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Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic

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Abstract The cool and short growing season that characterizes Arctic climates puts severe constraints on life cycles and reproduction in the Arctic flora. The timing of flowering is particularly critical and may affect both breeding system and reproductive success through the heavy penalties associated with later flowering. An 11-year study of 75 species in the central highland of Iceland showed that the onset of flowering varies greatly among years. The number of species in flower by the first week of July was closely correlated with air temperature (degree days above zero) in the preceding 5 weeks, but no correlations were found with degree days in May or with total degree days in the previous growing season. Time of snowmelt, which has widely been regarded as the environmental event initiating growth and flowering in alpine and arctic tundra, only had a significant effect when two exceptionally cold and late summers were included. The species studied, most of which have a wide distribution in the Arctic, are predicted to respond quickly to warmer spring and early summer temperatures. Accelerated phenologies may alter patterns of resource allocation, have implications for pollinators and pollinator-competition, and could increase the size, species richness and intraspecific genetic diversity of the soil seed bank.

Key words Flowering phenology · Iceland · Arctic · Global warming

Introduction

Patterns of plant phenology are related to the degree and nature of environmental variation and can be examined at different levels of organization, from single flowers, through individual plants, to populations and communities (Primack 1985). In the least seasonal climates, such as the moist tropics, no flowering season may be identifiable at the community level, flowering is often poorly synchronized among species, and individuals may flower at regular or irregular intervals of months or years. In contrast, plant communities in the highly seasonal desert and polar climates are characterized by a single compressed flowering period.

In the Arctic, the growing season is cool, short, and curtailed at both ends by subzero temperatures. This imposes major constraints on the Arctic biota and it has been suggested that because the growing season is so compressed, time can in itself be viewed as a kind of a resource for arctic, as well as alpine, plants (Galen and Stanton 1991). In a survey of the flora of north Sweden, Molau (1992) found that outbreeding populations flowered early, while apomictic and viviparous species were found among the late bloomers. He suggests that much of the great variation in reproductive patterns found among Arctic plants can be related to a single factor, flowering phenology.

Short and cool summers limit the production of viable seeds to exceptionally favourable years in many tundra populations (Bell and Bliss 1980; Philipp et al. 1990). Alpine snowbed populations have been found to produce fewer seeds than adjacent conspecific populations that can flower earlier (Totland 1994a). Seeds produced in the latest-melting parts of snowbeds may be smaller than those produced in earlier-melting parts (Galen and Stanton 1991) and hence of inferior quality. The limits on seed production in the Arctic may be manifest as a low frequency of years with viable seed crops, a low proportion of seed ripening, and reduced seed quality. Late-flowering individuals are likely to suffer disproportionately from all three, compared with individuals that bloom early in the season.

Thus, flowering phenology appears to be particularly critical in arctic plant populations, affecting both breeding system and reproductive success through the heavy penalties associated with late flowering. Time of flowering may be useful as a predictor of reproductive success and a key to understanding the reproductive

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ecology of the Arctic flora. However, there are very few records of flowering phenologies from the Arctic and little is known about variation in the onset of flowering and how this relates to environmental variables. Here, an 11-year record of annual fluctuations in the onset of flowering is presented for 75 species in the central highland of Iceland. The aims of the study were: first, to establish the degree of annual variation in phenology, and second, to relate this variation to environmental factors (temperature, precipitation, time of snowmelt and depth of thaw).

Materials and methods

Site and climate

The central highland of Iceland is an undulating plateau covered by glacial and glaciofluvial deposits. It is largely desert-like with continuous vegetation (i.e. vegetation approximating 100% cover) often limited to depressions in the landscape and to other areas with a high and stable water table (Thórhallsdóttir 1996). Thjórsárver comprises islands of vegetation immediately south of the Hofsjökull glacier cap, surrounded by gravelly and sandy barrens with <5% plant cover (Thórhallsdóttir 1994, 1996). The bulk of the continuous vegetation forms a 100-km^2 triangle between the tributaries of the glacial river Thjórsá (Fig. 1), west and immediately east of the main river. Small vegetation islands are found further east and south.

Palsas, which are large hummocks with a permafrost core that are characteristic of mires close to the climatic limits of permafrost (Washburn 1979), are common in Thjórsárver. They are mostly of low relief, 1–1.5 m high, but range in length from a few meters up to about 30 m or more. Permafrost may also occur in dry heath with thick moss sward. Of the 450 species making up the vascular plant flora of Iceland, 175 have been found in Thjórsárver. About half the vegetation area can be classified as wetland. Common wetland species include *Carex rariflora*, *C. lachenalii*, *C. nigra*, *Calamagrostis stricta*, *Eriophorum angustifolium* and *E. scheuchzeri*, with *Carex rostrata* and *C. lyngbyei* in the wettest parts. Willows (*Salix arctica*, *S. herbacea* and *S. lanata*) are often dominant on moist or dry ground, along with grasses and a variety of herbs.

The mean (24-h average) annual air temperature in Thjórsárver is estimated at about −0.8°C and annual precipitation at about 800 mm (Jónsson 1978; Thórhallsdóttir 1994; Iceland Meteorological Bureau, personal communication). Estimated 24-h means of monthly temperatures (°C, 1965–1990) from spring to autumn are 0.9°C in May, 5.4°C in June, 7.7°C in July, 6.8°C in August and 2.6°C in September. The mean number of degree days above zero from 1 May to 31 August 1983–1994 was 674.4 (minimum 506.4, maximum 785.2). The number of frost-free days from spring to autumn is about 40 (Iceland Meteorological Bureau, unpublished work) and the mean growing season length is probably about 2.5 months. On average, flat terrain is free of snow by early June (Jónsson 1978), with snow remaining longer in snowbeds.

Phenology

The data consist of 11-year records of which species (out of a total of 75) had come into flower at permanent sites by the first week of July. The sites were located in Thúfuver and Eyvindarver (Fig. 1) and the study extended from 1983 to 1994 (with the exception of 1992). For dicotyledons, a species was recorded as flowering if the petals were expanded. For sedges, grasses and rushes, flowering was recorded if the culm (bearing the inflorescence) was expanded.

Fig. 1 Location of the Thjórsárver nature reserve south of Hofsjökull ice cap in the central highland of Iceland. Vegetated land is *stippled*, rivercourses and lakes are *solid* (*E* Eyvindarver, *Th* Thúfuver)

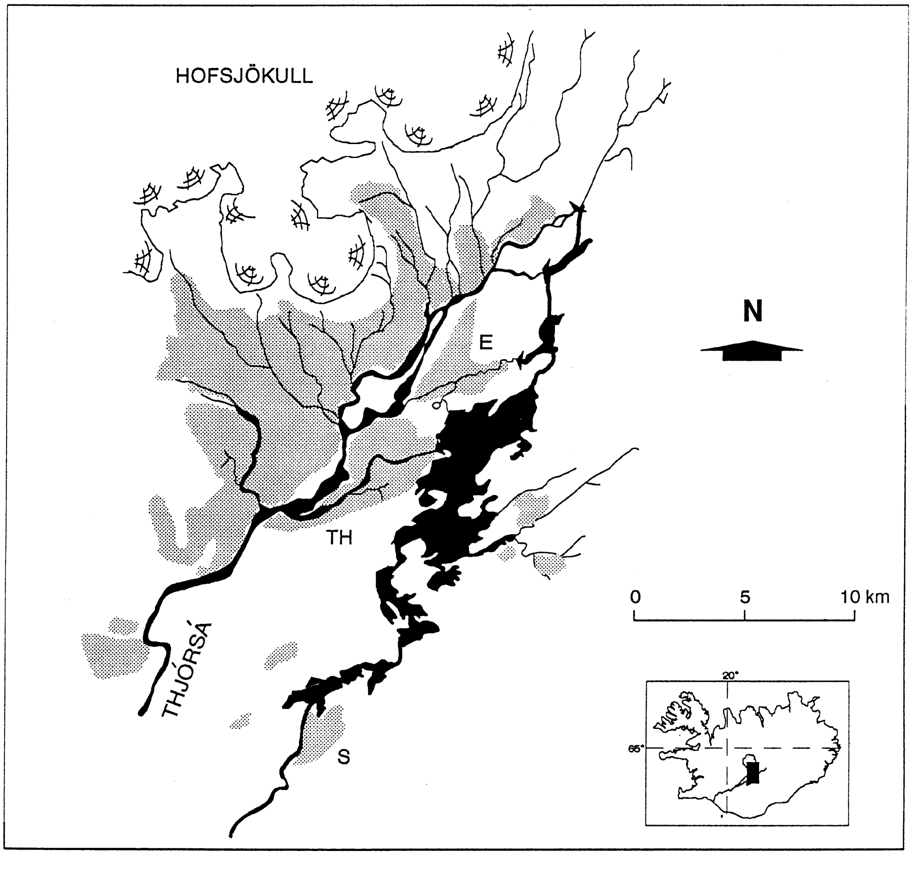

Table 1 The 75 species included in the 11-year survey, listed by frequency of flowering by 4–7 July

Species	No years in flower by 4–7 July
Empetrum nigrum	11
Salix arctica	10
Armeria maritima	9
Bartsia alpina	9
Erigeron uniflora	9
Harrimanella hypnoides	9
Luzula spicata	9
Pedicularis flammaea	9
Pinguicula vulgaris	9
Potentilla cranzii	9
Rumex acetosa	9
S. herbacea	9
S. lanata	9
S. phylicifolia	9
Saxifraga caespitosa	9
S. nivalis	9
S. oppositifolia	9
Silene acaulis	9
Tofieldia pusilla	9
Veronica alpina	9
Alchemilla vulgaris	8
Cardaminopsis petraea	8
Carex bigelowii	8
Cerastium alpinum	8
Dryas octopetala	8
Galium normanii	8
Juncus arcticus	8
Ranunculus acris	8
Thalictrum alpinum	8
Bistorta vivipara	7
Carex lyngbyei	7
Cerastium cerastoides	7
Eriophorum angustifolium	7
E. scheuchzeri	7
Saxifraga hirculus	7
S. stellaris	7
Sedum roseum	7
Sibbaldia procumbens	7
Silene maritima	7
Vaccinium uliginosum	7
Betula nana	6
Cardamine nymanii	6
Epilobium anagallidifolium	6
Festuca richardsonii	6
Geranium sylvaticum	6
Juncus biglumis	6
Kobresia myosuroides	6
Poa glauca	6
Taraxacum sp.	6
Viscaria alpina	6
Carex lachenalii	5
C. nigra	5
Luzula arcuata	5
Poa alpina	5
Pyrola minor	5
Sagina saginoides	5
Thymus arcticus	5
Deschampsia alpina	4
Calamagrostis stricta	3
Carex rufina	3
Festuca vivipara	3
Phleum alpinum	3
Ranunculus hyperboreus	3
Sagina nivalis	3
S. procumbens	3
Angelica archangelica	2
Euphrasia frigida	2
Hieracium spp	2
Parnassia palustris	2
Poa pratensis	2
Agrostis stolonifera	1
Epilobium latifolium	1
Hippuris vulgaris	1
Potentilla palustris	1
Sedum villosum	1

Silene maritima 7
Vaccinium uliginosum 7
Betula nana 6
Cardamine nymanii 6
Epilobium anagallidifolium 6

A species was scored as flowering if its populations were found in flower at any of the sites. Over a 6-year period (1984–1989), flowering, fruiting and seed dispersal were also recorded on 1–5 August and on 20–24 August.

For each species, the probability of randomly encountering a flowering individual will be influenced by its population size and proportion in flower. Low encounter probabilities could lead to a sampling bias against rare species and those with a low proportion of flowering individuals. I attempted to alleviate the possible bias against rare and sparsely flowering species in two ways. Firstly, a set route was followed on permanent sites so that the same populations were scored for flowering each year. Second, the 25 rarest out of an original set of 100 species were removed from the analysis. Of the remaining 75 species (Table 1), over two-thirds (52 species) occurred in more than 40 out of 203 squares in a 1-km^2 grid distribution map for the Thjórsárver flora (Jóhannsson et al. 1974). The distribution maps make it possible to test (although on a coarse scale) the relationship between frequent early flowering (this study) and commonness (i.e. number of grids occupied in Jóhannsson et al. 1974). There was a significant ($P < 0.001$), although weak ($r^2 = 0.158$) relationship between frequency of early July flowering and frequency in 1-km^2 grids but this may well reflect a real biological relationship between frequent early flowering and local population size. For example, Söyrinki (1938, p. 85–88) concluded that species close to their climatic limits in northern Finland had sparse or erratic flowering compared with the true Arctic species that were well within their distributional limits.

If some species do not flower annually, the record could also confound frequency of flowering and seasonal phenological variation. Flowering was much reduced in the very cold summers of 1983 and 1989. Thus, seven species were not found flowering in 1989 (a year when *Saxifraga oppositifolia* was still flowering on 24 August). Apart from these exceptionally cold years, 71 of the 75 species were recorded as flowering every year from 1984 to 1988, when late season records were collected in addition to the July census. The four species not recorded as flowering annually (*Potentilla palustris*, *Hippuris vulgaris*, *Carex rufina* and *Epilobium latifolium*) are all late bloomers and each of them missed out 1 year on the record. Thus, the overwhelming majority of the populations included flowered annually, failing to flower only in exceptionally cold years.

Environmental data

Temperature

The temperature record is based on three sources: (1) the Iceland Meteorological Bureau weather station at Hveravellir (about 55 km west of Thjórsárver, 64°52′N, 19°34′W, 640 m a.s.l.), (2) an automatic temperature station at Thórisós (at the same altitude, 582 m, as the study sites, 580–585 m, but 20 km further south, in operation since 1986, unpublished data from the National Power Company of Iceland), and (3) a small weather station operated in Thjórsárver from July to September 1972–1974 and 1982–1985. At the first two stations, 2 m air temperatures were recorded every 3 h and average monthly temperatures were calculated as means of the eight daily recordings. In Thjórsárver, recordings were made at 0900 and 2100 hours, i.e. twice every 24 h. To calculate monthly means, a correction factor must be added but since this has not been estimated for Thjórsárver, it had to be derived from the Hveravellir records.

There were close temperature correlations among all three stations. The relationship of monthly mean temperature at Thórisós (TT) to Hveravellir (TH) for 1986–1991 was: $TT = 0.41 + 1.036\ TH$ ($r^2 = 0.990$, $n = 59$). Using the Thjórsárver data, Jónsson (1978) concluded that the temperature difference between Thjórsárver and Hveravellir was 0.4, the same as that calculated between Thórisós and Hveravellir. Since the data from the permanently staffed station at Hveravellir are the most complete and accurate record, these were used for the analysis, modified by the above equation for the relationship between Thórisós and Hveravellir.

Precipitation and spring ablation

The closest weather station with a complete long-term climatic record is Hveravellir. Jónsson (1978) concluded that precipitation at Hveravellir and Thjórsárver was very similar. Data from Hveravellir (Iceland Meteorological Bureau, unpublished work) were used for monthly precipitation and for the time of snowmelt. Snow depth was monitored by 37 permanent stakes and the time of snowmelt was taken as the first day when all of these were free of snow.

Depth of thaw

Depth of thaw was recorded at 51 permanent points in 8 different plant communities on 4–7 July (see Thórhallsdóttir 1994 for details). Depth to the water table was used as a measure of soil moisture and was collected at the same sites (Thórhallsdóttir 1994).

Analysis

The relationship between the number of species in flower and environmental variables was tested by linear and multiple regression using SYSTAT.

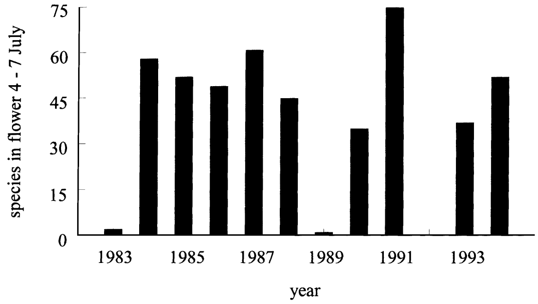

Fig. 2 The number of species in flower by 4–7 July 1983–1994. No data were collected in 1992

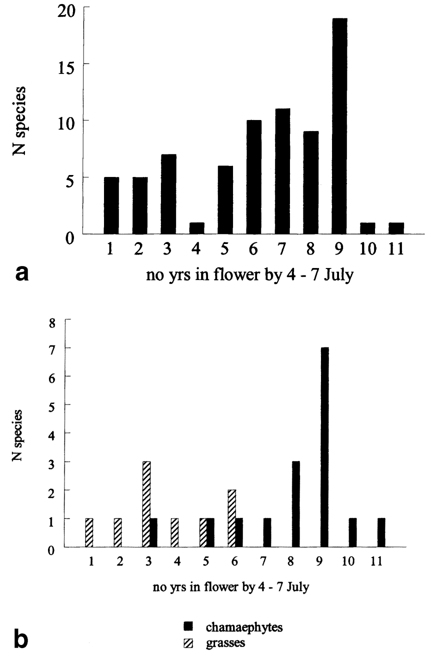

Fig. 3 a *Columns* show the frequency of flowering by 4–7 July over 11 years for the pool of 75 species. **b** *Solid columns* show the frequency of flowering by cushion plants and *hatched columns* the frequency of flowering by grasses (b)

Results

Annual variation

From 1983 to 1994, the number of species in flower by 4–7 July varied from a single species to all 75 that were included in the census (Fig. 2), with mean and median values of 42.5 (±6.9 SE) and 49 species respectively.

The species may be grouped according to flowering frequency (Table 1, Fig. 3a). *Empetrum nigrum* was the only species found flowering by the July census date in all 11 years. *Salix arctica* had flowered in all years except 1989. A large group of species flowered in 9 out of 11 years, missing the very cold summers of 1983 and 1989. About 50 species, equivalent to two-thirds of the species pool, had come into flower by early July in at least every other year. As might be expected, the group of consistent early bloomers were species characteristic of dry to mesic, but not wet, habitats. Cushion plants (chamaephytes) tended to flower early, but the grasses tended to flower late (Fig. 3b). The species pool contained 21 monocotyledon species (28% of the total), but of the 29 species found flowering in nine or more years, only 2 were monocots (about 7%).

The five species that were only found in bloom in 1991 usually flower at the very end of July or early August, e.g. *Epilobium latifolium*, *Potentilla palustris* and *Sedum villosum*. *Parnassia palustris* (in bloom in 2 years) usually flowers at the end of July.

Correlation with environmental factors

In separate linear regressions, the number of species in flower on 4–7 July did not show a significant relationship with (1) depth of thaw, (2) precipitation in May, (3) precipitation in June or (4) precipitation in May + June, nor with (5) degree days above zero (dd) in May (where $r^2 = 0.281$, $P = 0.094$). Date of snowmelt was significant only when the very cold and late summers of 1983 and 1989 were included (Fig. 4b).

Warmer temperatures in June and early July were associated with early flowering. Thus separate linear regressions of species in flower against degree days over the periods 1–15, 16–30 and 1–30 June, 1–5 July, 1 June–5 July, and 15 June–5 July gave statistically significant relationships in all cases. Including the whole period 1 June–5 July gave the best fit (Fig. 4a). The relationship remains significant even if the two cold summers of 1983 and 1989 are excluded ($y = -6.78 + 0.261x$, $r^2 = 0.619$, $P = 0.012$).

In most arctic species, flowering is a 2-year process with floral primordia formed in the first year (Söyrinki 1938, 1939; Sörensen 1941; Bliss 1971). Including total degree days for the previous growing season with current season degree days in the regression had no effect.

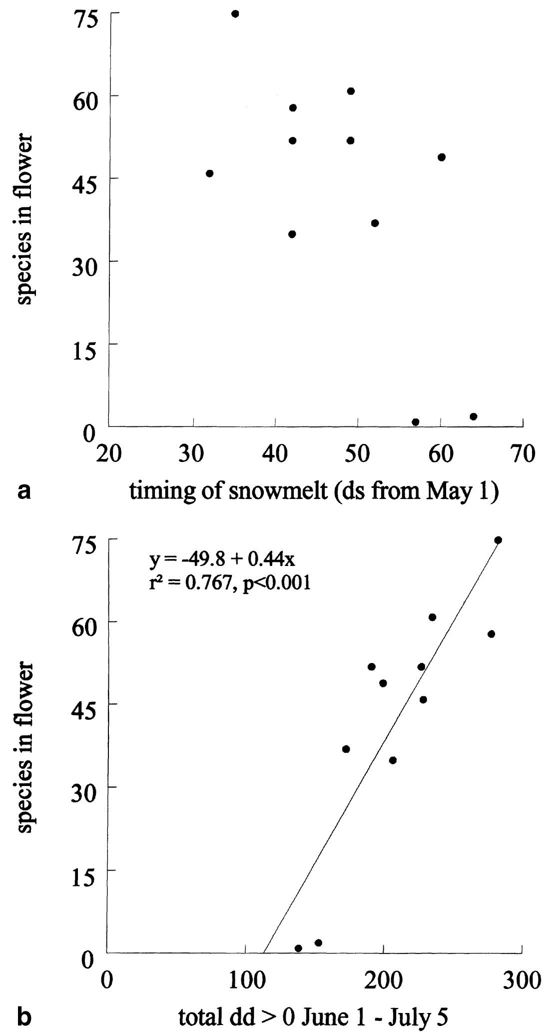

Fig. 4 The relationship between the number of species in flower by 4–7 July and **a** time of snowmelt (determined as the first day of snowfree ground and **b** degree days >0 from 1 June to 5 July

Discussion

The 11-year record presented here demonstrates wide annual variation in the onset of flowering among the 75 species, especially when scaled against the short growing season. For example, for the normally late-blooming *Epilobium latifolium* and *Sedum villosum*, the onset of flowering may vary by up to 4 weeks which in turn may amount to 40–50% of their growing season length in many years. The four species of willow present in Thjórsárver (*Salix arctica*, *S. herbacea*, *S. lanata* and *S. phylicifolia*) usually disperse their seed in late July but few other species have ripened seed before mid-August. Work on soil seed banks in the area (Thórhallsdóttir 1994), including dry *Salix* heath and *Carex bigelowii* heath, *Carex nigra* mire and a cottongrass mire, indicates that most species have small or no seed reserves in the soil. This is consistent with the hypothesis that little viable seed is produced in many years.

Temperature, photoperiod and rainfall are the three environmental factors that are recognized as triggers for flowering (Ratchke and Lacey 1985). Flowering time has also been shown to have a genetic basis in many species (Clausen and Hiesey 1958; Ratchke and Lacey 1985) but for others the effect of heredity has been inferred to be weak or absent (Galen and Stanton 1991). Many high-latitude species are known to require photoperiodic induction for flowering, but the strength and type of photoperiodic requirement varies and floral development can be stimulated via more than one route. In growth chambers, for example, high-Arctic populations of *Cerastium regalii* showed a short-day requirement for primary floral induction, although they probably never experience short-day stimulation in situ (Heide et al. 1990). Below 12°C, exposure to long days was sufficient to initiate flowering. In Norwegian alpine populations of *Carex bigelowii*, short days stimulated floral initiation and long days stimulated, but were not necessary for, further inflorescence development (Heide 1992).

In alpine tundra (Holway and Ward 1965; Billings and Mooney 1968), as well as in the Arctic (Billings and Mooney 1968; Wielgolaski and Kärenlampi 1975; Shaver and Kummerow 1992; Eriksen et al. 1993; Woodley and Svoboda 1994), snowmelt has been widely regarded as the environmental event initiating growth and flowering. Most of these studies looked at spatial rather than temporal variation, often by comparing the phenology of snowbed populations with that of adjacent conspecific populations outside snowbeds (e.g. Kudo 1991; Stenström and Molau 1992) or variation within snowbeds (e.g. Galen and Stanton 1991).

Here, cumulative degree days over the preceeding 5 weeks proved to be an excellent predictor of the number of species in flower. In continental areas with steep temperature gradients at the onset of the growing season and relatively warm summers, the effects of the timing of snowmelt (allowing light reception for photosynthesis) and of higher temperatures (allowing physiological activity) may not be easy to separate. In the maritime climate of Thjórsárver, the winters are not very cold but spring temperatures rise slowly and the onset of flowering is clearly not linked to snowfree conditions. Snowmelt is only likely to delay flowering after very cold springs with exceptionally late ablation. Although causal relationships cannot be established from correlations, the large amount of the variance in the onset of flowering that is explained by degree days, strongly implicates warming as the causal variable. This conclusion is supported by experimental evidence from *Dryas octopetala* in a polar semi-desert in Svalbard. There an increase in growing season temperatures by 3.5°C accelerated peak flowering times by at least 3 days and had strong effects on seed weight (Wookey et al. 1995) and on seed set (Wookey et al. 1993).

Global warming is expected to be most pronounced at high latitudes (Mitchell et al. 1990; Maxwell 1992). The implications for Arctic plant communities (Edlund and Alt 1989; Melillo et al. 1990), and productivity and plant growth (Melillo et al. 1990; Chapin et al. 1992) have received much attention, but raised temperatures may also affect the seasonal timing of developmental events. Most of the 75 species included here have a wide distribution in the Arctic, and over half are regarded as circumpolar (Hultén and Fries 1986). Higher temperatures in spring and early summer are likely to substantially affect the flowering phenology of these arctic species. With increasing temperatures, late flowering species, that now rarely ripen seed, may do so regularly. Given the low frequency of years with ripe seeds, current soil seed banks may often represent recruitment from no more than a few, seed crops, possibly only one. Increased frequency of seed set may increase the size, species richness and intraspecific genetic diversity of the soil seed bank. Accelerated phenologies may also alter patterns of resource allocation within plants, with earlier seed and fruit maturation leading to proportionally greater expenditure on reproductive tissue, possibly at the expense of vegetative or clonal growth (but see Wookey et al. 1995). Pollinators may benefit from increased densities of flowers. Diptera, the most important pollinators present in the Arctic (Hagerup 1951; Kevan 1972; Totland 1994b), are opportunistic in their visits, and changed patterns of flowering synchrony could lead to competition for pollinator services. Finally, increased frequency of seed set and larger seed crops may facilitate the potential migration of species in response to climatic warming (Melillo et al. 1990; Grabherr and Pauli 1994).

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