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Environmental control of phenological development in two *Lesquerella* species

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Abstract

Lesquerella fendleri and *Lesquerella mendocina* are two species with potential for domestication as crops for semiarid regions. Understanding the environmental influences on development is a critical step for the introduction of a wild species into cultivation. Under controlled conditions these species responded differently to temperature: *L. fendleri* phenological approach toward flowering responded linearly to temperature, whereas initiation of flowering in *L. mendocina* was relatively insensitive to temperature. *L. fendleri* exhibited a quantitative response to supra-optimal temperatures (with rate of development reduced with further increases in temperature) whereas *L. mendocina* showed a qualitative response, no flower development at supra-optimal temperatures. In this work undertaken in the field we studied phenological development in *L. fendleri* and *L. mendocina* as a function of planting date, quantified the time required to reach particular phenological stages under the various thermal environments, and compared these results with those previously obtained with controlled conditions. We also studied the influence of photoperiod on plant phenology in field situations and through experiments done under controlled conditions.

Development rate for both species varied with sowing date with plant cycles shorter in spring sown plants, even if measured in thermal time. *L. mendocina* plants sown in late spring displayed a biennial cycle. These results are consistent with those obtained under controlled conditions. However, cycle shortening in thermal time with delays in sowing date suggested that factors other than temperature also influenced phenology of these two species. Further studies under controlled conditions showed that phenological development of *L. fendleri* plants was also altered by photoperiod, with plants displaying a typical long-day response. At the highest temperatures used in these studies *L. mendocina* plants did not respond to photoperiod. The possibility that incident radiation is involved in *L. mendocina* response to sowing date is discussed.

Keywords: *Lesquerella fendleri*; *Lesquerella mendocina*; Development; Phenology; Photoperiod; Temperature

1. Introduction

Approximately one-third of the world's land area is arid and semiarid (Heathcote, 1983). Such areas are often utilized though over-exploitation and degradation can result from unsustainable agricultural practices. These same areas contain a numbers indigenous species with the potential for domestication as a source of specialty chemicals or other compounds that confer adaptability to harsh environments (Timmermann and Hoffmann, 1985). While several new industrial crops have been developed for warm-arid environments in recent years, there has been no parallel development of new crops for cold-arid environments, such as the extra-Andean Patagonia (Ravetta and Soriano, 1998; Zavala and Ravetta, 2000). Several species in the genus *Lesquerella* (Brassicaceae) could be an alternative for these

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environments (Rollins and Shaw, 1973; Dierig et al., 1996; Ploschuk et al., 2003). *Lesquerella fendleri* (A. Gray) S. Watson is native to the arid and semiarid regions of southwestern USA and its seeds contain significant amounts of hydroxy fatty acids (Thompson et al., 1989; Roetheli et al., 1991) used for the production of lubricants, plastics, protective coatings, surfactants and pharmaceuticals (Thompson, 1990). *L. fendleri* has been considered for domestication in the USA where it has high seed and oil yield, low seed dormancy and presents responsiveness to irrigation (Dierig et al., 1993; Hunsaker et al., 1998). Under cultivation *L. fendleri* behaves strictly as an annual, with all plants dying after seed maturity.

While *L. fendleri* yields under growing conditions similar to that of wheat and other small grains are high, when this species is grown as a spring crop in cooler climates yields are considerably lower (Dierig et al., 1993). A related species, *Lesquerella mendocina* (Phil.) Kurt, native to the 'Monte' region in Argentina, has been reported to behave as a perennial both in the wild (Correa, 1984) and under cultivation (Ploschuk et al., 2003). It also produces hydroxy fatty acids as the major oil constituent of the seeds but, unlike *L. fendleri*, has only recently been considered for domestication (Ploschuk et al., 2001).

One of the first steps for the introduction of a wild species into cultivation is to understand crop phenology and its environmental control, and then to avoid the coincidence of stages critical for yield determination with environmental conditions that can limit potential and actual yield in each particular area (Richards, 1991). Phenological development in other species of Brassicaceae is primarily affected both by photoperiod and temperature (Hodgson, 1978; Nanda et al., 1996).

Phenological responses to temperature in *L. fendleri* and *L. mendocina* under controlled condition reported by Windauer et al. (2004) were very different, this difference explaining in large measure the different growth habit displayed by these two species. *L. fendleri*'s phenological approach towards flowering responded linearly to temperature; in contrast, that of *L. mendocina* appeared relatively insensitive to temperature. To validate these results for plants growing under field conditions, we used successive planting dates designed to expose the plants to a wide range of thermal conditions. When other variables (i.e. water and nutrient availability) are held under control, this approach should also permit the detection of other environmental factors (i.e. photoperiod) that could be involved in the control of phenology. No experimental results assessing photoperiod influences on development have been reported in the literature for either *L. fendleri* or *L. mendocina*.

The objectives of this work were: (i) to study phenological development in *L. fendleri* and *L. mendocina* plants sown at successive planting dates, quantifying the time required to reach particular phenological stages under the various thermal environments and (ii) to detect the influence on plant phenology of other environmental factors (i.e. photoperiod).

2. Materials and methods

2.1. Field experiments

Field experiments were carried out during 1996 and 1997 for *L. fendleri*, and 1997 and 1998 for *L. mendocina* at the Facultad de Agronomía, Universidad de Buenos Aires (34°37′S, 58°20′W, alt. 25 m.o.s.l.) on a salty clay loam soil (Vertic Argiudoll).

Seeds of *L. fendleri* were provided by D. Dierig (USDA, WCL Phoenix, AZ) and came from multiplication plots in Phoenix, Arizona, established from seeds originally collected from native stands. Seeds of *L. mendocina* were collected from a native stand at Lihuel Calel, La Pampa, Argentina (37°57′S, 65°33′W).

There were eight sowing dates in 1996 for *L. fendleri*: 22 March, 12 April, 3 May, 23 May, 13 June, 27 July, 30 August and 31 October. In 1997, sowing dates for both *L. fendleri* and *L. mendocina* were: 24 March, 23 April, 26 May, 3 June, 2 August, 18 September and 17 November. During 1998, five sowings were performed for *L. mendocina* on 19 March, 20 April, 7 June, 4 August and 7 November.

Treatments were arranged in three randomized complete blocks. Each plot consisted of six lines, 0.2 m apart and 5 m long with a total density of 10 plants m^{-2}. In each plot, three lines were sown with seeds that had previously received a vernalization treatment, and three were sown with un-vernalized seeds. Vernalization treatment consisted of pre-germinating seeds maintained at 4 ± 1 °C in the dark for 14 days in Petri dishes containing wet cotton (Windauer et al., 2004). Un-vernalized seeds were pre-germinated for 2 days before sowing; as a result of this, both treated and untreated seeds were sown with a similar degree of hypocothyl and radicle protrusion.

Daily maximum and minimum temperatures were obtained from a meteorological station located 300 m from the experimental site and used to calculate daily mean temperatures. Photoperiod included twilight. Plots were irrigated as necessary throughout the season and hand-weeded with observations of phenological development made daily and dates of emergence (EM), first bud appearance (FBA), flowering (FL) and maturity (MA) were recorded. Plots were considered to have reached a given phase when 50% of the plants in the central rows reached that phase. Durations of the intervals between phases were measured in calendar days and in thermal time (TT). Thermal time was calculated using the T_b estimated by Windauer et al. (2004): 2.6 °C for the EM-FBA phase and 6.1 °C for the following phase (FBA-FL) for *L. fendleri*, while for *L. mendocina* a T_b of 3.6 °C was used for the phase FBA-FL. Thermal time for the phase EM-FBA had not been established in the case of *L. mendocina* due to the absence of

a significant relationship between developmental rate and temperature (Windauer et al., 2004).

Data analysis was carried out using ANOVA to determine differences in duration of the phases considered both in days and in TT. Regression analysis was used to estimate the effect of sowing date on the duration of each phenological phase and of the whole cycle, as well as to determine the effect of temperature on the rate of development.

2.2. Experiments under controlled conditions

2.2.1. General

Plants of both *Lesquerella* species were grown under two photoperiods and three temperature regimes in growth chambers (Biocontrol, Buenos Aires, Argentina). Seeds of *L. fendleri* and *L. mendocina* were pre-germinated and vernalized essentiality as previously described and then single seedlings transplanted into 1-L pots containing a mixture of vermiculite-moss:peat-moss (1:1) and placed into growth chambers, where photoperiod and temperature treatments were installed. Plants were watered daily with Hoagland solution.

The experiment consisted of a factorial combination of two species, two photoperiods and three temperatures. The photoperiod treatments were 8 and 18 h and the constant temperature regimes were 9, 16 and 24 (±0.5) °C. All plants received light of approximately 700 (mol m^{-2} s^{-1} for 8 h d^{-1}, with those plants allocated to the 18 h treatment illuminated with low intensity incandescent lamps during the other 10 h. Within each chamber, 10 plants per species were randomized and pots were rotated daily until flowering.

Phenological observations were carried out daily. Dates for FBA and FL were recorded and the duration of the phases was estimated in calendar days and TT. Corresponding rates of development were calculated as the reciprocal of the duration of each phase (Monteith, 1984). Analyses of variance considering temperature, photoperiod, species and their interaction effects were performed on all the variables. Linear regression analyses were used to estimate the association between variables.

3. Results

3.1. Field experiments

Temperatures during the experimental period, as well as annual variation of the photoperiod are shown in Fig. 1.

No differences in growth cycle duration were evident between vernalized and untreated controls (data not shown). Only changes in the rate of seedling emergence were found, that were attributed to a differential thermal time accumulation which might have occurred during vernalization. Data from both vernalized and non-vernalized controls were pooled for the rest of the analysis.

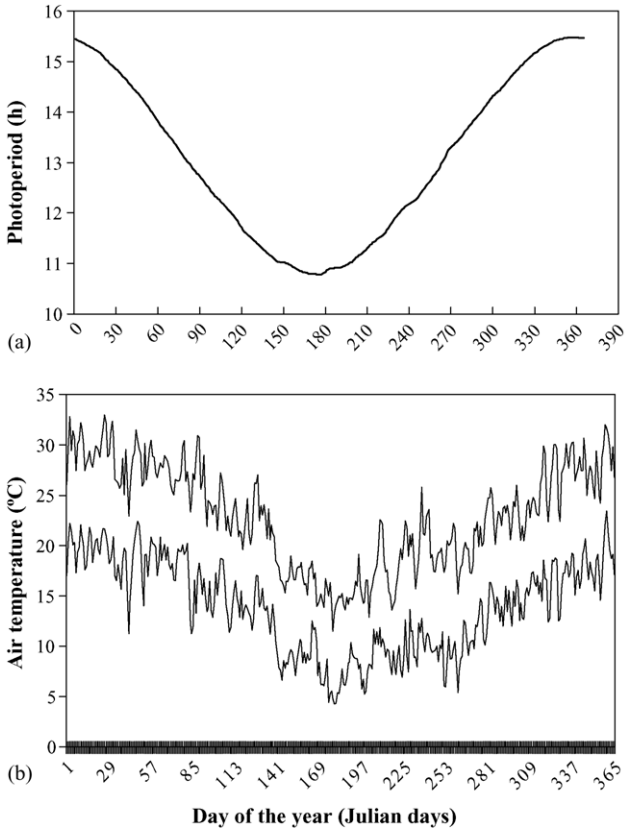

Fig. 1. Annual variation of the photoperiod (a) and daily maximum and minimum temperatures (b) during 1996–1997 at Buenos Aires (34°37′S, 58°20′W).

Essentially, all *L. fendleri* and *L. mendocina* plants behaved as annuals, the only exception being that of plants of *L. mendocina* sown at late spring (November, Fig. 2) behaved as biennials in both years.

L. fendleri showed a progressive reduction in the duration of its life cycle with delay in sowing date (Fig. 2). The linear relationship between sowing date and days to maturity obtained by regression analysis showed a reduction of 0.4 days (and 4.9 °C d) for every day's delay in sowing after 22

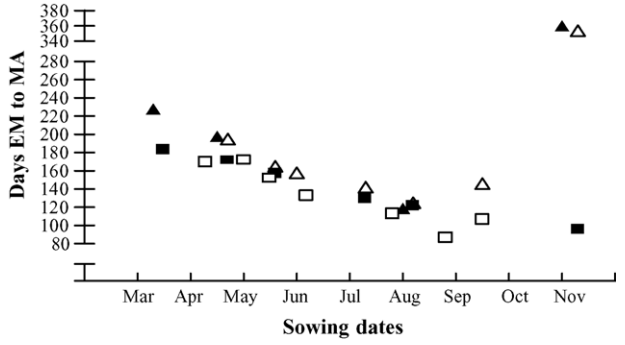

Fig. 2. Number of calendar days from emergence (EM) to maturity (MA) for *L. fendleri* (■, □) and *L. mendocina* (▲, △) grown in the field, for different sowing dates during 1996, 1998 (open symbols) and 1997 (closed symbols).

March ($P < 0.001$). A similar response was found in *L. mendocina* ($P < 0.001$) with a reduction of 0.7 days for every day's delay in sowing between 19 March and 8 August. The September and November sowing dates for *L. mendocina* showed a different response pattern during each experimental year: a significant increase ($P < 0.001$) in the duration of the growth cycle (Fig. 2) compared to that of plants from the earlier sowing dates. Moreover, plants sown in November (late spring) displayed a biannual cycle, flowering concurrently with plants sown the following March.

Independent of sowing date, plants of *L. mendocina* needed more days to complete their life cycle than *L. fendleri* plants (Fig. 2), although the magnitude of the difference was small in sowing dates going from March to August (14 ± 3.7 days).

When the life cycle of these plants were separated in three phases (EM-FBA, FBA-FL and FL-MA) it was only in the first of these phases that major differences were found.

As sowing date was delayed, the duration of EM-FBA decreased in *L. fendleri* plants, either if expressed in calendar days (Fig. 3) or in TT (data not shown). This reduction was particularly noticeable when comparing autumn with spring sowing dates (i.e. from 105 to 28 days and from 1271 to 498 °C d ($T_b = 2.6$ °C), for autumn and spring sowing dates, respectively (Fig. 3) and on average resulted in a reduction of 0.33 ± 0.03 days and 3.56 ± 0.40 °C d per day of delay in the sowing date. This reduction in the phase length was less significant when comparing the September, October and November sowing dates. *L. mendocina* required significantly more days to reach FBA than *L. fendleri* ($P < 0.001$) but as with *L. fendleri*, a reduction in the preflowering phase was found for *L. mendocina* plants sown between March and August, with extreme values of 136 and 63 days (0.42 ± 0.04 days per day of delay in the sowing dates, Fig. 3). Plants sown later than August displayed a reverse response during both experimental years, the number of days to reach FBA increased when sowing date was delayed ($P < 0.001$). Furthermore,

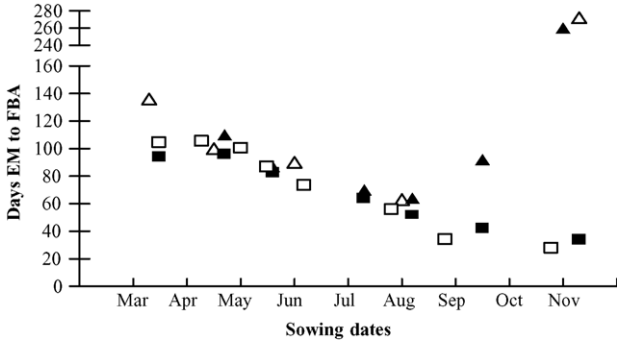

Fig. 3. Number of calendar days from emergence (EM) to floral buds appearance (FBA) for *L. fendleri* (■, □) and *L. mendocina* (▲, △) grown in the field, for different sowing dates during 1996, 1998 (open symbols) and 1997 (closed symbols).

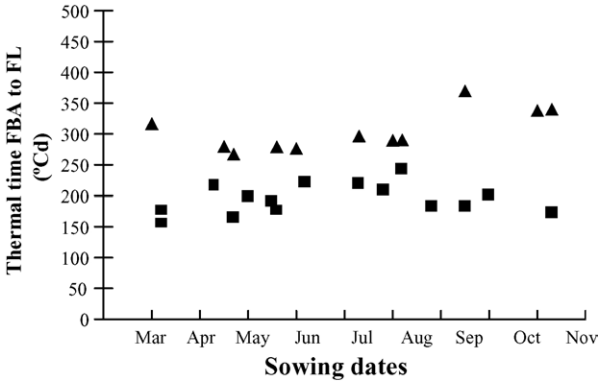

Fig. 4. Thermal time from floral bud appearance (FBA) to flowering (FL) during *L. fendleri* (■) and *L. mendocina* (▲) grown in the field for different sowing dates.

sowing in November resulted in plants with a biennial growth cycle that was displayed even by plants that had undergone vernalization.

Both species showed a similar response pattern during the FBA-FL phase, requiring progressively less time (days) to reach flowering when the sowing date was delayed. This response was strongly associated with daily temperatures during this phase. No significant differences were detected in the accumulated TT for the completion of the phase when the plants were sown at different dates, either for *L. fendleri* or for *L. mendocina* (Fig. 4), though *L. mendocina* plants required more TT to complete this phase than *L. fendleri* ones ($P < 0.001$; 195 ± 29 °C and 324 ± 36 °C d for *L. fendleri* and *L. mendocina*, respectively). Similarly, both species followed a similar pattern during the (FL-MA) phase, taking progressively less time to reach maturity as sowing date was delayed. This shortening could again be attributed to increases in temperature (data not shown).

In the case of *L. fendleri*, the reduction in the duration of the phase EM-FBA with delays in sowing date was also evident if that duration was expressed in thermal time (data not shown). Hence, the concurrence of another factor in addition to temperature was inferred from this response for the determination of the length of the phase EM-FBA. For the case of *L. mendocina* (though with the exception of late spring sowing dates) a reduction in the duration of the EM-FBA phase was also observed with delays in the sowing date. However, since the duration of this phase has been reported to be insensitive to temperature in the suboptimal range, an environmental factor other than temperature should have been responsible for this change in the length of the EM-FBA phase. As a first approach, we considered photoperiod as the only environmental factor modulating the developmental rate in *L. mendocina* subjected to suboptimal temperatures and that photoperiod, concurrently with temperature, would be controlling the phase length in *L. fendleri*. To test for these possibilities, we carried out experiments under controlled conditions varying temperature and photoperiod.

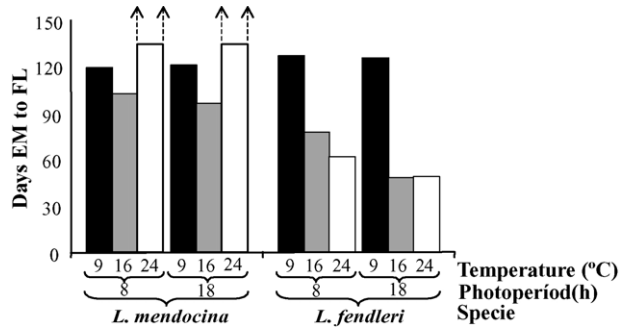

Fig. 5. Number of calendar days from emergence (EM) to flowering (FL) for both *Lesquerella* species for a combination of two photoperiods and three temperatures. Bars ending with arrows mean flowering was not reached before the experiment ended (180 days from sowing).

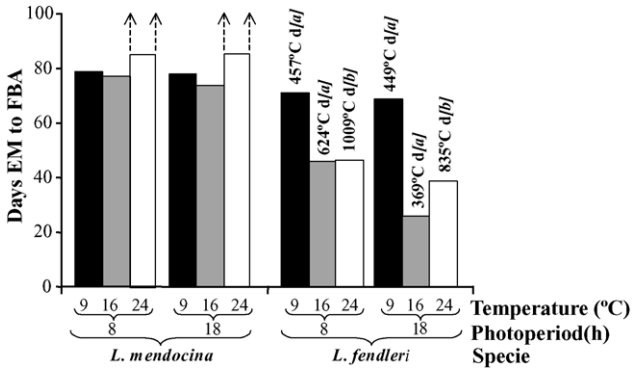

Fig. 6. Number of calendar days from emergence (EM) to floral buds appearance (FBA) for both species for a combination of two photoperiods and three temperatures. Bars ending with arrows mean flowering was not reached before the experiment ended. Figures above the bars represent the TT (T_b = 2.6 °C). [Different letters in each of these values mean significant differences in thermal time, between different thermal regimes for a single photoperiod.]

3.2. Experiments under controlled conditions

Responses to photoperiod and temperature under controlled condition were different depending on species. Both species displayed clear responses to temperature, showing shorter time to flowering when grown at higher temperatures, except that *L. mendocina* plants grown at 24 °C did not flower under any photoperiodic condition (Fig. 5). Cycle lengths were also similar for both species when grown at the lowest temperature; however, as temperature increased, time from EM to FL was always shorter in *L. fendleri* than in *L. mendocina* plants (Fig. 5).

Responses to photoperiod were strikingly different between species. *L. mendocina* did not show any sensitivity to photoperiod while *L. fendleri* plants displayed a marked quantitative long-day response. This response was clear at warm temperatures, however, and not at 9 °C, evidencing a strong interaction between photoperiod and temperature (Fig. 5).

When time to FL was split in two sub-phases, and the first sub-phase, EM-FBA, was analyzed, *L. mendocina* failed to show sensitivity both to temperature and photoperiod (Fig. 6), while *L. fendleri* evidenced a significant response to both factors with marked interaction between these factors (Fig. 6). *L. fendleri* did not respond to photoperiod at very low temperatures the magnitude of the photoperiodic effect was higher at 16 °C than at 24 °C. As shown by Windauer et al. (2004), thermal time was higher at 24 °C than at 16 °C at both photoperiods (Fig. 6), with optimum temperature for this early phase lower than 24 °C.

The duration of the sub-phase FBA to FL decreased in both species as temperature increased under all photoperiods (Fig. 7). *L. mendocina* plants were also insensitive to photoperiod in this reproductive sub-phase (Fig. 7). In contrast, *L. fendleri* plants displayed a response to both temperature and photoperiod and the interaction between both factors for the determination of the length of this reproductive phase. No photoperiod effect was detected at the lowest temperature (i.e. 9 °C), while photoperiod significantly affected time from FBA to FL at 16 and 24 °C (Fig. 7). As in the previous phase, the photoperiodic effect was greater at 16 °C than at 24 °C (Fig. 7).

A consequence of this photoperiod × temperature interaction in *L. fendleri*, is that TT accumulated for the FBA-FL, was different at 9 and 16 °C for an 8 h photoperiod (no significant difference was detected between TT required to complete either the EM to FBA or the FBA to Fl phase at 9 and 16 °C when plants were grown at 18 h photoperiod). It has been reported that base temperature over which TT is calculated might change under different daylengths (Slafer and Rawson, 1995a), suggesting that TT accumulated until flowering should not be calculated with a base temperature estimated under a single photoperiod.

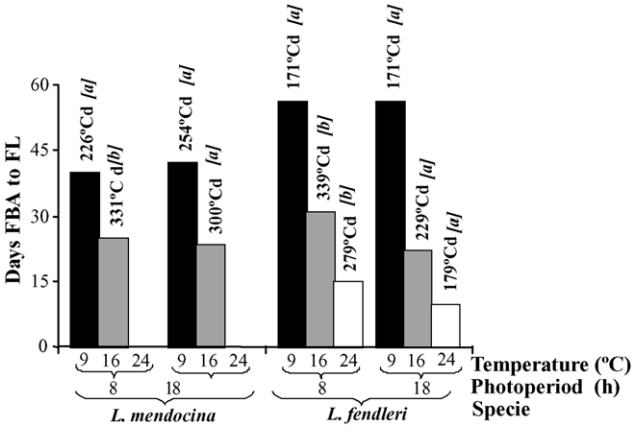

Fig. 7. Number of calendar days from floral buds appearance (FBA) to flowering (FBA) for both species for a combination of two photoperiods and three temperatures. Figures above the bars represent the TT (for T_b calculated in Windauer et al., 2004) for a wide set of temperatures under long days. [Different letters in each of these values mean significant differences in thermal time, between different thermal regimes for a single photoperiod.] No data are presented for *L. mendocina* at 24 °C, since plants did not reach the floral bud stage.

4. Discussion

Development rates for both *L. fendleri* and *L. mendocina* varied among sowing dates: as sowing dates were delayed from autumn to spring, plant cycles were shorter. The longest cycle was obtained with *L. mendocina* plants sown in September and November, which displayed a biennial cycle. This is consistent with our previous results obtained under controlled conditions: the optimum temperature for EM–FBA is ca. 20 °C for both species, but while responses to supra-optimal temperatures are quantitative in *L. fendleri*, the same responses are qualitative in *L. mendocina* (Windauer et al., 2004). Therefore, it could be hypothesized that in late sowings, when initial temperatures were relatively high, *L. mendocina* plants remained vegetative and displayed a biennial habit, because the phase EM-FBA in this species responds qualitatively to supra-optimal temperatures. Indeed, although the possibility of an unfulfilment of remaining vernalization requirements in spring sown *L. mendocina* cannot be totally ruled out, these results strongly support the conclusions obtained by Windauer et al. (2004). Furthermore, Ploschuk et al. (2001) reported the inability of *L. mendocina* plants to turn to the reproductive phase when grown under greenhouse conditions with temperatures above 24 °C and long photoperiods. Also in agreement with our present results, some field experiments carried out on *Brassica napus* (Thurling and Vijendra Das, 1977) and wheat (Marcellos and Single, 1971; Caos and Moss, 1991), showed that time to flowering was sharply delayed or no progression to flowering was recorded, under high temperatures common in late sowings, even under strongly inductive photoperiods.

Lack of response to vernalization in both species may be due to (i) pre-germinated seeds sown in early or late sowing dates, which consequently explored higher initial temperatures might have been completely de-vernalized (Mendham and Salisbury, 1995); this is not consistent with results obtained with other species, where the effect of de-vernalization was reported to be frequently incomplete and, moreover, de-vernalization response was non-uniformly distributed within the population (Loomis and Connor, 1992). None of these de-vernalization consequences have been found in our experiment. Or (ii) pre-germinated seeds sown in dates when temperatures were cold might (intermediate dates in this experiment) have been naturally vernalized thus overcoming the difference between vernalization treatments. This is highly unlikely since such a sensitivity to low temperatures should have been displayed as plants with the shortest cycle when having explored the initial coldest environment (i.e. those coming from June sowing dates); plants from June sowing dates had longer cycles than plants from August sowing dates.

Indeed, except when effective temperatures were above the optimum (sowing dates earlier than May, and plants sown after August), development variation was correlated to photoperiod (Fig. 5). Therefore, we assessed the influence of photoperiod on development of both species with experiments carried out under controlled conditions. Surprisingly, the two species of *Lesquerella* displayed a different response to photoperiod. Increasing or decreasing the photoperiod did not affect development towards flowering in *L. mendocina* plants (a neutral day plant). In contrast, *L. fendleri* plants displayed sensitivity to photoperiod, in agreement with responses to photoperiod reported for other species from the same family (Salisbury and Green, 1991; Nanda et al., 1996; Vilariño et al., 1998). Therefore, experiments under controlled conditions provided evidence that phenological responses to different sowing dates in *L. fendleri* were also controlled by photoperiod in addition to temperature.

In contrast to the results from field experiments where photoperiod appeared to affect only EM-FBA phase duration, *L. fendleri* showed a quantitative long-day response for both EM-FBA and FBA-FL sub-phases at intermediate temperatures under controlled conditions. The absence of a photoperiodical effect on the FBA-FL phase observed in the field experiment is in agreement with the results from field experiments reported by Nanda et al. (1996), but disagreed with other results from controlled experiments (Thurling and Vijendra Das, 1977) both in Brassicas. Same misleading results between controlled and field studies after floral differentiation have been reported for other crops (Manupeerapan et al., 1992; Slafer et al., 1994). A possible explanation could be related to interactions among other environmental factors and photoperiod in field conditions. Another explanation could be that photoperiods in controlled conditions remained constant during all the EM-FL phase, while photoperiods changed daily in the field. If photoperiod had a direct impact on EM-FBA, with a concomitant effect on the next sub-phase, results from field experiments could not be compared to results from controlled experiments where photoperiod is mostly constant both before and after FBA.

The rate of development in the phase EM-FBA turned out to be completely independent of temperature (in the suboptimal range) and photoperiod in *L. mendocina* plants. In addition, previous experiments with this species indicated that there was an optimum temperature lower to 24 °C and that responses to supra-optimal temperatures were strongly qualitative (Windauer et al., 2004); this was also observed in the present controlled experiment even under contrasting photoperiodical conditions. The experiments under controlled conditions also provided evidence that the factor associated to sowing date that accelerated phenology in *L. mendocina* when temperatures were suboptimum, was not photoperiod. Hence, some other factor should have been responsible for the shortening of the cycle of this species. This hypothetical factor might have been incident radiation, as it is strongly associated to photoperiod for a wide sowing dates range. Developmental response to radiation has been reported for other crops (Salisbury and Green, 1991, in rapeseed, Rawson, 1993 in wheat; Bertero, 2001 in quinoa). In this way, when sowings are delayed, mean photoperiod

increases, and so does mean radiation during the EM to FBA phase, resulting in an increasingly shorter phase length, until a change in the rate of development occurs when temperatures are above the optimum at latest sowings. The latter change in the rate of development might be due to an interaction between high temperatures and radiation, as a result of changes in the source/sink relationship (Rawson, 1993), thus leading to a biennial behavior in *L. mendocina* when it is sown in November. The effect of a source limitation (low radiation and/or high temperatures) on development is well documented for other species, e.g. *Deschampsia caespitosa* (Davey, 1987) and *Sinapsis alba* (see Bodson et al., 1977 for evidence of supplemental carbon hydrates modifying floral induction requirements in *S. alba*). Current experiments are devoted to test this hypothesis.

The information from our experiments allowed us to state (with assumptions that should be part of future hypothesis), which are the most outstanding traits to explain differences in the developmental pattern between the two species. *L. fendleri* is an annual species with responses to the photoperiod × temperature interaction similar to those found in other thoroughly studied species (Thurling and Vijendra Das, 1977; Major and Kiniry, 1991; Slafer and Rawson, 1995b), while the perennial *L. mendocina* would be in its first growth cycle a facultative biennial species. According to the environmental conditions, *L. mendocina* may behave as an annual (such as *L. fendleri*; autumn–winter sowings), as an annual but differently to *L. fendleri* (earliest autumn sowings), or a biennial (in very late sowings dates). The results found in this investigation will help to better delineate cropping strategies for both *Lesquerella* species, under different climates and sowing dates.

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