Chapter 3.5

HIGH ALTITUDE CLIMATES

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1. INTRODUCTION

Phenology at high altitudes differs from that in most other habitats in four significant ways. First, for much (sometimes the majority) of the calendar year these habitats may be under snow or ice, and there is little photosynthetic activity. Consequently (and second), there is a very short growing season delimited by a combination of temperature and snowpack. Third, this may be one of a few habitats where almost all phenology is tied to a single highly variable event, the timing of snowmelt; few high-altitude plants appear to exhibit photoperiodic responses for phenological events. And finally, high altitudes may differ from other habitats in the way that global climate change is affecting phenology.

What is a high altitude? The answer is not as obvious as it might seem. It probably makes more sense to use an ecosystem definition rather than an absolute altitude, as what constitutes a high altitude at high latitudes differs from a high altitude at mid- or low latitudes. For the purposes of this chapter we will consider "high altitude" to refer to alpine or montane ecosystems. Alpine is defined as the area above the natural limit of trees, and it extends over a wide latitudinal and altitudinal range. Another way of defining it, in climatic terms, is that its lower elevational limit corresponds well to the 10°C isotherm for the warmest summer month (Wardle 1974). The alpine

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shares many characteristics with high-latitude or arctic ecosystems (Bliss 1971, and see Chapter 3.4 in this book), but from a phenological perspective one big difference is the much longer day lengths during the arctic growing season. Montane ecosystems are less clearly defined, but would include the ecosystem between grasslands on the lower end and the alpine on the upper end; the term subalpine applies to the upper end of the montane.

There are not as many long-term studies of phenology at high altitudes as there are of low altitudes. In fact, there do not appear to be any studies longer than the one described in this chapter that was initiated in 1973. Thus some of the discussion in this chapter will be colored by the fact that Inouye has worked for most of his research career at a single high-altitude field station, the Rocky Mountain Biological Laboratory (RMBL). Perhaps the information in this chapter will help to stimulate the initiation of other studies.

2. THE HIGH-ALTITUDE CLIMATE

Mountains have been described as "generating their own climate", due to the effect of their mass on circulation patterns, precipitation, and radiation. This creates abundant variation of the climate within mountain regions, but also some general patterns that help to differentiate high altitude climate, and hence phenology, from that at lower altitudes. Kittel et al. (2002) go into detail about elevation dependence of climate, which can be attributed to factors at high altitudes such as closer contact to the free troposphere, decoupling from convective mixing of the lower troposphere, and snow-albedo feedback. Within the Rocky Mountains, there is a classic orographic precipitation pattern that creates increased precipitation on the west (windward) side of the mountains and a rain shadow on the east, although some winter air masses create up-slope conditions on the east side that generate precipitation there.

In all areas of the Rocky Mountains, total precipitation increases significantly with elevation (Kittel et al. 2002), with the highest precipitation occurring near the peak elevations (this is true for the Alps also, Theurillat and Guisan 2001, and in the Scandinavian mountains). Maximum and minimum temperatures decrease strongly with increasing altitude throughout the Rocky Mountains (Kittel et al. 2002), although there are some interesting variations. For example, variation of maximum temperatures decreases with elevation in the winter while that of minimum temperatures increases during the summer, and at lower elevations in the central Rockies, temperatures can be colder than those at similar elevations in the north (due to the influence of continental vs. maritime air masses).

An analysis of historical data shows that there are significant century-scale positive trends for annual and seasonal precipitation and mean minimum temperature in the U.S. Rocky Mountains (Kittel et al. 2002). Some of these are quite striking; in the northern and central Rockies summer precipitation has increased by 30% and 33% over the past century. There has also been a trend for increasing annual mean minimum temperature (0.7 – 0.9°C for the northern and central mountains). It is probable that these changes, and those forecast for the future, will have consequences for phenology at high altitudes. Giorgi et al. (1997) predicted similar changes for temperature over an altitudinal range in the Swiss Alps, and suggested "... that high elevation temperature change could be used as an early detection tool for global warming."

Both large- and small-scale events can affect high-altitude phenology. For example, the El Niño Southern Oscillation (ENSO) and the North Pacific Oscillation (or Pacific Decadal Oscillation) can affect winter precipitation in the Rocky Mountains. At the other extreme, microclimate can have very large effects. Areas where snow is deposited by wind (on the lee side of ridges, trees, etc.) can melt out much later than nearby sites, and deposition by snow slides and avalanches may create such deep snow depths that certain areas may not melt out at all in a given summer. Wagner and Reichegger (1997) found that a north-facing study site subject to deep snow deposition took about a month longer to melt out than sunlit sites. The cold water from melting snowbanks can have an effect on the phenology of plants it reaches. Holway and Ward (1963) found in an experimental study that meltwater resulted in delays of flowering in 12 of 14 species growing in irrigated plots (typically of about a week, but up to a month).

Another aspect of high-altitude phenology that is unique to areas with great topographic relief is the potential for phenological inversions. Thermal inversions through cold air drainage can have phenological consequences. Lynov (1984) reported statistically significant effects of such phenological inversions for eight species of trees and shrubs, with delays of 2 – 5 days in times of bud opening and flowering. Areas where this cold air collects are also described as frost hollows or frost pockets.

In the southern Colorado Rocky Mountains the ecosystem at 2900 m is sub-alpine, or montane, as trees are still common at this altitude. The date of first permanent winter snowpack at the RMBL averages about 4 November (range 15 October-24 November, data from 1974-2001), and the length of snowcover is about 200 days (range 165-233, data from 1975-2001). The mean date of first bare ground at a permanent snow measurement station is 21 May, with a range of 25 May to 19 June (data from 1975-2002). Summer precipitation also appears to play a role in some aspects of phenology at the RMBL. Precipitation for June-August at the NOAA weather station in

Crested Butte (2704 m, 9.5 km from RMBL) has averaged 13.5cm (range 5.3-22.3 cm, data from 1973-2001; the data for 2002 will probably set a new record low).

The influence of climate on the growing season, and hence on phenology, can also be seen by transplant experiments. Plants transplanted to lower altitudes will typically develop much sooner than those left in their native high-altitude sites (e.g., Wagner and Reichegger 1997).

3. LITERATURE REVIEW

Perhaps more than any other bioclimatic zone except high latitudes, phenological events at high altitudes are constrained by a short growing season, delimited by cold temperatures and snowpack. Time of snowmelt appears to have an almost universal effect on high-altitude phenology, and variation in phenology can usually be linked to variation in accumulation and then melting of snow, whether this is across time or space. This interaction has been reported by many studies, including Bliss (1956), Holway and Ward (1963, 1965), and Mark (1970). Canaday and Fonda (1974) found that the timing and duration of phenophases of a variety of subalpine plants in the Olympic Mountains (WA) were a function of snowmelt. In general terms Ratcliffe and Turkington (1989) found the same results, although they argue that the identity of dominant species and, to a lesser degree, aspect, are responsible for variations they observed in phenology. Some species tended to flower earlier on south-facing slopes, indicating the potential importance of aspect and microenvironment.

Most studies of phenology at high altitudes have been short (e.g., (Wielgolaski and Kärenlampi 1975); such studies can probably define relatively well the spatial pattern of snowmelt and hence phenology in a particular site, but longer studies are required to gain insights into the effects of climate variables on phenology. In one relatively long study, Walker et al. (1995) followed the phenology of two forbs for six years in five different plant communities and found significant differences among years and plant communities.

Phenophase condensation has been observed in several studies of alpine plants, with full development being accomplished more rapidly where snow persists longer. Examples of this have been reported by Knight et al. (1977, and references therein), and Billings and Bliss (1959). Snowmelt gradients are a common phenomenon at high altitude, as some areas will receive more or less snow and receive more or less insolation and result in earlier or later snowmelt. The consequences of these gradients have been investigated in several studies. Kudo (1992) investigated five herbaceous species along a

snowmelt gradient on Mt. Kaun in the Taisetsu Mountains of Hokkaido, where the snowfree period ranged from 55 to 95 days. The later snowmelt occurred, the later flowering and fruiting began, and in the plot that melted out last no species was able to mature all fruits because of the short growing season. In a study of 56 species over three years, Kudo also found that a shorter snow-free period reduced flowering and seeding (Kudo 1991).

Plants found in alpine tundra are often remarkable for the speed with which they can flower and fruit, but this adaptation is required for success given the short growing season (Bliss 1971; Wielgolaski and Kärenlampi, 1975). This early flowering is facilitated by the fact that floral initiation often occurs one or more years in advance of flowering; preformation of flower buds is characteristic of many high-altitude plants (e.g., Resvoll 1917; Forbis and Diggle 2001; Meloche and Diggle 2001, and see references in Bliss 1971).

The climate constraints of high altitudes could result in significant selection against late flowering, to allow sufficient time for the development of seeds before the first killing frost in the fall, and this may be why annual and even biennial plants are relatively uncommon at high altitudes (Bliss 1971; Jackson and Bliss 1982). Annuals may be restricted to sites that melt out early or that don't dry out early in the summer (Reynolds 1984). Some studies do show that most species in alpine communities initiate flowering rapidly after snowmelt, with relatively few species flowering late (e.g., Holway and Ward 1965; Billings and Mooney 1968; Totland 1993). In a few cases, plants may be able to initiate growth under the snow and get a head start on the growing season. Billings and Bliss (1959) found *Geum turbinatum*, *Carex elynoides*, and *Deschampsia caespitosa* growing under 1-5 cm of snow near the edge of a melting snowbank, and observed that the latter two of these had started growth under 50 cm of snow that did not become snow free for another four days. Young red leaves of *Polygonum bistortoides* were found under 110 cm of old snow (Mooney et al. 1981). Williams and Cronin (1968) found that *Delphinium* species could emerge and develop green cotyledons when snow melted to a depth of 30 cm or less, and Spomer (cited in Richardson and Salisbury 1977) found green plants of *Ranunculus adoneus* under 1m of snow. Arroyo et al. (1981) recorded the earliest-flowering alpine species in the Chilean Andes as actually blooming precociously under 5-6 cm of snow, and Bliss (1971) reported flowering by species of *Caltha* and *Ranunculus* under 10 cm or more of snow.

Theurillat and Schlüssel (2000) studied seven subalpine-alpine species in the Alps and characterized them by the number of degree-days to bud burst and the end of flowering. Each species differed in its requirements, but only *Vaccinium myrtillus* was closely tied to snowmelt, while the others fit heat sum models that depended on degree-days after a chilling requirement,

intensity of chilling from a threshold, or constant degree-days following thaw (Heide 1993; Myking and Heide 1995). It would be interesting to have some studies that have compared models of heat sums and time since snowmelt to see which works best for predicting phenology of a variety of species.

3.1 Temporal, Spatial, and Altitudinal Gradients

Plants growing in microsites with shorter growing seasons may be able to compensate somewhat by shortening the time before flowering starts, allowing them to complete seed production before the weather becomes unfavorable. Jackson and Bliss (1984) studied *Polygonum minimum*, a very small (<2 cm tall) subalpine annual plant at 3,000m in the Sierra Nevada. Its indeterminate growth pattern, and the fact that it can dehisce seeds in as little as two months after snowmelt, help it to survive the phenological constraints of its habitat. The indeterminate growth pattern permits plants to take advantage of longer growing seasons for increased seed production. Another example is provided by *Carex* species in the Austrian Alps (Wagner and Reichegger 1997).

However, if the microsite differences in snowmelt lead to significant differences in flowering time, the end result may be fitness differences among individuals flowering at different times, and eventually, divergence. This kind of differentiation has been seen in mountain environments in Japan (Kudo 1991), Colorado (Galen and Stanton 1991) and North Swedish Lapland (Stenström and Molau 1992). Galen and Stanton (1991) found fitness differences related to emergence phenology; plants in the latest-melting parts of snowbeds produced smaller seeds than earlier-flowering plants, and seed size was correlated with seedling survival rates.

Despite the potential advantages of early flowering, some species do seem to be able to withstand the constraints of late flowering. For example, *Gentianella caucasea* is an annual species found growing up to the subniveal zone in the Central Caucasus that can complete its life cycle with four to five weeks (Akhalkatsi and Wagner 1996). Different microclimates appear to have resulted in different phenotypes with significant differences in developmental times. Populations at the lower end of the altitudinal range take at least 24-25 days for floral bud formation, flowering, and fruit ripening, while those at high elevations flower about three weeks later than the earliest lower population and take only 18 days to complete reproduction. *Gentianella germanica*, a biennial species found at high altitudes in Europe and the Balkans, is unusual for its late flowering (August to the beginning of November when winter begins (Wagner and Mitterhofer 1998). Phenological differences in flowering between two morphs of this

species may be leading to their isolation. The Norwegian alpine species *Leontodon autumnalis* var. *taraxaci* also flowers late (Totland 1997).

Elevational gradients provide an interesting opportunity for phenological studies at high altitudes. Schuster et al. (1989) studied gene flow in limber pine (*Pinus flexilis*) over its altitudinal range (1650 m to 3350 m) in Colorado, and found that pollination phenology is strongly affected by altitude. Sites that differed in elevation by more than 400m did not usually have overlapping pollination periods, so gene flow by pollination was quite restricted. Mitton et al. (1980) found similar results for ponderosa pine trees (*Pinus ponderosa*). Hoffmann and Walker (1980) looked at phenology of two drought-deciduous shrubs along an altitudinal gradient on the Coastal and Andean Ranges of Chile. Vegetative growth at the upper limit (2000 m) started nine weeks later than at the lowest altitude (700 m), and lasted longer at the lower altitude, but flowering and fruiting occurred at about the same time at both ends of the gradient (perhaps indicating a dependence on day-length as a cue). Environmental gradients may produce some of the same effects as elevational gradients; for example, Stanton et al. (1997) suggested that differences in flowering time of *Ranunculus adoneus* along a snowmelt gradient could reduce opportunities for pollen transfer, and presented evidence for some genetic differentiation among early, middle, and late-melting cohorts. The longer growing season in early-melting sites enhanced vegetative growth at all life-history states and increased fecundity of seedlings (Stanton and Galen 1997).

3.2 Community-Level Patterns and Temporal Patterns

Relatively few community-level surveys of plant phenology have been made of alpine plants. Douglas and Bliss (1977) conducted weekly samples in 2x2m plots in the North Cascade Range of Washington and recorded times of vegetative growth, flowering, fruiting, seed dispersal, and dormancy of 32 species in weekly surveys. Most species flowered within 14-24 days following initiation of growth, remained in bloom for 8-20 days, and then had a 10-24 day fruiting stage prior to seed dispersal. This is also reported in various communities of the low alpine region in southern Norway (Wielgolaski and Kärenlampi 1975). Ratcliffe and Turkington (1989) used similar methods looked at 45 vascular plant species in southern British Columbia. Most species flowered between 15 and 40 days after snowmelt. Bauer (1983) reported data on the seasonal flowering phenology of 24 species of tundra plants visited by bumblebees, from weekly surveys.

Molau (1993) conducted a study of the relationships between flowering phenology and life history strategies of plants in high-altitude Sweden. Some of the immense variation among tundra species in reproductive traits

(e.g., seed:ovule and fruit:flower ratios) in this habitat is correlated with flowering phenology (which in turn is linked to snowmelt patterns). Early-flowering species show high outbreeding rates and low seed:ovule ratios, while late-flowering species showed the reverse. Apomixis and vivipary were restricted to late-flowering species, and ploidy levels increased from early- to late-flowering times.

Relatively little is known about phenology at high altitudes in the southern hemisphere, or in tropical areas. Inouye and Pyke (1988) did report phenological data for alpine Australia from a one-year study. Ralph (1978) found that plants of *Azorella* compacta (Apiaceae) flowered year-round in populations at 3960 and 4500 m. Phenological patterns of the high Andean Cordillera of central Chile were studied by Arroyo et al. (1981), who looked at 97 alpine species. They characterized these species as falling into nine different patterns of phenological behavior. The most common category was perennials that overwintered in a dormant state. At all sites they examined, there was a single prominent maximum in flowering activity, which was earlier on north-facing than south-facing slopes. An interesting observation about flowering longevity was that duration of flowering tended to be longer at higher altitudes (individual flowers lasted longer, and the total flowering period was also longer). (Gómez 1993 also saw longer flowering periods at higher altitudes.) Over their two-year study, they found that phenological patterns were "remarkably constant from one year to the next"; more than 90% of species had identical phenology in both years.

Melampy (1987) studied flowering phenology of *Befaria resinosa*, an ericaceous shrub of the eastern Andes of Colombia. This species seems to have two peaks of flowering each year, although one is more significant, and there was some suggestion from the data that the two peaks of rainfall might have been responsible for initiation of flowering. The weather at this 2200 m site is quite dry for much of the year, and 22% and 31% of the annual precipitation occurs during the two peaks. There are often sympatric congeneric wildflower species in high altitude habitats, and it's not surprising that in such cases they might flower at different times as a way to avoid competition for pollinators. Adams (1983) studied five sympatric species of *Pedicularis* (Scrophulariaceae) on Mount Rainier in the Washington Cascade Mountains, all of which are pollinated by bumblebees. Two bloom early in the growing season, one in mid-season, and two in late-season. At RMBL, pairs of *Mertensia* and *Delphinium* species include species that flower early and at mid-season (Inouye, unpublished).

Gómez (1993) investigated the effects of flowering synchrony on reproductive success of 80 *Hormathophylla spinosa* (Cruciferae) plants in the Sierra Nevada mountains of Spain. He measured flowering synchrony as the number of days that the flowering of an individual overlaps with the

flowering of every other plant in the sample, and found that synchrony ranged from 0.25 to 1.00, with more than 70% of plants having synchrony levels greater than 0.75. Plants with a lower degree of flowering synchrony were visited by more pollinators and also eaten by fewer herbivores, but the phenological traits did not affect female fertility so Gómez concluded that flowering synchrony in this species is not regulated by selective pressures from pollinators or herbivores.

Although it may be more common than the literature indicates, mast flowering does occur in at least some alpine or montane ecosystems. *Frasera speciosa* (Gentianaceae) has a flowering pattern that has been described as 'sporadic seasonal synchrony', in which significant flowering events of this long-lived monocarp occurs only once every several years (Beattie et al. 1973; Taylor and Inouye 1985). A similar flowering pattern, but with even longer intervals between significant flowering years, is seen in the lily *Veratrum tenuipetalum* (Inouye, unpublished observations). Mast flowering has also been reported from a few alpine species in New Zealand (Kelly et al. 2000; Rees et al. 2002)

4. FLOWERING PHENOLOGY IN THE COLORADO ROCKY MOUNTAINS

Inouye has conducted since 1973 a study of the timing and abundance of flowering by Rocky Mountain wildflowers, in permanent 2x2m plots near the RMBL. This site is located in the West Elk Mountains of Colorado, at an altitude of about 2,900m (38°57.5'N, 106°59.3'W). Every other day for most or all of the growing season all flowers in the plots are counted.

Phenology of flowering and many other events at this site is dependent on the amount of snow that fell during the previous winter and when that snow melts, as the growing season does not begin until the snow is gone. Since 1975 the annual snowfall (measured as daily snowfall or even more frequently during storms; unpublished data courtesy of Billy Barr) has ranged from 474-1641cm (mean = 1105). The date on which the permanent snowpack has begun has ranged from 15 October to 24 November (mean = 4 November), and the snow has disappeared from the measurement site as early as 25 April and as late as 19 June (mean = 24 May). Of course there is much variation in these dates across the landscape, with differences in microclimate, slope aspect, and snow deposition through wind activity resulting in some sites that hold or lose snow earlier or later.

One question that arises is whether the range of dates described here is typical of a longer-term period. Although we do not have snowfall data from RMBL earlier than 1975, a proxy for snowfall, the peak runoff in the

East River (which runs through the Lab) is measured at Almont, Colorado, and has been recorded continuously since 1935. The correlation between measurements of winter snowfall at RMBL and the peak runoff measured at Almont is strong (r^2 = .757, p = .0001). If peak runoff is then used to estimate historical snowfall at RMBL, we find that the period 1975 – 2002 contains both the maximum and minimum snowfall records for the 68 years of data. This could be an indication of the increased variation in precipitation that has been predicted by some models of global climate change.

For all species that we have examined so far, from the earliest flowering (*Claytonia lanceolata*) to the latest (*Artemisia tridentata*), the timing of flowering is strongly linked to the amount of snow that falls during the previous winter, and hence the timing of snowmelt. For some species the relationship is linear (e.g., *Delphinium nuttallianum*, Figure 1a), while for others it is curvilinear (e.g., *Mertensia ciliata*, Figure 1b). The curvilinear relationship seen for some species may indicate an interaction between temperature and number of days since snowmelt; in years with early snowmelt, it takes more days (i.e., more growing degree days) for some heat sum to be achieved before flowering begins. Such curvilinear relationships may characterize later-flowering species (e.g., Inouye et al. 2002), as we have not observed them yet in early-flowering species. This strong reliance on snowmelt as an environmental factor determining flowering time, seems to characterize all of the herbaceous species at this site, and possibly the relatively few woody ones as well. There do not seem to be species at this altitude that rely on day length for timing of flowering.

Another factor that is important in the abundance of flowers and is linked to phenology is frost (Inouye 2000). In some years frost can kill almost all of the buds of some species of wildflowers at RMBL, such as *Helianthella quinquenervis*, the aspen sunflower. In eight of the past 28 years there has been significant frost damage (Inouye, unpublished). The critical factor for this interaction between snow, frost, and flower abundance appears to be phenology. If there is sufficient snow during the winter, snowmelt, and hence the beginning of the growing season, will be delayed compared to those years with light snowpack. Hard frosts (e.g., temperatures down to -7° C) can occur as late as the third week in June. If plants begin growth too early in the season, they can have buds at a sensitive stage of development by the third week of June, and are then susceptible to frost damage. If there is sufficient snow to delay snowmelt, and hence the growing season, then development of frost-sensitive buds will be delayed beyond the time when frost is likely to occur. There is some evidence that frost risk at lower altitudes may be declining as a consequence of global climate change (Moonen et al. 2002).

Given that there is so much evidence supporting the dependence of high-altitude phenology on snowpack, it may be possible to use historical data on

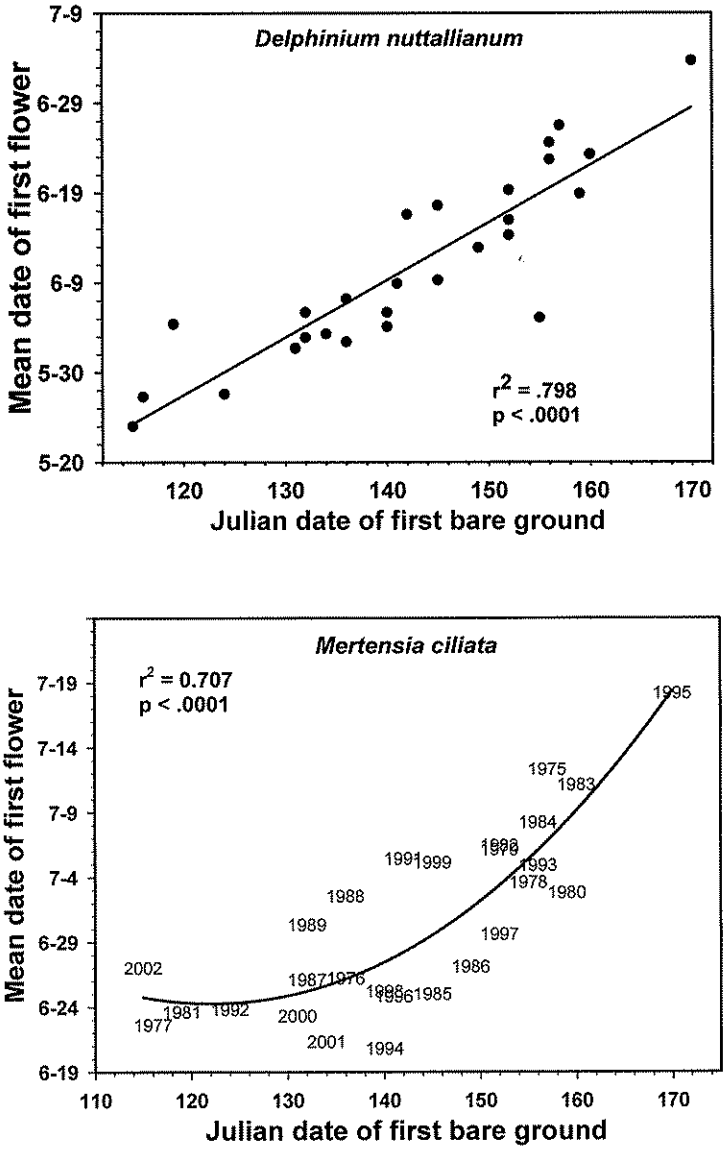

Figure 3.5-1. The relationship between the first date of bare ground and the date of first flower for a) *Delphinium nuttallianum* and b) *Mertensia ciliata.*

snowpacks in other areas to draw conclusions about historical patterns of phenology. For example, spring pulse dates of streamflow exhibit trends toward earlier spring timing, matching patterns of flowering by lilacs and honeysuckles in phenology studies (Cayan et al. 2001).

5. PHENOLOGY AND ANIMAL ECOLOGY

Although most of this review has focused on plant phenology, there are indications from the few available studies that animal phenology at high altitudes is also influenced by the same kinds of environmental cues that affect plants. Morton (1994) assessed timing of reproduction for both wild onion (*Allium validum*) and White-crowned Sparrows (*Zonotrichia leucophyrus oriantha*) at the same subalpine meadow in the California Sierra Nevada. Data from 21 years indicated that both flowering date and clutch initiation date were highly correlated with snow conditions (occurring later as snowpack increased).

Langvatn et al. (1996) found that plant phenology had important consequences for diet quality, and hence reproduction, for red deer. They found a negative correlation between various fitness measures for female red deer and growing degree-days during the summer. Their interpretation was that when herbage growth is retarded (via cooler weather) the digestibility of plants declines more slowly than in warm summers, resulting in a longer period with good grazing. Although this study was conducted at high latitude rather than high altitude, the same principle may apply at higher altitudes too. Merrill and Boyce (1991) make a similar story for high-elevation summer range for elk in the Yellowstone ecosystem, describing a link between heavy winter snowfall, delayed phenology the next summer, and consequent high-quality forage through late summer.

6. CLIMATE CHANGE AND PHENOLOGY IN THE COLORADO ROCKY MOUNTAINS

Inouye et al. (2000) reported that there was no sign of an effect of climate change on the phenology of wildflowers in the Rocky Mountains. This finding contrasts strongly with results from lower altitudes, where many studies have reported that phenological events are happening earlier than they used to (e.g., Bradley et al. 1999; Brown et al. 1999; Roy and Sparks, 2000; Peñuelas and Filella 2001; Sagarin and Micheli 2001; Fitter and Fitter 2002; Peñuelas et al. 2002; Walther et al. 2002). The paper by Inouye et al.

pointed out that this difference between low and high altitudes in phenological responses to climate change could cause problems for altitudinal migrants, and reported data suggesting that robins (*Turdus migratorius*) were showing effects of this change in synchrony.

The reason that flowering phenology was not changing at high altitudes is probably related to the trend observed for increased winter precipitation (see Figure 1 in Inouye et al. 2000, and Figure 3.4-4 in this book). Thus, even though air temperatures appeared to be warming, the net result was that there was no trend for earlier snowmelt dates (and hence phenology). Some models of global climate change predict increased precipitation. In contrast to flowering phenology, there is evidence that some animals are responding to warming temperatures with changes in phenology. Inouye et al. (2000) reported that marmots were emerging from hibernation significantly earlier than they did a few decades earlier, and therefore emerging when there was much more snow left on the ground than previously. Another change is seen in the emergence dates of a butterfly species that overwinters as adults. Emergence date has become significantly later during the period 1975 – 2002 (Figure 2), for reasons that are not clear. Emergence dates of ground squirrels and chipmunks from winter hibernation are also changing, but in the opposite direction from that of marmots (Billy Barr, unpublished). Apparently they are responding to different cues than the marmots, or they are responding differently to the same cues as marmots.

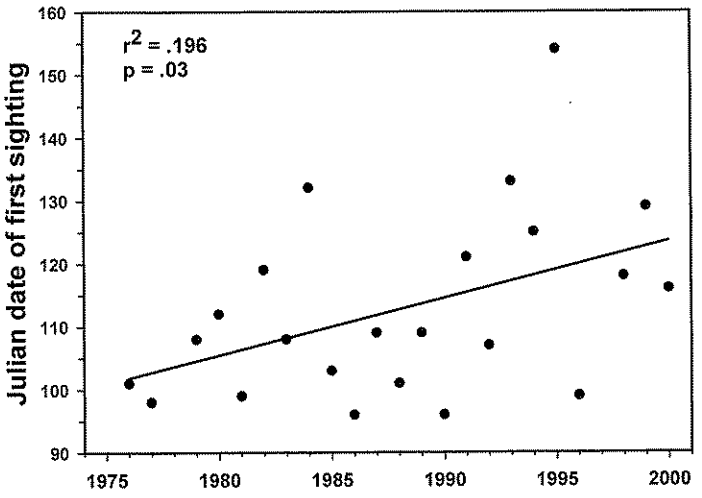

Figure 3.5-2. The change in emergence date for adults of the butterfly *Nymphalis milberti* at the Rocky Mountain Biological Laboratory. Unpublished data from Billy Barr.

If the emergence phenology of pollinators and herbivores is changing relative to their host plants and food plants, it seems likely that coevolved relationships may change significantly in the future. This kind of change in synchrony has also been reported from lower altitudes (Visser and Holleman 2001).

High-altitude aquatic habitats may also be showing signs of changing phenology. Caine (2002) reported that spring ice thickness on an alpine lake is declining at a rate of about 2 cm/yr, and the duration of ice cover also appears to be declining. Presumably a variety of aspects of plant and animal phenology in such alpine lakes is being influenced by the change in ice cover (which may be a consequence of increasing precipitation).

The changes that are predicted for distribution of alpine plants in the future as a consequence of climate change (e.g., Guisan and Theurillat 2000; Theurillat and Guisan 2001) will be in part a function of changes in phenology. The ultimate result is likely to be an overall trend for reduced availability of suitable habitat, and shifts in the distribution of species richness (either shifting upward or spreading out of patches) (Guisan and Theurillat 2000). There is some evidence that plants in the Swiss Alps may already be showing signs of such a shift upward in distribution (Hofer 1992; Grabherr et al. 1995; and Chapter 3.4 in this book).

7. CONCLUSIONS

The disappearance of snow cover appears to be the primary factor influencing phenology at high altitudes in the temperate zone. Not enough is known yet about other high-altitude areas without significant snow cover to confirm what is controlling their phenologies. One consequence of the importance of snow in controlling phenology is that flowering, and other phenological events involving both plants and animals, can be highly variable because of variation across years in snowpack depth and across space because of aspect and microsite differences in snow accumulation and melting. A consequence of this variation may be that no single set of phenological and physiological characteristics is optimally adapted to all of this variability, which would then encourage the evolution and maintenance of a diversity of adaptive strategies in high altitude communities.

Although the timing of events exhibits significant variation among years, their relative timing is much less variable. The sequence of flowering species is typically consistent across years, with the same species flowering each year in early, middle or late season. Variation across space is also consistent, as sites that tend to accumulate snow in one year are likely to do so in other years.

Lest flowering phenology at high altitudes be considered an esoteric topic, consider the economic importance of strawberry production. Strawberries used to be highly seasonal, but it is now possible to produce multiple crops across most temperate climates. This change is the result of developing new multiple-cropping cultivars with cyclic flowering. The genes for this change for all modern day-neutral cultivars come from a single clone of *Fragaria virginiana* ssp. *glauca* from the Wasatch Mountains of Utah (Sakin et al. 1997).

8. AVENUES FOR FUTURE INVESTIGATION

Experimental studies of phenology are rare, even though snowpack is relatively easily manipulated (e.g., Galen and Stanton 1993; Dunne et al. 2003), but they offer the potential to elucidate the significance of variation in phenology more quickly than observational studies. The International Tundra Experiment has investigated responses of tundra plants to simulated climate warming, but most of its sites are at high latitudes (Henry and Molau 1997). Suzuki and Kudo (2000) did carry out an experiment in Japanese alpine tundra using open top chambers and five species of shrubs. Although there was some evidence of earlier leafing and flowering, this was not a consistent response. Additional experimental studies are likely to provide interesting and novel results. It would be valuable to have additional long-term studies of phenology at high altitudes, not only of flowering and other phenological events for plants, but also for phenology of animals. Not much is known about the phenology of hibernating and migrating species, or insects at high altitudes. There are been some interesting reports of differences in phenological characteristics within species across altitudinal gradients, for example, that flowering may last longer at higher altitudes. Additional studies across such gradients would be useful to confirm this and other aspects of phenology.

Studies of the consequences of variation in phenology are uncommon. What are the consequences of flowering early or late, or at the tail vs. the peak of flowering time? What are the consequences of variation in time of emergence from hibernation or in arrival or departure of migrating species? Very little is known about what controls the phenology of high-altitude tropical ecosystems, where snow is not a significant controlling factor. Given that snow may play little or no role in some of those areas, what is the influence of other environmental variables? We suggest that future studies of high-altitude phenology will be particularly interesting in the context of climate change, and hope that this review will help to stimulate additional work on this topic.

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