

Do longer growing seasons give introduced plants an advantage over native plants in Interior Alaska?

Christa P.H. Mulder and Katie V. Spellman

Abstract: In interior Alaska, increases in growing season length and rapid expansion of introduced species are altering the environment for native plants. We evaluated whether earlier springs, warmer summers, and extended autumns alter the phenology of leaves and flowers in native and introduced forbs and shrubs in the boreal understory and open-canopy habitats, and whether the responses provide an advantage to either group. We tracked the phenology of 29 native and 12 introduced species over three years with very different spring, summer, and autumn conditions. The native species produced flowers (but not leaves) earlier than the introduced species, and both groups advanced leaf-out and flowering in the early-snowmelt year. However, shifts in phenology between early and late years were similar for both groups. There was no increase in fruit development rate for either group in the warm summer. In contrast, in the year with the extended autumn, the introduced plants extended leaf production and time of senescence much more than native species. While growth form and leaf habit could explain the differences in phenology between native and introduced groups in spring and summer, these traits could not account for differences in autumn. We conclude that in boreal Alaska extended autumns may benefit introduced species more than native ones.

Key words: boreal forest, climate change, deciduous, invasive plants, non-native plants, phenology.

Résumé : Dans l'Alaska intérieur, les augmentations de la durée de la saison de croissance et l'expansion rapide d'espèces introduites modifient l'environnement des plantes indigènes. Les auteurs ont évalué si des printemps hâtifs, des étés plus chauds et des automnes prolongés modifient la phénologie des feuilles et des fleurs d'herbes non graminéennes et d'arbustes indigènes et introduits des habitats de sous-bois boréal et de canopée ouverte, et si l'un ou l'autre groupe en tire un quelconque avantage. Ils ont suivi la phénologie de 29 espèces indigènes et 12 espèces introduites au cours de trois années caractérisées par des conditions printanières, estivales et automnales très différentes. Les espèces indigènes produisaient des fleurs (contrairement aux feuilles) de manière plus hâtive que les espèces introduites, et la sortie des feuilles et la floraison étaient devancées chez les deux groupes lors de l'année où la fonte des neiges a été hâtive. Toutefois, les changements dans la phénologie entre les années hâtives et tardives étaient similaires chez les deux groupes. Il n'y avait pas d'augmentation du taux de développement des fruits chez ces groupes lors de l'été chaud. Par contre, lors de l'année où l'automne s'est prolongé, les plantes introduites prolongeaient la période de production des feuilles et le temps de sénescence beaucoup plus que les plantes indigènes. Alors que la forme de croissance et le port de la feuille pourraient expliquer les différences de phénologie entre les groupes indigènes et les groupes introduits au printemps et à l'été, ces traits ne pourraient expliquer les différences observées en automne. Les auteurs concluent qu'en Alaska boréal, les automnes prolongés peuvent être davantage bénéfiques aux espèces introduites comparativement aux espèces indigènes. [Traduit par la Rédaction]

Mots-clés : forêt boréale, changements climatiques, décidu, plantes envahissantes, plantes non indigènes, phénologie.

Introduction

Boreal forest is the largest vegetation type in North America (comprising approximately 627 million ha, or 29% of the continent north of Mexico), but until recently the plant invasions in this vegetation type have received little attention because of the low number of introduced

species compared with other habitats (Villano and Mulder 2008; Sanderson et al. 2012; Spellman et al. 2014). However, rapid shifts in climate (Wolken et al. 2011), combined with increased fire frequency and extent (Kasischke et al. 2010) and increased anthropogenic activity have contributed to a rapid increase in the number

Received 20 November 2018. Accepted 29 March 2019.

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and extent of introduced species in the boreal forest region (Carlson and Shephard 2007; Sanderson et al. 2012). Historically, cool temperatures and very short growing seasons have likely limited the ability of introduced plants to reproduce. The growing season in Interior Alaska has become warmer and longer over the past 88 years. Since 1930, the cumulative growing degree days (sum of temperatures above 0 °C) has increased by 21% (4.3 degrees per year; Supplementary data, Fig. S1A¹) and the maximum number of consecutive days above freezing also increased by 21% (from 104 to 126 days; Supplementary data, Fig. S1B¹). Continued large increases in temperatures across the state are predicted over the next 80 years (Scenarios Network for Alaska and Arctic Planning 2017), suggesting increasingly hospitable growing season conditions for growth, reproduction, and spread of introduced plant species in interior Alaska.

An advance in the timing of leaf-out and flowering is one of the “fingerprints” of climate change (Parmesan and Yohe 2003). This phenomenon has been extensively studied in temperate (e.g., Bradley et al. 1999; Fitter and Fitter 2002; Menzel et al. 2006; Ge et al. 2011), alpine (e.g., Chapman 2013; CaraDonna et al. 2014; Hart et al. 2014), and subarctic (e.g., Bokhorst et al. 2011; Mulder et al. 2017) habitats, but boreal forest has received relatively little attention, and most boreal work has been based on remote sensing approaches rather than tracking of individual species (e.g., Park et al. 2015; Crabbe et al. 2016; but see Ovaskainen et al. 2013).

Species within a community differ in their responses to environmental variability, with some species showing little or no response to environmental shifts (e.g., Bradley et al. 1999; Fitter and Fitter 2002; Mulder et al. 2017). Introduced plants may be more plastic in the timing of leafing and flowering and have a greater ability to track environmental conditions (Willis et al. 2010; Wolkovich and Cleland 2011; Fridley 2012; Wolkovich et al. 2013); this may allow them to take advantage of “vacant phenological niches” that arise as earlier springs and later autumns result in suitable growing conditions when native species are not active (Wolkovich and Cleland 2011; Fridley 2012). Finally, in areas with short growing seasons (such as the boreal forest and arctic regions), a longer growing season may allow introduced species that were previously not able to flower and mature seeds within one season to do so. These mechanisms could result in an increased competitive advantage of introduced species relative to native species and ultimately a shift in community composition toward greater representation by introduced species.

The vast majority of high-latitude plant species, including boreal species, produce their leaf and flower buds at least a year prior to bud-burst (Sørensen 1941;

Hodgson 1966; Billings and Mooney 1968; C.P.H. Mulder and P.K. Diggle, unpublished data), and the timing of budburst is limited by snow melt and ground thaw for most species (Barr et al. 2009; Wipf 2010) rather than limited by photoperiod (Zohner et al. 2016; Richardson et al. 2018). Furthermore, while in temperate areas the chilling requirements for budburst may not be met in warm years (Heide 2003; Yu et al. 2010), the winter chilling capacity of the Subarctic probably greatly exceeds chilling requirements (Murray et al. 1989; Heide 1993). As a result, leaf production in spring tends to be rapid and highly synchronous across species (Wipf 2010; Park et al. 2015; C.P.H. Mulder's personal observation), and flower production peaks early in the season compared with other habitats (Bliss 1971; Wolkovich and Cleland 2011), as is expected given the short time period available for fruit and seed maturation. The start of the season (which we defined as five consecutive days above freezing to prevent inclusion of short above-freezing events in mid-winter) has varied by about a month over the past 88 years, and has shifted earlier by about a week (Supplementary data, Fig. S1C¹). We would expect changes in spring conditions to result in shifts in leaf and flower phenology that are synchronized across many species. However, warmer temperatures may trigger tissue de-hardening and increase the risk of damage from freeze-thaw cycles to vulnerable leaf and flower buds (e.g., Wipf et al. 2006; Augspurger 2009; Bokhorst et al. 2011; Richardson et al. 2018), and this may explain the lack of a response to shifts in time of snow melt in some species. Introduced species in interior Alaska originate from native ranges at lower latitudes. While the vast majority of native species are perennials (Hultén 1968), annuals are common among introduced species in interior Alaska (Carlson et al. 2005; AKEPIC 2018) and are likely to flower later because no flower buds are present at the start of the season. Furthermore, if the leaf and flower buds of perennial introduced species are less advanced in their development at the time of snowmelt than those of native species, we would expect to see later development overall and possibly weaker responses to earlier snow melt.

Development in plants is sped up under warmer temperatures because of temperature-dependent enzymatic catalytic reactions (Went 1953; Atkinson and Porter 1996), and an advance in the time of fruit production has also been found in numerous temperate and arctic communities (Menzel et al. 2006). For alpine and arctic species there is strong evidence that temperature (often expressed as cumulative temperature above a baseline temperature) drives plant phenology, especially for later stages of phenology such as fruit development (e.g., Huelber et al. 2006; Wipf 2010). If this is also the case for

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjbb-2018-0209>.

boreal forest species, then we might expect that phenology of later reproductive stages such as fruit ripening will be affected both by the time of snow melt (which affects flowering time) and by temperatures during fruit development. We might also expect introduced species that are adapted to the higher cumulative temperatures at lower latitudes to respond more strongly than native species to warm summers.

In interior Alaska, there is also considerable variation in the timing of the end of the growing season (a range of 45 days over the past 88 years, when defined as five consecutive days below freezing), but no evidence for a shift in the timing over this time period (Supplementary data, Fig. S1C¹). In autumn, deciduous boreal species initiate senescence and nutrient resorption while light is abundant and well before temperatures drop in most years, and the dominant cue for growth cessation and bud set is photoperiod (Lambers et al. 2008; Way and Montgomery 2015). While a meta-analysis demonstrated that high-latitude tree species show weaker phenological responses to temperature in autumn than low-latitude trees (Gill et al. 2015), an experimental study near the southern range of the boreal forest (northern Minnesota, 47°30'N) showed strong linear responses to temperature for woody species, but with greater delays under warming for understory shrubs than for tree species (Richardson et al. 2018). It is therefore unclear what drives senescence in understory plants in high-latitude boreal forest. Introduced woody deciduous species in temperate forests of the eastern United States show extended autumn leaf phenology compared with their native counterparts (Fridley 2012). Given the contradictory results for the strength of the response of high-latitude and boreal trees to variation in temperature, and lack of comparisons between native and introduced shrubs or forbs in boreal forest, a priori predictions for shifts under warming cannot be made.

A high proportion of native shrubs in Alaska (~27%) are evergreen (Viereck and Little 2007) and an additional subset of forbs retain their leaves over the winter (Hultén 1968); in years with an extended autumn these species may be able to prolong their period of active growth and photosynthesis with little risk. Many of these undergo "winter reddening" (increasing anthocyanin content) but it is unknown what triggers this process (Hughes 2011) and whether it is affected by warming.

In addition to nativity, two variables are likely to affect the responses of plants to interannual variation: leaf habit, and growth form. These classifications are associated with sets of functional traits that are largely independent of each other (Díaz et al. 2016); for example, woody plants have leaves that range from short-lived and highly resource acquisitive (e.g., high nitrogen content, low mass per area, low % fiber and lignin) to long-lived and highly resource conservative (e.g., low nitrogen content, high mass per area, high % fiber and lignin). Proportions

of species with specific growth forms and leaf life histories differ between native and introduced species in the boreal forest, both in Alaska in general and in our dataset. A high proportion of native understory species are shrubs, whereas the vast majority of introduced plants are forbs (or graminoids, which are not considered in this study) (Hultén 1968; Viereck and Little 2007; AKEPIC 2018). Furthermore, while most introduced species in interior Alaska are summergreen (producing leaves in spring and losing them in autumn), many native species are evergreen or wintergreen (Hultén 1968; Viereck and Little 2007; AKEPIC 2018; Table 1).

Plants that are closely related tend to flower and fruit at similar times, and, in general, earlier-flowering plants show a greater response to interannual variation in time of flowering (Davies et al. 2013). Timing of leaf-out is also phylogenetically conserved (Panchen et al. 2014). However, there is little evidence that variation in flowering times across years is phylogenetically conserved (Davies et al. 2013). Native and introduced species differ in their evolutionary histories: plants in the Fabaceae and Asteraceae are over-represented among introduced species relative to native species in Alaska's flora, whereas other families that are well-represented among native species (e.g., Ericaceae) are not represented among the introduced species (Carlson et al. 2005). Thus, we expect the average timing of leaf and flower production and senescence to differ between native and introduced species, but we have no predictions about the relative size of shifts in phenology between years.

While populations of introduced species are increasing rapidly across interior Alaska (AKEPIC 2018), very few populations have moved off the human footprint (Carlson and Shephard 2007; Conn 2008; AKEPIC 2018). The vast majority of species are ruderals associated with open canopy habitats such as river banks, recently burned forest, road edges, and trails (Villano and Mulder 2008; Bella 2011). Unlike in more southern parts of the state, there are very few instances to date where introduced species have colonized and persisted in boreal forest communities beyond the forest and disturbance edges (AKEPIC 2018). However, if longer growing seasons alter the competitive balance between introduced and native species, the risk of invasion may increase. Therefore, this study focuses on common native species found in a range of habitats (disturbed habitat, black spruce forest, and mixed deciduous/conifer forest) and compares their phenology with that of introduced species primarily associated with disturbed habitat (Table 1).

In this paper we tracked the development of leaves and flowers in 41 species over three growing seasons with very different weather patterns. We asked the following questions:

1. Do native and introduced species differ in their responses to interannual variation in spring, summer, and autumn conditions?

Table 1. Species used in the study.

Species	Family	Origin	Habitat	Growth form	Leaf habit	Plant LH	2013	2014	2015
<i>Achillea millefolium</i> var. <i>borealis</i>	Asteraceae	N	MF&I	F	S	P	x	x	x
<i>Arctous rubra</i>	Ericaceae	N	MF	DS	S	P	x	x	x
<i>Arctostaphylos uva-ursi</i>	Ericaceae	N	MF	DS	E	P	x	x	x
<i>Caragana arborescens</i>	Fabaceae	I	D	TS	S	P	x	x	x
<i>Castilleja caudata</i>	Orobanchaceae	N	MF	F	S	P	x	x	NA
<i>Chamaedaphne calyculata</i>	Ericaceae	N	BS	TS	E	P	x	x	x
<i>Chamerion angustifolium</i>	Onagraceae	N	D	F	S	P	x	x	x
<i>Chenopodium album</i>	Chenopodiaceae	I	D	F	S	A	x	x	x
<i>Cornus canadensis</i>	Cornaceae	N	MF	F	W	P	x	x	x
<i>Crepis tectorum</i>	Asteraceae	I	D	F	S	A	x	x	x
<i>Empetrum nigrum</i>	Empetraceae	N	BS	DS	E	P	x	x	x
<i>Eurybia sibirica</i>	Asteraceae	N	D	F	S	P	x	x	x
<i>Geocaulon lividum</i>	Santalaceae	N	MF	F	S	P	x	x	x
<i>Hedysarum alpinum</i>	Fabaceae	N	D	F	S	P	x	x	x
<i>Hedysarum boreale</i>	Fabaceae	N	D	F	S	P	x	x	x
<i>Iris setosa</i>	Iridaceae	N	D	F	S	P	x	x	x
<i>Lepidium densiflorum</i>	Brassicaceae	I	D	F	S	A/B	x	x	x
<i>Linnaea borealis</i>	Caprifoliaceae	N	MF	F	W	P	x	x	x
<i>Matricaria discoidea</i>	Asteraceae	I	D	F	S	A	x	x	x
<i>Medicago sativa</i> subsp. <i>falcata</i>	Fabaceae	I	D	F	S	A/P	x	x	x
<i>Melilotus albus</i>	Fabaceae	I	D	F	S	A/B/P	x	x	x
<i>Mertensia paniculata</i>	Boraginaceae	N	MF	F	S	P	x	x	x
<i>Orthilia secunda</i>	Ericaceae	N	MF	DS	W	P	NA	x	x
<i>Petasites frigidus</i>	Asteraceae	N	MF&BS	F	S	P	x	x	x
<i>Plantago major</i>	Plantaginaceae	I	D	F	S	P	x	x	x
<i>Polygonum aviculare</i>	Polygonaceae	I	D	F	S	A/P	x	x	x
<i>Comarum palustre</i>	Rosaceae	N	BS	F	S	P	x	x	x
<i>Rhododendron groenlandicum</i>	Ericaceae	N	MF&BS	TS	E	P	x	x	x
<i>Rhododendron tomentosum</i>	Ericaceae	N	BS	TS	E	P	x	x	NA
<i>Rosa acicularis</i>	Rosaceae	N	MF	TS	S	P	x	x	x
<i>Rubus arcticus</i>	Rosaceae	N	MF	F	S	P	x	x	x
<i>Rubus chamaemorus</i>	Rosaceae	N	BS	F	S	P	x	x	x
<i>Rubus idaeus</i>	Rosaceae	N	D	TS	S	P	x	x	x
<i>Shepherdia canadensis</i>	Eleagnaceae	N	MF	TS	S	P	x	x	x
<i>Solidago canadensis</i>	Asteraceae	N	D	F	S	P	x	x	x
<i>Taraxacum officinale</i>	Asteraceae	I	D	F	S	P	x	x	x
<i>Trifolium repens</i>	Fabaceae	I	D	F	S	P	x	x	x
<i>Vaccinium uliginosum</i>	Ericaceae	N	MF	TS	S	P	x	x	x
<i>Vaccinium vitis-idaea</i>	Ericaceae	N	MF&BS	DS	E	P	x	x	x
<i>Viburnum edule</i>	Adoxaceae	N	MF	TS	S	P	x	x	x
<i>Vicia cracca</i>	Fabaceae	I	D	F	S	P	x	x	x

Note: Scientific names follow the recommendations of the Integrated Taxonomic Information System (<https://www.itis.gov/>, accessed November 2018). Origin: N, native; I, introduced. Habitat types: MF, mixed deciduous and coniferous forest; BS, black spruce; D, disturbed habitat (e.g., along trails). Growth form: F, forb; DS, dwarf shrub; TS, tall shrub. Leaf habit: S, summergreen; E, evergreen; W, wintergreen. Plant life history (LH) based on the USDA PLANTS website (USDA, NRCS 2019): A, annual; B, biennial; P, perennial; for species with multiple codes listed in USDA PLANTS, we indicated life history strategy observed in our sites in **bold**. The last three columns indicate whether a species was included in that year or not.

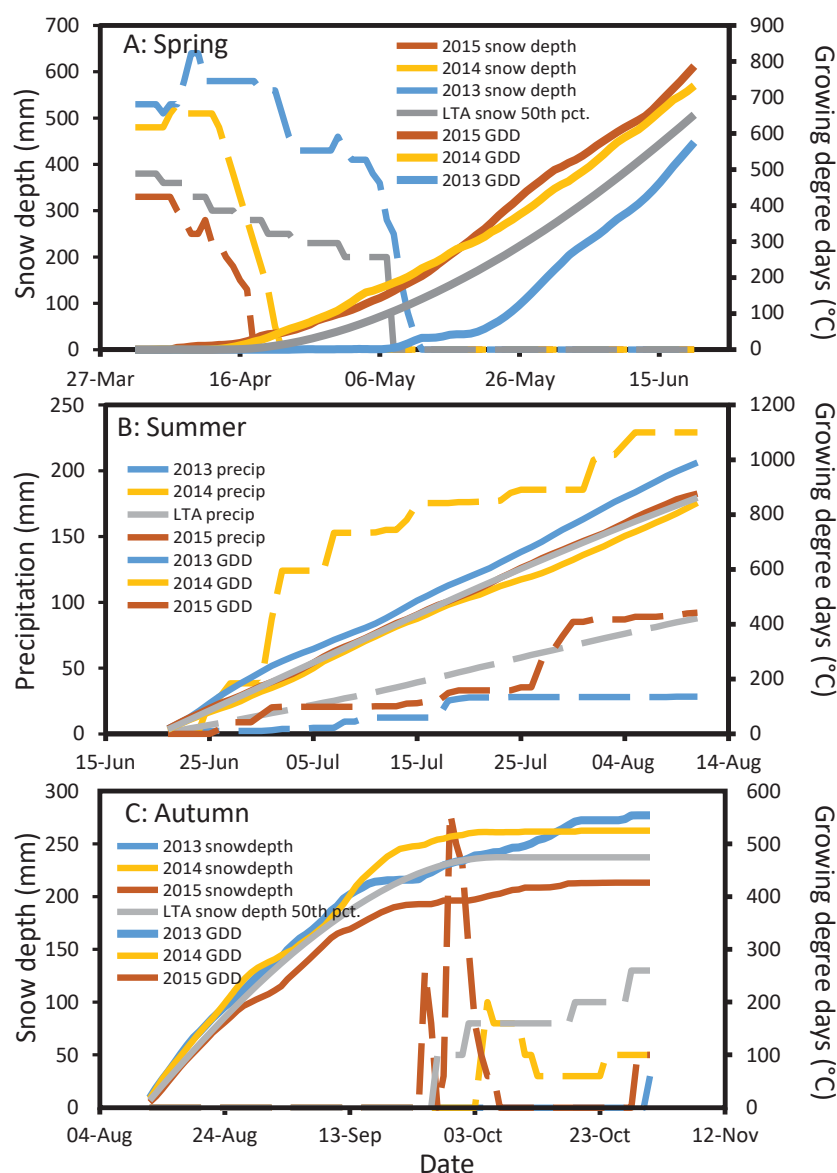
2. If there are differences in native and introduced responses, do these provide evidence for an advantage for either group (by increasing the growing season length for leaves or flowers/fruit)?
3. Do species with different growth forms or different leaf life histories differ in their responses to interannual variation in spring, summer, and autumn conditions? If so, can these explain differential responses of native and introduced species to environmental conditions?

4. Do species in different families differ in phenology? If so, can these help explain differences in phenology of native and introduced species?

Materials and methods

We collected phenological data for 41 plant species near Fairbanks, Alaska (64.8°N, 147.9°W) in 2013, 2014, and 2015. These years contrasted sharply in terms of spring, summer, and autumn conditions (Fig. 1). Spring came late in 2013 (cool temperatures and high snow, first

Fig. 1. Differences between years in spring (A), summer (B), and autumn (C) conditions compared with the long-term averages ("LTA", data from 1981–2010). Snow depth (left axis) indicates total snow pack present, while precipitation is cumulative. "LTA 50th pct" refers to the 50th percentile of daily nonzero snow depth for 29-day windows centered on each day. Growing degree days ("GDD", right axis) are cumulative degrees above 0 °C. Data are from the Fairbanks International Airport weather station and obtained via National Centers for Environmental Information.



snowfree day May 12), early in 2015 (warm temperatures and little snow, first snowfree day April 18), and was intermediate in 2014 (first snowfree day April 22; Fig. 1A). Summer was warmest and driest in 2013 and coolest and wettest in 2014 (Fig. 1B). In Interior Alaska, snow events in September may be followed by a period of snow melt, but historically once snow falls in late September or early October, the ground remains snow-covered until spring (Fig. 1C). In 2013, autumn was greatly extended, with above-freezing temperatures and no snow until the very end of October, whereas 2014 showed the more typical freeze-up and first snow in the first week October, and in 2015 autumn ended early with substantial autumn snow in the last week of September (Fig. 1C). These

three focal years encompassed a wide range of conditions for all three seasons when compared with the historical record (88 years). In spring, focal years encompassed the 16th–96th percentiles for the start of the season (five consecutive days > 0 °C), and the 28th–99th percentiles for first snowfree day. In summer, they encompassed the 55th–100th percentile for the warmest summer temperature (cumulative growing degrees with base = 0 °C for 21 June – 11 August), and the 3rd–100th percentile for precipitation. In autumn, they encompassed the 60th–91st percentile for the season end date (five consecutive days < 0 °C), and the 5th–94th percentile for first date with snow accumulation >10 cm in

Table 2. Definitions of phenological variables used.

Season	Variable name	Definition
Spring	<i>firstleaf</i>	Date of first fully expanded leaf
	<i>firstflower</i>	Date of first open flower
	<i>peakflower</i>	Date for which plant phenophase = 2 (open flower)
Summer	<i>firstunripe</i>	Date of first unripe fruit (swollen ovary)
	<i>firstripe</i>	Date of first ripe fruit
	<i>firstflower–firstunripe</i>	No. days from first open flower to first unripe fruit
	<i>halfripe</i>	Date for which phenophase = 4.5 (midway between 4 = unripe and 5 = ripe fruit)
	<i>peakflower–halfripe</i>	No. days between peak flower and half-ripe fruit
Autumn	<i>lastflower</i>	Date of last flower opening
	<i>lastleaf</i>	Date of last new leaf emerging
	<i>lastunripe</i>	Date of last new unripe fruit produced
	<i>senesce50</i>	First date on which 50% of leaves (or leaf area) in summergreen species had senesced
	<i>winterred</i>	Date on which wintergreen or evergreen species reached full winter reddening
Whole growth	<i>producelength</i>	No. days from <i>firstleaf</i> to <i>lastleaf</i>
	<i>greenlength</i>	No. days from <i>firstleaf</i> to <i>senesce50</i>

Note: Most variables were calculated as the mean date (or No. of days) for individual plants (replicates) of a given species in a given year. We estimated values for the variables *peakflower*, *halfripe*, and *senesce50* using linear regressions, based on plant phenophase values from all replicates of a given species in a given year.

autumn. Generally, warmer summers are also drier (Pearson's $r = 0.36$, $t_{[86]} = 3.62$, $P < 0.001$).

The 41 focal species included 29 native and 12 introduced nongraminoid understory species (Table 1). Introduced status was determined using Alaska Exotic Plants Information Clearinghouse (AKEPIC) at the Alaska Center for Conservation Science. Selection criteria for the species included: species had a wide distribution in the boreal forest (Hultén 1968); was abundant at our field sites; was easily accessible by foot trail at our sites; and at least five individuals were sexually reproductive. Introduced species selected included 8 of the 10 most common non-graminoid species in interior Alaska (based on frequency in Alaska's non-native flora inventory database; AKEPIC 2018). All but one introduced species were forbs; the single woody species, *Caragana arborescens*, is one of only two common invasive woody species in this area (the other, *Prunus padus*, is common along waterways but was not yet common in the areas we surveyed, or present only in a pre-reproductive stage). Of the introduced forbs, three are annuals and four can be annuals or perennials (Table 1); at our sites *Melilotus albus* is biennial, *Medicago sativa* is perennial, and *Lepidium densiflorum* and *Polygonum aviculare* are annual (K.V. Spellman's personal observation; Klebesadel 1992a, 1992b; AKEPIC 2018).

The dataset included 27 forbs, 9 "tall" shrubs (>0.5 m), and 5 dwarf shrubs (<0.3 m) (Table 1). Plants were classified following Chabot and Hicks (1982) as "summergreen" (leaves are produced in spring and lost in the autumn of the same year; maximum leaf age is <4 months; 32 species), "wintergreen" (leaves are produced in spring or early summer and retained during the winter; maximum leaf age = 1 year; 3 species) or "evergreen" (leaves are produced in spring or early summer and retained for >1 year; 6 species). For each species, data were collected in the habitat where it was most commonly found: black spruce forest, mixed white spruce/

deciduous forest, or in disturbed habitat (e.g., along trails) (Table 1). Data were collected at three main locations: within the Bonanza Creek Long Term Ecological Research site (64.70°N, 148.30°W), at a pull-out near the Bonanza Creek site (64.77°N, 148.28°W, and along the forested trail system on the UAF campus (64.86°N, 147.86°W).

In each year we monitored phenology from the date of first flower or leaf emergence to the date of 100% senescence or autumn snow. We tagged 5–10 ramets per species and counted the number of buds, flowers, or fruit on each plant using a scoring system for each phenophase (described in detail in Spellman and Mulder 2016): unopened buds (phenophase = 1), flowers (phenophase = 2), "petaldrop" (flowering completed but ovary not (yet) swollen; phenophase = 3), unripe fruit (phenophase = 4), and ripe fruit (phenophase = 5). A phenophase for each plant was calculated based on the weighted average of these phenophases (e.g., a plant with 2 buds and 1 flower would have a phenophase of 1.33). Where there were many reproductive units or inflorescences, percentages in each category were estimated visually. Similarly, we counted the number of emerging leaves, fully expanded leaves, percent leaf senescence (either as number of leaves that had turned colour or as the mean % of leaf area that had turned colour, depending on the species), and date of maximum winter reddening (*winterred*, only for evergreen and wintergreen species in 2014 and 2015).

We used the phenological data to calculate response variables. For spring we focused on the early stages of leaf and fruit production: date of first fully expanded leaf (*firstleaf*), date of first open flower (*firstflower*), and date of peak flower production (*peakflower*) (see Table 2 for details). For summer we focused on the time it took for plants to develop unripe and ripe fruits from flowers: number of days from first flower to first unripe fruit (*firstflower–firstunripe*), and number of days from peak

flowering to half ripe fruits (*peakflower-halfripe*). For autumn we focused on the cessation of leaf and flower production and preparation for winter, regardless of the time of year (i.e., some “autumn” responses occurred prior to “summer” responses). Autumn response variables were date of last new flower produced (*lastflower*), date of last new leaf (*lastleaf*), date of 50% senescence (*senesce50*; only for summergreen species), and date of maximum winter reddening (*winterred*, only for evergreen and wintergreen species in 2014 and 2015). We calculated two variables related to total growing season length: *leafprod*, the number of days during which new leaves are being produced (all species), and *greenlength*, the number of days between first leaf production and 50% senescence (summergreen plants only).

Analyses

To evaluate differences between native and introduced plants in their responses to interannual variation we ran a maximum-likelihood based mixed-effects model with nativity (native or introduced) as a fixed effect and year and species as random effects using the “lmer” function in the “lme4” package in R (R Development Core Team, version 3.5.2, 2018). We started with the full model (including nativity, year, nativity given the year, and species identity) and evaluated the impact of each term (except species identity) by dropping it from the model and comparing the simplified model to the more complex one using a chi-square value from a likelihood ratio test. A significant nativity-by-year term indicates that introduced species differ from native species in the strength and (or) direction of their response. We controlled the family-wise error rate by comparing the *P*-values from the set of 33 tests (11 response variables $\times$ 3 explanatory variables) to values generated using the Benjamini–Hochberg procedure (Benjamini and Hochberg 1995) with the false discovery rate set at 0.05. Sample size differed by response variable (e.g., in 2014 many species did not produce any fruit owing to low pollinator activity in bad weather, so sample size is greater for the “first flower” than the “first unripe fruit” variable).

To evaluate phenological responses by growth form or leaf habit regardless of nativity, we ran models that included growth form or leaf habit, plus year and species identity as random variables, and compared these models with models without growth form or leaf habit. Because all except one of the introduced species were summergreen forbs but many of the native species were deciduous or evergreen shrubs, differences between native and introduced species may simply reflect the different growth forms or leaf habits. Therefore, when differences by nativity were detected for the entire dataset we repeated our tests for nativity using only summergreen forbs. A small sample size and low overlap in plant families between our groups of native and introduced species precluded the type of explicit inclusion of phylogeny used in some studies (e.g., Wolkovich et al. 2013;

Panchen et al. 2014): of the 13 families represented by native species and six families represented by introduced species, only two (Asteraceae and Fabaceae) included representatives from both groups. We therefore could not formally evaluate the role of phylogeny in driving differences between native and introduced species, but simply test for an overall effect of including family as a random variable in models that also included year and species identity, and describe any patterns in families with at least three species that may help explain differences by nativity.

Results

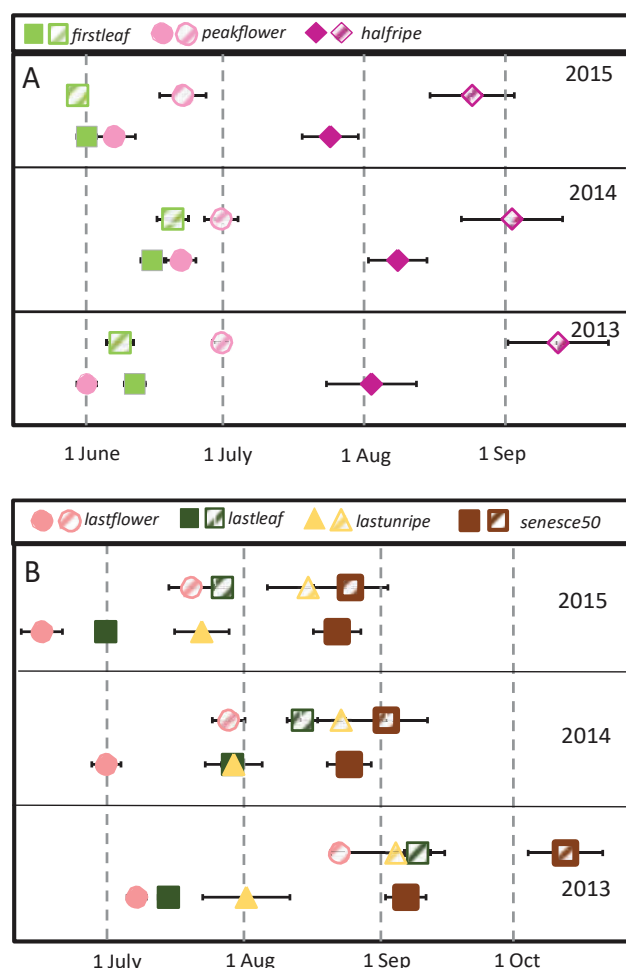
Spring

All three spring response variables (*firstleaf*, *firstflower*, and *peakflower*) differed between years, with earlier dates for 2015 (the early spring year) than for the other two years (Fig. 2A). Native and introduced species did not differ in *firstleaf*, but *firstflower* and *peakflower* were earlier in native species (Table 3; Fig. 2A). However, when the dataset was limited to deciduous forbs there were no differences by nativity (*firstflower*: $\chi^2 = 0.91$, $P = 0.34$; *peakflower*: $\chi^2 = 1.47$, $P = 0.23$). None of the spring response variables showed a significant interaction between nativity and year, indicating shifts between years were similar for native and introduced plants (Table 3; Fig. 2A).

There was a strong negative correlation between *firstflower* and the size of the shift from 2013 to 2015 (Pearson's $r = -0.63$, $n = 37$, $P < 0.001$), indicating that plants that flowered earlier showed greater interannual variation. In contrast, there was no correlation between *firstleaf* and the size of the shift between years (Pearson's $r = 0.15$, $n = 35$, $P = 0.39$). While *firstleaf* and *firstflower* themselves were not correlated (Pearson's $r = -0.13$, $n = 33$, $P = 0.47$), there was a marginally significant correlation between shifts for leaves and flowers (Pearson's $r = 0.32$, $n = 33$, $P = 0.067$): plants with high interannual variation in flowering also had high interannual variation in leaf-out. Leaf-out was highly synchronous in both native and introduced species, as was flowering for native species, but flowering was less synchronous in introduced species (Fig. 3). This pattern was consistent across years (data not shown), and species were fairly consistent in the order (out of 41 species) in which they flowered (average change in rank between years: 6.7 out of 41) but less consistent in the order in which they leafed out (average change of rank between years = 11.5). Within the introduced species, annuals tended to produce leaves early but did not show any pattern with respect to timing of flowering (Fig. 3, pink markers).

Growth form affected the absolute timing of flower production, as well as timing relative to leaf production (Table 4; Fig. 4A). Whereas dwarf shrubs produced flowers approximately 2 weeks prior to leaf production and tall shrubs almost simultaneously with leaf production, flower production in forbs occurred several weeks after

Fig. 2. Phenology of native and introduced species by year. Native species are indicated by solid markers and introduced species by hashed markers. Values are date means $\pm$ SEM. (A) Spring phenology: first leaf, peak flowering, and half-ripe fruit. (B) Fall phenology: last flower, last leaf, last unripe fruit, and 50% senescence (for summergreen species). Note that not all phenological stages are presented here; data on additional stages can be found in the Supplementary data, Table S1¹.



leaf production (≈ 22 days). Similarly, flower production occurred early and well before leaf production in evergreen plants, but the reverse was true for summergreen plants, with wintergreen plants showing an intermediate pattern (Fig. 4B), although these differences were not statistically significant after controlling for family-wise error rate (Table 4). Neither growth form nor leaf habit interacted with year, and family did not explain variation in these variables (Table 4).

Summer

Developmental time from *firstflower* to *firstunripe* or from *peakflower* to *halfripe* did not differ between native and introduced species (Table 3). There were no significant differences between years for either of the measures of developmental times (*firstflower*–*firstunripe* or *peakflower*–*halfripe*; Table 3). As a result, the timing for later stages of

reproductive development (*firstripe* and *halfripe*) mirrored that of earlier bud and flower stages: more advanced in 2015 than in the other two years, and more advanced in native than in introduced species (Fig. 2A for *halfripe*; see the Supplementary data, Table S1¹ for values for *firstunripe* and *firstripe*). There was no interaction between nativity and year for either variable (Table 3).

Tall and dwarf shrubs produced their first unripe fruit 3–4 weeks before forbs did (Supplementary data, Table S1¹), but there was no difference between growth forms in *firstflower*–*firstunripe* or *peakflower*–*halfripe*, and no interaction with year (Table 4). Leaf habit and family did not explain *firstflower*–*first unripe* or *peakflower*–*halfripe* (Table 4).

Autumn

Lastleaf and *lastflower* differed between years, with the latest cessation in 2013 (when above-freezing temperatures continued until the end of October) and the earliest cessation in 2015 (Table 3; Figs. 2B and 5A). Introduced species continued producing new leaves and flowers later than native species in every year, but there was a significant interaction between year and nativity only for *lastleaf*: the difference was much greater in 2013 (the year with extended warm temperatures) than in 2014 or 2015 (Table 3; Figs. 2B and 5A). When only summergreen forbs were compared, this interaction persisted: introduced species extended leaf production for 44 days in 2013 compared with 2015 (the difference was 14 days for native species) ($\chi^2_1 = 10.34$, $P = 0.001$).

Introduced plants produced their last unripe fruit later than native plants, but there were no differences between years, and no interaction between year and nativity (Table 3).

To evaluate the extent to which indeterminate leaf production explained these results, we calculated the number of days between production of a least 5% of leaves and at least 85% of leaves in 2014, the year with the closest to average weather (we used 5%–85% rather than 0%–100% to prevent a single very early leaf or a few very late leaves from driving results). This produced a continuum of values from 0 (all leaves observed on a single date) to 60 (almost continuous leaf production). For introduced species this measure of within-plant leaf synchrony was almost twice as long as for native species (27.6 ± 5.3 days vs. 16.0 ± 3.1 days), but there was no relationship between this measure of leaf synchrony and the shift in *lastleaf* between 2013 (the earliest year) and 2015 (the latest year; Pearson's $r = 0.33$, $t_{[28]} = 1.7$, $P = 0.08$).

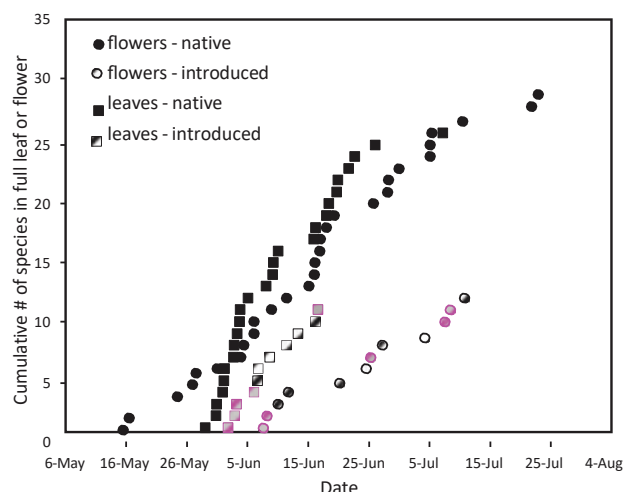
Forbs produced their last flowers later than tall shrubs, but there was no interaction with year (Table 4; Fig. 4C). Evergreen species ceased flower production earlier than summergreen or wintergreen species, but again there was no interaction with year (Table 4; Fig. 4D). For *lastleaf* there was no significant effect of growth form or leaf habit, nor any interaction with year for either (Table 4; Figs. 4C and 4D). Family did not affect *lastleaf*,

Table 3. Results of tests for effects of nativity, year, and their interaction on response variables.

Season	Variable	N	Nativity (df = 1)		Year (df = 1)		Nativity by year interaction (df = 3)	
			χ^2	P	χ^2	P	χ^2	P
Spring	<i>firstleaf</i>	36	0.27	0.604	33.00	<0.001	1.24	0.743
	<i>firstflower</i>	41	5.81	0.016	28.44	<0.001	1.43	0.697
	<i>peakflower</i>	41	7.11	0.008	30.81	<0.001	0.37	0.947
Summer	<i>firstflower–firstunripe</i>	40	0.33	0.565	<0.01	0.999	<0.01	0.999
	<i>peakflower–halfripe</i>	36	2.16	0.141	<0.01	0.999	<0.01	0.999
Autumn	<i>lastflower</i>	41	19.07	<0.001	41.84	<0.001	4.51	0.211
	<i>lastleaf</i>	35	15.56	<0.001	16.54	<0.001	10.22	0.017
	<i>lastunripe</i>	40	15.01	<0.001	2.72	0.099	0.96	0.812
	<i>senesce50</i>	29	7.54	0.006	17.91	<0.001	10.39	0.016
	<i>winterred</i>	8	NA	NA	7.41	0.006	NA	NA
Whole season	<i>leafprod</i>	36	12.03	<0.001	1.88	0.171	21.09	<0.001
	<i>greenlength</i>	27	3.34	0.068	17.44	<0.001	11.54	0.009

Note: Models included species identity as a random variable. *P*-values in **bold** indicate significant differences following a Benjamini–Hochberg procedure with a false discovery rate of 0.05. *N*, number of species.

Fig. 3. Cumulative number of species with fully expanded leaves or in full flower over time by origin (native or introduced). Pink markers (with a grey background) represent annuals. Dates are means across all years.



but it did affect *lastflower* (Table 4). For families with three or more species, the families that ceased flower production the earliest were the Ericaceae (on average 13 June, $n = 3$) and Rosaceae (19 June, $n = 5$), and the latest were the Asteraceae (28 July, $n = 6$) and Fabaceae (29 July, $n = 7$). *Lastunripe* was not explained by growth form, leaf habit, or family (Table 4). When only deciduous forbs were used, introduced plants continued to produce their last unripe fruit later than native plants ($\chi^2 = 10.68$, $P = 0.0001$).

In summergreen species the timing of 50% leaf senescence (*senesce50*) differed between years and between native and introduced species, with a strong interaction between year and nativity (Table 3). In 2013 (the late-autumn year), introduced species delayed leaf senescence for ≈ 35 days longer than native species, while in 2014 and 2015 the difference was small (8 and 3 days resp.; Fig. 2B). When only deciduous forbs were evalu-

ated, the difference between *senesce50* in native and introduced species remained statistically significant ($\chi^2 = 4.92$, $P = 0.027$), but there was no longer a significant interaction with year ($\chi^2 = 6.19$, $P = 0.10$). There was no effect of growth form or family on timing of leaf senescence. Species that retained their leaves over the winter reached winter reddening in 2014 later than in 2015 by more than a month (≈ 34 days), but there were no differences between leaf habits or growth forms (Tables 3 and 4).

The number of days during which new leaves were produced (*leafprod*) was greater for introduced species than for native species, and there was a strong interaction with year: in 2013 introduced species approximately doubled the number of days on which leaves were produced compared to 2014, whereas native species showed little change from year to year (Table 3; Fig. 5A). There were no differences between growth forms or leaf life histories, and when only deciduous forbs were included, *leafprod* was still greater for introduced species than for native species ($\chi^2 = 7.17$, $P = 0.007$). *Leafprod* did differ by family (Table 4): of those families represented by at least three species, the Ericaceae had the shortest period of leaf production (mean = 33 days, $n = 8$), Rosaceae (mean = 42, $n = 5$) and Asteraceae (mean = 45, $n = 5$) were intermediate, and Fabaceae (mean = 79, $n = 7$) had by far the longest period. Results for the number of days during which plants had green leaves (*greenlength*) showed a similar interaction between year and nativity: *greenlength* was greatly extended for introduced plants in 2013, whereas native species showed a small shift between years (Table 3; Fig. 5B). There were no significant differences across all years between native and introduced species or between growth forms or families (Tables 3 and 4).

Discussion

Native vs. introduced species

Spring

Both native and introduced species responded strongly to interannual variation in spring; as expected, they

Table 4. Effects of growth form, leaf habit and family on phenology.

Season	Variable	N	Growth form (df = 2)		Growth form by year interaction (df = 6)		Leaf habit (df = 2)		Leaf habit by year interaction (df = 6)		Family (df = 1)	
			χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P
Spring	<i>firstleaf</i>	36	4.98	0.083	2.58	0.859	8.05	0.018	8.60	0.197	1.75	0.185
	<i>firstflower</i>	41	21.62	<0.001	6.80	0.339	7.84	0.020	4.19	0.651	6.52	0.011
	<i>peakflower</i>	41	17.17	<0.001	4.70	0.582	6.11	0.047	0.09	0.999	4.20	0.040
Summer	<i>firstflower–firstunripe</i>	40	0.76	0.684	5.20	0.518	0.51	0.775	4.44	0.617	0	1
	<i>peakflower–halfripe</i>	36	1.37	0.503	2.27	0.893	4.89	0.087	<0.01	0.999	1.07	0.302
Autumn	<i>lastflower</i>	41	21.25	<0.001	0.95	0.987	8.31	0.016	0.39	0.999	9.00	0.003
	<i>lastunripe</i>	35	1.19	0.551	0.84	0.991	0.03	0.983	1.24	0.975	0.41	0.520
	<i>lastleaf</i>	40	1.70	0.428	7.25	0.203	1.89	0.389	0.91	0.989	3.22	0.072
	<i>senesce50</i>	29	0.48	0.788	2.18	0.902	NA	NA	NA	NA	3.53	0.060
	<i>winterred</i>	8	3.73	0.155	1.28	0.973	0.09	0.767	2.84	0.242	NA	NA
Whole season	<i>leafprod</i>	36	2.56	0.277	10.28	0.113	3.08	0.214	2.92	0.819	4.08	0.043
	<i>greenlength</i>	27	1.16	0.560	2.54	0.863	NA	NA	NA	NA	2.69	0.101

Note: Models include year and species identity as random variables. *P*-values in **bold** indicate significant differences following a Benjamini–Hochberg procedure with a false discovery rate of 0.05. Analyses marked with “NA” were not run because only one level of the variable existed. *N*, number of species.

flowered and produced leaves earliest in the year with the earliest snow melt (2015; Fig. 2A). In general, native plants produced flowers (but not leaves) earlier than introduced plants, but there was no difference in the size of the shift between years (as indicated by the lack of an interaction) for either leaf-out or flowering. Furthermore, when the comparison was limited to summer-green forbs there was no difference between native and introduced plants in flowering phenology, suggesting that the earlier mean flowering time of native species is driven by the high proportion of shrubs and low proportion of forbs compared with introduced species, rather than by inherent differences between the nativity groups. There was, however, no evidence that the annuals were driving the delay in flowering or leaf-out for introduced species. Overall, these results provide no support for an advantage for either group under earlier springs. These results differ from several studies in temperate environments that found earlier flowering times and greater interannual variation in response to temperature in introduced compared with native species (Willis et al. 2010; Wolkovich et al. 2013). However, they are consistent with Fridley (2012), who compared woody native and introduced species in temperate deciduous forest and found that native species similarly had earlier budburst than introduced species but showed no difference in the size of the response to interannual variation (Fridley 2012).

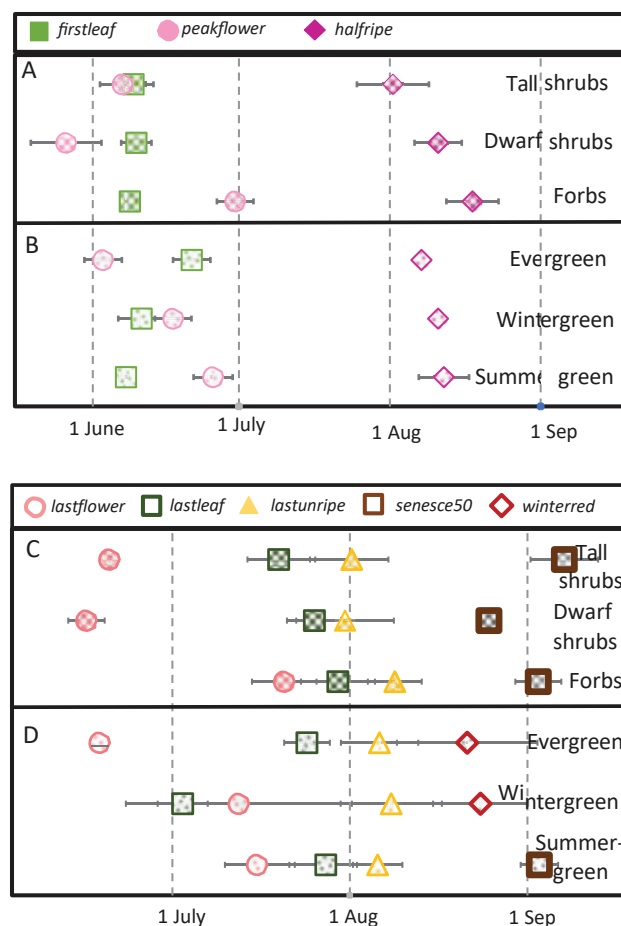
In temperate habitats, species show strong differences in leaf-out phenology that can be attributed to phylogeny, deciduousness, and growth habit (Panchen et al. 2014). However, in high-latitude species the very short growing season forces all species to flower early and synchronously compared with other habitats (Wolkovich and Cleland 2011), and this is reflected in our dataset

(Fig. 3). Many boreal forest species initiate leaf and flower buds in June of the year prior to flowering and are well-developed at the start of the winter (P.K. Diggle, E. Schaub, and C.P.H. Mulder, unpublished data for 8 species also included in this dataset). These species’ buds likely expand as soon as water is available to plants (Barr et al. 2009). The role of timing of ground thaw is evident from our data: 2014 and 2015 had very similar spring air temperatures but 2014 had a much greater snow load, and flowering and leaf-out were delayed. The crucial role of snow depth complicates predictions for future flowering times: while spring temperatures in interior Alaska are expected to continue to increase and agreement between models is fairly good, precipitation in winter is also expected to increase (potentially countering the impact of warmer temperatures) and model agreement is poor (SNAP 2017).

Summer

We had expected faster fruit development in the record warm summer (2013), but there were no detectable differences between years, and there was no interaction between nativity and year. It is possible that the very dry conditions in 2013 (3rd percentile in total precipitation) countered any positive effects of temperature on rate of development; given that temperature and precipitation are negatively correlated, these two variables are confounded. Overall, these results suggest that, at least over the range of moderate to warm temperatures, timing of fruit ripening is driven by spring conditions and timing of flowering, and they provide no support for an advantage of either group under warmer summers. While a large European dataset found earlier fruit ripening under warmer temperatures (Menzel et al. 2006), the correlation with temperature was weaker for fruit ripening

Fig. 4. Phenology of species by leaf habit and growth form. Values are date means $\pm$ SEM. (A) Spring phenology by growth form: first leaf, peak flowering, and half-ripe fruit. (B) Spring phenology by leaf habit. (C) Fall phenology by growth form: last flower, last leaf, last unripe fruit, 50% senescence (for summergreen species), and winter reddening (for wintergreen and evergreen species). (D) Fall phenology by leaf habit. Note that not all phenological stages are presented here; data on additional stages can be found in the Supplementary data, Table S1¹.

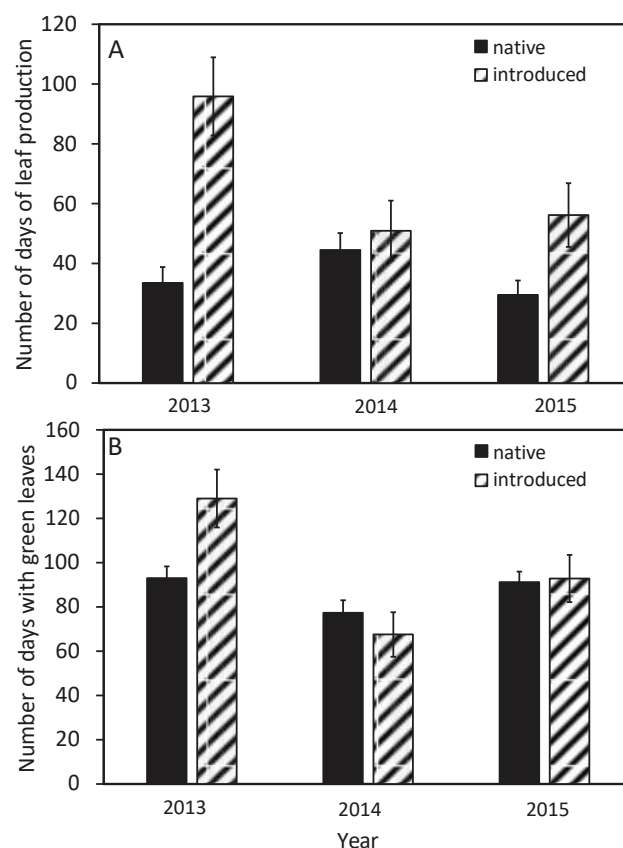


than for flowering, and weaker for wild plants than for agricultural species. Furthermore, the regression coefficient for fruit ripening in that study was similar to that for flowering (-2.18 ± 0.34 vs. -2.52 ± 0.07), suggesting that these results were also mainly driven by the timing of flowering rather than a change in developmental rates.

Autumn

Both native and introduced plants responded to prolonged above-freezing temperatures in autumn by extending the time of leaf and flower production and delaying senescence or winter reddening, with our data suggesting introduced species taking greater advantage of the extra time. Introduced species not only consistently continued leaf and flower production and delayed leaf senescence for longer than native species, they also showed a greater shift for leaf production in the year with the extended warm period in autumn (2013). It is

Fig. 5. Leaf production and retention by native and introduced plants in each year. (A) Number of days during which plants produced new leaves (*leafprod*). (B) Number of days during which plants had green leaves (*greenlength*). Values are the mean $\pm$ SEM.



possible that summer temperatures, which were extremely high in 2013, also played a role in delaying autumn phenology. And unlike for spring phenology, differences in autumn phenology persisted when the comparison was limited to summergreen forbs, indicating that growth form and leaf habit cannot account for differences in how native and introduced species respond to environmental conditions in autumn. Introduced species were less synchronous in leaf production than native species in the year with close-to-average environmental conditions, but there was substantial overlap between the two groups. Furthermore, there was no relationship between our measure of leaf synchrony and the size of the shift in last leaf production between the earliest and latest years, so leafing strategy does not provide insights into why native and introduced species differ.

A number of the introduced species have been used in agriculture or as ornamentals (e.g., *Melilotus albus* and *Trifolium repens* were developed as crops whereas *Caragana arborescens* is a commonly used as an ornamental hedge), likely resulting in selection for continuous flower production. In addition, a high proportion of introduced species are members of the Fabaceae or Asteraceae, the two families with the latest flower production.

However, while flowering was extended in 2013 compared with the other two years, fruit production (as measured by the timing of the last unripe fruit) was not, suggesting a lack of pollinators or insufficient time to develop fruits from late flowers. Because flower production that does not result in fruit production represents a (small) cost, there is again no evidence for a reproductive advantage for introduced species within a single longer growing season, and possibly even a disadvantage.

Extended leaf production was not explained by any plant traits investigated beyond nativity. A meta-analysis by Gill et al. (2015) found that while overall senescence has shifted earlier over time for deciduous trees, there has been no such shift for high-latitude species. Together these results suggest that there are inherent differences between high-latitude native forbs and shrubs and lower-latitude introduced species in their ability to adjust date of senescence in response to interannual variation in autumn conditions, most likely due to a strong constraint imposed by photoperiod, as has been found for boreal tree species (Stinziano and Way 2014; Way and Montgomery 2015). While using photoperiod as a cue to initiate senescence protects the plant from the loss of nutrients prior to resorption in the case of an early frost, it may severely limit the ability of plants to respond to longer autumns, at least in the short term (Way and Montgomery, 2015).

The impact of longer autumns on potential productivity was substantial: while in 2014 (the year that was closest to average conditions) the number of days during which new leaves were produced differed by a week between introduced and native species, in 2013 (the year with the extended autumn) the difference was more than three-fold (32 vs. 96 days; Fig. 5A). Introduced and native plants had similar periods with green leaves in 2014 and 2015, but in 2013 this period was 47% longer in introduced than in native species (Fig. 5B). These results again mirror the comparison of native and introduced deciduous woody plants by Fridley (2012). In that study, photosynthetic measurements demonstrated that this extended green period for introduced woody species resulted in significant net carbon gain (the difference between carbon fixation and respiration) (Fridley 2012). Whether this is the case in interior Alaska is not clear. During the period of interest (September and October), photoperiod drops very rapidly (from 14 h 36 min on 1 September, to 11 h 17 min on 1 October, and to 8 h 3 min on 30 October), and even when temperatures are above freezing, they are low (e.g., in 2013, the extended autumn year, mean air temperature was 6.7 °C in September and 2.3 °C in October). However, leaf temperature may be higher than air temperature. Determining to what extent the extended leaf availability results in increase carbon gain in introduced plants would require direct measurements of carbon fixation and respiration during this period.

Some groups of native plants may also benefit from extended autumns. Winter reddening (monitored only in 2014 and 2015) was greatly delayed in 2014 compared with 2015 in both evergreen and wintergreen species (by 45 days and 18 days resp.; compare with the 6 day difference in date of 50% leaf senescence in summergreen species). Winter reddening is thought to provide photoprotection under cold, dry, and bright conditions (see review in Hughes 2011) but there is little information available on how winter reddening affects photosynthetic rates. There is therefore the potential for extended autumns to increase carbon fixation in the fall, but direct measurements of photosynthesis during the fall season are needed to evaluate this.

In summary, there is no evidence for an advantage to either native or introduced species of earlier springs or warmer summers, as both groups respond similarly to interannual variation. There is also no evidence that an extended autumn season increases the period of fruit production in either group, and since introduced species continue to produce flowers but cannot extend fruit production, there may be a small cost within a single year. The most likely advantage of extended autumns for introduced species is greater carbon gain in forbs, as leaves continued to be produced and retained into September and even October. Similarly, we have some indications that extended autumns may result in a longer period for photosynthesis in evergreen and wintergreen native species. However, more research is needed to determine whether this results in a greater net carbon gain. Furthermore, since there is not (yet) clear evidence for a delay in winter over the past 88 years in Interior Alaska, these results may simply point out one of the ways that introduced plants can expand by taking advantage of years with late starts to winter, even in the absence of climate change.

Growth form and leaf habit

Tall shrubs had the earliest flower production, followed by dwarf shrubs and then forbs (Fig. 3B). The difference between tall shrubs and forbs was approximately three weeks. Forbs carry their preformed buds belowground and woody species aboveground, but this difference in flowering may not simply be the result of physiological constraints associated with moving buds from belowground to aboveground. Leaf production showed a very different pattern: forbs and shrubs leafed out at the same time, and considerably earlier than dwarf shrubs. Instead (or additionally), the difference in timing may be the result of different life history strategies. First, on average, forbs have a shorter lifespan than deciduous woody species (Kikuzawa and Ackerly 1999), so that the loss of all flowers to a spring freezing event represents a relatively larger cost to forbs than to the longer-lived woody species. Under this scenario, we would expect a conservative approach to flower emergence, delaying it until the chances of flower loss are

small. Second, almost all the forbs were summergreen, and summergreen species developed fruits much faster than did evergreen species, making it possible for plants to delay flowering without increasing the risk of unripe fruit loss due to autumn freezing events.

This same risk–benefit argument can also explain the timing of leaf-out in plants with different life histories. Evergreen species produced leaves later than summergreen species, and wintergreen species were intermediate. Evergreen species already have winter-hardened leaves on the plant at the start of spring; delaying the production of new leaves represents only a small opportunity cost, whereas the loss of leaves that can last up to three years (C.P.H. Mulder, unpublished data) to spring freezing events would represent a very large cost. Hence, we would expect delay of leaf production. Wintergreen species similarly start the spring with leaves already present, but each leaf represents a smaller investment; this intermediate cost of leaf loss to spring freezing events is consistent with an intermediate timing of new leaf production. Our results are consistent with others studies that have similarly shown earlier leaf-out in summergreen compared with evergreen species (Davi et al. 2011; Panchen et al. 2014).

Under the hypotheses just presented, leaf and flower phenology may show opposite responses: some species (e.g., evergreen woody species) produce flowers early and leaves late, whereas others (e.g., deciduous forbs) produce leaves early and flowers late. This is born out in our dataset, where there was no correlation between the timing of leaf and flower production in spring. We might also expect a stronger response to environmental variation in species that have a “risky” strategy (produce flowers or leaves early) compared with those who have a “conservative” strategy (produce flowers or leaves late; Fridley 2012). The evidence for this was mixed. Consistent with earlier studies (Pau et al. 2011; Davies et al. 2013; Mulder et al. 2017), early-flowering species responded more strongly to interannual variation in temperature than later-flowering species, but this was not true for leaf emergence. Furthermore, we might expect the interannual variation to be uncorrelated for leaves or flowers given that their timing is uncorrelated, but the size of the shift between years was marginally positively correlated for leaves and flowers: a species that showed a strong response to environmental variation did so in both leaf and flower emergence date.

The ability of plant traits to explain differences by nativity was strongly season-dependent. Our pool of introduced species lacked evergreen or wintergreen species and included only a single shrub species; both growth form and leaf habit helped explain why introduced species produced flowers but not leaves later than native species did, and why they delayed senescence and extended leaf production in 2013. However, while for spring variables these plant traits were sufficient to ex-

plain differences by nativity (there were no significant differences between native and introduced summergreen species), this was not the case for fall variables: there were significant differences between native and introduced summergreen species.

Study limitations

Our study used a nonrandom, nonexhaustive selection of native and introduced species; while these did represent the dominant or most abundant species in the understory and ruderal communities in our sites, it is possible that the particular selection of species influenced the outcomes. Only one woody species was included in our introduced species group, and no graminoids or trees were included; it is therefore not possible to extrapolate to all species. While summergreen introduced species were, by their very nature, ruderal, some of the summergreen native species were not. And while the three focal years differed greatly, we did not have any extremely cold years, so our conclusions are limited to the moderate to warm part of the range. All of these caveats deserve further exploration.

Implications for plant communities

Our results suggest that earlier springs are unlikely to result in any changes in plant composition based on the species we studied (but note that we did not include graminoids or trees in our dataset). In contrast, extended falls have the potential to benefit two groups: forbs, especially introduced forbs, which were able to extend leaf production and delay senescence, and evergreen species, which delayed winter reddening. The group least likely to benefit are deciduous shrubs. However, whether these responses translate into increased plant productivity for any group will depend on whether leaves that are active in late fall, when temperatures are near freezing and light levels are dropping rapidly, have a positive carbon balance. Studies that focus on directly measuring carbon fixation late in the season would allow us to quantify the actual benefit of retaining green leaves. Furthermore, because introduced plants have green leaves at a time when native species do not, land managers may be able to detect, inventory, and manage their populations more easily than if this were not the case, which could slow down their expansion.

Acknowledgements

We thank Morgan Cain, Stephen Decina, Patricia Hurtt, Brennan McKinnon, Katie Moeller, the Mulder-Uliassi family, and the Spellman-Villano family for assistance collecting field data. We thank the citizen scientists from the Melibee Project and Project Brown-down for the conversations that inspired this study, and J. Fridley, and M. Carlson for discussions at the start of

the project and constructive comments on an earlier draft. Funding was provided by the Bonanza Creek LTER (NSF grant No. DEB-1026415).

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