influenced by night temperature. Thousand seed weight tended to decrease with falling night temperature during anthesis (Table 6).

As an average for cv. Løfar and Leif, seed set at upper, intermediate and lower nodes in the panicle was 53, 63 and 60 %. Seed set was lower at floret position 7 than at more basal positions in spikelets from both cultivars (Fig. 6).

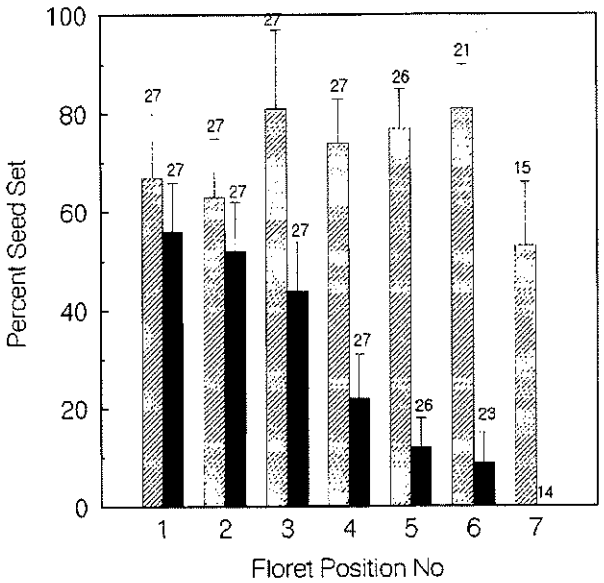


**Figure 4. Percent seed set (+ S.E.) at various floret positions in spikelets of intact and detached panicles of *Bromus inermis* cv. Manchar. Figures above bars denote the number of floret positions studied. Experiments in Oregon = intact panicles, ■ = detached panicles)**

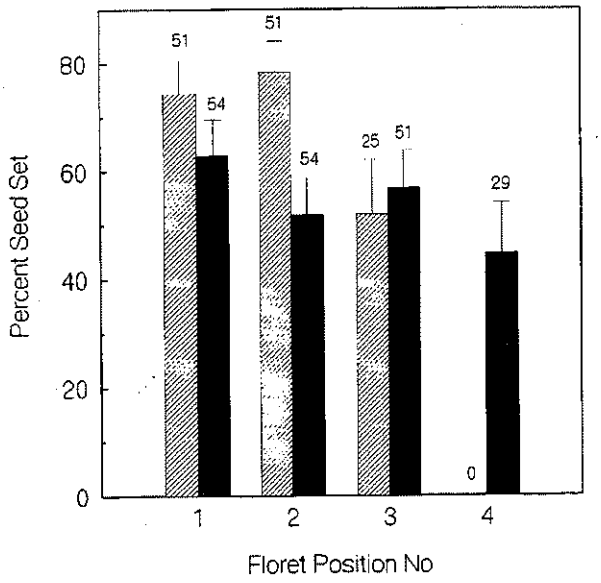


**Figure 5. Percent seed set (+ S.E.) at various floret positions in spikelets of *Poa pratensis* cv. Lavang and Leikra. Figures above bars denote the number of floret positions studied. Experiments in Oregon. ( = cv. Lavang, ■ = cv. Leikra)**

**Table 3. Florets per spikelet, percent seed set, seed moisture content at harvest, seed yield per panicle, seed number per panicle, thousand seed weight and germination in *Poa pratensis* cv. Lavang and Leikra.**

| | Cultivar | | LSD |
|---|---|---|---|
| | Lavang | Leikra | P<0.05 |
| Florets per spikelet | 2.3 | 3.5 | 0.4 |
| Seed set (%) | 71 | 56 | 9 |
| Seed moisture content at harvest (%) | 20 | 16 | ns |
| Seed yield per panicle (mg) | 34 | 65 | 12 |
| Seed number per panicle (calc.) | 121 | 234 | 45 |
| Thousand seed weight (mg) | 281 | 279 | ns |
| Germination, 10 days | 74 | 43 | 12 |
| Germination, 28 days | 85 | 82 | ns |

**Table 4. Effect of night temperature on percent seed set, seed moisture content at harvest, seed yield per panicle, seed number per panicle, thousand seed weight, and germination after 10 and 28 days in intact panicles of *Poa pratensis*. Data are means of cv. Lavang and Leikra.**

| | Night temperature, °C | | | LSD |
|---|---|---|---|---|
| | 5 | 10 | 15 | P<0.05 |
| Seed set (%) | 66 | 62 | 63 | ns |
| Seed moisture content at harvest (%) | 19 | 21 | 15 | ns |
| Seed yield per panicle (mg) | 57 | 43 | 49 | ns |
| Seed number per panicle (calc.) | 186 | 163 | 182 | ns |
| Thousand seed weight (mg) | 302 | 270 | 267 | ns(P=0.06) |
| Germination, 10 days | 52 | 58 | 65 | ns(P=0.14) |
| Germination, 28 days | 83 | 80 | 87 | ns |

**Table 5. Spikelets per panicle, florets per spikelet. percent seed set, seed yield per panicle, seed number per panicle, thousand seed weight and germination in *Bromus inermis* cv. Løfar and Leif.**

| | Cultivar | | LSD |
|---|---|---|---|
| | Løfar | Leif | P<0.05 |
| Spikelets per panicle | 62.4 | 58.4 | ns |
| Florets per spikelet | 5.5 | 4.2 | 0.6 |
| Seed set (%) | 56 | 62 | ns |
| Seed yield per panicle (mg) | 267 | 227 | ns(P=0.08) |
| Seed number per panicle (calc.) | 64 | 55 | ns |
| Thousand seed weight (mg) | 4195 | 4111 | ns |
| Germination, 10 days | 75 | 82 | 6 |
| Germination, 28 days | 78 | 88 | 6 |

**Table 6. Effect of night temperature on percent seed set, seed yield per panicle, seed number per panicle, thousand seed weight and germination in *Bromus inermis*. Data are means of cv. Løfar and Leif.**

| | Night temperature, °C | | | Outdoor | Sign. |
|---|---|---|---|---|---|
| | 2 | 6 | 10 | control | |
| Seed set (%) | 60 | 55 | 67 | 55 | ns |
| Seed yield per panicle (mg) | 253 | 219 | 276 | 240 | ns |
| Seed number per panicle (calc.) | 63 | 53 | 65 | 57 | ns |
| Thousand seed weight (mg) | 4017 | 4117 | 4240 | 4238 | ns(P=0.07) |
| Germination, 7 days | 76 | 78 | 78 | 81 | ns |
| Germination, 21 days | 81 | 85 | 82 | 85 | ns |

### *Poa pratensis*

The examined characters were generally not affected by night temperature, and data are therefore not shown.

## DISCUSSION

The detrimental effect of spring frosts on panicle production and seed yields of *Lolium perenne*, *Poa pratensis* and *Dactylis glomerata* is well documented (Hill, 1980; Heide, 1980, Niemeläinen, 1991). Promoted by indications in the literature (Hampton & Hebblethwaite, 1983; Elgersma *et al.*, 1989), this research was conducted to test the hypothesis that low, non-freezing temperatures also depress seed yields if they occur during or shortly after anthesis. The results do not verify the hypothesis.

In the first experiment conducted with *Bromus inermis* in Oregon, each panicle was harvested 28 days after the first sign of anthesis in that specific panicle. Grabe (1956) found that maximum seed weight in *Bromus inermis* was achieved 17 or 18 days after anthesis; hence four weeks was considered more than sufficient to attain physiological maturity in the present study. The high seed moisture contents at harvest clearly indicate that this assumption was wrong, especially for night temperatures of 5 and 10°C. Whereas Grabe (1956) worked with individual florets, whole panicles with at least one week's variation in anthesis were used in the present investigation, and there is little doubt that low night temperature prolonged not only the period from heading to anthesis (Fig. 2), but also the duration of flowering and the period from anthesis to maturity. It is therefore not surprising that thousand seed weight and seed yield per panicle increased with increasing night temperature in this particular experiment. A higher loss of small and immature seeds during cleaning explains why seed number per panicle also tended to decrease with lower night temperature. However, this can not be interpreted as an effect of night temperature on seed set.

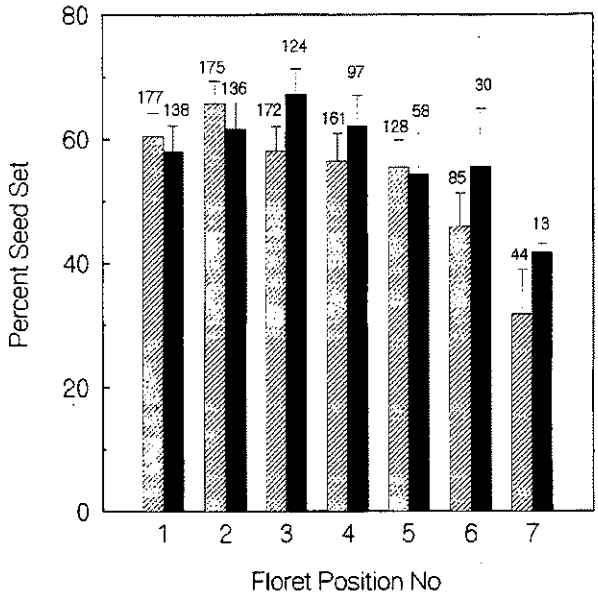


**Figure 6. Percent seed set (+ S.E.) at various floret positions in spikelets of *Poa pratensis* cv. Løfar and Leif. Figures above bars denote the number of florets positions studied. Experiments in Norway. ( = cv. Løfar, ■ = cv. Leif)**

Unlike *Bromus inermis*, seeds of *Poa pratensis* were mature at harvest, and there was no significant effect of night temperature on seed moisture content (Table 4). In this species, most seeds at 20/15°C probably reached their maximum dry weight several days before harvest. The higher seed weights at 20/5 and 20/10°C can be explained by longer seed filling periods; at these temperatures harvest was also deferred to 31 and 35 days after anthesis. It is a common experience that low temperatures and long seed filling periods give the highest seed weight both in cereals and grasses (Kolderup, 1979; Wiesner and Grabe, 1972; Akpan and Bean, 1980).

The lack of any effect of low, non-freezing night temperature on seed set complies with Domingo (1944) who was unable to emasculate flowers of *Bromus inermis* by exposing them to 0°C. Although low temperature delays the phenological development and retards pollen tube growth (Elgersma *et al.*, 1989), this does not necessarily imply reduced seed set and seed yield (Elgersma *et al.*, 1993).

According to Burbidge, Hebblethwaite and Ivins (1978) approximately 60 % of the florets in seed crops of *Lolium perenne* are capable of being fertilized. In *Poa pratensis* Maun *et al.* (1969) reported an average seed set of 63, 67 and 63 % after exposure to 21, 27 and 32°C, respectively. Knowles and Baenziger (1962) obtained an average seed set of 62 % in northern strains of *Bromus inermis*. These figures are in general agreement with the average of 62 % seed set in *Bromus inermis* and 64 % in *Poa pratensis* as determined by the present examinations of intact panicles.

A calculation of the realised seed number per panicle as a percentage of the potential seed number per panicle (i.e. the product of spikelets per panicle and florets per spikelet) resulted in much lower values for seed set in *Bromus inermis*, on average only 34 and 21 % in the experiments in Oregon and Norway, respectively. To a certain extent, the difference between these two ways of determining seed set can be explained by the fact that only primary panicles, most of them fairly large, were selected for the counting of spikelets and florets. However, it is also likely that many light seeds were removed together with empty florets during seed threshing and cleaning (Meijer, 1985; Horeman, 1989).

In contrast to the experiments conducted by Elgersma and van Hateren (1991) and Elgersma *et al.* (1993), the use of detached spikelets and panicles was not very successful in the present investigation. In the case of whole detached panicles, percentage seed set was less than one half compared to intact panicles (Table 2), and with divided panicles it was even lower. The lower seed set and seed weight in detached panicles can clearly be ascribed to shortage of water and nutrients, and this situation probably occured before anthesis was finished. The drop in seed set from the top to bottom of each panicle and, most notably, from the base to the apex within each spikelet (Fig. 4), is compatible with Knobloch (1944) who found that anthesis in *Bromus inermis* proceeds basipetally from the top spikelets down the panicle but acropetally within each spikelet. Elgersma *et al.* (1993) reported no problem of desiccating spikelets, but their studies were restricted to the four bottom floret positions, and the spikelets were kept on water for only seven days.

The results from divided panicles and the close correlation between seed set in primary and secondary panicles on the same plant (Fig. 3) suggest that variation in fertility in *Bromus inermis* is mostly of genetic origin. One contributing factor might well be irregularities during meiosis in this octoploid species (Elliott and Love, 1948). Selection of high fertility plants offers considerable scope for seed yield improvements in *Bromus inermis* (Knowles and Baenziger, 1962). This is probably also the case in *Poa pratensis*, although variation for seed set seems to be smaller in this largely apomictic species (Nissen, 1950; van Wijk, 1985).

The variation in seed set depending on spikelet and floret position (Figs. 4-6) complies with earlier studies in *Lolium perenne* (Anslow, 1963; Hampton and Hebblethwaite, 1985; Elgersma *et al.*, 1993) and *Bromus inermis* (Knowles and Baenziger, 1962). Burbidge *et al.* (1978) observed a much stronger drop in seed set from the base to the apex in each spikelet, and they ascribed this to lower assimilate supply to the upper florets. On the other hand, Marshall and Ludlam (1989) found that all florets were equally prone to abortion which they considered was due to genetic factors associated with outbreeding rather than shortage of nutritients. The present results represent a compromise between the two views, seed set being approximately equal at all floret positions except the one or two terminal ones.

Although not directly related to seed set, the problems of flower induction of *Bromus inermis* and *Poa pratensis* under artificial conditions became very apparent during these experiments. For *Bromus inermis* it seems crucial that the short day treatment is started before plants have developed false stems (Heide, 1984). It is also noteworthy that the artificial induction treatment imposed on Løfar in Oregon produced only 32.6 spikelets per panicle as compared to 62.4 spikelets per panicle under natural induction conditions in Norway. In *Poa pratensis* the temperate cultivar Leikra needed longer exposure to low temperature and short days than the arctic cultivar Lavang, which in fact seemed to be overinduced as primary induction under artificial light conditions was extended to 10 weeks.

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