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For everything there was a season: phenological shifts within the flora of the Tetons

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Abstract Around the world, phenology — the timing of ecological events — is shifting as the climate warms. This can lead to a variety of consequences for individual species and entire ecological communities, most notably when asynchronies develop between plants and animals that depend upon each other (e.g. nectar-consuming pollinators). Grand Teton National Park biologists have identified this topic ("effect of earlier plant flowering on pollinators and wildlife") as one of their priority research needs. We have gathered, digitized, and quality-controlled phenological observations of first flowering dates collected by Frank Craighead, Jr. in the 1970s, before significant warming occurred. First flowering date for 87% of a 72-species data set correlates significantly with spring temperatures in the 1970s, suggesting that these plants should now be flowering earlier and will continue to flower earlier in the future. This year we began standardized phenological observations of these 72 species in the same location and initiated a citizen science program. Our proposed next steps are to: (1) gather and analyze further historical records of plant phenology; (2) conduct 3-5 additional years of contemporary observations; (3) link plant phenological changes with potential cascading impacts on pollinators and foragers; (4) model phenology under future climate change scenarios; and (5) implement a long-term citizen science program in the Tetons.

Introduction

Climate change is threatening biodiversity, globally and in the Rocky Mountains (Bloom, 2016). Climatic changes such as the earlier arrival of spring snowmelt (Hall et al., 2015) and advancing spring onset (Monahan and Fisichelli, 2014) are leading to changes in plant and animal interactions (Armstrong et al., 2016; Dillon, 2011; Middleton et al., 2013), plant reproductive success (Inouye, 2008), and disturbances such as larger wildfires (O'Leary et al., 2016). Around the world, phenology — the timing of ecological events — is shifting as global and local climates warm (Parmesan and Yohe, 2003). Examples of phenology include when plants leaf out, first flower, or reach peak flowering; when insects emerge, metamorphose, pollinate, and reproduce; or when migrating birds arrive on breeding grounds. Although some species' phenologies are closely linked to temperature and climatic events such as snow cover (O'Leary et al., 2018; Sherwood et al., 2017; Willis et al., 2008), other species' phenologies can be driven by day-length cues. As the climate warms, this can result in phenological mismatches or novel synchronies between species (Deacy et al., 2017). Observed shifts in phenology are often the first signs that climate change is impacting natural populations and may be an early warning of future population declines or local extinctions (Willis et al., 2008).

Detailed historic phenology data are rare, but in Grand Teton National Park (GTNP) we have the opportunity to capitalize on data gathered by ecologist

Frank Craighead, Jr. in the 1970s. These data served as the basis of his popular book *For Everything There is a Season* (Craighead, 1994) which gives a week-by-week account of ecological events that are likely to be occurring in the Grand Teton-Yellowstone area. Similar phenology notes have been used to compare past and present patterns in a handful of other locations around the United States. These include Henry David Thoreau's notes from Massachusetts (see Primack and Miller-Rushing, 2012 for a synthesis of findings), Aldo Leopold's notes from Wisconsin (Bradley et al., 1999), and the notes of the Smiley brothers in New York (Cook et al., 2008). To our knowledge, no such comparative study has been undertaken in the Rockies; the Craighead notes provide us with an opportunity to examine changes in phenology in one of the most celebrated and biologically intact ecosystems in the world.

Within the Greater Yellowstone Ecosystem (GYE) and GTNP, there is currently little understanding of how climate change is affecting plant and animal phenology or potential asynchronies between these guilds. One prominent study concluded that more rapid spring green-up is negatively impacting migratory elk populations in the GYE (Middleton et al., 2013). This study relied on remotely sensed data of aggregate vegetation greenness, rather than considering individual plant species. A more detailed understanding of how plant phenology is changing at the species level — and what it means for the myriad species that depend on these plants in the GYE — is needed in order for managers to anticipate and mitigate impacts of these changes. GNTP biologists have identified this topic ("effect of earlier plant flowering on pollinators and wildlife") as one of their priority research needs. Previous work has begun to shed light on how warming temperatures in GTNP may impact plant nectar production and pollinator resources (Debinski et al., 2014; Dillon, 2011; Monahan et al., 2016; Sprayberry et al., 2016). However, as yet, there has been no thorough investigation of how plant phenology at the species level has changed as temperatures have warmed over the last 40 years in GTNP. Our work directly addresses this research gap.

Demonstrating and untangling the effects of changes in phenology requires long-term data on a variety of species. Thus, our study must span several more years to address our primary research question: 1) How has plant phenology, on a species level, shifted now relative to the 1970s in the Tetons? 2017 marked the first of 3-5 years of planned contemporary observations to compare to Craighead's dataset. We are compiling additional historic data through investigation of herbarium records and naturalist notes. Beyond comparing to historic data, we seek to create a new standardized baseline of phenology in GTNP, with data made freely available through the United States National Phenological Network (US-NPN). Once we have gathered substantial historic and contemporary observations, we will be able to answer our additional research questions: 2) What climate variables (e.g. spring temperature, precipitation as snow, timing of snowmelt) are most closely related with plant flowering times? 3) What are the plasticity and predicted future flowering times for ecologically important plant species in the Tetons? 4) And importantly, what are the likely consequences of current and future changes in plant phenology for key pollinators (e.g. hummingbirds, bumblebees) and other wildlife (e.g. sage-grouse, bears)? This year demonstrated the first of many successful years of contemporary observations. Preliminary results demonstrate that individual species respond vastly differently to temperature cues, indicating certain species may fare worse than others in a changing climate depending on their plasticity.

The reputation of Frank Craighead, a renowned biologist in the GYE and long-time resident of the Tetons, and the accessibility of our field site lends this project perfectly for citizen science and community engagement in climate change research. Citizen science, which engages non-professional scientists in one or more stages of scientific research, has made substantial contributions to scientific understanding and conservation management (Bonney et al., 2014; McKinley et al., 2015) and is an effective form of science outreach. Through research, outreach, and key partnerships, we aim to better understand ecological relationships and assist in the mitigation of climate change impacts on the plants and wildlife of the GYE.

Methods

Historical collections

Since 2015, we retrieved, entered, and quality-controlled nearly 800 observations that Frank Craighead Jr. made of plant flowering and fruiting dates in the 1970s and in 1988. Craighead's notes included 258 species of flowering plants. Plant observations were scored as representing first presence of leaves, first presence of buds, first flower, peak flower, and occurrence of fruits or seeds. Where available, location data and any other notes were recorded. Most observations were made in Grand Teton National Park near Blacktail Butte. We are interested in Craighead's data as a "baseline" of plant phenology patterns before climate change had started to significantly warm spring temperatures.

All data were sorted by species, year, and ecological event. We identified the species that had at least two (preferably three) observations from the 1970s - sufficient replication to make contemporary comparisons. Many of these species also have observations from 1988 (the same year as the massive Yellowstone wildfires), an unusually dry and hot spring/summer that is often considered a harbinger of future conditions under a warming climate (Westerling et al., 2011).

We analyzed the available first flowering data to examine (a) how well spring temperatures predicted first flowering time, and (b) whether differences in flowering time were significantly different between 1988 and the available dates from the 1970s. We calculated the average minimum and maximum temperatures for March-June of each year for Teton County using the TopoWX surface, and used linear regressions to relate temperature to first flowering date for each species. Average minimum temperature was consistently a better predictor than average maximum temperature, so we report only results from the former. Within each species, we calculated the difference in first flowering date between the following pairs of years (years for which there was adequate data): 1988-1975, 1988-1976, 1988-1979. We then calculated the average difference in first flowering date across all species and related it to the difference in mean minimum temperature for each year pair.

We found that there were many common and important species for which Craighead had not collected multiple years of data. Thus, of the 258-total species recorded, we identified 54 species with 3 or more years of observations. To that we added an additional 18 common and ecologically important species with one to two years of observations, for a total of 72 species as candidates for a full research program that compares past with present phenology (Supplemental Material: Species List). We plan to build the historic dataset over the next several years from additional sources, including herbarium records.

Contemporary observations

In spring 2017, we initiated contemporary observations of the selected 72 species, more than 40 years after Craighead's initial observations. Using historic information, we identified the locations visited by Craighead and created a standardized transect to walk from his home through sagebrush steppe vegetation towards the summit of Blacktail Butte located near Moose, Wyoming in GTNP. Blacktail Butte is an isolated outcrop of vegetated limestone with elevations ranging from 1,990-2,343 m in the heart of the GYE, centered between the Beartooth-Absaroka Range to the north, the Gros Ventre Range to the east, the Snake River Range to the south, and the Tetons to the west. The location and topographic variation of the formation harbors a great seasonal diversity of plants and wildlife.

We divided the transect (2.7 km one way) into 5 specific sites representing a variety of ecosystem types, (Figure 1). Each site contains a subset of the total 72 species. For each species we recorded the presence or absence of each phenological phase (phenophase) including vegetative, budding, flowering, peak flower, fruiting, and senescence/withering. Peak flower is defined as when at least 50% of inflorescences are open in flower, as opposed to buds (Primack et al., 2004). While we do not have historic data on all of these phenological stages, it is important to begin tracking changes in all of these parameters, as peak flowering date and seeding/fruiting date

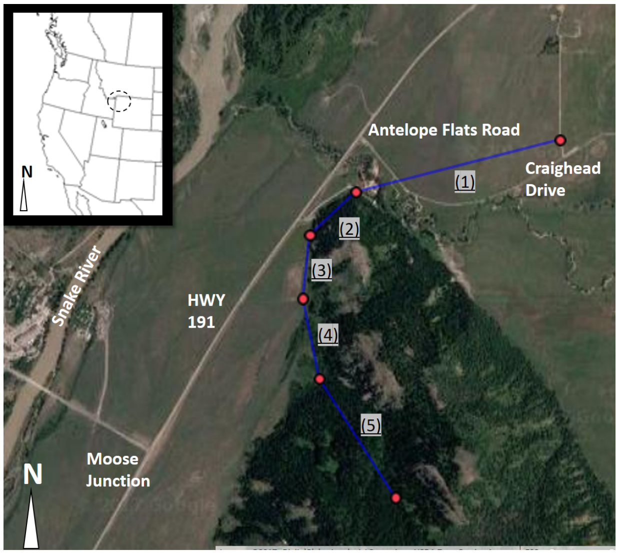

Figure 1. Phenological observation sites for 72 species of flowering plants within Grand Teton National Park. Phenophases for individual species were collected across the 5 site locations encompassing a diversity of ecosystems: (1) Craighead Cabin sagebrush steppe (2) Lower Blacktail Butte sagebrush steppe (3) Lower Blacktail Butte forest (4) Aspen grove and (5) Upper Blacktail Butte montane forest. Each site contains a subset of the total 72 species.

have important consequences for species of birds, mammals, and insects that feed upon plant resources such as nectar and fruits (Aldridge et al., 2011; Deacy et al., 2017; Dillon, 2011; Kearns et al., 1998). Further, these phenophases can shift in response to climate change (CaraDonna et al., 2014).

From March 31 to October 30, we collected phenological observations at all 5 sites on Blacktail Butte once every 3-7 days, for a total of 55 observation dates; this captured the entire flowering period of all 72-target species. We made a total of 5,227 species-level observations over the course of the field season. Over 95% of observations were made by a single researcher, Bloom, minimizing observer effects. We also captured coarse-scale weather observations, naturalist observations, and hundreds of photographs.

Citizen science program

We identified nine species of flowering plants as suitable for a citizen science program open to the public. Our goal is to set up a "phenology walk," ideally retracing Craighead's steps, along which citizen scientists can gather phenology data. In 2017 we developed instructions using photos, diagrams, maps of collection sites, and step by step instructions for making field observations on these 9 species using a standardized datasheet (available on request from T. Bloom) and began training citizen scientists.

Preliminary Results and Discussion

Historic collections

The majority of plants for which we have historic data (n=49) exhibited a statistically significant sensitivity to spring temperatures. First flowering date for 87% of these species was negatively correlated with mean spring temperatures, meaning warmer temperatures related to earlier flowering times (Figure 2). In many cases there were only 3 data points available, reducing the power to detect statistically significant trends; nevertheless, many regressions were statistically significant and had high R^2 values. Some species had remarkably tight correlations with temperature data (e.g. *Amelanchier alnifolia; Epilobium angustifolium; Heracleum lanatum; Hydrophyllum capitatum; Potentilla gracilis*; Figure 1). Other species did not show much relationship at all with temperature (e.g. *Prunella vulgaris; Prunus virginiana; Shepherdia canadensis*; Figure 1).

The slope of these regressions also varied (Figure 2 and 1). Species with particularly steep slopes – indicating high sensitivity to temperature – were *Orogenia linearifolia, Viola adunca, Lomatium ambiguum, Galium boreale, Geum triflorum, Taraxacum officinale,* and *Arnica cordifolia*.

Across all species analyzed, first flowering time was, on average, 25.1 days earlier in 1988 compared to 1975. Even 1979, which was only 1.4 °F cooler than 1988, had first flowering dates averaging 12 days later than in 1988 (Figure 3).

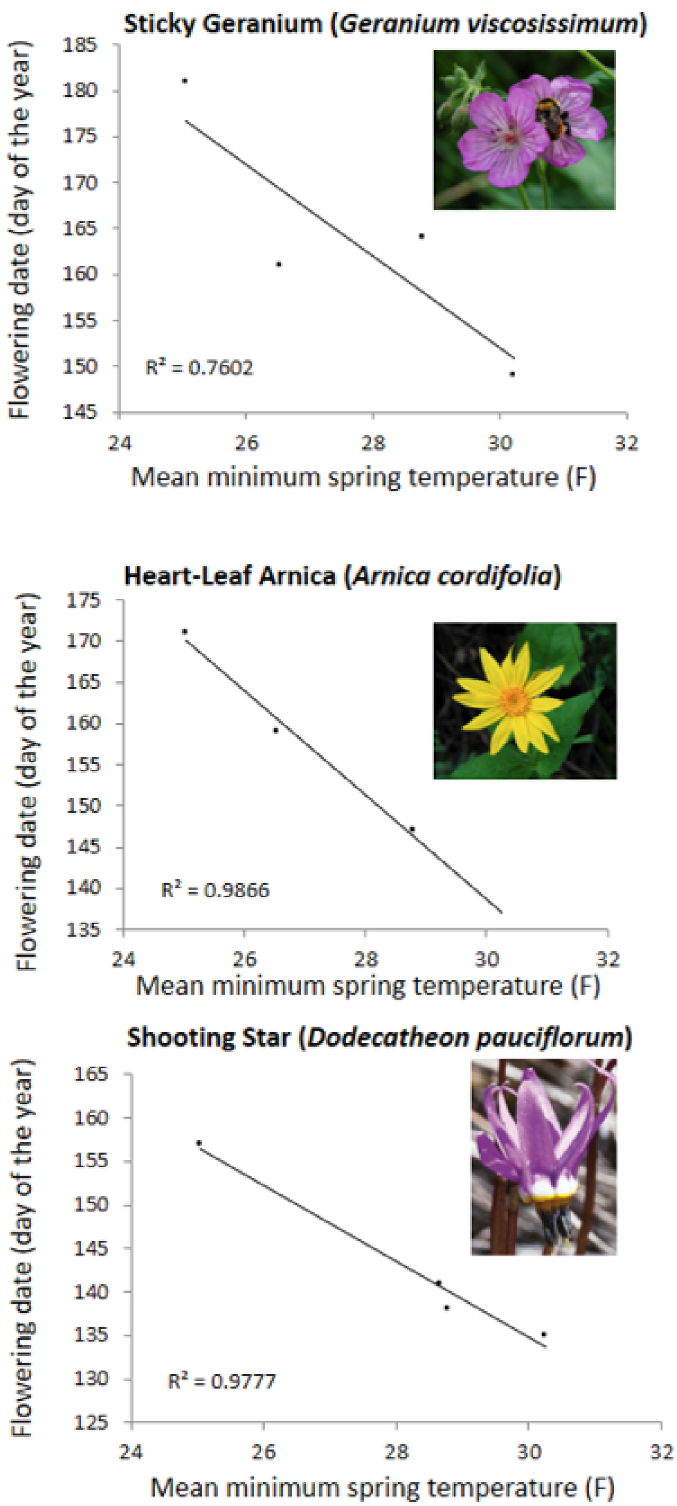

Figure 2. Regressions of first flowering date against mean minimum temperature during spring months (March-June). Flowering dates were sampled in five years: 1975, '76, '77, '79, and '88.

Contemporary observations

The short sampling period, a single season, limits our ability to conduct a complex analysis. However, it is interesting to note that we observed many species in flower well before Craighead ever did. For example, we observed *Fritillaria pudica*, an early-spring flower, flowering on April 17, 2017, a full 17 days earlier than the earliest Craighead record. We observed another spring flower, *Ranunculus glaberrimus*, in bloom as early as April 7, 2017 - six days before Craighead observed it in the extreme year of 1988, and 14-21 days before he observed it flowering in the 1970s. We observed the first flowers of *Amelanchier alnifolia* (serviceberry) on May 25th, the same day Craighead observed the first flower of this species in 1988, and more than 7 days earlier than he observed it any year in the 1970's. All three of these species have first flower dates that are strongly negatively correlated with spring temperature (Figure S1). Interestingly, the first flower of *Prunus virginiana* (chokecherry) showed no strong relationship to temperature in our regressions (R^2=0.127) and was first observed in 2016 on June 14, which is 2-6 days later than any observation by Craighead, suggesting other mechanisms may be driving phenology for this species.

Serviceberry and chokecherry fill similar ecological niches, with fruits serving as important food sources for many species, including bears. Early flowers may result in earlier fruits that disappear before the food source is needed most in the months leading up to hibernation. Previous research demonstrates that plants with phenology that is plastic to temperature shifts fare better under a warming climate, and those that cannot rapidly adapt may experience declines in abundance and even local extinction events (Willis et al., 2008). This logic suggests that serviceberry may fare better than chokecherry under continued climate change.

The early flowering times we observed for many species are especially interesting considering 2016/2017 was a heavy snowfall season for the Tetons; thus it is not unreasonable to predict that flowering times in low snowpack years could be

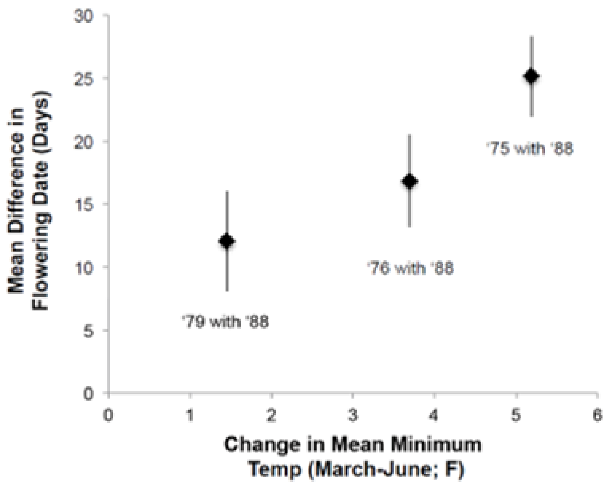

Figure 3. Mean +-SE difference in first flowering date (in pairwise year comparisons) for 49 species of plants as a function of difference in mean minimum temperature during spring (March-June) months. First flowering dates from 1988 are compared against earlier, cooler years.

substantially earlier than what was observed in the 1970s. Snowmelt timing may be a more important driver of phenology than temperature for many species (O'Leary et al., 2018; Sherwood et al., 2017). Such large shifts in flowering time as we are already starting to observe may result in large phenological mismatches or novel synchronizations between plants, pollinators, and foragers (Deacy et al., 2017; Debinski et al., 2014).

Citizen science and outreach

We succeeded in training 55 individual citizen scientists to collect data on 9 common species on Blacktail Butte this season. Many citizen scientists returned to the field repeatedly over the course of the season, completing standardized datasheets for future analysis. Citizen scientists in 2017 made 102 observations over 11 total days throughout the season. Preliminary examinations indicate that our citizen scientists are accurately collecting phenology data on target taxa that do not greatly differ from the observations of our primary researchers. Our efforts have proven the feasibility of a successful citizen science project in the Tetons, and we plan to grow our program over the coming years, tying it in with the USNPN and the Nature's Notebook digital application. This can serve as a permanent repository for citizen science data and offers many data visualization and interpretation tools for citizen scientists and educators.

Conclusions

This year is the first of 3-5 subsequent collection years aimed at creating a database that will allow us to compare contemporary phenology with historic data. It will also serve as a new highly systematic baseline for the phenology of common plant species found in GTNP. Our observations will be shared with the United States National Phenological Network (USNPN) and the GYE NPS Inventory and Monitoring Program, contributing to rapidly growing national databases.

We have already observed that many species are flowering earlier now than they were in the 1970s. It is likely that the phenology of certain plants is no longer lining up in timing with other important ecological events such as the arrival of migratory birds, the pollination habits of insects, and feeding behaviours of ungulates and bears. Our results indicate that individual species respond differently to spring temperatures, and thus will respond differently to future climate change in the Rocky Mountains as well (Figure S1).

Assessing the plasticity of certain species to increases in temperature could help managers mitigate impacts of climate change, and better understand phenological mismatches. Our study will help to reveal these patterns, providing valuable insight on management decisions such as revegetation or assisted migration plans in the GYE. We also aim to increase overall science literacy and awareness of climate change through continued outreach efforts.

Future Work

We have started gathering additional historical data by accessing the herbarium records of local flowering plants. This will expand the scope of historical data to other locations in GTNP, to additional species, and to more years from the past. Furthermore, this will allow us to examine changes in a broader set of phenological stages, which will likely reveal more clear patterns on the regional effect of climate change (Calinger et al., 2013). Much of the Craighead data are observations of first flowering date, while herbarium specimens can provide data on peak flowering date, fruiting, and seeding. We will compile, georeference, and datamine all relevant records for our focal species from GTNP, Bridger Teton National Forest, the Murie Collections, and the Consortium of the Rocky Mountain Herbaria. We will also continue to seek out other sources by word of mouth. Often individuals have made their own phenological observations over the years, and these informal data sources can be valuable and rich (Primack et al., 2004).

Once all historic data and at least three years (but ideally five years) of contemporary data have been gathered, we will be able to compare historic (pre-climate change) baseline data with contemporary flowering dates in order to answer the question of whether and how much earlier plants are flowering now than in the past. Our plot-based observations of phenology will also support spatial models of species-specific spring greening, which are currently proposed by The National Science Foundation and United States Geologic Survey (USGS) researchers. By serving as source data for model fitting and ground-truth observations for post-hoc validation, our observations will improve our understanding of phenology of the GYE beyond the Blacktail Butte study area.

Further, we plan to tie our plant phenology observations to pollinator and foraging studies in order to better understand interspecific interactions, partnering with other experts in the field. We plan to incorporate pollinator observations and abundance counts for important functional groups such as bumble bees (*Bombus* spp.) and butterflies (*Lepidoptera* spp.), following principles and protocols described in (Sprayberry et al., 2016) and Lebuhn et al. (2013).

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Table S1. List of plants included in the study.

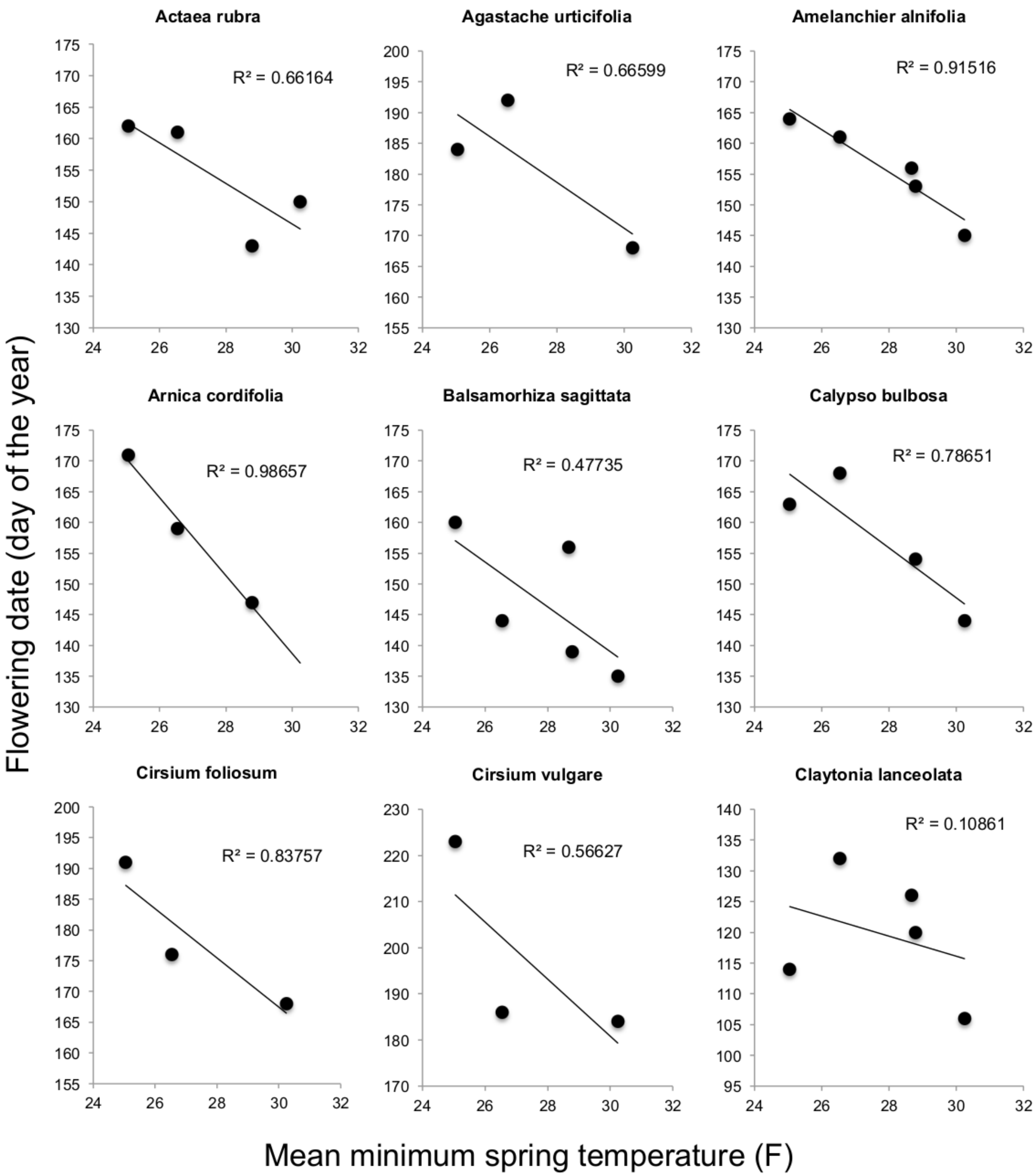
Scientific name (Craighead)	Current scientific name	Common name
Acer glabrum	*Acer glabrum*	mountain maple
Achillea millefolium	*Achillea millefolium*	yarrow
Aconitum columbianum	*Aconitum columbianum*	monkshood
Actaea rubra	*Actaea rubra*	red baneberry
Agastache urticifolia	*Agastache urticifolia*	giant hysop
Amelanchier alnifolia	*Amelanchier alnifolia*	saskatoon serviceberry; western serviceberry
Arenaria congesta	*Eremogone congesta*	ballhead sandwort
Arnica cordifolia	*Arnica cordifolia*	heartleaf arnica
Aster engelmannii	*Eucephalus engelmannii*	Engelmann aster
Balsamorhiza sagittata	*Balsamorhiza sagittata*	arrowleaf balsamroot
Calypso bulbosa	*Calypso bulbosa*	fairy slipper
Campanula rotundifolia	*Campanula rotundifolia*	harebell
Carduus nutans	*Carduus nutans*	musk thistle
Castilleja chromosa	*Castilleja chromosa*	low paintbrush
Castilleja linariifolia	*Castilleja linariifolia*	Wyoming Indian paintbrush
Castilleja miniata	*Castilleja miniata*	giant red Indian paintbrush
Chrysothamnus nauseosus	*Ericameria nauseosa*	rubber rabbit brush
Cirsium foliosum	*Cirsium foliosum*	elk thistle
Claytonia lanceolata	*Claytonia lanceolata*	spring beauty
Clematis hirsutissima	*Clematis hirsutissima*	hairy clematis; sugarbowl
Crepis acuminata	*Crepis acuminata*	tapertip hawksbeard
Delphinium nelsonii	*Delphinium nelsonii*	larkspur
Dicentra uniflora	*Noccaea montana*	steer's head
Disporum trachycarpa	*Disporum trachycarpa*	fairy bells
Dodecatheon pauciflorum	*Dodecatheon pauciflorum*	shooting star
Epilobium angustifolium	*Chamerion angustifolium*	fireweed
Eriogonum umbullatum	*Eriogonum umbullatum*	sulfer-flower buckwheat
Fragaria vesca	*Fragaria vesca*	woodland strawberry
Frasera speciosa	*Frasera speciosa*	green gentian
Fritillaria atropurpurea	*Fritillaria atropurpurea*	leopard lily; spotted fritillary
Fritillaria pudica	*Fritillaria pudica*	yellow fritillaria
Galium boreale	*Galium boreale*	northern bedstraw

Continued on next page

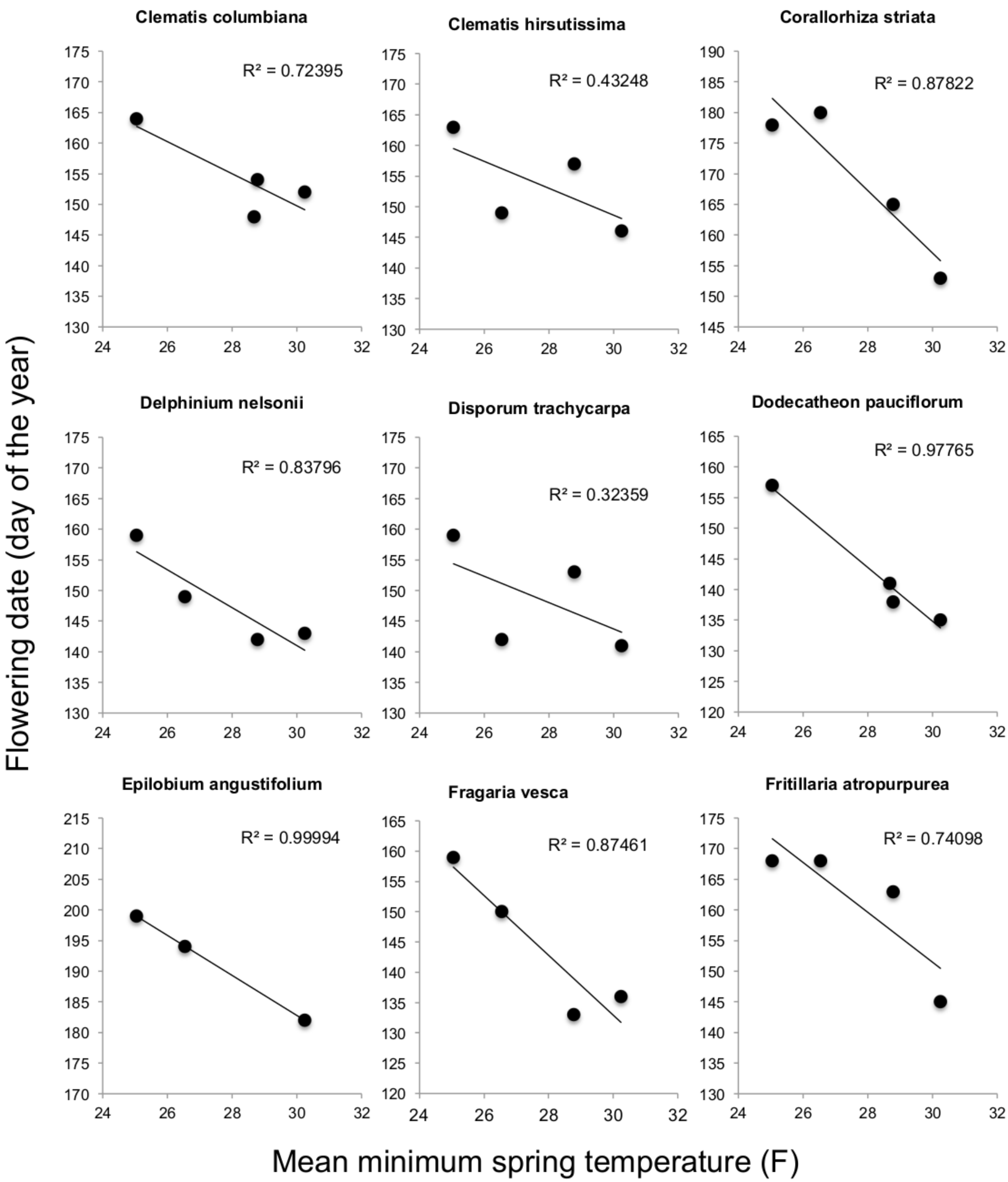
Scientific name (Craighead)	Current scientific name	Common name
Geranium viscosissimum	*Geranium viscosissimum*	sticky purple geranium
Geum triflorum	*Geum triflorum*	old man's whiskers; long-plumed avens; prairie smoke
Gilia aggregata	*Gilia aggregata*	scarlet gilia
Helianthella uniflora	*Helianthella uniflora*	one flower sunflower
Heracleum lanatum	*Heracleum maximum*	cow parsnip
Hydrophyllum capitatum	*Hydrophyllum capitatum*	waterleaf; ballhead waterleaf
Linum lewisii	*Linum lewisii*	Lewis/blue/prairie flax
Lithophragma parviflorum	*Lithophragma parviflorum*	star flower; woodland star
Lithospermum incisum	*Lithospermum incisum*	narrowleaf stoneseed; Gromwell; puccon
Lonicera involucrata	*Lonicera involucrata*	black twinberry
Lonicera utahensis	*Lonicera utahensis*	Utah honeysuckle
Lupinus argenteus	*Lupinus argenteus*	silvery lupine
Lupinus sericeus	*Lupinus sericeus*	silky lupine
Mahonia repens	*Mahonia repens*	creeping barberry; Oregon grape, holly grape
Mertensia ciliata	*Mertensia ciliata*	mountain bluebelle
Mimulus guttatus	*Mimulus guttatus*	Yellow monkey flower
Noccaea fendleri	*Noccaea montana*	alpine pennycress
Orogenia linearifolia	*Orogenia linearifolia*	snow drops, Indian potato
Perideridia gairdneri	*Perideridia montana*	gardners yamha; common yampha
Phlox hoodii	*Phlox hoodii*	Hood's phlox
Phlox longifolia	*Phlox longifolia*	long-leaved phlox
Potentilla arguta	*Potentilla arguta*	tall cinquefoil
Potentilla gracilis	*Potentilla gracilis*	slender cinquefoil
Prunus virginiana	*Prunus virginiana*	black chokecherry
Purshia tridentata	*Purshia tridentata*	antelope bitterbrush
Ranunculus glaberrimus	*Ranunculus glaberrimus*	sagebrush buttercup
Ribes lacustre	*Ribes lacustre*	prickly current
Rosa woodsii	*Rosa woodsii*	woods' rose
Rubus parviflorus	*Rubus parviflorus*	thimble berry

Continued on next page

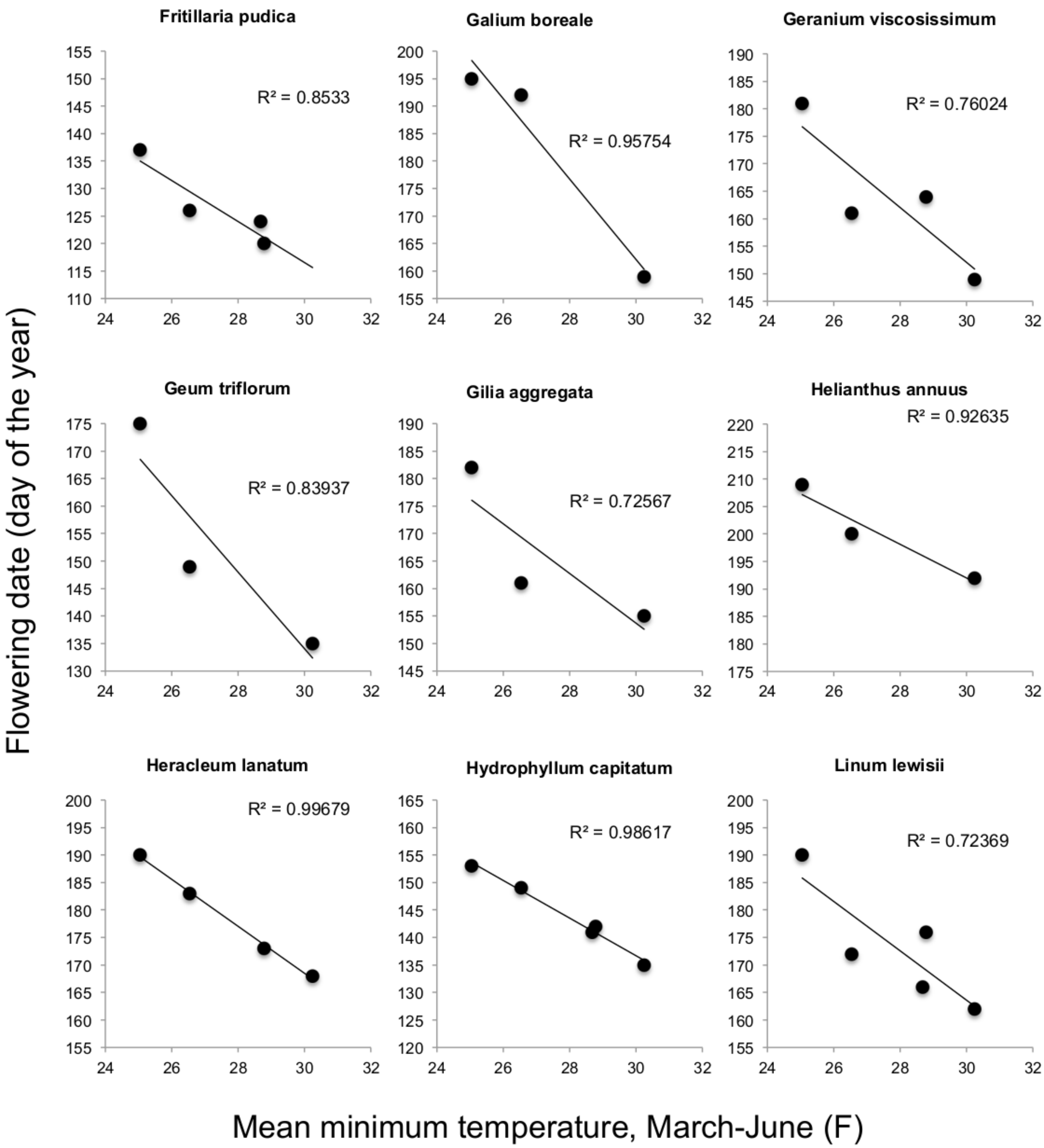
Scientific name (Craighead)	Current scientific name	Common name
Sedum lanceolatum	*Sedum lanceolatum*	spearleaf stonecrop; yellow stonecrop
Shepherdia canadensis	*Shepherdia canadensis*	buffalo berry
Smilacina racemosa	*Maianthemum racemosa*	feathery false lily of the valley; false solomon's seal
Smilacina stellata	*Maianthemum stellatum*	wild lily of the valley
Symphoricaros oreophilus	*Symphoricaros oreophilus*	mountain snowberry
Taraxacum officinale	*Taraxacum officinale*	dandelion
Tragopogon dubius	*Tragopogon dubius*	yellow salsify
Vaccinium membranaceum	*Vaccinium membranaceum*	huckleberry
Viola adunca	*Viola adunca*	early blue violet, or hookedspur violet
Viola nuttallii	*Viola nuttallii*	yellow violet; Nuttall's violet
Wyethia amplexicaulus	*Wyethia amplexicaulus*	mule's ear



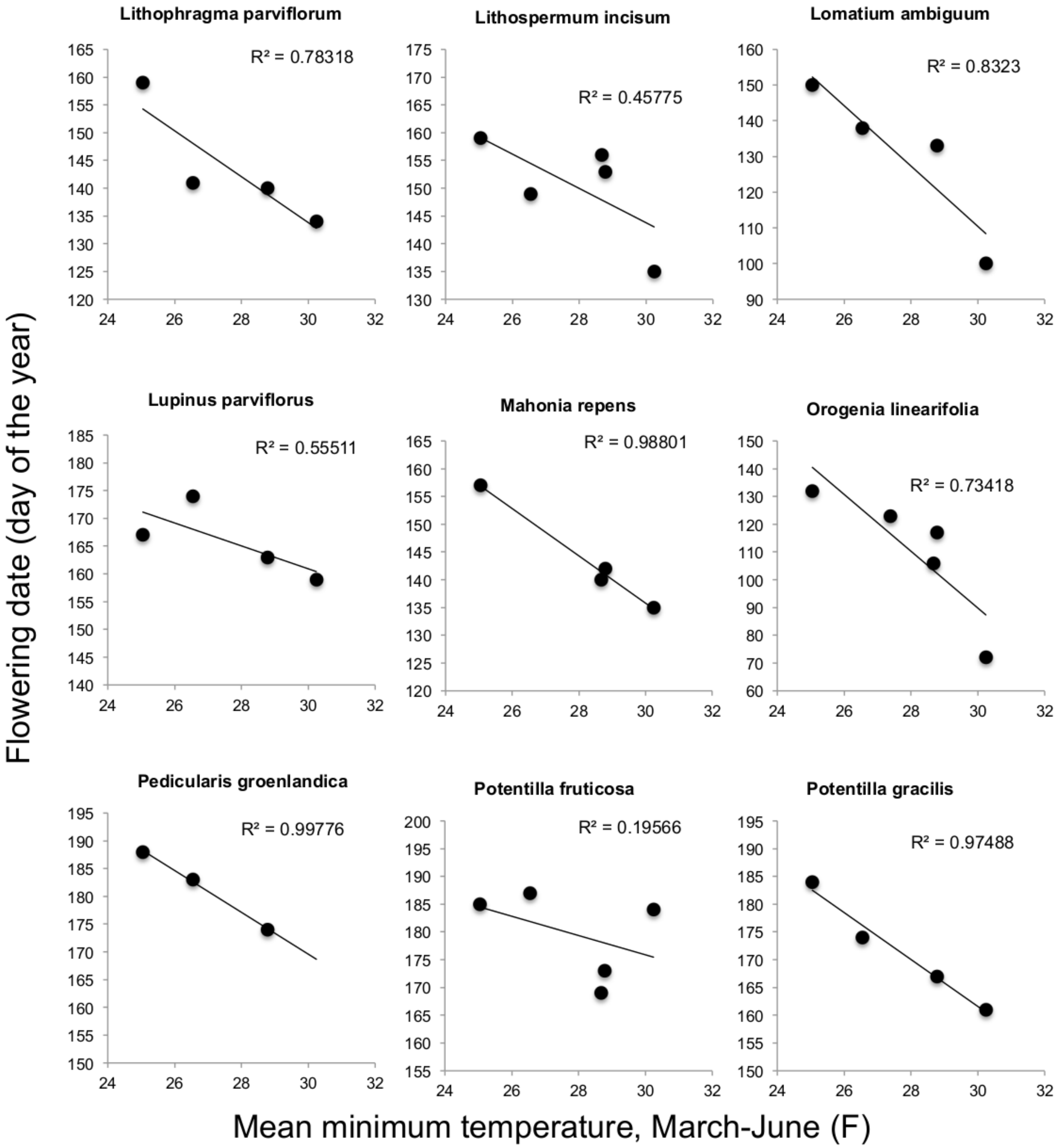
Supplemental Materials, Figure 1



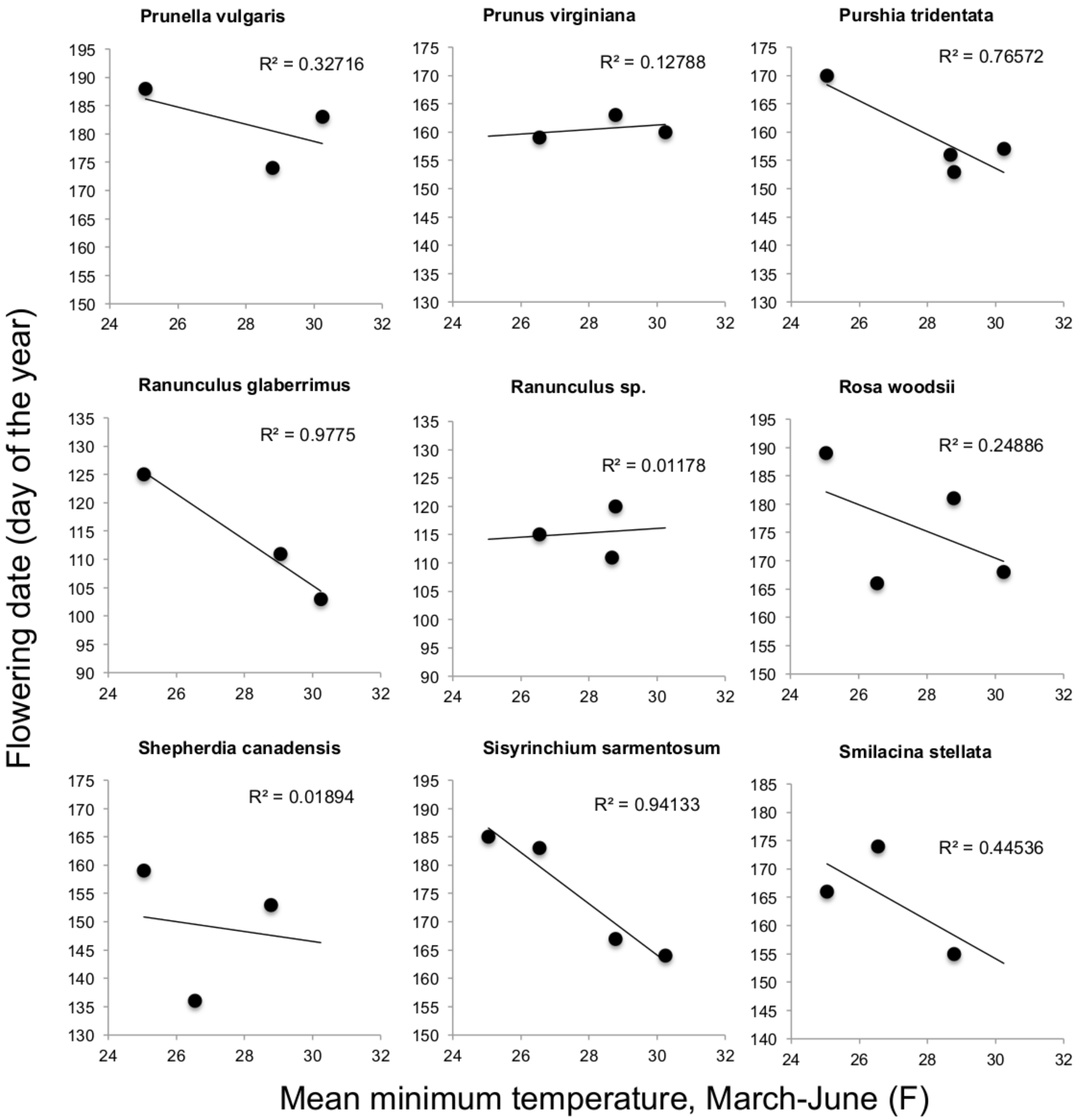
Supplemental Materials, Figure 1. (cont.)



Supplemental Materials, Figure 1. (cont.)



Supplemental Materials, Figure 1. (cont.)



Supplemental Materials, Figure 1. (cont.)