MASTER'S THESIS

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EFFECTS OF FORECASTED CLIMATE CHANGE ON A BUTTERFLY-PLANT INTERACTION IN THE NORTH CASCADES NATIONAL PARK

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by
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Abstract

Climate change can impact butterfly populations by shifting butterfly and plant phenologies relative to each other and by shortening the growing season. These impacts are expected to be greatest at high latitudes and elevations. I studied the effects of Julian date, soil moisture, and stream proximity on the phenology of common red paintbrush, *Castilleja miniata*, a host plant of the Anicia checkerspot, *Euphydryas anicia*, at two subalpine meadow sites in the North Cascades National Park. I considered 14 models that include the following variable combinations to predict growing season length:

1) Julian date,
2) soil moisture,
3) proximity to streams,
4) soil moisture and proximity to streams,
5) Julian date and proximity to streams,
6) Julian date and soil moisture,
7) Julian date, soil moisture, and proximity to streams.

I used multi-model inference to determine the relative importance of Julian date, soil moisture, and proximity to streams. I used Akaike's Information Criterion to select the best models from the candidate set. Julian date is the most important variable, followed closely by soil moisture. The model-averaged prediction for growing season length for plants in moist soils is 9.5 days longer than for plants in dry soils. Contemporary and forecasted climate change effects on *C. miniata* phenology suggest that a substantial amount of current habitat will become unsuitable for *E. anicia* due to advancement and shortening of the growing season.

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Introduction

Climate change

Global climate change could affect most species and ecological processes on the planet. Although we are committed to much greater climate changes than those observed to date (IPCC 2001), many ecological impacts of contemporary climate change are apparent. These include changes in species physiology, phenology, distributions, community composition, and ecosystem structure and function (Hughes 2000; McCarty 2001; Parmesan and Yohe 2003; Root *et al.* 2003). The magnitude of the impacts of climate change to terrestrial ecosystems in the coming century is expected to be second only to habitat destruction (Sala *et al.* 2000). Many species will not be able to cope with the effects of changing temperature and precipitation regimes. Thomas *et al.* (2004) predict that 15-37% of species are committed to climate change induced extinction in the next 50 years.

To date, only a small fraction of the forecasted climate changes and resultant biotic impacts have been observed, but many effects are clear already (Walther *et al.* 2002). Warmer temperatures have advanced the phenologies of plants, birds, and squirrels (Bradley *et al.* 1999; Beaubien and Freeland 2000; Fitter and Fitter 2002; Berteaux *et al.* 2004; Davies *et al.* 2005; Delbart *et al.* 2006) and shifted butterfly and bird ranges toward the poles (Hill *et al.* 1999; Parmesan 1999; Thomas and Lennon 1999; Crozier 2004b; Peterson *et al.* 2004; Davies *et al.* 2005). Climate change has caused extinction of butterfly populations (McLaughlin *et al.* 2002) and loss of habitats (Wilson *et al.* 2005).

Much remains uncertain about the nature and magnitude of biotic impacts of climate change. The effects of climate change on biodiversity are expected to have large regional variation, particularly in areas vulnerable to biotic exchange (Sala *et al.* 2000). Additionally, the interactive effects of climate change combined with other drivers, such as habitat destruction due to land use, on biodiversity are uncertain (Sala *et al.* 2000). Climate envelope models, used to forecast risk of species extinction, project changes that vary in magnitude and direction (Araújo *et al.* 2005). The spatial and temporal extent of these changes exceeds current knowledge about ecological interactions, which magnifies uncertainty in forecasted biotic responses to climate change (Walther *et al.* 2002).

Climate change: PNW regional forecasts

The present Pacific Northwest climate is characterized by mild wet winters and warm dry summers (Waring and Franklin 1979; Kruckeberg 1991). Most annual precipitation occurs in winter, which falls as snow in montane environments. Snow accumulation strongly influences plant characteristics and phenologies. In many montane habitats, deep snowpacks linger into late spring or early summer, which reduce the snow-free growing season and moisten soils during the dry season. Short growing seasons prevent tree establishment (Peterson and Peterson 2001; Kulla 2006) and facilitate establishment of meadows dominated by herbaceous annuals and perennials. These meadows provide habitat for many butterfly species.

Current and future climatic changes will alter conditions that determine the distribution of montane meadow habitats and phenologies of the plants and butterflies inhabiting them. A warming trend is apparent already: data from 113 Pacific Northwest weather stations in the U.S. Historic Climate Network reveal a regional mean temperature increase of 0.82ºC during the 20th Century (Mote *et al.* 2003). Simulations using global climate models (GCMs) suggest this warming trend will continue in the Pacific Northwest, producing an increase of 1.5ºC to 3.2ºC by 2040s decade (Mote *et al.* 2003), or an average increase of 2.5ºC resulting from a doubling of atmospheric CO_2 concentration (Leung and Wigmosta 1999). The magnitude of warming is expected to be greater in winter than in summer and at high elevations than at lower areas (Kim *et al.* 2002).

Forecasts of future precipitation regimes are more complex and less certain, but several outcomes consistently emerge from simulations using either GCMs or regional climate models (RCMs). First, little change in summer precipitation is forecast (Mote *et al.* 2003). Second, increases in winter precipitation are forecast (Leung and Ghan 1999; Leung and Wigmosta 1999; Kim *et al.* 2002; Mote *et al.* 2003). By the 2020s, winter (Oct.-Mar.) precipitation forecasted from eight GCMs increased by a mean of +8% over current values, with a range of +2% to +18% (Mote *et al.* 2003). Similar forecasts were obtained for the 2040s: -2%, +9%, +22% for low, mean, and high forecasts, respectively (Mote *et al.* 2003). For a watershed adjacent to the eastern boundary of Mt. Rainier National Park, simulated precipitation using an RCM with doubled atmospheric CO_2 concentration increased 7.0% (to 2092 mm, from 1956 mm; Leung and Wigmosta 1999).

Forecasted changes in temperature and precipitation combine to produce a decrease in Pacific Northwest snowpacks. Decreasing snowpacks became apparent in the 20th Century, during which the snow water equivalent of Pacific Northwest snowpacks decreased by 0.25 to 0.51 centimeters per year (Cowles *et al.* 2002). Despite increases in forecasted winter precipitation, warmer temperatures will cause more of that precipitation to fall as rain (Leung and Ghan 1999; Leung and Wigmosta 1999; Kim *et al.* 2002; Mote *et al.* 2003), except at elevations above 2500 meters (Kim *et al.* 2002). The result is a forecasted decrease in snowpack by 50% (Leung and Ghan 1999) or 60% (Leung and Wigmosta 1999).

Butterflies as model systems

Butterflies are often used to study the effects of climate change because of their sensitivity to climatic variables. Temperature strongly affects butterflies throughout their life histories. Direct or indirect effects of temperature have been observed in choice of oviposition sites, egg-laying rates, larval development and survival rates, and range shifts and expansions (Dobkin *et al.* 1987; Ayres and Scriber 1994; Parmesan 1999; Fleishman *et al.* 2000; Crozier 2003, 2004b; Davies *et al.* 2006). Precipitation influences larval development and survival by controlling host plant phenology (Rodriguez *et al.* 1994). Individual host plants are usually the sole source of food for prediapause larvae because inter-plant distances often exceed larval dispersal ranges (Weiss and Murphy 1988). Larvae are unable to travel far to locate a new host if their natal plant becomes defoliated or senescent (Dethier 1959; Wiklund 1977; Cain *et al.* 1985; Cappuccino and Kareiva 1985; Hayes 1985). Larvae of some species must reach a particular instar prior to diapause (Singer 1972; Weiss *et al.* 1987; Hunter and McNeil 1997). If a host plant senesces before larvae reach diapause, the larvae starve unless they find another suitable plant. Starvation is the usual outcome because inter-plant distances often exceed larval dispersal ranges (Weiss and Murphy 1988; but see Singer 1972; Hellman 2002)

The close link between larval survival and host plant senescence is well studied in the checkerspot butterfly *Euphydryas editha bayensis*. In California's serpentine soils, the main host plant of this butterfly, *Plantago erecta*, grows on both north- and south-facing slopes. Water and temperature exposure vary across these topographical aspects; south-facing slopes are usually warmer and have drier soils as a result of more direct insolation than cooler north-facing slopes. *P. erecta* on south-facing slopes are exposed to less water and higher temperatures than plants on north-facing slopes. Consequently, these south-slope plants have a more advanced phenology (2.5 to 4 wk earlier than north-facing slopes) (Dobkin *et al.* 1987; Weiss *et al.* 1988). While postdiapause larvae develop rapidly on warm south-facing slopes, prediapause mortality of *E. editha* is much higher on these slopes because plants senesce earlier than on north-facing slopes (Dobkin *et al.* 1987; Weiss *et al.* 1988). The timing of senescence, influenced by slope, aspect, and climatic variables, plays a dominant role in determining butterfly population dynamics in *E. editha* by influencing prediapause larval survival (Singer 1972; Weiss *et al.* 1988; Cushman *et al.* 1992).

Butterflies are an ideal model system because the natural history of many species is well understood. Long-term studies on butterfly populations have led to detailed knowledge of their ecology, life history, and population dynamics (see Ehrlich and Hanski 2004). *Euphydryas* species are particularly well studied in areas of larval development, survival, and host plant interactions; the research already conducted on these butterflies provides an excellent foundation for further study of the biotic effects of climate change.

Butterfly habitats are easily defined and delineated because the larval stage is highly dependent upon host plants. As adults, most butterflies are generalists and can find food in the form of nectar, rotting fruit, and sap; however, larvae are usually specialist feeders and some require a specific host plant (Pyle 2002). Since larvae are closely tied to their host as their food source, the plant's distribution defines the potential distribution of the butterfly. This distribution is further limited by climatic factors such as temperature (Crozier 2004b; Davies *et al.* 2005, 2006).

The literature on butterfly response to climate change is large and growing. Researchers have identified range shifts, expansions and contractions of distributions, habitat loss, and local extinctions due to changes in climate (Singer and Thomas 1996; Boggs and Murphy 1997; Thomas *et al.* 1998; Hill *et al.* 1999; Parmesan *et al.* 1999; Roy and Sparks 2000; Kerr 2001; Roy *et al.* 2001; Hellman 2002; Hill *et al.* 2002; McLaughlin *et al.* 2002; Crozier 2003; Konvicka *et al.* 2003; Oberhauser and Peterson 2003; Crozier 2004, 2004b; Peterson *et al.* 2004; Stefanescu *et al.* 2004; Davies *et al.* 2005; Wilson *et al.* 2005, Davies *et al.* 2006). Butterflies are sensitive to climate change; understanding their responses to climate change, especially through interactions with host plants, will aid in forecasting how other species will respond.

Phenology of alpine plants in response to climate change

Species at high altitudes and latitudes are expected to undergo rapid change due to greater magnitudes of warming (Kim *et al.* 2002; Thuiller *et al.* 2005). Timing of snowmelt is determined by amount of snowpack (Ostler *et al.* 1982; Price and Waser 1998). In the North Cascades, as well as in other montane areas, plant phenologies are closely related to snowmelt timing and early season temperature regimes (Billings and Bliss 1959; Canaday and Fonda 1974; Fareed and Caldwell 1975; Douglas and Bliss 1977; Ostler *et al.* 1982; Galen and Stanton 1991; Kudo 1992; Walker *et al.* 1995; Price and Waser 1998; Inouye *et al.* 2002; Totland and Alatalo 2002; Dunne *et al.* 2003). Shallow snowpacks melt early and typically result in an earlier growing season than heavy snowpacks (Price and Waser 1998; Arft *et al.* 1999; Inouye *et al.* 2002; Dunne *et al.* 2003). Shallow snowpacks also are correlated with drier growing season soils and high moisture stress in plants (Ostler *et al.* 1982; Dunne *et al.* 2003). Heavy snowpacks and late snowmelt delay emergence and germination (Fareed and Caldwell 1975; Kudo 1992; Price and Waser 1998) and also decrease alpine plant cover and production (Billings and Bliss 1959; Ostler *et al.* 1982), except in dry soils where cover and production are enhanced due to increased soil moisture (Fareed and Caldwell 1975; Ostler *et al.* 1982).

The effects of snowpack and snowmelt on alpine plant phenologies can vary based on how strongly soil moisture depends on snowmelt. Summer precipitation can be critical to alpine plants, particularly after snowmelt when soils begin to dry (Galen and Stanton 1991; Walker *et al.* 1995). While plant phenology in mesic soils is typically not affected by summer snowmelt (Canaday and Fonda 1974), summer precipitation increases plant cover and production in soils that dry after snowmelt (Billings and Bliss 1959; Ostler *et al.* 1982). Plants growing in rapidly drying soils depend on heavy snowpack and late snowmelt to escape drought conditions and early senescence.

The timing of plant senescence is influenced by several factors; knowing their relative importance will help project how senescence will be affected by climate change. If senescence is regulated predominantly by day length rather than temperature or precipitation, climate change might have little effect on the timing of senescence. For example, Bradley *et al.* (1999) found that plants with phenologies regulated by factors other than temperature did not have springtime advancement in phenophases. Alternatively, if plant phenologies are influenced strongly by climate variables, then climate change could alter the phenological overlap between host plants and larvae. In this case, determining the magnitude of phenological shifts would be important in assessing potential butterfly range shifts and extinction risk in forecasted climate regimes.

Effects of forecasted climate changes on butterfly-plant interaction

Effects of forecasted climate change on plant and insect phenologies will be complex. First, growing seasons will begin earlier due to hastened melting of shallower snowpacks. Second, plant senescence will commence earlier because soil moisture derived from melting snow will become depleted sooner. In the vicinity of meadow streams, the latter will be compounded by a reduction in summer streamflow (Kim *et al.* 2002; Mote *et al.* 2003). The temporal shift in the growing season caused by such substantial snowpack reductions could be as much as two weeks: 30% snowpack reductions were found to hasten the snowfree date by five days (Ostler *et al.* 1982). The temporal shift in plant senescence likely will be even greater, because warmer temperatures would hasten soil drying (Peterson and Peterson 2001; Mote *et al.* 2003).

Shrinking snowpacks and shifting plant phenologies may reduce the distributions of some montane butterflies. Local persistence of univoltine butterflies requires phenological overlap between larvae and larval host plants sufficient for larvae to complete development before plant senescence. Climatic changes forecasted for the Pacific Northwest could reduce the overlap between plant and larval phenologies, and thereby convert some meadows from source habitats to sinks. Earlier melting of shallower snowpacks would induce plants to emerge earlier and in cooler weather that would retard larval development. With summer precipitation expected to remain low, soils could dry and plants could senesce before most larvae complete development. This shift in plant phenologies from summer toward spring would be exacerbated by hastened rates of soil drying due to warmer temperatures (Peterson and Peterson 2001; Mote *et al.* 2003). Consequently, larvae might not survive in otherwise suitable meadows containing larval host plants. Shrinking snowpacks would expose additional meadow habitat at higher elevations, but the loss of larger meadow areas at lower elevations due to earlier drying and forest expansion (Peterson and Peterson 2001) would cause a net loss in butterfly habitat area. Warmer temperatures could create suitable habitat on north-facing slopes that are currently too cold for butterflies. This would require a shift in the current distribution of host plants, but it is uncertain if this shift could occur rapidly enough to mitigate the loss of suitable habitat on south-facing slopes. The implications for climate change suggest a need to determine the extent of phenological shift in plants as well as the magnitude of shift due to soil drying.

Knowledge gaps

Despite well-studied life histories and distributions in many areas, there are gaps in current knowledge with respect to butterfly responses to climate change. Butterfly responses to changing precipitation are poorly understood relative to responses to temperature. Most studies of butterfly responses to climate change have focused on the effects of temperature changes, but changes in precipitation patterns can be as important. Precipitation largely affects butterfly larval development via host plants, through changes in the initiation and length of the growing season. Shorter growing seasons caused by droughts narrow the window of successful development time for larvae (Weiss *et al.* 1987). Conversely, wet weather delays larval development in *Euphydryas editha* by limiting the time larvae are exposed to warming insolation (Dobkin *et al.* 1987). Also, if there are more cloudy days, adults may have less time for mating and oviposition (Cappuccino and Kareiva 1985). Few studies have addressed how changes in precipitation will affect butterfly survival (McLaughlin *et al.* 2002; Oberhauser and Peterson 2003). Most studies on precipitation and plant phenology have focused on snowpack depths and the initiation of the growing season. More research is needed to determine how precipitation influences the end of the growing season.

Large temporal shifts in the growing seasons of host plants could increase the extinction risk of many butterfly populations. Further research on the effects of precipitation on butterflies and their host plants is warranted because phenological shifts are expected to be a common response to climate change (Hughes 2000). Research is needed to address how regional changes in temperature and water availability caused by climate change will affect butterfly distributions and abundances. Particular needs include determining how changes in precipitation timing and quantity could threaten butterfly populations by reducing the overlap between larval and plant growing seasons. These effects are likely to be greatest on dry slopes, where soil moisture is determined by recent precipitation and time since snowmelt, and least near streams, where soil moisture persists at higher levels.

Changes in the timing and duration of plant and butterfly phenologies have potential to reduce the suitable habitat available for butterflies. Precipitation changes can affect the date of growing season onset, length of the growing season, and butterfly development times. These changes would leave fewer areas where the overlap between plant and butterfly phenologies is sufficient to support larval development. Research is needed to determine how climate change will alter habitat and distributions, possibly causing local and/or regional reductions in habitat.

There is a need for research on butterfly distributions and responses to climate change in the North Cascades National Park (NOCA). Aside from the Slate Peak area, butterfly occurrence and distributions in the majority of the park are unknown (Pyle 2002). Information on butterfly distributions and their responses to climate change will fill a gap in the biotic inventory recently conducted in the park and complement other NOCA research projects (NPS 2000). Additionally, the North Cascades is an ideal location to study climate change due to its complex topography, moderately high latitude, and abundance of butterfly species. Climate change is expected to be more complex in mountainous environments and greater in northern latitudes. More research is needed to understand how species will respond in these sentinel locations.

This study

In this study I investigated the effects of Julian date, soil moisture, and proximity to streams on the phenology of *Castilleja miniata*, a host plant of *Euphydryas anicia* larvae. My study had three main objectives,

1. to determine the relative importance of Julian date, soil moisture, and proximity to streams on *C. miniata* phenology
2. to use the best model or model set to predict *C. miniata* growing season length in moist areas near streams and dry areas far from streams
3. to assess effects of forecasted climate change on survival of pre-diapause *E. anicia* larvae.

I identified mechanisms whereby Julian date, soil moisture, proximity to streams, and combinations of these variables could determine *C. miniata* phenology. Then I translated those mechanisms into a set of linear and nonlinear models.

I used multi-model inference to determine the relative importance of Julian date, soil moisture, and proximity to streams. I used Akaike's Information Criterion to select the best model or model set from a set of candidate models which contained all possible combinations of the following variables: Julian date, soil moisture, and proximity to streams.

Methods

Study subjects

The checkerspot butterfly, *Euphydryas anicia*, has a wide range in western North America, occurring in varied habitats including sage steppe, deserts, high grasslands, canyons, edges of conifer forests, alpine meadows, and mountain summits (Pyle 2002). Adult *E. anicia* females lay eggs during late spring/early summer. During the summer, prediapause larvae feed mainly on inflorescences of plants of the family Scrophulariaceae, including species of *Castilleja* and *Penstemon*, until late summer when they diapause under rocks or leaf litter (Figure 1). Larvae remain in diapause through winter until they emerge the following spring and continue feeding and basking until they pupate and eclose as adults (Figure 1).

Castilleja miniata is a perennial hemiparasitic herb distributed throughout western North America. It occurs in the Pacific Northwest in low to high elevation meadows (Pojar and MacKinnon 1994). *C. miniata* is dormant through the winter and emerges after snowmelt in spring (Figure 1). It blooms during the summer and senesces in late summer/early fall (Figure 1).

Study sites

Study sites were located in the south unit of the North Cascades National Park (Figure 2). *E. anicia* were present at both sites. The complex topography of the area and high variability in soil moisture regimes create a variety of alpine plant community types (Douglas and Bliss 1977). At a climate sensor near these sites (Harts Pass SNOwpack TELemetry data (SNOTEL); Natural Resources Conservation Service, 2004) mean annual precipitation was 133.6 cm and mean annual snowfall was 117.9 cm over the years 1982-2005. All sites had SSW aspect. Study sites at Easy Pass were at elevations of 1850-2050m and had a 30-40° slope (Figure 3). Sites at Hidden Meadows were at an elevation of 1950m and had a 13° slope (Figure 4).

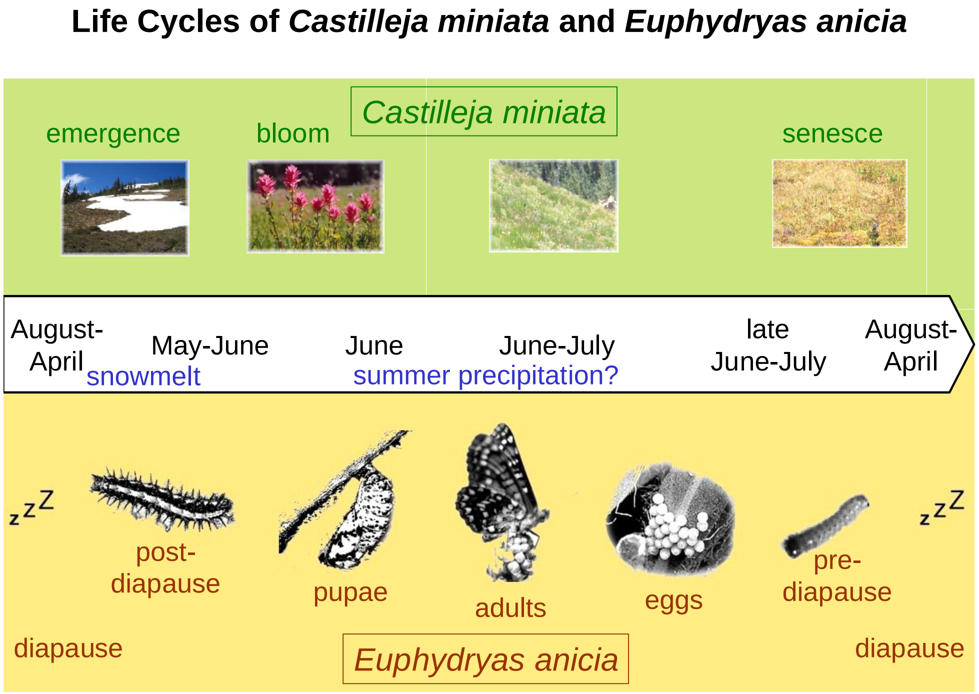

Figure 1. Observed life cycle of *E. anicia* and *C. miniata* relative to snowmelt at Easy Pass and Hidden Meadows, NOCA, 2004.

Table 1. Sample size and dates for set-up and sampling at study sites in the North Cascades National Park in 2004.

		Sampling Dates			
Study Site	**Set-up dates**	**1st**	**2nd**	**3rd**	**4th**
Easy Pass	7/20-7/21	7/29	8/3	8/10	8/27
Hidden Meadows	7/26	8/4	8/11	8/28	-

Field methods

I studied host plant phenology of *C. miniata* in relation to soil moisture. During the summer of 2004 at Easy Pass, I randomly selected 34 plants from moist soils and 35 from dry soils. At Hidden Meadows, I randomly selected 34 plants from moist soils and 36 from dry soils. Moist soils were located near a persistent stream. I only used plants that were non-senescent, had at least one inflorescence, and had no larvae or visible signs of larval feeding (frass). Because of my criteria for plant selection, it is possible that samples were biased towards plants that were not chosen as hosts by adult butterflies or moths. If adult butterflies or moths consistently selected plants of high quality as oviposition sites, plants available for my study may have been biased toward somewhat lower quality.

I classified inflorescence phenology independently and generally following Starr et al. (2000): 0= non-senescent, 1= < 50% senescent, 2= > 50% senescent, and 3= fully senescent. For plants growing in moist soils, I recorded the distance from each plant to the stream. Plants growing in dry soils were at least 50 m away from streams so individual distances were not recorded. Soil moisture was measured at the base of each plant weekly (study sites were inaccessible one week: 8/16-8/22, due to mudslides) from late July to late August using a ThetaProbe and HH2 Moisture Meter from Delta T Devices Ltd (Cambridge, England) (Table 1). Measurements were taken during the day between 1130 and 1600. Six soil samples were collected from moist and dry areas at each site (24 samples total) and analyzed to confirm organic soil types.

Map of Study Site Locations

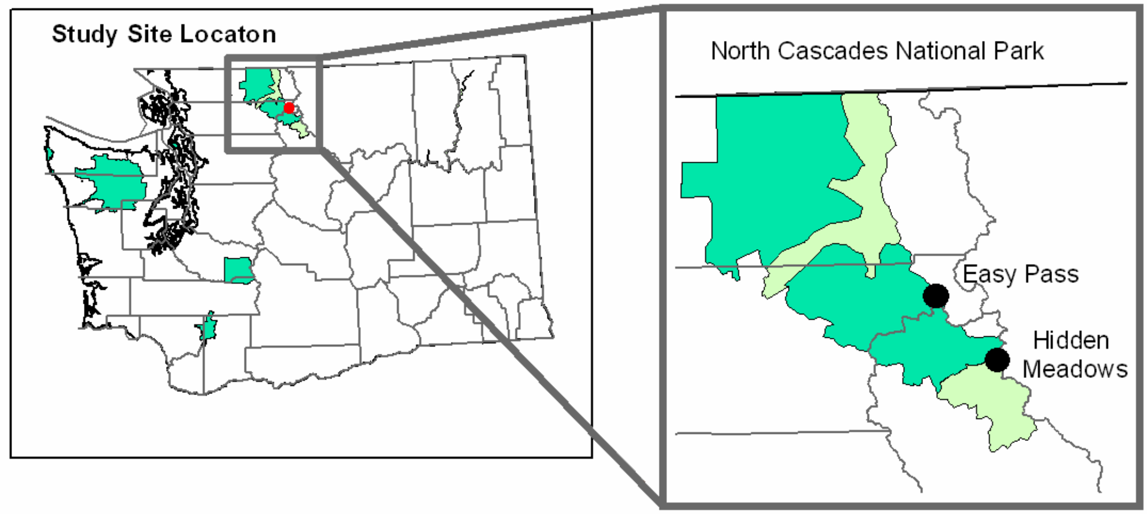

Figure 2. Study site locations in the North Cascades National Park

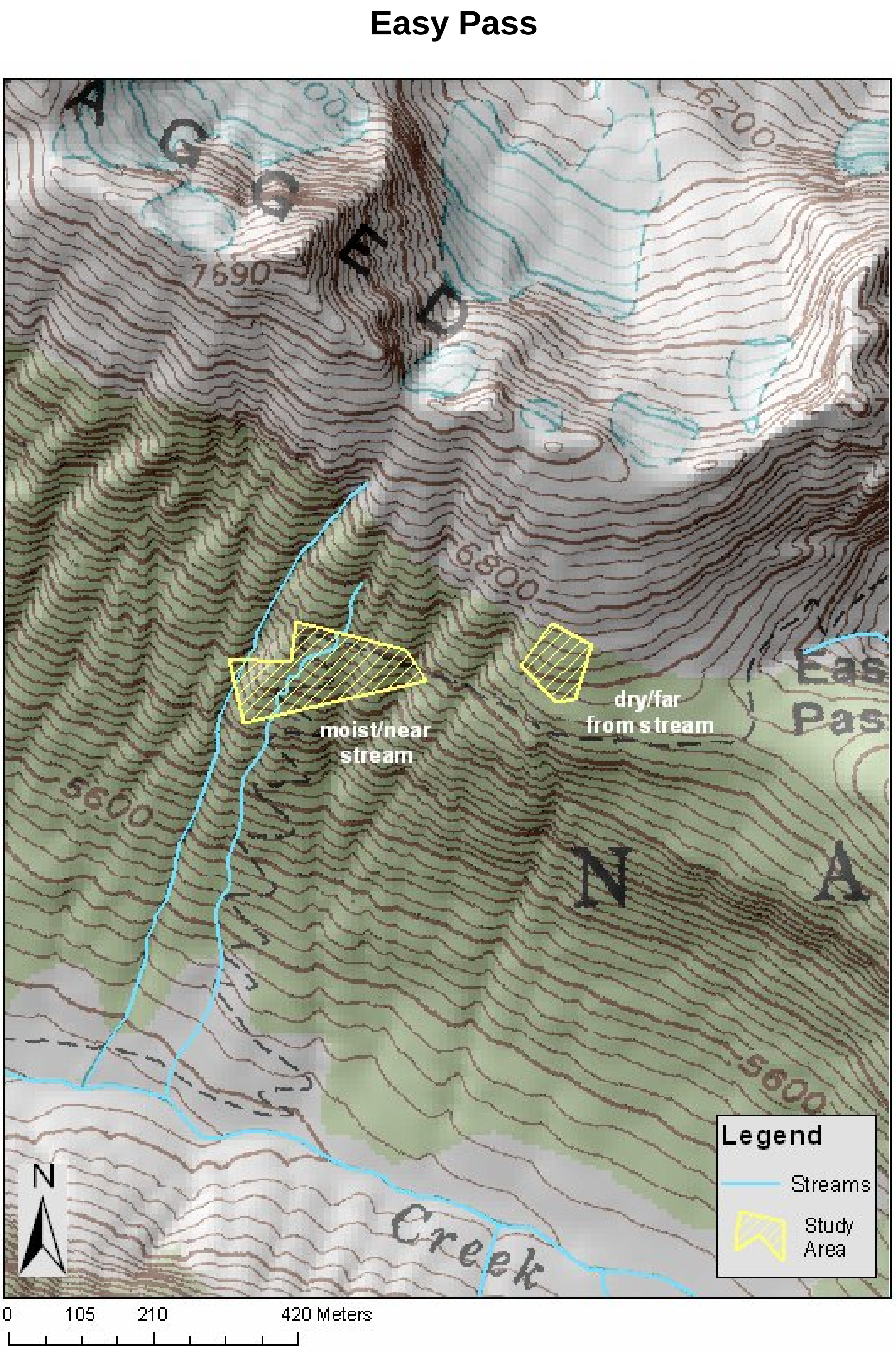

Figure 3. Easy Pass study site. Note two study areas: moist area near stream and dry area far from stream.

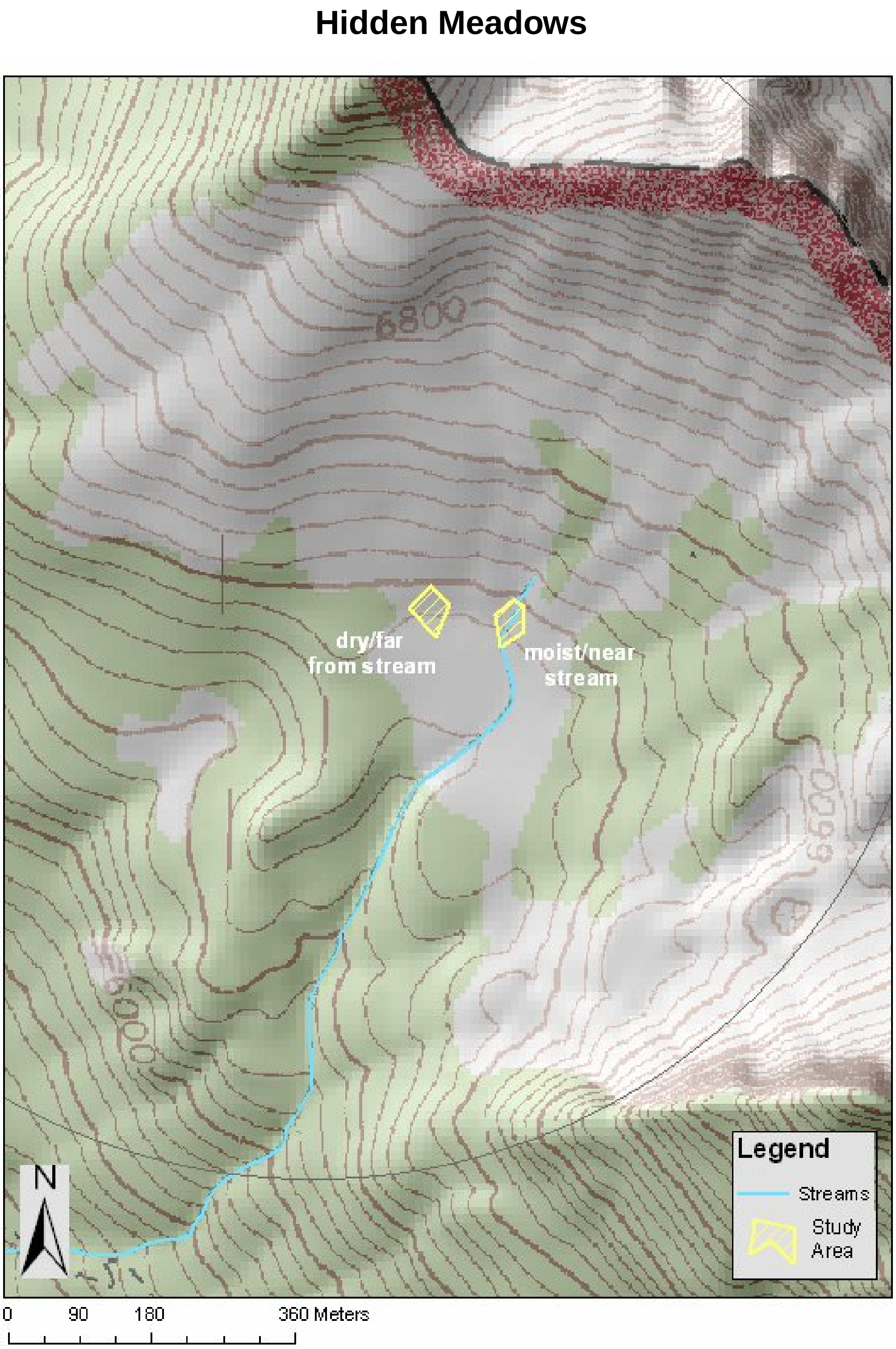

Figure 4. Hidden Meadows study site. Note two study areas: moist area near stream and dry area far from stream.

Model development

I developed and analyzed a series of models to determine the relative importance of various factors on plant phenological progression and to forecast development time available to pre-diapause larvae. The response variable in all models was plant phenological state, for which values of 0, 1, 2, and 3 were given respectively to plants in which no flowers were senescent, less than half of all flowers had senesced, more than half of all flowers had senesced, and all flowers had senesced. Predictor variables included one or more of the following three: (1) Julian date, (2) soil moisture content (0 to 100%), and (3) linear distance (meters) from the nearest streambank. Each model represented a plausible mechanism whereby predictor variables determine plant phenological state. Table 2 lists the seven sets of predictor variable considered and the mechanism represented by models containing each set.

Table 2. Variable combinations and mechanisms proposed as determinants of plant phenology. The following variable abbreviations are used: "date" = Julian date – 200, "moisture" = soil moisture content, "distance" = linear distance (m) from nearest streambank.

Hypothesis	Variables	Mechanism
1	date	Senescence is timed to decreasing day length, or time since emergence, photoperiod, or cumulative degree days, regardless of soil conditions.
2	moisture	Senescence is driven by decreasing soil water availability.
3	distance	Senescence is driven by drying soils and air, which are delayed near streams.
4	moisture, distance	Senescence is driven by water availability in soil and air, regardless of day length, emergence date, photoperiod, or cumulative degree days.
5	date, distance	Senescence due to decreasing day length, increasing time since emergence, photoperiod, or cumulative degree days is delayed by soil moisture and/or humid air near streams.
6	date, moisture	Senescence due to decreasing day length, increasing time since emergence, photoperiod, or cumulative degree days is delayed by moist soils.
7	date, moisture, distance	Senescence due to decreasing day length, increasing time since emergence, photoperiod, or cumulative degree days is delayed by both soil moisture and proximity to streams.

For each set of predictor variables listed in Table 2, I developed both linear and nonlinear models. Linear models describe relationships between plant phenology and the predictor variable(s) in the simplest possible form: a linear monotonic phenological progression with time, soil desiccation, and distance from water. Table 3 lists linear models for each of the seven variable combinations considered.

Table 3. Linear models for plant phenological status (*Y*) as determined by Julian date (*c*), soil moisture (*m*), and/or distance from the nearest streambank (*d*). In the models below, *a, β, γ,* and *δ* are fitted parameters and *ε* is residual variation.

Hypothesis	**Model**
(1) date	$Y_{ij} = \alpha + \beta c_i + \varepsilon_{ij}$
(2) moisture	$Y_{ij} = \alpha + \beta m_i + \varepsilon_{ij}$
(3) distance	$Y_{ij} = \alpha + \beta d_i + \varepsilon_{ij}$
(4) moisture, distance	$Y_{ijk} = \alpha + \beta m_i + \gamma d_j + \varepsilon_{ijk}$
(5) date, distance	$Y_{ijk} = \alpha + \beta c_i + \gamma d_j + \varepsilon_{ijk}$
(6) date, moisture	$Y_{ijk} = \alpha + \beta c_i + \gamma m_j + \varepsilon_{ijk}$
(7) date, moisture, distance	$Y_{ijkl} = \alpha + \beta c_i + \gamma m_j + \delta d_k + \varepsilon_{ijkl}$

In nonlinear models, I used sigmoid functional forms to represent phenological progression. Sigmoid functions may represent plant development more realistically than linear relationships, because sigmoid curves can depict entirely non-senescent plants early in the growing season or in moist soils, and a lingering tail of late-senescing plants. In multivariate nonlinear models 5, 6, and 7, I treated moisture and/or distance as modifiers of the sigmoid relationship between date and phenology, whereby moisture or distance advance or delay the senescence midpoint. Table 4 lists the nonlinear models I developed for each of the seven variable combinations considered.

Table 4. Nonlinear models for plant phenological status (*Y*) as determined by Julian date (*c*), soil moisture (*m*), and/or distance from the nearest streambank (*d*). In the models below, *a, β,* and *γ* are fitted parameters and *ε* is residual variation.

Hypothesis	**Model**
(1) date	$Y_{ij} = \frac{\alpha c_i^2}{\beta + c_i^2} + \varepsilon_{ij}$
(2) moisture	$Y_{ij} = \frac{\alpha m_i^2}{\beta + m_i^2} + \varepsilon_{ij}$
(3) distance	$Y_{ij} = \frac{\alpha d_i^2}{\beta + d_i^2} + \varepsilon_{ij}$
(4) moisture, distance	$Y_{ijk} = \frac{\alpha m_i^2}{\beta / d_j + m_i^2} + \varepsilon_{ijk}$
(5) date, distance	$Y_{ijk} = \frac{\alpha c_i^2}{\beta / d_j + c_i^2} + \varepsilon_{ijk}$
(6) date, moisture	$Y_{ijk} = \frac{\alpha c_i^2}{\beta / m_j + c_i^2} + \varepsilon_{ijk}$
(7) date, moisture, distance	$Y_{ijkl} = \frac{\alpha c_i^2}{\beta / d_j + \gamma / m_k + c_i^2} + \varepsilon_{ijkl}$

Model selection and analysis

I conducted model selection, analysis, and multi-model inference using information-theoretic methods (Burnham and Anderson 2002). These methods identify the optimal balance between model parsimony and accuracy of fit and facilitate simultaneous evaluation of multiple hypotheses. Information-theoretic methods address my research objectives better than statistical hypothesis testing for three reasons. First, unlike statistical hypothesis testing, information-theoretic methods allow direct comparisons of the relative importance of several mechanisms that may affect larval survival (Burnham and Anderson 2001). Second, information-theoretic methods also facilitate multi-model inference, which can be applied to predict plant senescence using models for all mechanisms considered in proportion to their relative importance. Third, information-theoretic methods provide a more comprehensive evaluation of uncertainty in model selection and inference, which is central to climate change research in general and to my work in particular.

My approach is summarized in the steps listed in Table 5, which are explained in the text below.

Table 5. Sequential steps I applied in model selection and multi-model inference.

1 For a given model, estimate parameter values and residual variation using data points (*n* = 132) selected at random from all plant data collected (*n* = 441).

2 Repeat step (1) a total of 6000 times, sampling with replacement from the original data set.

3 From results of (2) determine bootstrapped estimates of parameter values and residual error. Using estimated residual error, calculate log-likelihood for the given model.

4 Repeat (1-3) for all models.

5 Calculate the Akaike's Information Criterion (AIC_c) score and ΔAIC_c for each model.

6 Calculate the Akaike weight (*w*) for each model, which yields the probability that a given model is the best among all models considered, as determined by Kullbach-Leibler information theory.

7 Determine the confidence set for the best model.

8 Determine the relative importance of each predictor variable considered (date, moisture, distance), independent of any particular model.

9 Use model averaging to develop robust estimates for maximum time available for larval development (time to plant senescence). Develop these estimates for both dry and moist sites.

I performed all bootstrap sampling and model fitting using *R* statistical software (version 2.2.0, R Development Core Team, 2005), which is a dialect of the *S* programming language. Code for all *R* functions used in my analysis is listed in Appendix B of this thesis.

Step 1: Model fitting. For a given linear model and bootstrapped sample (*n*=132, the number of individual plants included in my study), I estimated parameters and residual error using the linear model function (`lm`) in *R*. I fit nonlinear models using the nonlinear least squares regression function (`nls`) in *R*. I determined the log-likelihood of linear and nonlinear models using the `logLik` function.

Step 2: Bootstrap sampling. I repeated model fitting with 6000 bootstrapped samples (n=132, drawn from 441 total measurements) for each model. I used bootstrap sampling to avoid violating the regression assumption of independence among data points (Efron and Tibshironi 1993), because the 132 plants in my study were measured up to four times each.

Step 3: Bootstrap estimates. I determined bootstrapped estimates of parameter values and model log-likelihood by calculating mean values for model fits to the 6000 samples performed for each model. I determined variance in log-likelihood for each model similarly.

Step 4: Bootstrap estimates for all models. To avoid bias in comparing models (Anderson and Burnham 2002), all models were fit to the same plant phenology data.

Step 5: AIC calculations. I used Akaike's Information Criterion (AIC) as an estimator of the Kullbach-Leibler distance for each model (Burnham and Anderson 2002). A small AIC value implies strong empirical evidence for a given model. Because bootstrapped sample size was small relative to number of parameters in some models ($n/K < 40$), I used the small sample bias adjustment, AIC_C.

$$\mathrm{AIC_c} = -2\log_e[L(\hat{\theta} \mid data)] + 2K + \frac{2K(K+1)}{n-K-1} \tag{1}$$

where:

$\hat{\theta}$ = estimated model parameters

$\log_e[L(\hat{\theta} \mid data)]$ = log-likelihood, maximized over all θ

K = number of parameters in model, including estimated residual error

To simplify interpretation, I rescaled AIC_C values to give the best model a score of zero:

$$\Delta_i = \mathrm{AIC}_{c_i} - \min \mathrm{AIC}_c . \qquad (2)$$

Step 6: Akaike weights. I calculated the Akaike weight (*w*) for each model, which gives the likelihood of a given model relative to all *T* models considered. This is equivalent to the probability that a given model is the best among all models considered, as determined by Kullbach-Leibler information theory (Anderson *et al.* 2000).

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{t=1}^{T}\exp\left(-\frac{1}{2}\Delta_t\right)} \qquad (3)$$

Step 7: Confidence set for the best model. Three methods have been suggested for determining the set of models to include in the confidence set for the best model according to Kullbach-Leibler information theory (Burnham and Anderson 2002). I used the method of likelihood-based inference, which enjoys the strongest support by statistical theory (Burnham and Anderson 2002). In this method, the likelihood of a given model (g_i) is compared to the likelihood of the Kullbach-Leibler best model (g_{min}). If the ratio of these two likelihoods exceeds a threshold (*C*), then the given model is included in the confidence set.

$$\frac{L(g_i \mid x)}{L(g_{\min} \mid x)} > C \qquad (4)$$

where *x* are the data.

There is no standard value for the threshold (*C*). I used $C = 1/10$ as a threshold evidence ratio.

Step 8: Determine relative importance of date, moisture, and distance. I used multi-model inference to compare the importance of each variable in driving changes in plant phenology. To determine relative importance of a variable, I summed Akaike weights (w_i) of each model containing that variable. Because each variable was included in exactly four linear and four nonlinear models, this multi-model comparison is free of bias due to differential opportunity among variables included. The resulting predictor weight, or sum of weights for each variable, is a number between zero and one. Predictor weights can be used to sort variables in order of relative importance and to make quantitative comparisons of their relative importance (Burnham and Anderson 2001).

Step 9: Estimate available development time using model averaging. I used multi-model inference in the form of model-averaging to predict plant senescence and time available for larval development. Predictions generated by each model are weighted by strength of evidence for that model using Akaike weights:

$$\hat{\bar{\theta}} = \sum_{i=1}^{T} w_i \hat{\theta}_i \tag{5}$$

where:

$\hat{\theta}$ = predicted senescence date, θ
$\hat{\bar{\theta}}$ = model averaged estimate of θ
w_i = Akaike weight of model i
T = number of models considered

Model-averaged predictions often are less biased and more precise than predictions made from the best individual model (Burnham and Anderson 2002).

I calculated the uncertainty in the model-averaged senescence prediction using the standard deviation (SD) of predicted onset of senescence ($\hat{y}$=2.75). Plant phenological state of y=2.75 is used as onset of senescence because some models did not reach a value of y=3.0. I calculated the minimum and maximum predicted date of senescence at moist areas near streams (moisture = 90%, distance = 0.5m) and dry areas far from streams (moisture = 10%, distance = 50):

$$x_{\min} = \frac{\hat{y} - (\alpha + S_\alpha) - (\gamma - S_\gamma)m - (\delta + S_\delta)d}{\beta + S_\beta} \tag{6}$$

$$x_{\max} = \frac{\hat{y} - (\alpha - S_\alpha) - (\gamma + S_\gamma)m - (\delta - S_\delta)d}{\beta - S_\beta} \tag{7}$$

where:

$\hat{y} =$ phenology at onset of senescence (2.75)
$\alpha =$ y-intercept
$S_\alpha =$ SD of the intercept
$\gamma =$ coefficient of moisture
$S_\gamma =$ SD of the coefficient of soil moisture
$m =$ soil moisture in dry or moist areas
$\delta =$ coefficient of distance
$S_\delta =$ SD of the coefficient of distance
$d =$ distance from stream for near and moist or far and dry areas
$\beta =$ coefficient of date
$S_\beta =$ SD of the coefficient of date

Results

Soil moisture, distance, and date

Soil moisture gradually decreased as distance from stream increased, but some areas far from streams had moderately moist soils (Figures 5, 6). Soil moisture near streams was always highly variable (Figures 5, 7, 8), while those far from streams usually had low variance, particularly on the steeper slopes at Easy Pass (Figures 7, 8). Soil moisture for the last sampling dates (Julian dates 240 and 241) was higher most notably in the far sites (Figures 7, 8). Four nearby SNOTEL data stations measured a range of 0.3-1.0 inches of precipitation on 8/24 and a range of 0.1-1.7 inches of precipitation on 8/25, just prior to 8/28, the last sampling date (Swamp Creek, Harts Pass, Rainy Pass, and Park Creek Ridge SNOTEL data; Natural Resources Conservation Service, 2004).

Easy Pass vs. Hidden Meadows

Soils at far distances from streams were always drier at Easy Pass than at Hidden Meadows (Figures 7, 8). Soil moisture near streams at Easy Pass was more variable than at Hidden Meadows, but soil moisture far from streams was more variable at Hidden Meadows than at Easy Pass (Figures 7, 8). Throughout the study, the proportion of plants in each phenological stage was similar between sites (Figure 9).

Modeling

Based on the mean Δ_i values for AIC_C and the Akaike weights (w_i), two models stand out as the best of the candidate set, model 7: the linear global model (Δ_i=0.00, w_i=0.577), and model 6: a linear model including date and moisture (Δ_i=0.71, w_i=0.405) (Table 6).

Model 7 is only 1.43 times more likely than model 6 (evidence ratio = w_7/w_6 = 0.577/0.405) to be the best given the data and candidate model set, but it is 41.15 times more likely to be the best compared to third-ranked model 8 (evidence ratio = 0.577/0.014). The evidence ratios imply that while models 6 and 7 clearly are superior to the other models considered, there is uncertainty about which of models 6 or 7 is best. The ranking of models 6 and 7 might change given another replicate dataset.

The remaining models are unlikely to be the best model as indicated by their Δ_i values ($\Delta_i > 7$); however, the Δ_i values of the top 5 ranked models are all within one standard deviation of the Δ_i value for the highest-ranked model 7 (Table 6). The high variances in Δ_i values suggest that each of the models 1, 5, 6, 7, and 8 could potentially be the best model if other replicate datasets were available. Additionally, based on the adjusted R^2 values (range: 0.434 - 0.460), the highest-ranked linear models 1, 5, 6, and 7 fit the data similarly well and substantially better than the remaining linear models (Table 6).

The confidence set for the best model (Δ_i <1) consists of models 6 and 7, although the large variation in the Δ_i values of these models indicates some uncertainty about the confidence set. The coefficient values for models 6 and 7 are:

(6) date, moisture $Y_{ijk} = -0.432 + 0.067c_i + 0.012m_j + \varepsilon_{ijk}$

(7) date, moisture, distance $Y_{ijkl} = 0.162 + 0.062c_i + 0.005m_j + 4.053\text{E-}6d_k + \varepsilon_{ijkl}$

where c = date, m = dryness, and d = distance from stream.

Date is the most important variable, followed closely by soil moisture, and then distance from a stream (Table 7, Figure 10). Due to the high variation in Δ_i values it is likely that there is also high variation in the relative importance of the variables, although it is unlikely that the ranking of the variables' relative importance would change. Models including date always rank better than models without, and the univariate date models are ranked third and fourth whereas the univariate moisture and distance models are the lowest ranked models (Table 6). Similarly, all models with high adjusted-R^2 values include date as a variable but only some include soil moisture or distance.

The model-averaged prediction of the number of days to senescence for moist soils near streams is 9.54 days longer than for dry soils far from streams (Table 8, Figure 11). Senescence is defined as phenology = 2.75; the maximum level of senescence attained by some models. Each week plants advance 0.443 phenology units, and with every 10% decrease in soil moisture, plants advance 0.078 phenology units (calculated from the weighted parameter estimates of models 6 and 7).

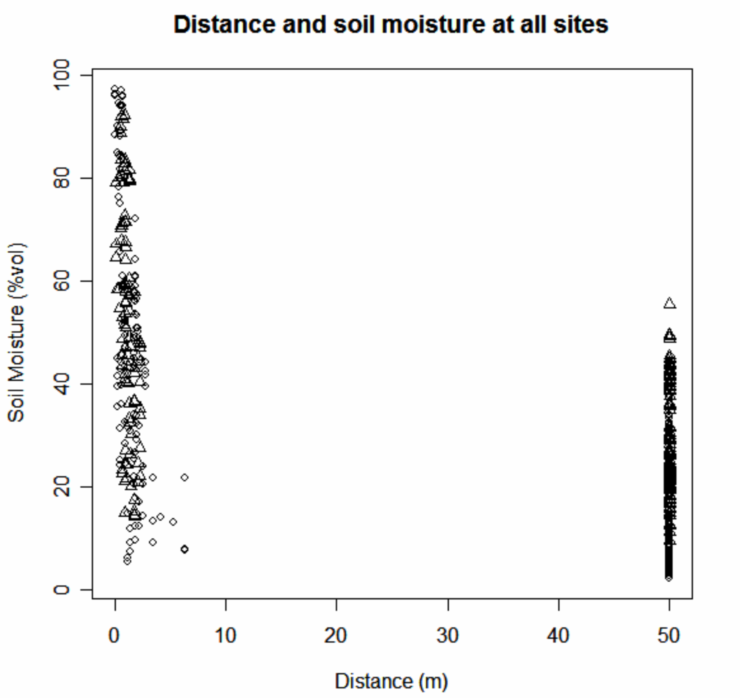

Figure 5. Distance and soil moisture at Easy Pass and Hidden Meadows during July and August 2004. Circles are Easy Pass data and triangles are Hidden Meadows data.

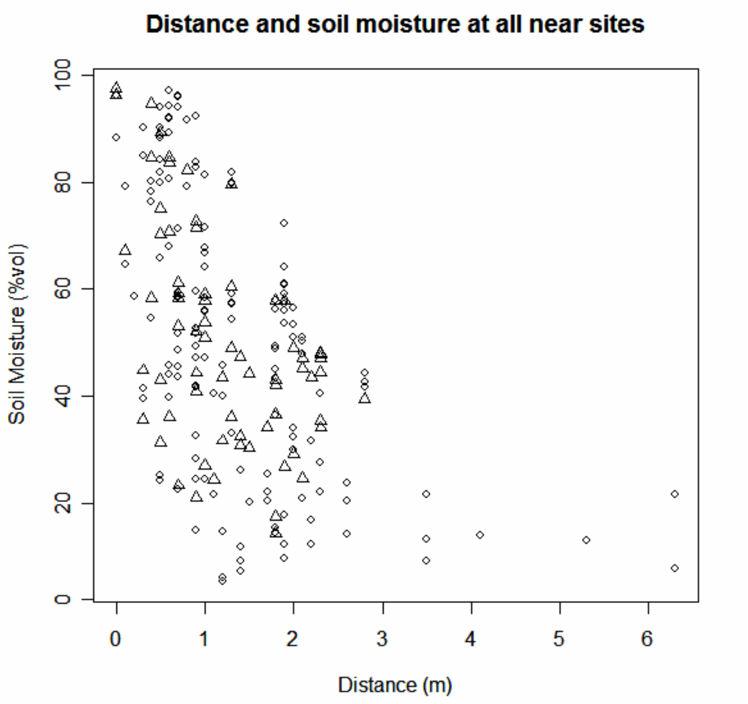

Figure 6. Distance and soil moisture at Easy Pass and Hidden Meadows during July and August 2004, only near streams. Circles are Easy Pass data and triangles are Hidden Meadows data.

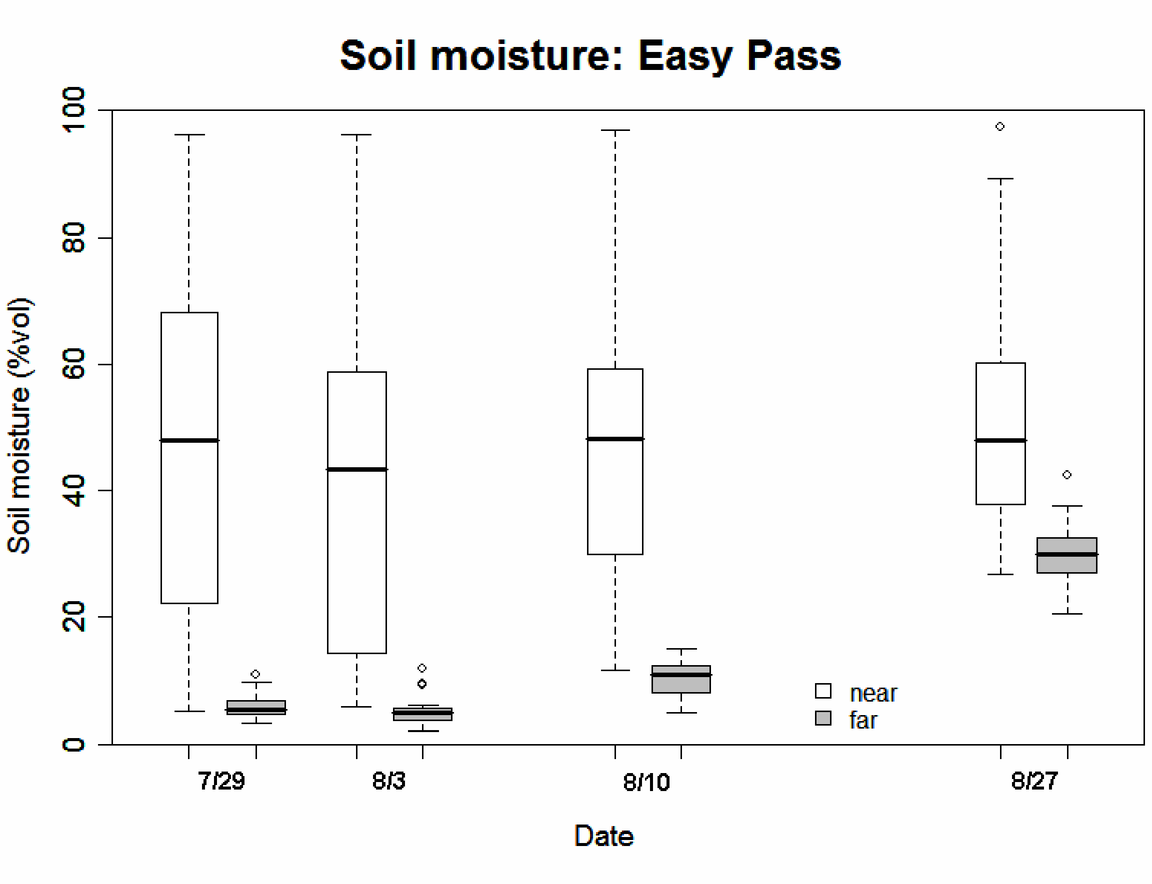

Figure 7. Soil moisture at Easy Pass, areas near and far from streams during 2004.

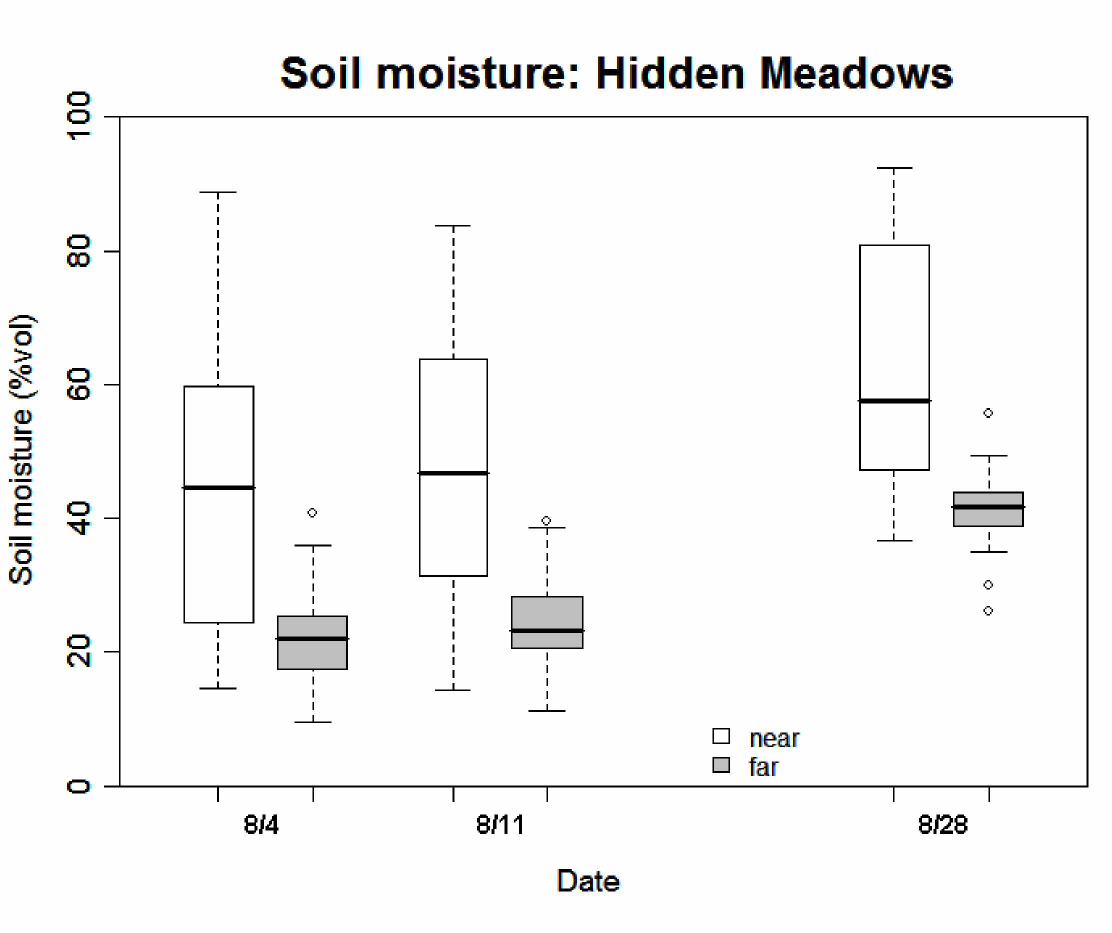

Figure 8. Soil moisture at Hidden Meadows, areas near and far from streams during 2004.

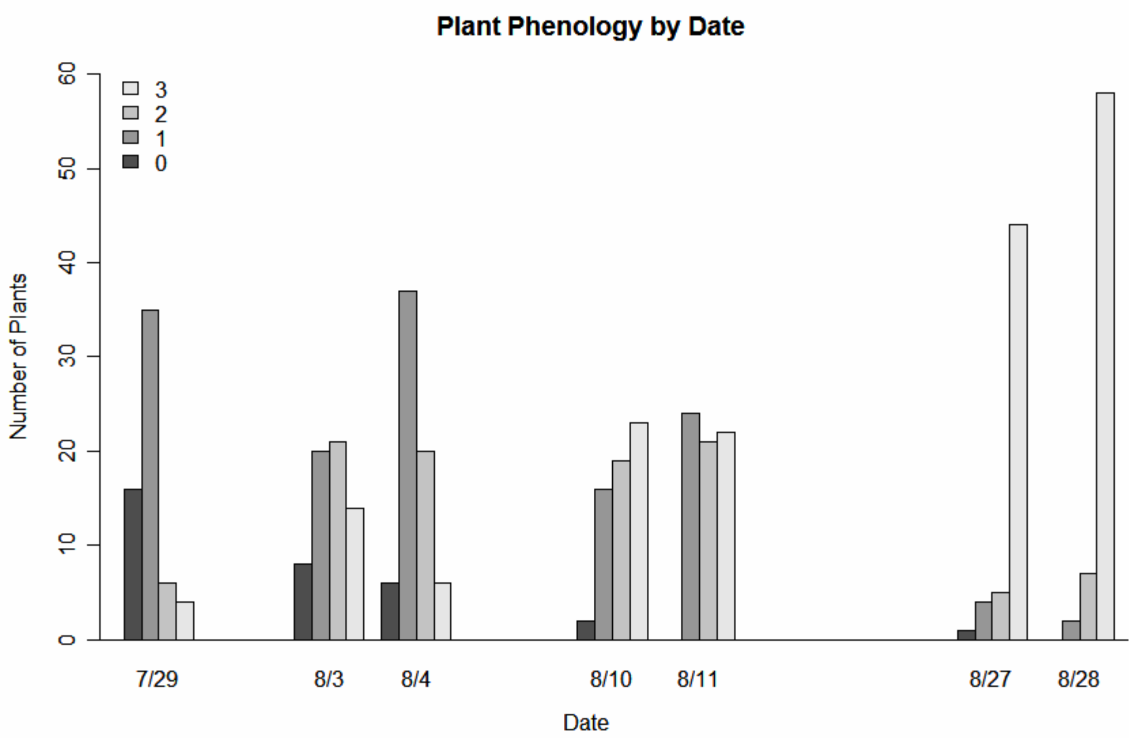

Figure 9. Proportion of *C. miniata* in each phenological stage by sampling date. Bar shade indicates phenological stage. Sampling dates 7/29, 8/3, 8/10, and 8/27 were at Easy Pass, and sampling dates 8/4, 8/11, and 8/28 were at Hidden Meadows.

Table 6. Summary of candidate models for predicting phenology of *C. miniata*, including the maximized log-likelihood (log(L)), the number of parameters (K_i), Akaike's Information Criterion for small samples (AIC_C), the simple difference values (Δ_i) for AIC_C, and the Akaike weights (w_i). Mean values are from 6000 bootstrap samples of 132 data points selected from total data set of n=441.

	Model	**log(L)***	$\mathbf{K_i}$	$\mathbf{AIC}_C$*	Δ_i*	w_i	**Rank**	**Adj. R^2**
ID	**Linear models**							
1	date	-150.21 ± 8.55	3	306.60 ± 17.10	10.41 ± 17.10	0.003	4	0.441
2	moisture	-194.12 ± 4.86	3	394.43 ± 9.72	98.24 ± 9.72	0.000	14	0.001
3	distance	-184.22 ± 5.39	3	374.62 ± 10.78	78.43 ± 10.78	0.000	11	0.056
4	moisture, distance	-180.39 ± 5.31	4	369.09 ± 10.62	72.90 ± 10.62	0.000	10	0.009
5	date, distance	-151.04 ± 8.25	4	310.40 ± 16.50	14.21 ± 16.50	0.000	5	0.434
6	date, moisture	-144.29 ± 8.24	4	296.90 ± 16.49	0.71 ± 16.49	0.405	2	0.460
7	date, moisture, distance	-142.86 ± 8.25	5	296.19 ± 16.50	0.00 ± 16.50	0.577	1	0.442
	Sigmoid models							
8	date	-148.72 ± 8.41	3	303.63 ± 16.82	7.43 ± 16.82	0.014	3	-
9	moisture	-184.25 ± 6.69	3	374.69 ± 13.38	78.50 ± 13.38	0.000	12	-
10	distance	-187.56 ± 8.26	3	381.30 ± 16.51	85.11 ± 16.51	0.000	13	-
11	moisture, distance	-180.90 ± 8.48	3	367.98 ± 16.96	71.79 ± 16.96	0.000	9	-
12	date, distance	-174.83 ± 8.17	3	355.84 ± 16.33	59.65 ± 16.33	0.000	8	-
13	date, moisture	-157.39 ± 7.53	3	320.97 ± 15.07	24.77 ± 15.07	0.000	6	-
14	date, moisture, distance	-158.48 ± 10.70	4	325.28 ± 21.40	29.08 ± 21.40	0.000	7	-

* Values are mean ± standard deviation.

Table 7. Relative importance of the variables Julian date, soil moisture, and distance from streams in predicting *C. miniata* plant phenology. Relative importance is the sum of the Akaike weights of the models containing the specified variable.

	Relative importance of variables		
Model ID	w_i **date**	w_i **moisture**	w_i **distance**
1	0.003	-	-
2	-	0.000	-
3	-	-	0.000
4	-	0.000	0.000
5	0.000	-	0.000
6	0.405	0.405	-
7	0.577	0.577	0.577
8	0.014	-	-
9	-	0.000	-
10	-	-	0.000
11	-	0.000	0.000
12	0.000	-	0.000
13	0.000	0.000	-
14	0.000	0.000	0.000
Sum	1.000	0.982	0.578

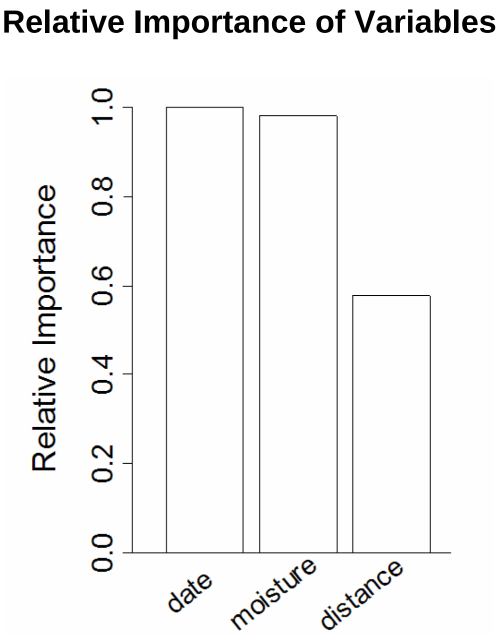

Figure 10. Relative importance of variables Julian date, soil moisture, and distance from streams in predicting *C. miniata* plant phenology.

Table 8. Model averaged prediction of number of days (θ) to senescence (phenology = 2.75) for *C. miniata* in moist soils near streams and dry soils far from streams. The model averaged predictions are the sum of the products of predicted days * Akaike weights for each model.

	θ (d)			**θ * w_i (d)**	
Model ID*	**near/moist**	**far/dry**	w_i	**0.5 m, 90% moist**	**50 m, 10% moist**
1	37.01	37.01	0.003	0.118	0.118
5	40.24	35.57	0.000	0.019	0.017
6	45.51	31.47	0.405	18.429	12.744
7	40.69	34.02	0.577	23.492	19.640
8	39.80	39.80	0.014	0.558	0.558
13	105.41	35.14	0.000	0.000	0.000
14	104.71	33.66	0.000	0.000	0.000
model averaged**				42.617 ± 8.028	33.077 ± 1.154

*only models that included the date variable were used in the model averaged prediction; model 12 never attains senescence and therefore is not included in the model averaged prediction.

**model averaged predictions ± uncertainty in the date of senescence, derived from the standard deviation of predicted onset of senescence (Y=2.75).

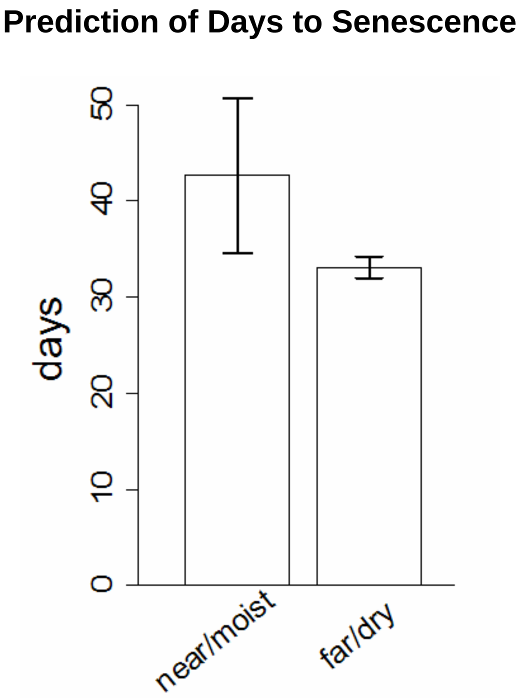

Figure 11. Model averaged prediction of number of days to senescence for *C. miniata* in moist soils near streams and dry soils far from streams. Error bars represent 1 standard deviation.

Discussion

Best predictors of phenology

This study shows that Julian date and soil moisture are the best predictors of *C. miniata* phenology. Distance from stream was the least important variable and its effect in the global linear model is minimal (slope value = 4.053E-6). Soil moisture had a stronger influence on plant phenology than proximity to stream, which indicates that summer precipitation played an important role in regulating phenology at these study sites, particularly the dry areas. Also, stream proximity did not always correlate well with soil moisture. The study site at Hidden Meadows was at the base of a hillside and had a 20-30°-shallower slope than Easy Pass study sites that were nearer to the top of the slope. Similarly, plant water stress was found to be less at the base of slopes than upslope (Douglas and Bliss 1977).

The growing season of *C. miniata* was constrained by both soil moisture and date. Low soil moisture advanced the date of senescence of plants in dry areas. This is consistent with studies that show the strong influence of summer precipitation in maintaining adequate soil moisture after snowmelt (Billings and Bliss 1959; Jackson and Bliss 1984). The importance of date suggests that in moist areas *C. miniata* phenology is constrained by circannual factors; at some point late in the growing season, day length will cue plant senescence. Other montane herbaceous plants also use day length as a phenological cue (Starr *et al.* 2000; Keller and Körner 2003).

Difference between dry and moist areas

Based on the model-averaged prediction, *C. miniata* inflorescences in moist soils senesced ~10 days later than those in dry soils. This agrees with studies that have found that increasing soil moisture leads to week- to month-long delays in flowering phenology (Holway and Ward 1963) and that experimental warming and associated low soil moisture induce early plant senescence (Zavaleta *et al.* 2003).

Adverse effects have been observed in diverse annual and perennial species, which have suffered leaf death, seedling mortality, and early senescence. The primary cause of *Ranunculus adoneus* seedling mortality was late season drought (Galen and Stanton 1991). Dry soils resulting from early snowmelt and minimal summer precipitation caused the death of 25% of *Penstemon heterodoxus* study plants (Jackson and Bliss 1984). Dry soils hasten senescence or dormancy in many plants (Newman 1965, 1967; Fischer and Kohn 1966; Lavender *et al.* 1968; Stinson 2004). Johnson and Billings recorded later dormancy in alpine plants during a wet year (1962). Herbs and a grass under high water stress (7% soil moisture) began senescing about 20 days earlier than plants with adequate moisture (Mott and McComb 1975). Soil moisture decreased to low levels at my study areas, as low as 2.1% at Easy Pass. As reported for other regions and species, dry soils at my sites caused early plant senescence. This hastened senescence by an average of 10 days; this was smaller than that observed elsewhere (e.g. Mott and McComb 1975), but unusual late season rains in 2004 likely extended the growing season in my study sties. Summer precipitation also has been shown to maintain plant growth at other Pacific Northwest sites after snowmelt ceases to moisten soils.

Results in context of forecasted climate changes

Earlier senescence of *C. miniata* plants in dry areas suggests that further reductions in growing season in those areas due to forecasted climate change could preclude butterfly survival. The forecasted 50-60% reduction in snowpack (Leung and Ghan 1999; Leung and Wigmosta 1999) would advance the initiation of the growing season for *C. miniata*. Unfortunately, the forecasted increase in temperature would not be enough to cause the same advancement in larval butterflies. Although warmer temperatures would speed larval development somewhat, thereby providing some compensation for reduced phenological overlap, this compensation likely would be limited because the magnitude of warming would be small relative to cooling caused by a several week advance in phenology. In addition, larval development would be slowed further by greater cloud cover prevalent earlier in summer, which would reduce opportunities for larvae to bask in direct insolation. It is possible that plant development might proceed slowly due to the cool temperatures of an early growing season, but the warmer temperatures later in the growing season combined with drier soils would result in early senescence and an overall shortened growing season.

Net shift in phenology for dry and moist areas

Greening in North American plants has advanced 7-8 days over the past 60 years (Bradley *et al.* 1999; Beaubien and Freeland 2000). In the next 50 years, snowpacks in the Pacific Northwest are expected to become 50-60% shallower (Leung and Ghan 1999; Leung and Wigmosta 1999) resulting in a minimum ten-day advance in the snow-free date (from Ostler *et al.* 1982; 30% reduction in snowpack = five-day advance in snowfree date). This is a net shift of 17-18 days in the onset of phenology and does not address compounding effects of more rapid snowmelt due to increased temperatures. Increased temperatures are also likely to cause earlier soil drying during the growing season (Peterson and Peterson 2001; Mote *et al.* 2003), thereby advancing the date of senescence in plants (Mott and McComb 1975). Development times for *E. anicia* have not been measured, but the development times of other *Euphydryas* species are well documented (Table 9).

Table 9. Development time of *Euphydryas* species.

	Development time (days)*		
Stage	***E. editha***	***E. chalcedona***	***E. phaeton***
Egg	13.3	-	21
Prediapause larva	21	24.4	20.7
Both (egg to diapause)	34.3	-	41.7

* from Labine 1968; Singer 1972; Singer and Ehrlich 1979; Stamp 1981; Williams *et al.* 1983; Stamp 1984; Dobkin *et al.* 1987; Weiss *et al.* 1988; Bowers *et al.* 1992; Fleishman *et al.* 1999; Hellman 2002. *E. editha* and *E. chalcedona* populations were located in central California, *E. phaeton* populations were from New York and Virginia.

The expected net shift in phenology from forecasted climate change represents a substantial portion of the development time of butterfly larvae from egg to diapause, although the development times do not include the time required for postdiapause larval growth, the pupal stage, and the adult stage. The growing season is brief; any additional shifting and condensing has the potential to reduce time available for larvae to develop.

The effects of earlier plant phenology on post-diapause larval development might depend on soil moisture. Plant growth in the moist areas at Easy Pass began earlier and ended later in the growing season than in dry areas. These areas could provide habitat for *E. anicia* larvae that would not be available in dry areas early and late in the season.

Contemporary and forecasted climate change will likely cause a considerable reduction in suitable habitat for *E. anicia*. The time interval available for larval development on south slopes will become earlier and shorter due to earlier growing season initiation coupled with earlier onset of senescence due to low soil moisture. Growth rates of postdiapause larvae will slow due to a shift in the start of the growing season to weather with greater cloud cover and lower temperatures. Prediapause larvae will face greater risk of starvation due to hastened plant senescence, which will be driven by dry soils caused by low snowpacks and increased temperatures. Plants growing in dry areas in my study senesced 9.5 days earlier than plants in moist areas. While plants growing in moist areas (near streams, at slope bases) will likely support successful larval development, plants in dry areas will not remain edible long enough for larvae to reach diapause. This represents a major reduction in suitable habitat on south-facing slopes for *E. anicia* populations in the North Cascades due to climate change.

Uncertainties

Climate change forecasts generated by GCMs and RCMs contain greater uncertainty in precipitation than temperature (Kusnierczyk and Ettl 2002; Leung *et al.* 2003; Coquard *et al.* 2004). Changes in precipitation are more difficult to forecast than changes in temperature, particularly in topographically complex areas like the North Cascades. Forecasting plant responses compounds uncertainty in climate forecasts because plant phenologies are more sensitive to changes in moisture than temperature (Kusnierczyk and Ettl 2002). Uncertainty in forecasting biotic responses to climate change is exacerbated by the anticipated increase in precipitation variability (Easterling *et al.* 2000), which has been shown to hasten butterfly population extinctions (McLaughlin *et al.* 2002).

Results of multi-model inference are constrained by the model set considered (Anderson and Burnham 2002); the importance of excluded variables cannot be determined.

Temperature may be a better predictor of plant senescence than Julian date or soil moisture (Zavaleta *et al.* 2003; but see Kusnierczyk and Ettl 2002; Totland and Alatalo 2002), but my analysis cannot be used to assess the relative importance of temperature because it was not included in any model. In my study system, Julian date and soil moisture seem to be the primary determinants of phenology, particularly senescence. Other studies indicate that temperature has a greater influence on plant phenology than Julian date or precipitation (Fareed and Caldwell 1975; Thórhallsdóttir 1998), but they focused on the phenology of flowering and reproduction rather than senescence. Nevertheless, increased temperatures are likely to exacerbate forecasted reductions in soil moisture because experimental warming has led to drier soils (Chapin *et al.* 1995; Harte *et al.* 1995).

If the Pacific Northwest climate changes as forecasted, early *C. miniata* senescence in response to dry soils will adversely affect *E. anicia* butterfly larvae. Other plants in the system might react differently to low snowpack and warmer temperatures, particularly plants that are more drought tolerant than *C. miniata*. Jackson and Bliss (1984) studied different montane plant life forms and found differential responses to drought: some senesced early and others did not senesce until late in the growing season. Perhaps other plants with higher drought tolerance in these study meadows can serve as persistent green hosts, although field surveys did not identify any known alternative hosts of *E. anicia* (Pyle 2002) at the study sites.

My study focused on butterfly habitat on south-facing slopes. While most north-facing slopes do not currently support habitat for *E. anicia*, it is possible that climate change could make these areas more suitable. North-facing slopes in the North Cascades have less sun exposure and snowpacks that persist longer into the growing season than south-facing slopes. Because of these environmental differences, the vegetation communities differ by slope exposure (Douglas and Bliss 1977). If north-facing slopes do become more suitable for *C. miniata* and *E. anicia* with changes in climate, it is uncertain how soon these populations can become established.

My data were highly variable leading to adjusted R^2 values for linear models ranging from 0.001 to 0.460 (also see Fig 11). Heterogeneity in individual plant responses was combined with rounding error associated with the scale I used to measure phenological status. Although heterogeneous rounding errors reduce accuracy in determining the rate of senescence, my primary objectives were to determine the date that plants senesced and became inedible to butterfly larvae, as well as the difference in that date for plants growing in moist vs. dry soils. Most plants that had at least some brown flowers were given a score of 1 or 2 (1 = 1-49% flowers brown; 2 = 50-99% flowers brown). Only plants that had no flowers senescent or all flowers senescent were scored 0 or 3. It was easy to determine that none or all flowers were brown, but the rounding error with plants at intermediate levels of flower senescence was much greater.

Future research would benefit from modifications to this study. I measured soil moisture weekly and missed one week late in the growing season. Measuring soil moisture more often, particularly near the end of the growing season would give better resolution to the relationship between senescence and soil moisture. Plant phenology should also be measured more precisely and monitored over multiple growing seasons; this study included data from only one season. Future studies should include more climatic variables, such as ambient air and soil temperature because these variables influence plant phenology in other systems (Holway and Ward 1965; Fareed and Caldwell 1975; Thorhalsdottir 1998; Sandvik and Totland 2000; Dunne *et al.* 2003; Zavaleta *et al.* 2003). A logical next experiment would be to determine the survival of butterfly larvae on plants growing in moist and dry areas. This would address how a shorter growing season affects larval survival. In addition, an experiment to determine postdiapause larvae development rates during early and late growing season conditions would be helpful. Also, studying effects of forecasted climate change on north-facing slopes would help determine the potential of those areas to become suitable habitat. Other plant species that are hosts for insect larvae in subalpine meadow habitats should be studied to better understand the effects of climate change on these plant-insect communities.

Statistical violations

In this study I used linear and nonlinear regression to determine the fit of each model. My data violate the assumptions of normality and homogeneity of variances, and two variables are significantly correlated. While linear and nonlinear regression are generally robust to violations of the normality assumption, heteroscedasticity can increase the chances of over-estimating actual effects. Soil moisture and distance from stream are correlated (Kendall's tau= 0.527, $p < 2.2E\text{-}16$), but I included both variables to determine if phenology was influenced by environmental factors associated with stream proximity such as nutrient availability, air temperature, and relative humidity (Hogg 1993; Ledwith 1996; Cirmo and McDonnell 1997; Liu *et al.* 2004). The inclusion of both variables has likely inflated variances, standard errors and parameter estimates because soil moisture and stream proximity are redundant, however, since the variables are not highly correlated (Kendall's tau < 0.7) this is not likely to be problematic. In addition there is heterogeneous rounding error in my dependent variable. Linear regression was used with similar data (phenology scored by stage of flowering/fruiting) in other studies published recently in peer-reviewed journals (Price and Waser 1998; Dunne *et al.* 2003); these studies do not address the rounding error.

References

Anderson, DR, Burnham KP, Thompson WL. 2000. Null hypothesis testing: Problems, prevalence, and an alternative. *J. Wildl. Manage.* 64: 912-923.

Anderson DR, Burnham KP. 2002. Avoiding pitfalls when using information-theoretic methods. *J. Wildl. Manage.* 66: 912-918.

Araujo MB, Whittaker RJ, Ladle RJ, Erhard M. 2005. Reducing uncertainty in projections of extinction risk from climate change. *Global Ecol. Biogeogr.* 14: 529-538.

Arft AM, Walker MD, Gurevitch J, Alatalo JM, Bret-Harte MS, Dale M, Diemer M, Gugerli F, Henry GHR, Jones MH, Hollister RD, Jónsdóttir IS, Laine K, Lévesque E, Marion GM, Molau U, Mølgaard P, Nordenhäll U, Raszhivin V, Robinson CH, Starr G, Stenström A, Stenström M, Totland Ø, Turner PL, Walker LJ, Webber PJ, Welker JM, Wookey PA. 1999. Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecol. Monogr.* 69: 491-511.

Ayres MP, Scriber JM. 1994. Local adaptation to regional climates in *Papilio Canadensis* (Lepidoptera: Papilionidae). *Ecol. Monogr.* 64: 465-482.

Beaubien EG, Freeland HJ. 2000. Spring phenology trends in Alberta, Canada: links to ocean temperature. *Int. J. Biometeorol.* 44: 53-59.

Berteaux D, Réale D, McAdam AG, Boutin S. 2004. Keeping pace with fast climate change: Can arctic life count on evolution? *Integr. Comp. Biol.* 44: 140-151.

Billings WD, Bliss LC. 1959. An alpine snowbank environment and its effects on vegetation, plant development, and productivity. *Ecology* 40: 388-397.

Boggs CL, Murphy DD. 1997. Community composition in mountain ecosystems: climatic determinants of montane butterfly distributions. *Global Ecol. Biogeogr. Lett.* 6: 39-48.

Bowers MD, Stamp NE, Collinge SK. 1992. Early stage of host range expansion by a specialist herbivore, *Euphydryas phaeton* (Nymphalidae). *Ecology* 73: 526-536.

Bradley NL, Leopold AC, Ross J, Huffaker W. 1999. Phenological changes reflect climate change in Wisconsin. *PNAS* 96: 9710-9704.

Burnham KP, Anderson DR. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildl. Res.* 28: 111-119.

Burnham KP, Anderson DR. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd ed., Springer-Verlag, New York.

Cain ML, Eccleston J, Kareiva PM. 1985. The influence of food plant dispersion on caterpillar searching success. *Ecol. Entomol.* 10: 1-7.

Canaday BB, Fonda RW. 1974. The influence of subalpine snowbanks on vegetation pattern, production, and phenology. *Bull. Torrey Bot. Club* 101: 340-350.

Cappuccino N, Kareiva P. 1985. Coping with a capricious environment: a population study of a rare pierid butterfly. *Ecology* 66: 152-161.

Chapin FS, III, Shaver FR, Giblin AE, Nadelhoffer KJ, Laundre JA. 1995. Responses of Arctic Tundra to Experimental and Observed Changes in Climate. *Ecology* 76: 694-711.

Cirmo CP, McDonnell JJ. 1997. Linking the hydrologic and biogeochemical controls of nitrogen transport in near-stream zones of temperate-forested catchments: a review. *J. Hydrol.* 199: 88-120.

Coquard J, Duffy PB, Taylor KE, Iorio JP. 2004. Present and future surface climate in the western USA as simulated by 15 global climate models. *Climate Dynamics* 23: 455-472.

Cowles MK, Zimmerman DL, Christ A, McGinnis DL. 2002. Combining snow water equivalent data from multiple sources to estimate spatio-temporal trends and compare measurement systems. *J. Agric. Biol. Environ. Stat.* 7: 536-557.

Crozier L. 2003. Winter warming facilitates range expansion: cold tolerance of the butterfly *Atalopedes campestris*. *Oecologia* 135: 648-656.

Crozier L. 2004. Field transplants reveal summer constraints on a butterfly range expansion. *Oecologia* 141: 148-157.

Crozier L. 2004b. Warmer winters drive butterfly range expansion by increasing survivorship. *Ecology* 85: 231-241.

Cushman JH, Boggs CL, Weiss SB, Murphy DD, Harvey AW, Ehrlich PR. 1992. Estimating female reproductive success of a threatened butterfly: influence of emergence time and host plant phenology. *Oecologia* 99: 194-200.

Delbart N, Le Toan T, Kergoat L, Fedotova V. 2006. Remote sensing of spring phenology in boreal regions: A free of snow-effect method using NOAA-AVHRR and SPOT-VGT data (1982-2004). *Remote Sensing Environ.* 101: 52-62.

Davies ZG, Wilson RJ, Coles S, Thomas CD. 2006. Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *J. Anim. Ecol.* 75: 247-256.

Davies ZG, Wilson RJ, Brereton TM, Thomas CD. 2005. The re-expansion and improving status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain: a metapopulation success story. *Biol. Cons.* 124: 189-198.

Dempster JP. 1997. The role of larval food resources and adult movement in the population dynamics of the orange-tip butterfly (*Anthocharis cardamines*). *Oecologia* 111: 549-556.

Dethier VG. 1959. Food-plant distribution and density and larval dispersal as factors affecting insect populations. *Can. Entomol.* 91: 581-596.

Dobkin DS, Olivieri I, Ehrlich PR. 1987. Rainfall and the interaction of microclimate with larval resources in the population dynamics of checkerspot butterflies (*Euphydryas editha*) inhabiting serpentine grassland. *Oecologia* 71: 161-166.

Douglas GW, Bliss LC. 1977. Alpine and high subalpine plant communities of the North Cascades range, Washington and British Columbia. *Ecol. Monogr.* 47: 113-150.

Dunne JA, Harte J, Taylor KJ. 2003. Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods. *Ecol. Monogr.* 73: 69-86.

Easterling DR, Evans JL, Groisman PY, Karl TR, Kunkel KE, Ambenje P. 2000. Observed variability and trends in extreme climate events: A brief review. *Bull. Am. Meterol. Soc.* 81: 417-425.

Efron B, Tibshirani RJ. 1993. *An Introduction to the Bootstrap*, Chapman and Hall, New York.

Ehrlich PR, Hanski I. (Eds.) 2004. *On the Wings of Checkerspots: A Model System for Population Biology.* Oxford University Press, Oxford.

Fareed M, Caldwell MM. 1975. Phenological patterns of two alpine tundra plant populations on Niwot Ridge, Colorado. *Northwest Science* 49: 17-23.

Fischer RA, Kohn GD. 1966. The relationship of grain yield to vegetative growth and post-flowering leaf area in the wheat crop under conditions of limited soil moisture. *Austr. J. Agri. Res.* 17: 281-295.

Fitter AH, Fitter RSR. 2002. Rapid changes in flowering time in British plants. *Science.* 296: 1689-1691.

Fleishman E., Murphy DD, Austin GT. 1999. Butterflies of the Toquima Range, Nevada: distribution, natural history, and comparison to the Toiyabe Range. *Great Basin Nat.* 59: 50-62.

Fleishman E, Launer AE, Weiss SB, Reed JM, Boggs CL, Murphy DD, Ehrlich PR. 2000. Effects of microclimate and oviposition timing on prediapause larval survival of the Bay checkerspot butterfly, *Euphydryas editha bayensis* (Lepidoptera: Nymphalidae). *J. Res. Lepid.* 36: 31-44.

Galen C, Stanton ML. 1991. Consequences of emergence phenology for reproductive success in *Ranunculus adoneus* (Ranunculaceae). *Am. J. Bot.* 78: 978-988.

Harte J, Torn MS, Chang F, Feifarek B, Kinzig AP, Shaw R, Shen K. 1995. Global warming and soil microclimate: Results from a meadow-warming experiment. *Ecol. Appl.* 5: 132-150.

Hayes JL. 1985. Egg distribution and survivorship in the pierid butterfly, *Colias alexandra*. *Oecologia* 66: 495-498.

Hellman JJ. 2002. The effect of an environmental change on mobile butterfly larvae and the nutritional quality of their hosts. *J. Anim. Ecol.* 71: 925-936.

Hill JK, Thomas CD, Huntley B. 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proc. R. Soc. Lond. B* 266: 1197-1206.

Hill JK, Thomas CD, Fox R, Telfer MG, Willis SG, Asher J, Huntley B. 2002. Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proc. R. Soc. Lond. B* 269: 2163-2171.

Hogg EH. 1993. An arctic-alpine flora at low elevation in Marble Canyon, Kootenay National Park, British Columbia. *Can. Field Nat.* 107: 283-292.

Holway JG, Ward RT. 1963. Snow and meltwater effects in an area of Colorado alpine. *Am. Midland Nat.* 69: 189-197.

Hughes L. 2000. Biological consequences of global warming: is the signal already apparent? *Trends Ecol. Evolut.* 15: 56-61.

Hunter MD, McNeil JN. 1997. Host-plant quality influences diapause and voltinism in a polyphagous insect herbivore. *Ecology* 78: 977-986.

Inouye DW, Morales MA, Dodge GJ. 2002. Variation in timing and abundance of flowering by *Delphinium barbeyi* Huth (Ranunculaceae): the roles of snowpack, frost and La Niña, in the context of climate change. *Oecologia* 130: 543-550.

Intergovernmental Panel on Climate Change (IPCC). 2001. Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York.

Jackson LE, Bliss LC. 1984. Phenology and water relations of three plant life forms in a dry tree-line meadow. *Ecology* 65: 1302-1314.

Johnson PL, Billings WD. 1962. The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. *Ecol. Monogr.* 32: 105-135.

Keller F, Körner C. 2003. The role of photoperiodism in alpine plant development. *Arctic, Antarctic, Alpine Res.* 35: 361-368.

Kerr JT. 2001. Butterfly species richness patterns in Canada: energy, heterogeneity, and the potential consequences of climate change. *Cons. Ecol.* 5: 10-. [online] URL: <http://www.consecol.org/vol5/iss1/art10/>.

Kim J, Kim TK, Arritt RW, Miller NL. 2002. Impacts of increased atmospheric CO2 on the hydroclimate of the western United States. *J. Climate* 15: 1926-1942.

Konvicka M, Maradova M, Benes J, Fric Z, Kepka P. 2003. Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale. *Global Ecol. Biogeogr.* 12: 403-410.

Kruckeberg AR. 1991. *The Natural History of Puget Sound Country*. Univ. Washington Press, Seattle.

Kudo G. 1992. Performance and phenology of alpine herbs along a snow-melting gradient. *Ecol. Res.* 7: 297-304.

Kulla C. 2006. “Twentieth-century climate change in the eastern North Cascades and subalpine forest expansion”. M.S. Thesis. Western Washington University, Bellingham, WA. pp. 78.

Kusnierczyk ER, Ettl GJ. 2002. Growth response of ponderosa pine (*Pinus ponderosa*) to climate in the eastern Cascade Mountains, Washington, USA: Implications for climatic change. *EcoScience* 9: 544-551.

Labine PA. 1968. The population biology of the butterfly, *Euphydryas editha*. VIII. Oviposition and its relation to patterns of oviposition in other butterflies. *Evolution* 22: 799-805.

Lavender DP, Ching KK, Hermann RK. 1968. Effect of environment on the development of dormancy and growth of Douglas-fir seedlings. *Bot. Gaz.* 129: 70-83.

Ledwith T. 1996. *Watershed Management Council Networker* 6: 6-7.

Leung LR, Ghan SJ. 1999. Pacific northwest climate sensitivity simulated by a regional climate model driven by a GCM. Part II: 2xCO_2 simulations. *J. Climate* 12: 2031-2053.

Leung LR, Wigmosta MS. 1999. Potential climate chance impacts on mountain watersheds in the Pacific Northwest. *J. Am. Water Res. Assoc.* 35: 1463-1471.

Leung LR, Qian Y, Han J, Roads JO. 2003. Intercomparison of global reanalyses and regional simulations of cold season water budgets in the western United States. *J. Hydrometeorol.* 4: 1067-1087.

Liu F, Williams MW, Caine N. 2004. Source waters and flow paths in an alpine catchment, Colorado Front Range, United States. *Water Resourc. Res.* 40: 16-.

McCarty JP. 2001. Ecological consequences of recent climate change. *Cons. Biol.* 15: 320-331.

McLaughlin JF, Hellman JJ, Boggs CL, Ehrlich PR. 2002. Climate change hastens population extinctions. *PNAS* 99: 6070-6074.

McLaughlin JF, Hellman JJ, Boggs CL, Ehrlich PR. 2002b. The route to extinction: population dynamics of a threatened butterfly. *Oecologia* 132: 538-548.

Moore SD. 1989. Patterns of juvenile mortality within an oligophagous insect population. *Ecology* 70: 1726-1737.

Mote PW, Parson EA, Hamlet AF, Keeton WS, Lettenmaier D, Mantua N, Miles EL, Peterson DW, Peterson DL, Slaughter R, Snover AK. 2003. Preparing for climatic change: The water, salmon, and forests of the Pacific Northwest. *Climatic change* 61: 45-88.

Mott JJ, McComb AJ. 1975. Effects of moisture stress on the growth and reproduction of three annual species from an arid region of western Australia. *J. Ecol.* 63: 825-834.

National Park Service (NPS). 2000. Research Catalog: A comprehensive manual of natural and cultural Study opportunities within Mount Rainier, North Cascades, and Olympic National Parks [online]. URL: <http://www.nps.gov/noca/rescat.htm>.

Natural Resources Conservation Service. 2004. Historical Daily SNOTEL Data Tables [online]. URL: < http://www.wcc.nrcs.usda.gov/snow/>.

Newman EI. 1965. Factors affecting the seed production of *Teesdalia nudicaulis*: II. Soil moisture in spring. *J. Ecol.* 53: 211-232.

Newman EI. 1967. Response of *Aira praecox* to weather conditions: I. Response to drought in spring. *J. Ecol.* 55: 539-556.

Oberhauser K, Peterson AT. 2003. Modeling current and future potential wintering distributions of eastern North American monarch butterflies. *PNAS* 100: 14063-14068.

Ostler WK, Harper KT, McKnight KB, Anderson DC. 1982. The effects of increasing snowpack on a subalpine meadow in the Uinta Mountains, Utah, U.S.A. *Arctic Alpine Res.* 14: 203-214.

Parmesan C, Ryrholm N, Stefanescu, C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L Kullberg J, Tammaru T, Tennent WJ, Thomas JA, Warren M. 1999. Polewards shifts in geographic ranges of butterfly species associated with regional warming. *Nature* 399: 579-583.

Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42.

Peterson AT, Martínez-Meyer E, González-Salazar C, Hall PW. 2004. Modeled climate change effects on distributions of Canadian butterfly species. *Can. J. Zool.* 82: 851-858.

Peterson DW, Peterson DL. 2001. Mountain hemlock growth responds to climatic variability at annual and decadal time scales. *Ecology* 82: 3330-3345.

Pojar J, MacKinnon A. *Plants of the Pacific Northwest Coast: Washington, Oregon, British Columbia, and Alaska*. Vancouver, B.C.: Lone Pine Publishing, 1994.

Price MV, Waser NM. 1998. Effects of experimental warming on plant reproductive phenology in a subalpine meadow. *Ecology* 79: 1261-1271.

Pyle RM. 2002. *The Butterflies of Cascadia: A Field Guide to All the Species of Washington, Oregon, and Surrounding Territories*. Seattle, WA: Seattle Audubon Society.

R Development Core Team. 2005. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: <http://www.R-project.org>.

Rodriguez J, Jordano D, Fernandez Haeger J. 1994. Spatial heterogeneity in a butterfly-host plant interaction. *Ecology* 63: 31-38.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421: 57-60.

Roy DB, Rothery P, Moss D, Pollard E, Thomas JA. 2001. Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *J. Anim. Ecol.* 70: 201-217.

Roy DB, Sparks TH. 2000. Phenology of British butterflies and climate change. *Global Change Biol.* 6: 407-416.

Sala OE, Chapin FS, III, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770-1774.

Sandvik SM, Totland Ø. 2000. Short-term effects of simulated environmental changes on phenology, reproduction, and growth in the late-flowering snowbed herb *Saxifraga stellaris* L. *Ecoscience* 7: 201-213.

Singer MC. 1972. Complex components of habitat suitability within a butterfly colony. *Science* 176: 75-77.

Singer MC, Ehrlich PR. 1979. Population dynamics of the checkerspot butterfly *Euphydryas editha*. 1979. *Fortschritte der Zoologie* 25: 52-60.

Singer MC, Thomas CD. 1996. Evolutionary responses of a butterfly metapopulation to human- and climate-caused environmental variation. *Am. Nat.* 148: S9-S39.

Stamp NE. 1981. Parasitism of single and multiple egg clusters of Euphydryas phaeton (Nymphalidae). *J. New York Entomol. Soc.* 89: 89-97.

Stamp NE. 1984. Interactions of parasitoids and checkerspot caterpillars *Euphydryas* spp. (Nymphalidae). *J. Res. Lepid.* 23: 2-18.

Starr G, Oberbauer SF, Pop EW. 2000. Effects of lengthened growing season and soil warming on the phenology and physiology of *Polygonum bistorta*. *Global Change Biol.* 6: 357-369.

Stefanescu C, Herrando S, Páramo F. 2004. Butterfly species richness in the north-west Mediterranean Basin: the role of natural and human-induced factors. *J. Biogeogr.* 31: 905-915.

Stinson K. 2004. Natural selection favors rapid reproductive phenology in *Potentialla pulcherrima* (Rosaceae) at opposite ends of a subalpine snowmelt gradient. *Am. J. Bot.* 91: 531-539.

Totland Ø, Alatalo JM. 2002. Effects of temperature and date of snowmelt on growth, reproduction, and flowering phenology in the arctic/alpine herb, *Ranunculus glacialis*. *Oecologia* 133: 168-175.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, Siqueira MFD, Grainger A, Hannah L, Hughes L, Huntley B, Jaarsveld ASV, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE. 2004. Extinction risk from climate change. *Nature* 427: 145-148.

Thomas CD, Lennon JJ. 1999. Birds extend their ranges northwards. *Nature* 399: 213.

Thomas CD, Hill JK, Lewis OT. 1998. Evolutionary consequences of habitat fragmentation in a localized butterfly. *J. Anim. Ecol.* 6: 485-497.

Thórhallsdóttir TE. 1998. Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic. *Oecologia* 114: 43-49.

Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC. 2005. Climate change threats to plant diversity in Europe. *PNAS* 102: 8245-8250.

Virtanen T, Neuvonen S. 1999. Performance of moth larvae on birch in relation to altitude, climate, host quality and parasitoids. *Oecologia* 120: 92-101.

Walker M, Ingersoll RC, Webber PJ. 1995. Effects of interannual climate variation on phenology and growth of two alpine forbs. *Ecology* 76: 1067-1083.

Walther G, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J, Hoegh-Guldberg O, Bairlein F 2002. Ecological responses to recent climate change. *Nature* 416: 389-395.

Waring RH, Franklin JF. 1979. Evergreen coniferous forests of the Pacific northwest. *Science* 204: 1380-1386.

Weiss SB, Murphy DD. 1988. Fractal geometry and caterpillar dispersal: or how many inches can inchworms inch? *Funct. Ecol.* 2: 116-118.

Weiss SB, Murphy DD, Ehrlich PR, Metzler CF. 1993. Adult emergence phenology in checkerspot butterflies: the effects of macroclimate, topoclimate, and population history. *Oecologia* 96: 261-270.

Weiss SB, Murphy DD, White RR. 1988. Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. *Ecology* 69: 1486-1496.

Weiss SB, White RR, Murphy DD, Ehrlich PR. 1987. Growth and dispersal of larvae of the checkerspot butterfly, *Euphydryas editha*. *Oikos* 50: 161-166.

Wiklund C. 1977. Oviposition, feeding and spatial separation of breeding and foraging habitats in a population of *Leptidea sinapis* (Lepidoptera). *Oikos* 28: 56-68.

Williams, KS, Lincoln DE, Ehrlich PR. 1983. The coevolution of *Euphydryas chalcedona* butterflies and their larval host plants: I. Larval feeding behavior and host plant chemistry. *Oecologia* 56: 323-329.

Wilson RJ, Gutiérrez D, Gutiérrez J, Martinez D, Agudo R, Monserrat VJ. 2005. Changes to the elevational limits and extent of species ranges associated with climate change. *Ecol. Lett.* 8: 1138-1146.

Zavaleta ES, Thomas BD, Chiariello NR, Asner GP, Shaw MR, Field CB. 2003. Plants reverse warming effect on ecosystem water balance. *PNAS* 100: 9892-9893.

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Appendix A: Plant Phenology Data

Table 10. Plant phenological state for *C. miniata* at Easy Pass dry area.

Date	% in state 0	% in state 1	% in state 2	% in state 3
203	100	0	0	0
211	10	60	17	13
216	0	20	43	37
223	0	3.3	33	63
240	0	0	3.3	97

Table 11. Plant phenological state for *C. miniata* at Easy Pass moist area.

Date	% in state 0	% in state 1	% in state 2	% in state 3
203	100	0	0	0
211	42	58	0	0
216	33	46	17	4.2
223	8.3	50	38	4.2
240	4.2	17	17	63

Table 12. Plant phenological state for *C. miniata* at Hidden Meadows dry area.

Date	% in state 0	% in state 1	% in state 2	% in state 3
208	100	0	0	0
217	14	60	20	5.7
224	0	49	31	20
241	0	2.9	20	77

Table 13. Plant phenological state for *C. miniata* at Hidden Meadows moist area.

Date	% in state 0	% in state 1	% in state 2	% in state 3
208	100	0	0	0
217	3.1	44	41	13
224	0	22	31	47
241	0	3.1	0	97

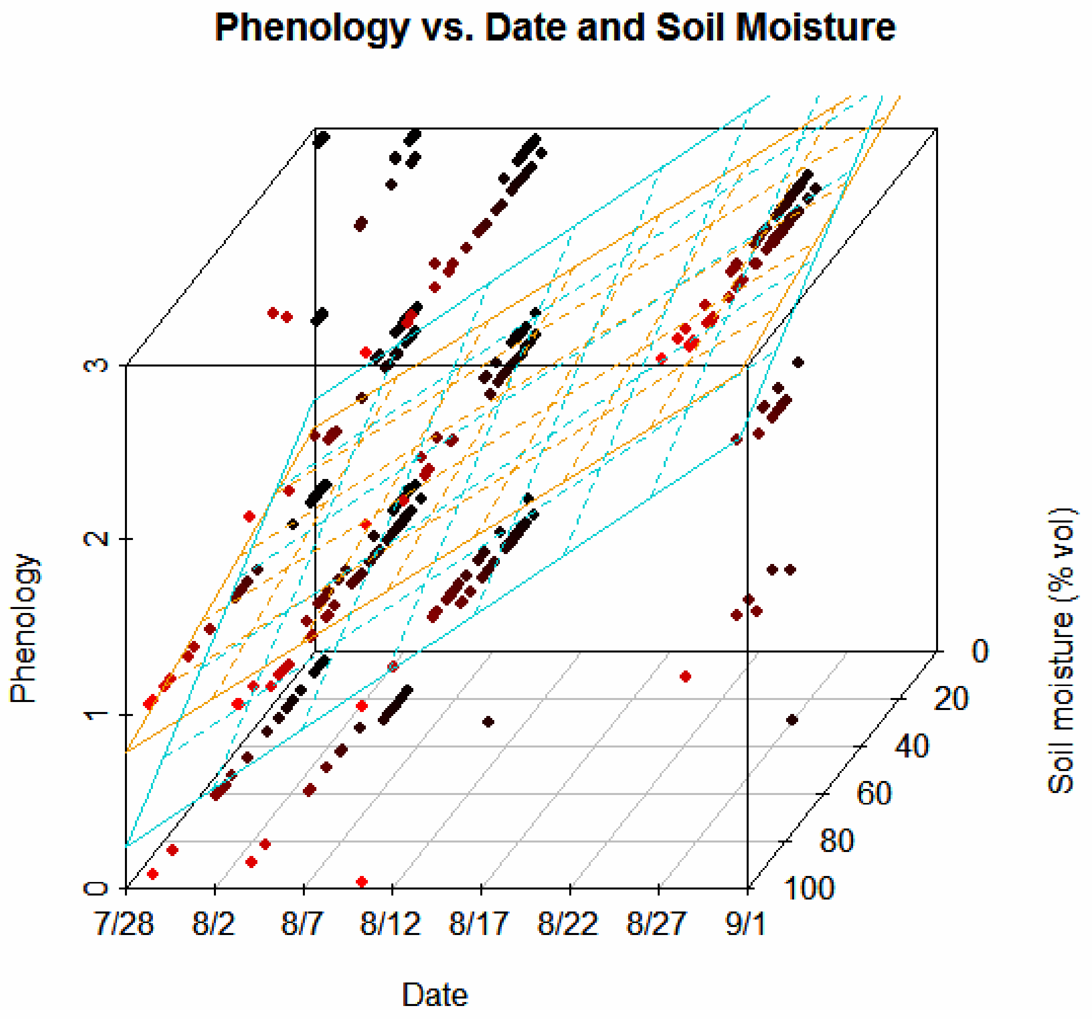

Figure 12. Phenology of plants by date and soil moisture (n=441). Color of data point indicates level of moisture (100-0% = red-black). Planes are model 6 equation (blue): $Y_{ijk} = -0.432 + 0.067c_i + 0.012m_j + \varepsilon_{ijk}$, and model 7 equation (orange): $Y_{ijkl} = 0.162 + 0.062c_i + 0.005m_j + \varepsilon_{ijk}$, where c = date, m = moisture. The distance variable in model 7 was excluded because its effect was minimal (slope = 4.053E-6). Phenology scores correspond to percent flower senescence: 0 = 0%, 1 = 1-49%, 2 = 50-99%, 3 = 100%.

Appendix B: R Code

Table 14. *R* functions used in this analysis.

Function name	**Purpose**
`boot*`	generate a specified number of bootstrap replicates of a statistic applied to data
`coef`	extract model coefficients
`data`	loads specified datasets
`lm`	fit linear models
`logLik`	extract maximized log-likelihood
`mean`	compute the arithmetic mean
`nls`	fit non-linear models
`read.table`	reads a file in table format and creates a dataframe from it
`sample`	take a sample of a specified size from a dataset with or without replacement
`summary`	produce a summary of results from model fitting function
`var`	compute the variance

*S original by Angelo Canty <cantya@mcmaster.ca>. R port by Brian Ripley <ripley@stats.ox.ac.uk>. (2005). boot: Bootstrap R (S-Plus) Functions (Canty). R package version 1.2-24.

Table 15. Dataset names and variables.

Dataset name	**Dataset variables**
`pdist`	distance
`pdry`	moisture
`pdrydist`	moisture and distance
`pdate`	date
`pdatedry`	date and moisture
`pdatedist`	date and distance
`pdatedistdry`	date, distance, and moisture

Step-by-step example of data analysis using the R software.

1. A sample of data from `pdatedistdry.dat` dataset file (y = phenology, x = date, w = distance, and z = moisture):

```
y x w z
1 16 2.6 85.76
2 16 3.5 86.73
3 16 4.1 86.07
2 17 1.4 73.77
```

2. Read in `pdatedistdry.dat` file and create `pdatedistdry` dataframe:

```
pdatedistdry<-read.table("C:/pdatedistdry.dat",T)
```

3. Enter function to output maximized log-likelihood, linear model coefficients, and adjusted R^2 value for linear model:

```
linearpdatedistdry.lik.coef<-function(data,i){
     d<-data[i,]
     pdatedistdry.lm<-lm(y~ x + w + z, data=d)
     c(logLik(pdatedistdry.lm),
     coef(pdatedistdry.lm),
     summary(pdatedistdry.lm)$adj.r.squared)
}
```

4. Enter function to output maximized log-likelihood, and non-linear model coefficients for sigmoid model:

```
sigmoidpdatedistdry.lik.coef<-function(data,i){
     d<-data[i,]
     pdatedistdry.nls<-
     nls(y~ (a * x^2) / ((b / w) + (c / z) + x^2),
     data=d, start = list(a = 3, b = 10, c = 20),
     trace=FALSE, control=list(maxiter=100))
     c(logLik(pdatedistdry.nls),
     coef(pdatedistdry.nls))
}
```

5. Enter function to bootstrap the `pdatedistdry` dataset. The bootstrap function is specified here to randomly sample with replacement 132 data points out of a total of 441 and apply the `linearpdatedistdry.lik.coef` function or the `pdatedistdry.lik.coef` function to the bootstrap sampled data. The bootstrap function repeats this sampling 6000 times.

```
linearpdatedistdry.boot<-
boot(data=pdatedistdry[sample(441,132),],
statistic=linearpdatedistdry.lik.coef, R=6000)
```

6. The mean and the variance of the maximized log-likelihood, linear and non-linear model coefficients, and adjusted R^2 values are computed:

```
mean(linearpdatedistdry.boot$t[,1])
var(linearpdatedistdry.boot$t[,1])
```

```
mean(linearpdatedistdry.boot$t[,2])
var(linearpdatedistdry.boot$t[,2])
etc.
```