

Ecotypic Variation among European Arctic and Alpine Populations of *Oxyria digyna*

Author: Heide, Ola M.

Source: Arctic, Antarctic, and Alpine Research, 37(2) : 233-238

Published By: Institute of Arctic and Alpine Research (INSTAAR),
University of Colorado

URL: [https://doi.org/10.1657/1523-0430\(2005\)037\[0233:EVAEAA\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2005)037[0233:EVAEAA]2.0.CO;2)

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Ecotypic Variation among European Arctic and Alpine Populations of *Oxyria digyna*

Ola M. Heide

Department of Ecology and
Natural Resource Management,
Agricultural University of Norway,
P. O. Box 5003, N-1432 Ås, Norway.
ola.heide@ina.nlh.no

Abstract

Morphological and physiological variation of four geographically separated European populations of *Oxyria digyna* (L.) Hill (Polygonaceae) ranging from 45 to 78°N latitude were studied in controlled environments. Characters such as the presence of rhizomes, variable stamen number, few inflorescence branches, and low leaf length/width ratio were found to be common to northern populations. Perennating buds were formed under short day (SD) conditions in all populations across the temperature range (9–21°C), while induction of dormancy required the combination of SD and low temperature. Dormancy release of dormant buds required long day (LD) conditions only. The species was found to be a short-long-day plant for flowering control, the SD requirement being quantitative while the subsequent LD requirement is obligatory. Both the SD flowering response and the fecundity of flowering decreased clinally with increasing latitude of population origin, while the critical daylength for secondary floral induction showed a parallel increase. With some minor modifications, these results agree with earlier findings with North American populations. It is concluded that the obligatory LD requirement for flowering has been a limiting factor for the southward geographic distribution of the species, and that the photoperiodic control of flowering and winter dormancy renders *Oxyria* particularly well adapted to resist potential negative effects of rising global temperature.

Introduction

Genetic differentiation into environmentally determined ecological races or ecotypes is a common phenomenon in plants with wide geographic distribution. The ecotype concept was introduced by Turesson (1922) who defined it as the “genotypic response to the various environments where the species is found.” Today the concept is generally accepted and many of its physiological aspects have been studied in natural and controlled environments. Thus, environmental adaptation to latitudinally and altitudinally determined climatic factors such as light and temperature is well documented in trees and shrubs (Håbjørg, 1972; Heide, 1974; Howe et al., 1995), as well as forbs (Mooney and Billings, 1961; Cumming 1969; Li et al., 1998), and grasses (Evans, 1939; Heide, 1994).

A classical ecotype analysis was done by Mooney and Billings (1961) with North American populations of *Oxyria digyna* Hill., a perennial, herbaceous member of the Polygonaceae with a circum-boreal arctic-alpine distribution of wide latitudinal range (Hultén and Fries, 1986). Using populations with origins ranging from California and Colorado in the south to Point Barrow, Alaska and Thule, Greenland in the north (41–78°N), and from sea level to nearly 4000 m a.s.l., they could demonstrate clinal variations in developmental characters such as flowering and dormancy control, metabolic processes such as photosynthesis and respiration, as well as seasonal changes in tissue chemical composition. Morphologically, however, the populations fell into a southern and a northern morphological group with a geographic dividing line confined to southern Alberta, coinciding with the extent of the maximum Pleistocene glaciation in the area.

In order to simulate alpine and arctic environments Mooney and Billings (1961) established an “alpine chamber” with 18°C/5°C day/night temperature and a photoperiod of 15 h, and an “arctic chamber” with day/night temperature of 13°C/2°C and a 24-h photoperiod. A third growth chamber provided constant 10°C and 12-h photoperiod

(later changed to 17 h). However, since temperature and daylength conditions were varied simultaneously with this set-up, it did not allow separation of temperature and daylength effects and their interactions.

With the availability of modern phytotron facilities, a similar *Oxyria* ecotype analysis under more adequate environment control conditions appeared to be desirable. Therefore, a comparable analysis has been done with European ecotypes which represent a similar latitudinal range of geographic distribution. Special emphasis was focused on flowering physiology and phenotypic plasticity of the populations. The results are discussed in relation to potential effects of the current global warming (Serreze et al. 2000), and the geographic distribution of the species.

Materials and Methods

Seeds of the *Oxyria digyna* populations listed in Table 1 were collected in the field. Each sample was collected from a number of plants covering an area of several square meters. When necessary, further seed multiplication was done in isolated phytotron compartments by open pollination of 15 to 20 plants.

The cultivation experiments were carried out in the Ås phytotron in daylight compartments combined with adjacent growth rooms for photoperiodic manipulations. After germination at 21°C, seedlings were raised at 18°C in 24-h photoperiod for 4 wk before the experimental treatments were started (except for Experiment 1 in which seedlings were exposed to different daylength and temperature conditions from germination). The plants were grown singly in 8 cm plastic pots in a peat-based potting compost. All plants received natural spring or summer daylight for 10 h d⁻¹ (0800–1800 h). Whenever the quantum flux in the daylight compartments went below 150 µmol m⁻² s⁻¹ during cloudy days, an additional 125 µmol quanta were automatically added by high pressure metal halide lamps (Osram HQI-BT, 400W).

TABLE 1

Geographic origin of the *Oxyria* populations used for the experiments.

Population name	Geographic origin	Latitude (N)	Longitude (E)	Altitude (m a.s.l.)
Col du Lautaret	Hautes Alps de Provence, France	45°05'	06°25'	2200
Finse	Hardangervidda, Ulvik, Norway	60°35'	07°30'	1300
Grytøy	Harstad, Norway	68°50'	16°20'	430
Svalbard	Longyearbyen, Svalbard	78°10'	15°30'	20

Daylength extensions were established by incandescent lamps at an irradiance of about $12 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$, whereas short days (SD) were provided by moving plants into darkness during the night. This ensured that all experimental plants received a similar dose of photosynthetic active radiation regardless of the photoperiodic conditions. Temperatures were controlled to $\pm 1.0^\circ\text{C}$, and a water vapor pressure deficit of 530 Pa was maintained at all temperatures.

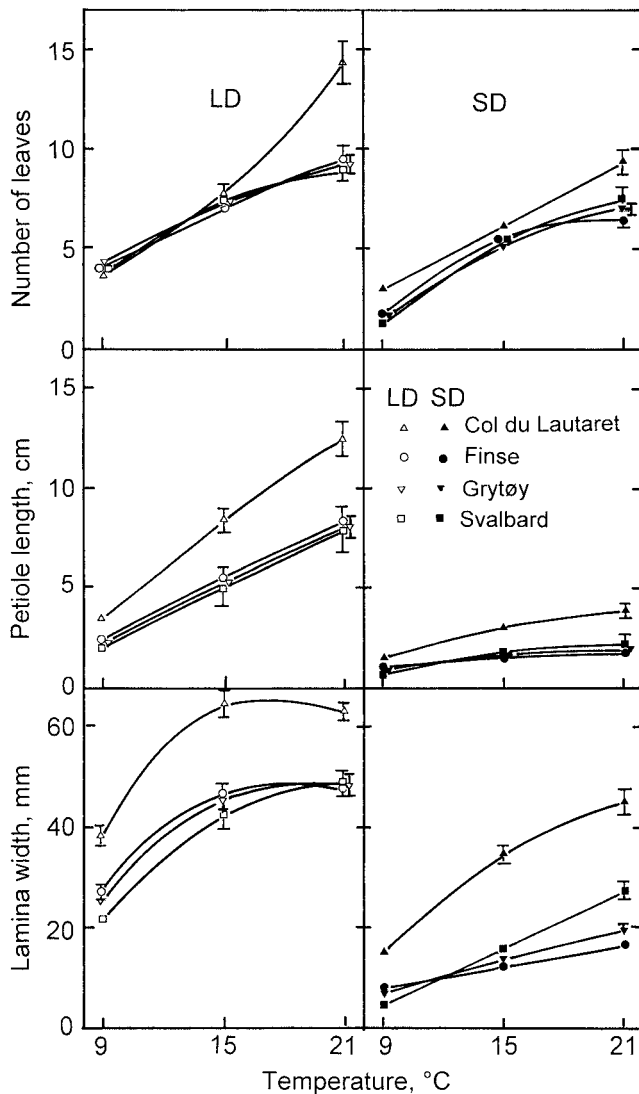


FIGURE 1. Effects of temperature and daylength on leaf production and leaf dimensions in four populations of *Oxyria*. Data for the largest leaf in each plant after 6 wk of cultivation from time of germination. Means \pm SE of 10 plants in each treatment.

TABLE 2

Leaf length/leaf width ratios and number of branches per inflorescence of the *Oxyria* populations. Leaf length/width ratios are means \pm SE for all temperatures and day-length conditions in Experiment 1, while number of inflorescence branches are weighted treatment means \pm SE for all experiments.

Population	Length/width ratio	Inflorescence branches
Col du Lautaret	0.53 ± 0.02	4.0 ± 0.3
Finse	0.47 ± 0.02	4.3 ± 0.4
Grytøy	0.47 ± 0.02	5.2 ± 0.2
Svalbard	0.47 ± 0.02	2.8 ± 0.3

Flowering was monitored by daily observations of inflorescence appearance and anthesis. Percentage of flowering plants and number of flowering stems per plant were used as the main criteria of flowering, with days to inflorescence appearance as an additional criterion. Morphological characters such as number of stamens and number of inflorescence branches were recorded in all experiments. In addition, number of leaves, petiole length, lamina length, and width were recorded for the largest leaf after 6 wk of cultivation in Experiment 1. At the termination of this experiment plants were also examined for the presence or absence of rhizomes.

Experiments were of the split-plot design with temperature as the main plot factor and daylength and populations as subplots. Ten evenly sized plants were used per treatment. One experiment (Exp. 4) was repeated in time. Quantitative data were subjected to analyses of variance (ANOVA) according to standard procedures using a SYSTAT Inc. version 0.5 program package. For experiments that were not replicated in time, the main effects were tested against their interactions with plant number (replicate) within treatment.

Results

EXPERIMENT 1

An initial experiment with three temperature (9, 15, and 21°C) and daylength conditions applied from the time of germination was set up to examine morphological characters and their phenotypic plasticity as well as the general growth and development performance of the populations. After 6 wk of cultivation, leaf numbers were recorded and the dimensions of the largest leaf were measured for all plants. The results in Figure 1 show that leaf production increased with the temperature in all populations, although it leveled off somewhat at the highest temperature in the northern populations. Leaf production was also significantly greater in LD than in SD for all populations (Fig. 1). SD conditions also induced the formation of perennating buds at all temperatures, the response being strongest in the northern populations and at low temperature (data not shown). At 15 and 21°C the plants continued leaf production in SD and retained a rosette of functional leaves, whereas at 9°C they ceased growing after formation of three to four leaves and went completely dormant.

All these growth responses are reflected in the leaf dimension data in Figure 1. In LD the plants formed loose rosettes of leaves with long petioles and relatively large laminae. Whereas petiole length increased linearly with temperature across the range of temperatures, lamina width (and length) leveled off above 15°C (Fig. 1). Both petiole length and lamina width were significantly larger ($P < 0.01$) in the Col du Lautaret population than in the northern ones. Also leaf length/leaf width ratio was slightly, but significantly, larger ($P < 0.05$) in the French population than in the other three which did not vary among themselves for any of these characters (Table 2). Although both lamina length and width increased with increasing temperature and daylength, their ratio was not significantly affected

TABLE 3

Number of flowering stems per plant in four *Oxyria* populations grown under different temperature and daylength conditions from germination. Means \pm SE of 10 plants per treatment. The SD-LD plants received 8 wk of 10-h SD before transfer to 24-h LD.

Temperature (°C)	Photoperiodic conditions	Population			
		Col du Lautaret	Finse	Grytøy	Svalbard
9	Continuous SD	0	0	0	0
	SD-LD	1.2 \pm 0.1	2.2 \pm 0.2	1.2 \pm 0.1	0
	Continuous LD	1.8 \pm 0.3	2.9 \pm 0.3	2.8 \pm 0.4	0.5 \pm 0.4
15	Continuous SD	0	0	0	0
	SD-LD	5.6 \pm 0.7	4.8 \pm 0.8	5.0 \pm 0.9	3.5 \pm 0.5
	Continuous LD	2.4 \pm 0.4	4.4 \pm 0.6	3.9 \pm 0.7	4.0 \pm 0.6
21	Continuous SD	0	0	0	0
	SD-LD	7.4 \pm 0.7	5.7 \pm 0.6	5.1 \pm 0.6	3.3 \pm 0.6
	Continuous LD	1.3 \pm 0.1	3.2 \pm 0.3	3.8 \pm 0.9	4.0 \pm 0.8

by these environmental factors. Rhizomes were formed on all or nearly all plants of the three northernmost populations, whereas no rhizomes were found on the population from the French Alps (data not shown).

No flowering took place in continuous SD in any of the populations. However, dissections of several plants revealed that they all had advanced inflorescence primordia in SD, and transfer to LD after 8 wk of SD treatment resulted in rapid growth activation and flowering (Tables 3, 4). All plants flowered also in continuous LD, and at 9°C the number of inflorescences was as high in LD as after transition from SD to LD. However, at higher temperatures the dual photoperiodic treatment became increasingly more favorable for flowering, the effect being most pronounced in populations originating from lower latitudes (Table 3). The number of flower stems decreased with increasing latitude of population origin, especially at high temperatures and long photoperiods. This resulted in a significant ($P < 0.01$) two-factor interaction of temperature \times daylength as well as a significant three-factor interaction ($P < 0.01$) of temperature \times daylength \times population for the flower stem data.

Inflorescence appearance (heading) was enhanced by temperature increase from 9 to 15°C, but showed little further advancement with a further increase to 21°C (Table 4). Heading and flowering was earliest in continuous LD for all temperatures and populations, although inflorescence initiation obviously was earliest in SD. Thus, upon transfer to LD heading occurred within 1 to 2 wk at 15 and 21°C. Under all conditions inflorescence appearance was increasingly delayed with increasing latitude of origin of the populations, even with nonlimiting 24-h photoperiod (Table 4).

Flower and inflorescence characters studied by Mooney and Billings (1961), were also studied in this and the following experiments. Number of inflorescence branches was found to be significantly lower in Svalbard than in the other populations (Table 2). Temperature and daylength had no significant effects on branch numbers, except in cases of marginal flowering that was associated with abnormal inflorescences with few or no branches (data not shown). Flowers of the Svalbard population also had a variable number of stamens, while the other populations always had the full complement of six. Thus, flowers situated at the base of the inflorescence (the first to reach anthesis), usually had aborted stamens in the Svalbard population. In some, stamen abortion was complete so that only rudimentary stamen filaments were present, the flowers thus becoming functionally female only, whereas other flowers had two normal stamens. In all cases, however, flowers situated at terminal positions of the inflorescences had the full complement of six stamens.

TABLE 4

Days to inflorescence appearance in four *Oxyria* populations grown under different temperature and daylength conditions from germination. Means \pm SE of 10 plants per treatment. The SD-LD plants received 8 wk of 10-h SD before transfer to 24-h LD.

Temperature (°C)	Photoperiodic conditions	Population			
		Col du Lautaret	Finse	Grytøy	Svalbard
9	Continuous SD	>120	>120	>120	>120
	SD-LD	86.7 \pm 1.2	111.4 \pm 2.9	107.3 \pm 3.1	>120
	Continuous LD	71.5 \pm 0.8	83.4 \pm 1.4	96.1 \pm 1.5	115.5 \pm 5.6
15	Continuous SD	>120	>120	>120	>120
	SD-LD	62.3 \pm 0.6	70.1 \pm 1.3	73.0 \pm 1.4	95.1 \pm 4.1
	Continuous LD	53.3 \pm 1.8	61.4 \pm 1.3	65.9 \pm 1.7	79.1 \pm 2.2
21	Continuous SD	>120	>120	>120	>120
	SD-LD	62.9 \pm 0.4	73.7 \pm 1.9	75.8 \pm 1.7	94.4 \pm 2.9
	Continuous LD	53.8 \pm 1.5	67.0 \pm 1.4	69.6 \pm 1.0	81.5 \pm 2.9

Variations in stamen number did not appear to be influenced by temperature and daylength conditions (data not shown).

EXPERIMENT 2

In this experiment the plants were raised at 18°C for 4 wk before the plants were exposed to SD at 15°C for 3, 5, 7, and 9 wk for primary induction while a control group was maintained in LD for 9 wk at 15°C. As in the previous experiment, the plants formed perennating buds in SD but continued leaf production at this temperature and maintained a rosette of active leaves as the older leaves senesced and wilted. The results in Figure 2 show that flowering increased progressively with increasing SD exposure in all populations. Compared with similar treatments of germinating seedlings (Table 3), these larger plants formed many more flower stems. Three weeks of SD induction was marginal for inflorescence initiation. In population Col du Lautaret flowering was saturated with 7 wk of SD, while it increased markedly with a further increase to 9 wk in the others. Again, the degree of flowering decreased with increasing latitude of origin of the populations, with a parallel reduction in the flowering response to SD (Fig. 2). As in the previous experiment, heading (and flowering) were later the higher the latitude of origin of the population. Time to inflorescence appearance after transfer to LD decreased with increasing SD exposure, although a minimum time was reached after 5 or 7 wk of SD in the southernmost populations (Fig. 2).

EXPERIMENT 3

This experiment examined the effect of temperature on the SD induction of flowering. Four-week old plants were exposed to SD for 9 wk at temperatures of 9, 15 and 21°C. The results in Figure 3 show that temperatures over this range did not greatly modify the response to SD, although the response varied somewhat among the populations. (Main effect of temperature and temperature \times population interaction both significant at $p < 0.05$). Population Col du Lautaret had the highest number of flower stems, the number increasing slightly across the temperature range, population Finse had an intermediate number of flower stems with an optimum at 15°C, while the Svalbard population formed relatively few flower stems regardless of the temperature. At 21°C the number of flower stems was quite variable in the latter two populations (Fig. 3).

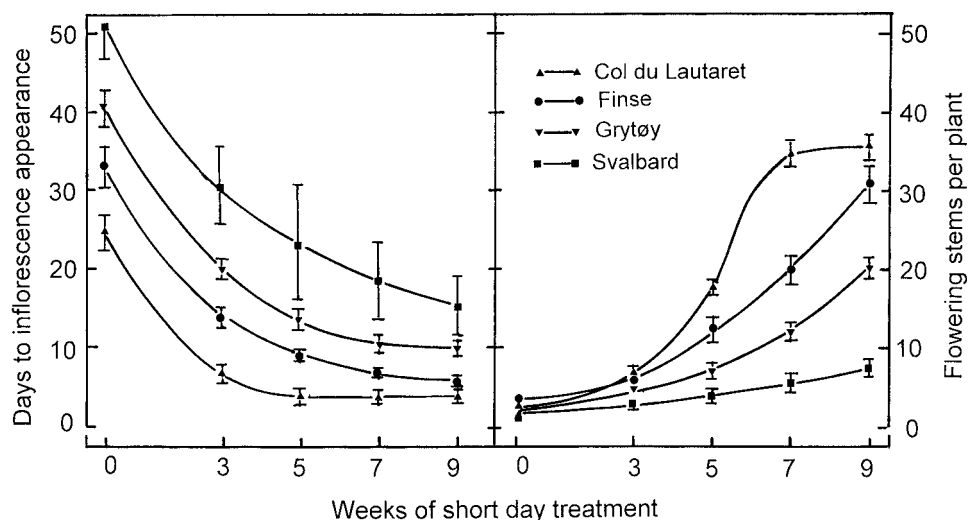


FIGURE 2. Flowering response of four *Oxyria* populations to increasing SD exposure at 15°C followed by LD at 18°C. Days to inflorescence appearance refer to days from end of SD treatment for the SD treated plants, and days from start of the 15°C temperature treatment for the LD treated plants. Means \pm SE for 10 plants in each treatment.

EXPERIMENT 4

The critical daylength for secondary induction of flowering of the populations was examined in a last experiment. After SD induction for 9 wk at 15°C the plants were exposed to a range of photoperiods at 18°C as shown in Figure 4. Both percentage flowering plants and number of flower stems per plant decreased with decreasing photoperiod in all populations. However, the critical daylength for 50% flowering increased from about 14 h in population Col du Lautaret to 15 h in Finse and 18 h in populations Grytøy and Svalbard. Only a few plants formed a single stunted flower stem at 12 and 14 h daylength. Confirming the results of the previous experiments, the magnitude of flowering was again found to decrease steadily with increasing latitude of population origin (Fig. 4). Time to inflorescence appearance and flowering increased with decreasing photoperiod in parallel with the decline in the magnitude of flowering (data not shown).

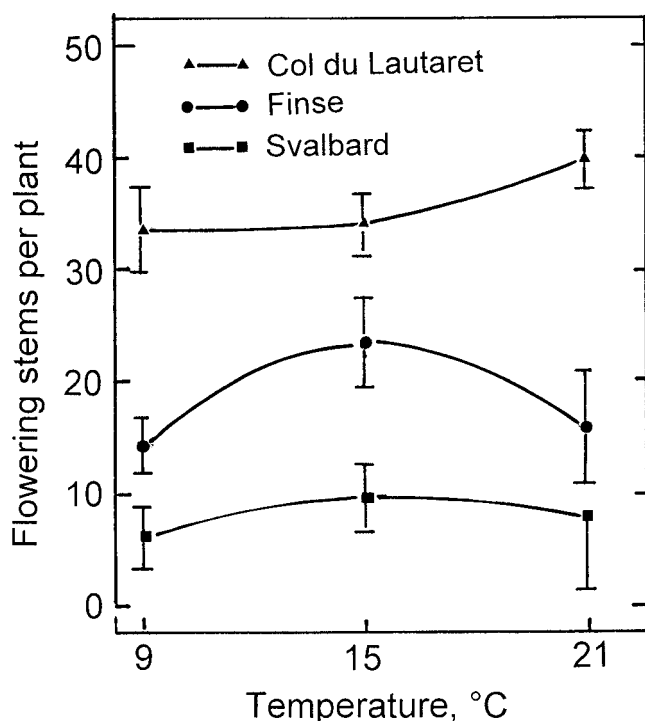


FIGURE 3. Temperature effects on the flowering response to 9 wk of SD exposure in three populations of *Oxyria*. Means \pm SE for 10 plants in each treatment.

Discussion

With some modifications, the present results with European populations of *Oxyria* confirm the ecotype variation reported for North American populations by Mooney and Billings (1961). Morphologically, however, the European ecotypes could not be separated into a distinct northern and a southern group, as the partitioning varied with the morphological characters studied. For all leaf characters studied the Col du Lautaret population from the French Alps was clearly different from the populations from continental Norway and Svalbard (Table 2, Fig. 1). The French population was also the only one that did not form rhizomes. On the other hand, the Svalbard population was the only one with variable stamen number, and it also differed from the other populations by having fewer inflorescence branches (Table 2). Thus, the French population differed from all the others in some characters while the Svalbard population differed from all the others in other characters. Differences in glaciation history and different trends in temperature change relative to latitude between the two continents might be possible reasons for such variations in ecotype segregation. Nevertheless, the presence of rhizomes, variable stamen number, low number of inflorescence branches, and low leaf length/width ratio were all found to be "northern" characters in both North American and European *Oxyria* populations, although the dividing lines varied.

The phenotypic plasticity of these morphological characters varied. Whereas characters such as stamen number, presence or absence of rhizomes, and number of inflorescence branches were non-plastic, leaf dimensions were strongly modified by environmental factors such as temperature and daylength (Fig. 1). Population differences were, however, not altered by such environmental influences. Such findings emphasize the role of phenotypic plasticity in plant adaptation and evolution (De Jong 1995).

As reported by Mooney and Billings (1961), *Oxyria* plants form perennating buds in SD. However, at temperatures of 15 and 21°C the plants remained active and continued to produce new leaves in SD, the induction of dormancy requiring the combination of SD and low temperature (9°C). Under such conditions all the leaves senesced and wilted and bulb-like buds were formed. When transferred to LD these buds were immediately activated, confirming that their dormancy release do not require chilling, but is fully controlled by long photoperiods (Heide, 2001).

Whereas Mooney and Billings (1961) considered *Oxyria* a long-day plant, the present results show that it actually is a short-long-day plant (Tables 3, 4, Fig. 2), the SD requirement being quantitative while the LD requirement is obligatory (Fig. 4). Although some flowering takes place also in continuous LD (Table 3), flowering was strongly

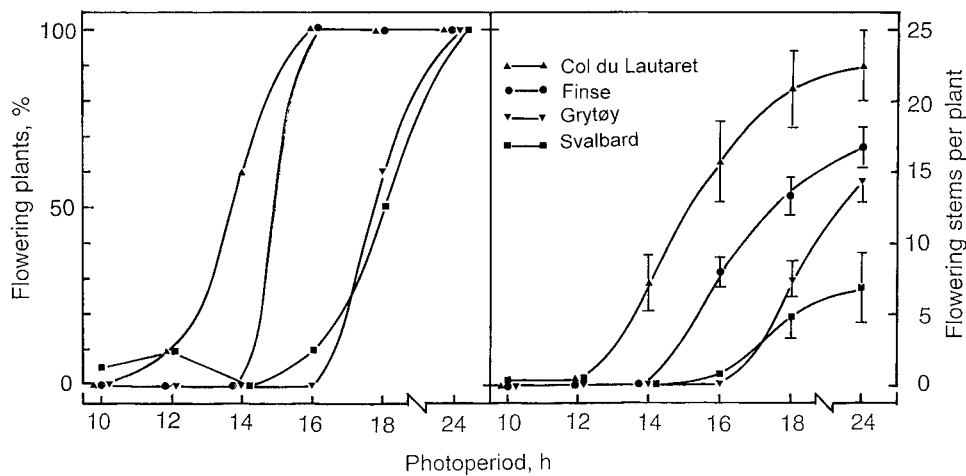


FIGURE 4. Critical photoperiods for secondary floral induction at 18°C for four populations of *Oxyria*. The plants had previously been exposed to SD for 9 wk at 15°C. Weighted means \pm SE for two experiments, each with 10 plants per treatment.

stimulated by increasing SD exposure followed by LD (Fig. 2). This SD floral induction response was greatest in the southernmost population and decreased clinally with increasing latitude of population origin, the Svalbard population being only weakly responsive to SD (Figs. 2, 4). Dissections revealed that not only floral induction, but also initiation and differentiation of inflorescences take place in SD so that fully differentiated, advanced inflorescence primordia were formed under SD conditions. The dual floral induction mode was in fact also suggested by the data of Mooney and Billings (1961) as their plants flowered rapidly and profusely when the photoperiod was changed from 12 to 17 h after several weeks of cultivation. The present results also confirm the clinal increase in photoperiodic requirements for flowering from the southern to the northern populations of this species as reported by Mooney and Billings (1961). Thus, the critical daylength for LD secondary induction of flowering increased from 14 h in the French population to 18 h in the two northernmost populations (Fig. 4). These critical daylengths agree well with the daylength conditions at the time of snowmelt in snowbed sites at the respective locations, although the Svalbard population seldom will experience photoperiods below 24 h in the nonfrozen condition.

The abundance of flowering decreased clinally with increasing latitude of population origin (Figs. 2–4), as also found by Mooney and Billings (1961). Reduced fecundity of flowering in the high-latitude populations was, however, compensated for by vegetative reproduction by rhizomes. Such a trade-off between flowering and vegetative reproduction was also observed in other arctic-alpine species such as *Carex bigelowii* (Heide, 1992) and *Phleum alpinum* (Heide and Solhaug, 2001), and would appear to have adaptive advantages in marginal temperature environments where flowering and seeding becomes unreliable.

On the basis of studies of flowering requirements of plants with a bipolar geographic distribution, I have argued that only plants that are able to flower and set seed under the SD conditions of the tropical highlands seem to have been able to migrate across the equator (Heide, 2002). The present results with *Oxyria digyna* tend to support this hypothesis. With its wide range of geographic distribution on both the American and Eurasian continents (Hultén and Fries, 1986), the species should have been in an excellent position for penetrating into the Southern Hemisphere. The obligatory LD requirement for flowering and dormancy release of the species would, however, have limited its southward distribution and effectively prevented such an event.

Photoperiodic control of flowering and winter dormancy is of obvious significance in a changing environment for synchronizing plant development with seasonal change. The mechanism will be of

particular importance under conditions of global warming, as photoperiodic conditions will remain unchanged under such a scenario. Since photoperiod has proved to be the main factor controlling flowering and reproduction as well as winter dormancy in *Oxyria*, and thereby its southward geographic distribution, it can be predicted that the current climatic warming (Serreze et al., 2000) would have relatively minor consequences for the biogeography and structure of *Oxyria* populations. The species' robust flowering response to temperature (Fig. 3), and the absence of a chilling requirement for dormancy release of resting winter buds, and its replacement by photoperiodic control, would ensure the maintenance of a regular and normal growth and flowering rhythm during warmer summers, stable winter dormancy during milder winters, and timely and temperature-independent growth initiation in warmer springs. Therefore, it seems that *Oxyria* is a species that is particularly well adapted to resist potential negative effects of rising global temperature.

Acknowledgments

I thank Dr. Line Nybakken for seed collection of the populations Col du Lautaret, Finse, and Svalbard.

References Cited

- Cumming, B. G., 1969: *Chenopodium rubrum* L. and related species. In Evans, L. T. (ed.), *The Induction of Flowering: Some Case Histories*. Melbourne: Macmillan, 156–185.
- De Jong, G., 1995: Phenotypic plasticity as a product of selection in a variable environment. *American Naturalist*, 145: 493–512.
- Evans, M. W., 1939: Relation of latitude to certain phases of the growth of timothy. *American Journal of Botany*, 26: 212–218.
- Håbjørg, A., 1972: Effects of photoperiod and temperature on growth and development of three latitudinal and three altitudinal populations of *Betula pubescens* Ehrh. *Meldinger fra Norges Landbrukshøgskole*, 51: 1–27.
- Heide, O. M., 1974: Growth and dormancy in Norway spruce ecotypes (*Picea abies*). I. Interaction of photoperiod and temperature. *Physiologia Plantarum*, 30: 1–12.
- Heide, O. M., 1992: Experimental control of flowering in *Carex bigelowii*. *Oikos*, 65: 371–376.
- Heide, O. M., 1994: Control of flowering and reproduction in temperate grasses. *New Phytologist*, 128: 347–362.
- Heide, O. M., 2001: Photoperiodic control of dormancy in *Sedum telephium* and some other herbaceous perennial plants. *Physiologia Plantarum*, 113: 332–337.
- Heide, O. M., 2002: Climatic flowering requirements of bipolar sedges

- Carex* spp. and the feasibility of their trans-equatorial migration by mountain-hopping. *Oikos*, 99: 352–362.
- Heide, O. M. and Solhaug, K. A., 2001: Growth and reproduction capacities of two bipolar *Phleum alpinum* populations from Norway and South Georgia. *Arctic, Antarctic, and Alpine Research*, 33: 173–180.
- Howe, G. T., Haccett, W. P., Furnier, G. R., and Klevorn, R. E., 1995: Photoperiodic responses of a northern and a southern ecotype of black cottonwood. *Physiologia Plantarum*, 93: 695–708.
- Hultén, E. and Fries, M., 1986: *Atlas of North European Vascular Plants North of the Tropic of Cancer*. Vol. I. Königstein: Koeltz Scientific Books. 180 pp.
- Li, B., Suzuki, J.-I., and Hara, T. 1998: Latitudinal variation in plant size and relative growth rate in *Arabidopsis thaliana*. *Oecologia*, 115: 293–301.
- Mooney, H. A. and Billings, W. D., 1961: Comparative physiological ecology of arctic and alpine populations of *Oxyria digyna*. *Ecological Monographs*, 31: 1–29.
- Serreze, M. C., Walsh, J. E., and Chapin, F. S., III, et al., 2000: Observational evidence of recent change in the northern high-latitude environment. *Climatic Change*, 46: 159–207.
- Turesson, G., 1922: The genotypical response of the plant species to the habitat. *Hereditas*, 3: 211–350.

Ms submitted July 2003