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RESEARCH ARTICLE

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Phenological Patterns Differ between Exotic and Native Plants: Field Observations from the Sapphire Mountains, Montana

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ABSTRACT: We collected plant phenology data in the Sapphire Mountains, Montana, USA, by monitoring developmental stages of 101 native species and 21 exotic species during weekly visits to the sites from March to November 2013. We compared the start, end, and length of the emergence, flowering, and seed maturation phases for exotic and native plants. Short-lived forbs, perennial forbs, and perennial grasses were analyzed separately. Exotic plants emerged earlier, began and ended flowering later, and had later ends to emergence and dispersal phases across all functional group comparisons. The emergence phase for exotic perennial forbs averaged 13.8 weeks longer than for native perennial forbs, the flowering phase was 3.4 weeks longer, and the seed dispersal phase was 8.3 weeks longer. The window for emergence and flowering for forbs, shrubs, and grasses (March to November) did not differ between natives and exotics. The results generally support the conclusion that the exotics have an advantage over the natives in priority of growth and wider niche breadth, rather than occupying vacant niches. Seed set time varied in duration from 1 to 23 weeks from April to November. Our results provide insights into invasion mechanisms and selection of native plant materials to compete with invasive species. We discuss implications for seed collection and herbicide timing.

Index terms: herbicide timing, microsite variation, native seed collection, phenology, plants

INTRODUCTION

Plant phenology, the seasonal timing of plant developmental stages, influences plant community dynamics and determines resource availability to herbivores and pollinators. Increased attention has been directed to differences in native and exotic plant phenology and how those differences affect invader abundance (Godoy et al. 2009b; Wolkovich and Cleland 2010; Wainwright et al. 2012). Specific exotic plants have been shown to have earlier or later flowering periods (Godoy et al. 2009a, 2009b; Pearson et al. 2012) and earlier germination than native species (Wainwright et al. 2012; Wainwright and Cleland 2013), but the generality of these observations has not been investigated.

The geographic origin of plant species influences phenology, as plants have evolved to the climatic conditions of their native range (Rathke and Lacey 1985; Godoy et al. 2009a). Though plants can change through selective pressure, they often retain the phenological patterns of their original range when they occupy a new range (Franks et al. 2007; Maron et al. 2007; Godoy et al. 2009a; Lesica and Kittelson 2010). Life history strategy also creates disparate phenological patterns (Jia et al. 2011). For example, annual grasses will allocate more resources to reproduction than perennial grasses that must invest in maintenance for longevity.

While most studies focus on one particular temporal phenological stage, usually the flowering stage, none have focused on how lengths of all stages vary through a growing season. Timing and duration trends of all plant phenological stages may inform us how exotic invaders compete with and displace natives. For example, a longer period of flowering and seed dispersal aids genetic mixing in invasive populations and allows the invader to take advantage of a wider array of favorable conditions across a growing season (Cadotte et al. 2006). A longer length of emergence period could give greater access to limited resources and, thus, increase fecundity (Cadotte and Lovett-Doust 2002).

We measured phenological traits for an entire growing season to test whether exotic species differ in timing and phase length compared to native species and whether these differences occur at the species functional group level. We considered exotic species in this study as any alien-origin plant species, whether it was invasive, noxious, or benign. Along with collecting species-level phenology in communities where nonnative species threaten the integrity of ecosystem function, an aim of this study was to understand plant phenology in regards to restoration of native plant communities in degraded systems. Though research has highlighted the importance of plant phenology for management applications (Ghersa and Holt 1995; Ansquer et al. 2009; Pearson et al. 2012), a gap remains in the knowledge of phenological patterns of native and exotic plants in the northern Rocky Mountains. For example, restoration aimed at filling niche space to best use available resources must account for both spatial and temporal plant relationships. Restoration maximizing niche space requires knowledge of phenological differences. Also, there is a notion among managers that windows exist for herbicide applications when damage to native plant populations can be minimized because problematic exotic plants are active aboveground while most native plants are dormant (Rice et al. 1997). These opportunities are referred to as "management windows" and would occur in cases where exotics occupied a vacant temporal niche in the community (Wolkovich and Cleland 2010). We found no comprehensive phenology data to support the existence of management windows, but we evaluate this concept.

METHODS

Study Site

This study was conducted at MPG Ranch in the Northern Sapphire Mountains of western Montana (Table 1, Figure 1). The ranch is a 3800-ha conservation property with topography that varies from flat bottomland to gentle foothills and forested mountain slopes. A combination of agricultural land, sagebrush steppe, riparian forests, dry open forests, and moist mixed coniferous forests dominate the landscape. Mean annual precipitation ranges from 300 mm on the valley floor to 350 mm on mountain summits, and mean temperatures in nearby Missoula for July and January are 19.4 °C and −4.7 °C, respectively. Cold moist winters, when most precipitation occurs, contrast with hot, dry summers.

Phenology study areas centered on 15 sites representative of habitats in the lower to upper montane rangeland (Table 1). Each area encompassed approximately 730 m^2. Native species richness ranged from 7 to 40 species across the sites. Exotic species, mainly *Centaurea stoebe* L. (spotted knapweed), *Euphorbia esula* L. (leafy spurge), *Bromus tectorum* L. (cheatgrass), *Sisymbrium altissimum* L. (tumble mustard), and *Potentilla recta* L. (sulfur cinquefoil) comprised 1%–84% of the plant cover (% cover from point-in-

Table 1. Survey site characteristics.

	Coordinates				Number of species per plot		
Site	Latitude	Longitude	Elevation (m)	Ecological system	Native	Exotic	Total
1	46.68605°	−113.98506°	1308	Rocky Mountain Montane-Foothill Deciduous Shrubland	36	14	50
2	46.70457°	−114.00040°	1480	Rocky Mountain Lower Montane, Foothill, Valley Grassland	29	6	35
3	46.70369°	−114.00676°	1325	Montane Sagebrush Steppe	26	3	29
4	46.70436°	−114.00352°	1386	Montane Sagebrush Steppe	41	8	49
5	46.69840°	−114.01187°	1233	Montane Sagebrush Steppe	34	9	43
6	46.69531°	−114.01762°	1172	Montane Sagebrush Steppe	4	7	11
7	46.68076°	−113.99016°	1267	Montane Sagebrush Steppe	10	8	18
8	46.67767°	−113.99591°	1189	Montane Sagebrush Steppe	14	11	25
9	46.67811°	−113.99272°	1223	Montane Sagebrush Steppe	11	8	19
10	46.71383°	−113.99976°	1491	Montane Sagebrush Steppe	18	9	27
11	46.71152°	−113.99572°	1468	Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest	40	8	48
12	46.70501°	−113.98061°	1748	Rocky Mountain Subalpine-Upper Montane Grassland	28	4	32
13	46.70722°	−113.98124°	1817	Rocky Mountain Subalpine-Upper Montane Grassland	32	3	35
14	46.71428°	−113.99657°	1539	Rocky Mountain Lower Montane, Foothill, Valley Grassland	18	6	24
15	46.71472°	−113.99338°	1544	Rocky Mountain Lower Montane, Foothill, Valley Grassland	21	6	27

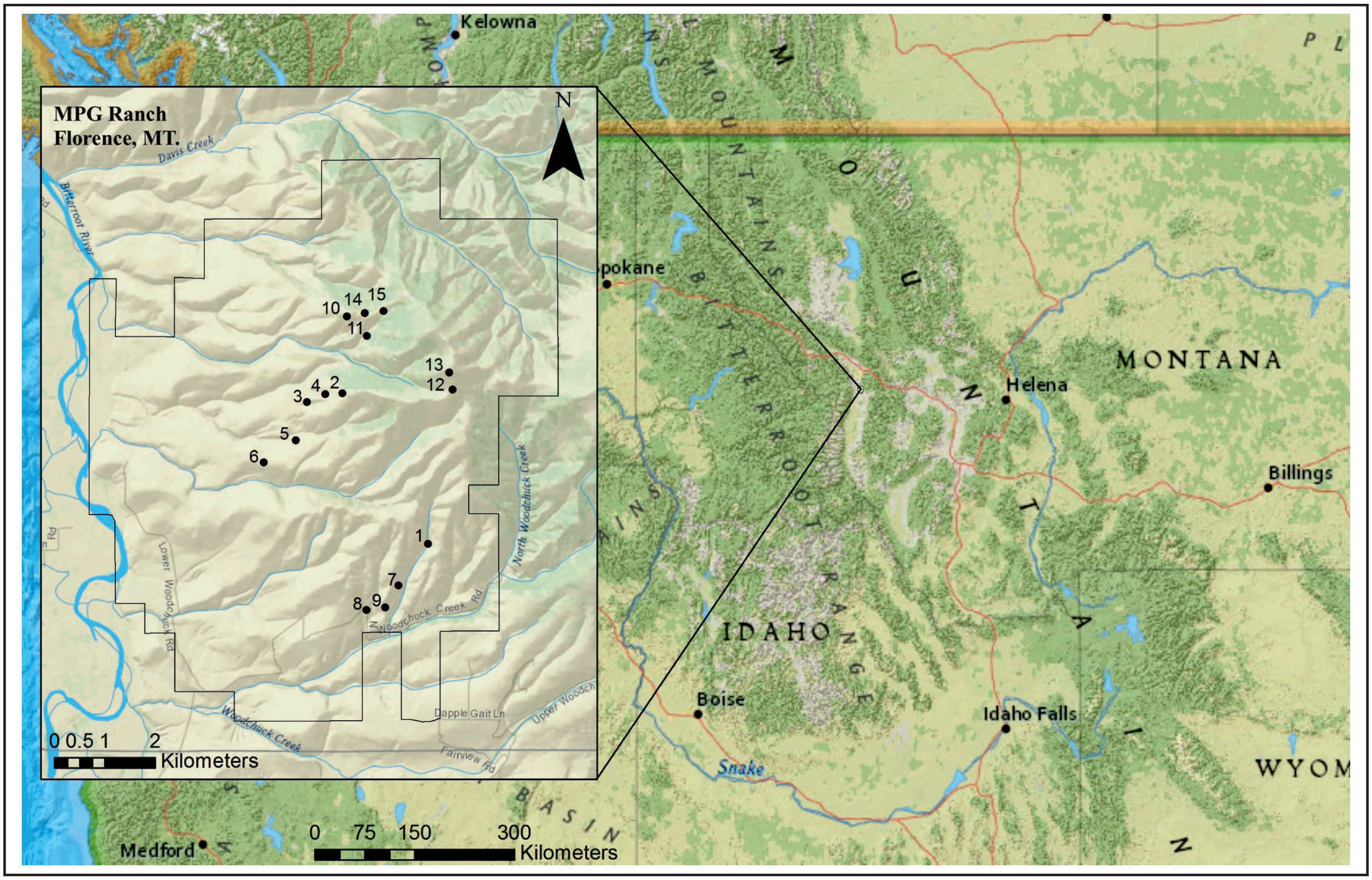

Figure 1. Study site locations within the boundary of MPG Ranch, Montana, USA.

tercept transect data, unpublished). Site elevation ranged from 1172 m to 1817 m (Table 1). Soil temperature and weather data can be accessed from http://livecams.mpgranch.com.

Field Sampling

We assigned each species encountered at each site to the category (or categories) emergent, budding, flowering, fruiting, mature seed, senesced, and fall growth/fall germination, weekly from 10 March 2013 to 23 November 2013. We visited sites the same day each week (±2 days). Phases were not mutually exclusive; we recorded each phase presented per species by site. Phenological stage was considered present if at least 80% of the individuals at the site were in the stage, to minimize noise from intraspecific variation.

Plants with green tissue were recorded as emergent. Budding plants had immature reproductive structures and closed sepals. Flowering plants were considered those with mature bloom and developed floral structures (i.e., anthers, stigma, petals). The fruiting period was recorded as the period with fruit after the flower withered, regardless of fruit maturity. Mature seed was recorded for fruiting plants with mature, collectable seed. We recorded plants with withered non-green vegetation as senesced. Fall regrowth was assigned to those plants that showed new vegetative growth in the fall. We recorded fall germination for plants that sprouted new seedlings in the fall.

Data Analysis

Homogeneity of variance within functional groups and differences in the number of native and exotic species in functional groups presented a challenge to analysis. For example, there were 60 native perennial forbs represented at three or more study sites. Only four exotic perennial forbs were detected (*C. stoebe*, *E. esula*, *Silene latifolia* Poir. [bladder campion], and *P. recta*). *Centaurea stoebe*, *E. esula*, and *P. recta* were well represented, but *S. latifolia* was only present at one site and was not observed in all stages. Differences in sample numbers between plant functional groups caused the data to violate the ANOVA assumptions of normality and homogeneity of variance. This problem could not be corrected by data transformations. For these reasons, we analyzed the data using nonparametric methods. We applied a Kruskal–Wallis *H* test to determine differences in duration and timing of phenological phases between functional groups (short-lived or perennial; forb or graminoid) and species origin (native or exotic). When species occurred at more than one site, average values were used to minimize noise across sites. A Mann–Whitney *U* test was used to test differences between subgroups. We discuss the phenology of plants within functional groups in relation to the distribution of the native plants within the same functional group. These analyses were performed with SPSS version 20.

RESULTS

Flowering Phenology

Flower duration, the number of weeks a species was in bloom, was charted for each study species by life form (Appendix). Flower duration for each species was the first week of occurrence to the last week of occurrence across all sites. Short-lived forbs included annuals and biennials. Perennial native forbs and native short-lived forbs flowered from March to September (Appendix). Exotic perennial forbs flowered from May to November, and exotic short-lived forbs flowered from March to November. Duration of flowering for native forbs was 2–18 weeks depending on the species, and flowering duration for exotic forbs was 2–31 weeks depending on the species (Appendix). Native perennial graminoids flowered from the end of April to the beginning of August. Exotic perennial graminoids flowered from the end of April to the beginning of July (Appendix). Duration of flowering for native perennial graminoids was 1–10 weeks and flowering duration of exotic perennial graminoids was 1–9 weeks (Appendix). Native shrubs flowered from the end of April to the beginning of November. Flower duration for shrubs was 3–13 weeks. Exotic annual grasses flowered from May to June, flower duration was 1–7 weeks (Appendix).

Phenology of Native vs. Exotic Functional Groups

We compared growth phases of the three functional groups with native and exotic representatives: short-lived forbs, perennial forbs, and perennial graminoids. Exotic and native species exhibited disparate phenology for the periods of emergence, flowering, and mature seed (Figures 2 and 3), while budding, fruiting, senescence, fall growth, and fall emergence did not differ among groups and are not reported. The

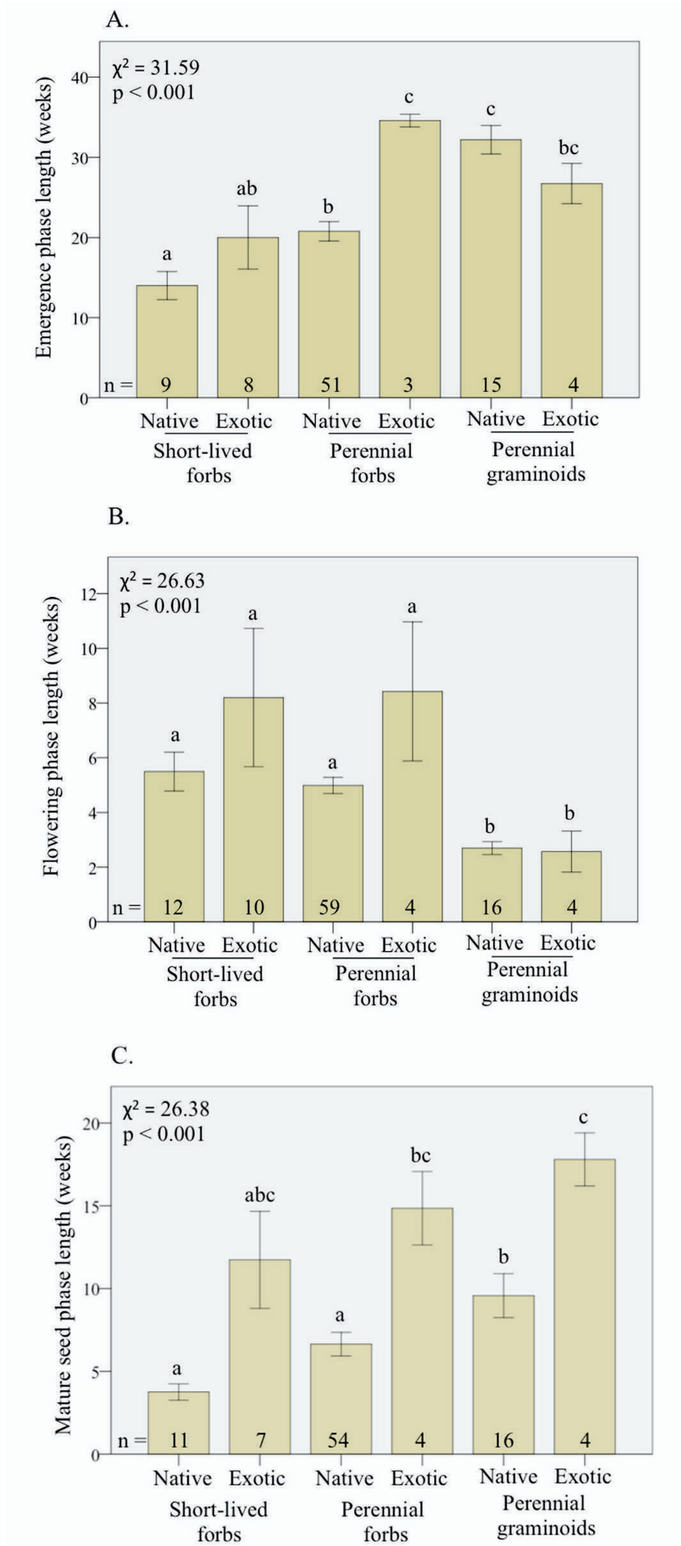

Figure 2. Mean duration of phenology phases of native and exotic functional groups: short-lived forbs, perennial forbs, and perennial graminoids (+/− 1 SE). Different letters indicate significant differences (*P* < 0.05). Phenology phases represented are (A) emergent phase length, the period of time when plant species have green plant tissue; (B) flowering phase length, the period of time when plant species have developed floral structures; and (C) mature seed phase length, the period of time when fruiting plant species have mature, collectible seeds.

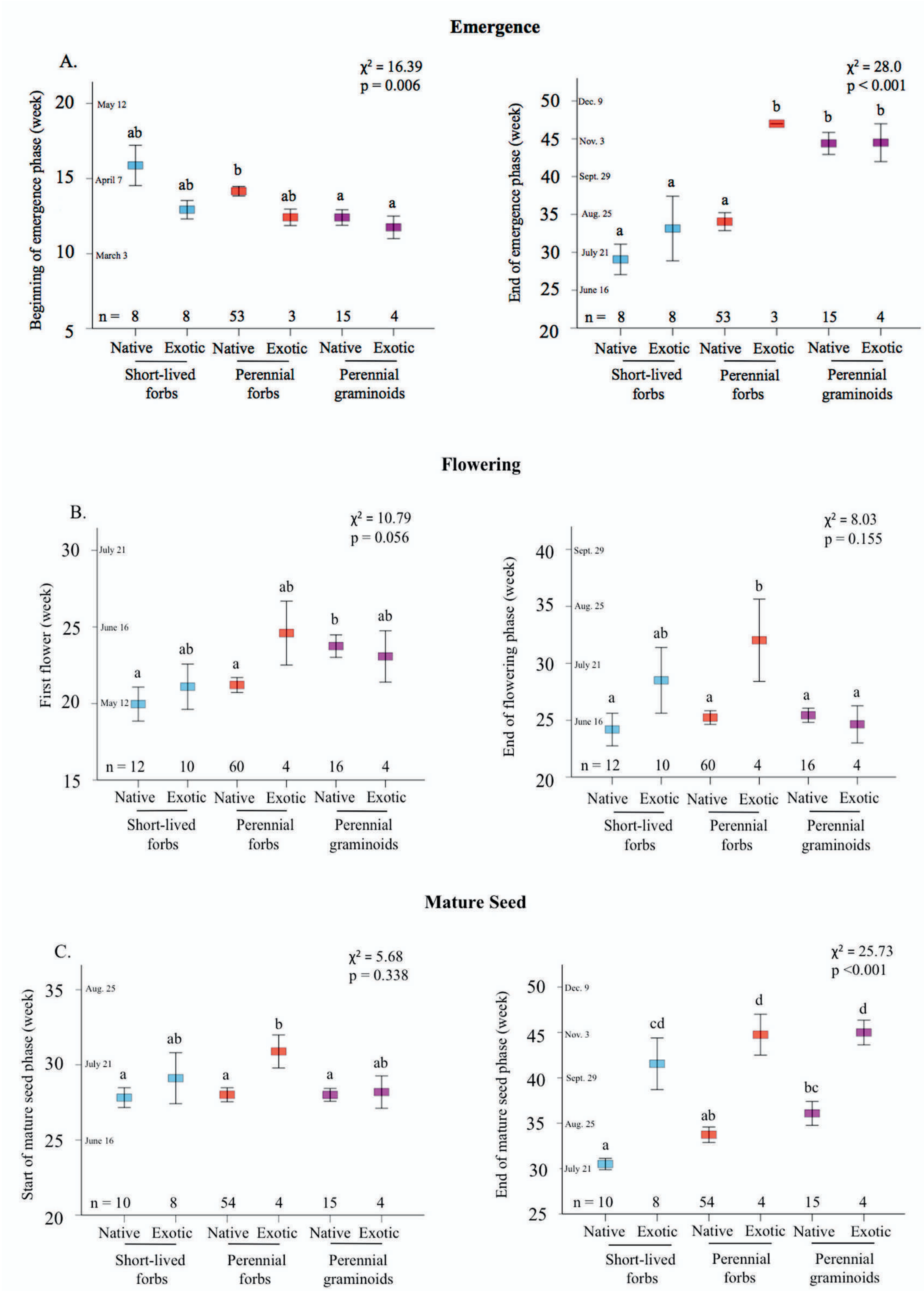

Figure 3. Mean timing (phase start and phase end) of phenology phases of native and exotic functional groups: short-lived forbs, perennial forbs, and perennial graminoids (+/− 1 SE). Different letters indicate significant differences (*P* < 0.05). Phenology phases represented are (A) the start and end of the emergence phase, when plant species have green plant tissue (start) and when green tissue is gone (end); (B) the start and end of the flowering phase, when plant species develop the first floral structures (start) and when the last floral structures are gone (end); and (C) the start and end of the mature seed phase, when plant species have the first mature, collectible seeds (start) and when the last mature seeds drop (end).

rest of this section will discuss differences between exotic and native short-lived forbs, perennial forbs, and perennial graminoids.

Short-Lived Forbs

The emergence phase length and beginning and end of the emergence phase were similar for native and exotic short-lived forbs (Figures 2 and 3). Flowering periods and the beginning and end of the flowering periods were similar for native and exotic short-lived forbs (Figures 2 and 3). The biggest differences between native and exotic short-lived forbs were noted for the mature seed phase. The exotic short-lived forbs trended toward holding mature seed longer than natives ($Z = -1.87$, $P = 0.069$; Table 2, Figure 2). The mature seed phase ended significantly later for exotic short-lived forbs than natives ($Z = -2.38$, $P = 0.016$; Table 2, Figure 3). Most of the exotic short-lived forbs had mature seed for most of the growing season, 11.7 weeks (SD ±M7.77). The native short-lived forbs held seed for a window

Table 2. Phase lengths, beginning and end week for the phenological phases of short-lived forbs, perennial forbs, and perennial graminoids.

	n		Mean (standard deviation)		Mann–Whitney *U*	
Phenological phase	**native**	**exotic**	**native**	**exotic**	***Z***	***p***
Short-lived forbs						
Emergence						
Length (weeks)	9	8	14.0 (5.24)	20.0 (11.2)	−1.3	0.2
Start (week)	8	8	15.9 (3.80)	12.9 (1.74)	−1.49	0.161
End (week)	8	8	29.1 (5.69)	33.1 (12.1)	−0.158	0.878
Flowering						
Length (weeks)	12	10	5.49 (2.45)	8.20 (8.00)	−0.33	0.771
Start (week)	12	10	20.0 (3.85)	21.1 (4.67)	−0.4	0.72
End (week)	12	10	24.2 (4.97)	28.5 (9.11)	−1.45	0.159
Mature seed						
Length (weeks)	11	7	3.75 (1.63)	11.7 (7.77)	−1.87	0.069
Start (week)	10	9	27.8 (2.08)	29.1 (5.09)	−0.9	0.4
End (week)	10	8	30.5 (1.97)	41.6 (8.05)	−2.38	0.016
Perennial forbs						
Emergence						
Length (weeks)	51	3	20.8 (8.64)	34.6 (1.38)	−2.25	0.019
Start (week)	53	3	14.2 (2.32)	12.4 (0.946)	−1.54	0.133
End (week)	53	3	34.1 (8.62)	47. 0 (0.000)	−2.31	0.015
Flowering						
Length (weeks)	59	4	4.99 (2.26)	8.42 (5.08)	−1.45	0.146
Start (week)	60	4	21.2 (3.77)	24.6 (4.17)	−1.55	0.127
End (week)	60	4	25.2 (4.69)	32.0 (7.22)	−2.4	0.012
Mature seed						
Length (weeks)	54	4	6.64 (5.27)	14.9 (4.44)	−2.54	0.007
Start (week)	54	4	28.0 (3.43)	30.9 (2.21)	−2.12	0.032
End (week)	54	4	33.7 (6.26)	44.8 (4.50)	−2.68	0.004
Perennial graminoids						
Emergence						
Length (weeks)	15	4	32.2 (6.87)	26.7 (5.00)	−1.6	0.124
Start (week)	15	4	12.4 (2.01)	11.8 (1.50)	−1.08	0.307
End (week)	15	4	44.4 (5.63)	44.5 (5.00)	−0.07	0.961
Flowering						
Length (weeks)	16	4	2.69 (0.938)	2.57 (1.50)	−0.52	0.617
Start (week)	16	4	23.8 (2.94)	23.1 (3.35)	−0.28	0.82
End (week)	16	4	25.4 (2.50)	24.6 (3.27)	−0.57	0.617
Mature seed						
Length (weeks)	16	4	9.57 (5.31)	17.8 (3.21)	−2.22	0.022
Start (week)	15	4	28.0 (1.65)	28.2 (2.15)	−0.65	0.53
End (week)	15	4	35.1 (5.10)	45.0 (2.72)	−2.41	0.014

of less than a month at 3.75 weeks (SD ±S1.63). *Erodium cicutarium* (L.) L'Her. ex Aiton (storksbill) was one of the plants contributing to this statistic, though other short-lived exotics mirrored this pattern. *Erodium cicutarium* did not hold seed from single flowers through the growing season; instead the plants had cycles of flowering and fruiting that continuously kept mature seed present for 11 weeks.

Perennial Forbs

Three exotic perennial forbs dominate many plant communities across the study area and our region. These are *C. stoebe*, *E. esula*, and *P. recta*. Of these, *C. stoebe* and *E. esula* are the most abundant and problematic. One other exotic perennial forb, *S. latifolia*, was detected at a study site. Unlike the other three forbs, *S. latifolia* poses little threat to invasion in our rangelands (pers. obs.). Due to the uneven numbers of species in the native versus the exotic perennial forb groups (Table 2), we describe the differences between the exotic and native perennial forbs as a group (Table 2) and individually (Table 3). Overall, the exotic forbs remained active longer (emergence phase $Z = -2.25$, $P = 0.019$; Figure 2), flowered later ($Z = -2.4$, $P = 0.012$; Figure 3), and retained mature seed more than twice as long as the native perennial forbs ($Z = -2.54$, $P = 0.007$; Figures 2 and 3).

Centaurea stoebe's emergent growth phase lasted more than 14 weeks longer than the mean of the native perennial forbs (Table 3). *Centaurea stoebe*'s flowering phase was 9 weeks longer than the mean of the natives and it carried mature seed for twice as long as the native mean (13.9 weeks for *C. stoebe*, compared to 6.64 weeks for the native perennial forbs; Table 3).

Euphorbia esula's emergent growth phase was also longer than the mean of the native perennial forbs (34.5 weeks; Table 3). The mean of the *E. esula* flowering period was twice as long as the mean of the native perennial forb flowering period (Table 3). *Euphorbia esula* carried mature seed for longer and later than the mean of the natives, but only by about 2.5 weeks (Table 3).

Table 3. Phase lengths, start week, and end week for native perennial forbs and exotic perennial forbs.

	Emergence			Flowering			Mature seed		
	Length (weeks)	Start (week)	End (week)	Length (weeks)	Start (week)	End (week)	Length (weeks)	Start (week)	End (week)
Native perennial forbs									
n	51	53	53	59	60	60	54	54	54
mean	20.80	14.20	34.10	4.99	21.20	25.20	6.64	28.00	33.70
s.d.	8.60	2.30	8.60	2.30	3.80	4.70	5.30	3.40	6.30
Spotted knapweed (*Centaurea stoebe*)									
n	13	13	13	13	13	13	13	13	13
mean	36.00	12.00	47.00	14.70	31.50	39.50	13.90	34.10	47.00
s.d.	2.00	2.00	0.00	2.20	3.50	3.70	0.28	0.28	0.00
Leafy spurge (*Euphorbia esula*)									
n	2	2	2	4	4	4	4	4	4
mean	34.50	13.50	47.00	9.50	20.30	28.80	9.00	30.00	38.00
s.d.	0.71	0.71	0.00	0.58	0.96	0.50	1.40	0.82	2.00
Bladder campion (*Silene latifolia*)									
n	0	0	0	1	1	1	1	1	1
mean	n.d.	n.d.	n.d.	7.00	22.00	28.00	29.00	19.00	47.00
s.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Sulfur cinquefoil (*Potentilla recta*)									
n	4	4	4	4	4	4	4	4	4
mean	33.30	11.80	38.80	2.50	27.00	28.50	17.50	30.50	47.00
s.d.	0.50	1.50	5.60	1.30	1.20	0.58	0.58	0.58	0.00
Sticky cinquefoil (*Potentilla glandulosa*)									
n	1	1	1	1	1	1	1	1	1
mean	21.00	16.00	36.00	4.00	24.00	27.00	19.00	29.00	47.00
s.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Slender cinquefoil (*Potentilla gracilis*)									
n	n.d.	n.d.	n.d.	1	1	1	1	1	1
mean	n.d.	n.d.	n.d.	3.00	26.00	28.00	9.00	33.00	41.00
s.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.

We monitored only one population of *S. latifolia* in this study and it was not detected until the budding stage, so emergence data is not presented. Anecdotally, *S. latifolia* flowered for about as long as the natives, but held mature seed from the end of the flowering period until the end of the growing season (29 weeks; Table 3).

Differences in phenology between *P. recta* and the native perennial forbs were not as large as between *C. stoebe*, *E. esula*, and the native perennial forbs. *Potentilla recta* was also the only perennial exotic forb with congeneric species in the study: *Potentilla glandulosa* Lindl. (sticky cinquefoil) and *Potentilla gracilis* Douglas ex Hook. (slender cinquefoil). *Potentilla recta*'s period of emergence was longer than the mean of the natives by 12 weeks and longer than the congeneric *P. glandulosa*, which was emerged for a period close to the mean of the native perennial forbs (21 weeks; Table 3). *Potentilla recta* and its congeners all held mature seed for longer than the mean of the natives, with *P. recta* and *P. glandulosa* averaging 17.5 and 19 weeks, respectively (Table 3).

Perennial Graminoids

The exotic perennial grasses in the study area were *Poa bulbosa* L. (bulbous bluegrass), *Thinopyrum intermedium* (Host.) Barkworth & Dewey (intermediate wheatgrass), *Poa pratensis* L. (Kentucky bluegrass), and *Agropyron cristatum* (L.) Gaertn. (crested wheatgrass). Most grasses, and all the exotics, were emerged through the growing season, flowered approximately the same time, and displayed similar phenology throughout the growing season with the only exception being with the time that exotics held mature seed. Exotic graminoids held seed more than 10 weeks longer than natives ($Z = -2.41$, $P = 0.014$; Figure 3).

Mature Seed Collection

Mature seed data for native species are presented in Table 4. When the species occurred at more than one site, we combined mature seed data to show the interval of when mature seed was available for collection. Mature seed period varied in duration (1–23 weeks) and time (April–November). When species occurred at multiple sites with similar habitats, we charted whether we observed variability in phenological stages between sites. We defined this variability as greater than or equal to two weeks' difference between the start of phenological stage. If we observed phenological variability across sites, the species was suspected to show microsite sensitivity. Microsite sensitivity occurs when species respond to specific environmental cues at a microsite level, such as aspect or shade (Titus and Tsuyuzaki 2003) or when competition between species varies on small scales (Larigauderie and Richards 1994). Some species showed these differences in phenological patterns at every stage across microsites, and others only for certain stages (Table 4).

Peak Emergence and Management Windows

We also examined peak emergence periods for native and exotic grasses and forbs to gauge differences by functional group. We considered peak emergence to be when most species were emergent with any green tissue across sites. The peak emergent period for native forbs and shrubs was from late May to early June, and the period of least activity was at the beginning and end of the growing season, early March and mid-October to November (Figure 4). The peak emergent period of exotic forbs was April to early May and the period of least activity was March and late October through November. The period when exotic forb emergence was highest and native forb emergence was lowest was late March and mid-October to November. The peak emergent period of native grasses was early May to late June, but remained high throughout the growing season (Figure 4). The peak emergent period of exotic grasses was mid-April to early June, and period of least activity was early to mid-August to mid-September (Figure 4). The period when exotic grass presence was highest and native forb presence was lowest was in early March (Figure 4).

DISCUSSION

Phenology of Native and Exotic Plants

Our study presents an extensive account of phenological stages for 101 native species and 21 exotic species through one growing season at a western Montana rangeland. In the plant communities studied here, exotic perennial forbs have longer periods of emergence than native perennial forbs. We found that in each functional group exotics have longer periods of mature seed and a later end of dispersal period than natives. Exotic forbs tend to emerge earlier, begin and end flowering later, and their dispersal phase tended to start later.

We divided plants into functional groups for comparisons. Though the number of exotic perennial forbs in the sample was only four, these plants are abundant across the study sites. A longer window of emergence, flowering, and seed dispersal gives the exotic perennial forbs greater access to resources, pollinators, and a longer window for seed to move to new locations. For example, some of the trends of the perennial forb functional group were driven by *C. stoebe*, whose phenology was very different from most native perennial plants. For *C. stoebe*, the flowering and mature seed phases happened concurrently, and were longer and later than for native perennial forbs. This extended cycle of flowering, fruiting, and seeding could allow for more genetic mixing between and within populations as different pollinators and dispersers move through the system. At the beginning and end of the flowering period for *C. stoebe,* only a few flowers were found in the populations at the study sites. This forces pollinators to move long distances between flowers, facilitating long-distance pollen dispersal. During the height of the flowering period, flowers are abundant, ensuring that pollinators do not need to travel far and the plants within a local population will be genetically well mixed (Godoy et al. 2009a). Flowering when most natives are fruiting reduces pollinator competition and allows for more pollination success for exotics (Godoy et al. 2009b; Pearson et al. 2012).

Table 4. The window of time when mature seed was collectible from native study species and the variability of all phenology phases across sites. The microsite sensitivity, when phenology phase start differed across sites by more than two weeks (yes or no). If microsite sensitivity was observed for a particular phase, the phase is noted: EM: emergent phase, BU: budding phase, FL: flowering phase, FR: fruiting phase, MS: mature seed phase, SE: senescent phase.

Scientific name	Common name	Life form	Date of first mature seed	Duration of mature seed (weeks)	Observed microsite sensitivity (≥2 weeks)	Observed phase variability
Acer glabrum	Rocky Mountain maple	shrub	18-Aug	14	N/A	
Achillea millefolium	western yarrow	forb	11-Aug	15	Yes	EM, BU, FR, MS SE
Agastache urticifolia	giant horsemint	forb	21-Jul	10	Yes	EM, BU, FL
Agoseris glauca	false-dandelion	forb	9-Jun	2	N/A	
Allium cernuum	nodding onion	forb	21-Jul	18	Yes	BU, FL
Amelanchier alnifolia	saskatoon	shrub	7-Jul	11	N/A	
Antennaria dimorpha	low pussytoes	forb	28-Apr	6	N/A	
Antennaria rosea	rosy pussytoes	forb	9-Jun	9	Yes	FR, MS
Antennaria umbrinella	umber pussytoes	forb	9-Jun	9	Yes	FL, FR, MS
Arenaria congesta	ballhead sandwort	forb	30-Jun	8	Yes	EM, BU, FL, FR, MS, SE
Aristida purpurea	three-awn	graminoid	14-Jul	19	No	
Arnica sororia	twin arnica	forb	16-Jun	9	Yes	FL, BU, MS, SE
Artemisia dracunculus	wild tarragon	shrub	10-Nov	2	No	
Artemisia frigida	fringed sagebrush	shrub	3-Nov	3	No	
Artemisia tridentata	big sagebrush	shrub	3-Nov	3	No	
Astragalus inflexus	hairy milkvetch	forb	21-Jul	2	No	
Astragalus miser	timber milkvetch	forb	30-Jun	3	Yes	FR, SE
Balsamorhiza sagittata	balsamroot	forb	16-Jun	9	Yes	EM, BU, FL, FR, MS, SE
Bouteloua gracilis	blue grama grass	graminoid	21-Jul	6	Yes	MS
Bromus carinatus	mountain brome	graminoid	7-Jul	16	Yes	EM
Carex filifolia	threadleaf sedge	graminoid	7-Jul	6	N/A	
Carex geyeri	elk sedge	graminoid	16-Jun	5	N/A	
Carex petasata	Liddon's sedge	graminoid	7-Jul	7	No	
Castilleja hispida	harsh paintbrush	forb	14-Jul	10	N/A	
Chrysothamnus viscidiflorus	green rabbitbrush	shrub	15-Sep	10	No	
Clarkia pulchella	pink fairies	forb	28-Jul	3	N/A	
Collinsia parviflora	blue-eyed Mary	forb	16-Jun	8	Yes	EM, FL, FR, MS, SE
Collomia linearis	narrow-leaved collomia	forb	7-Jul	6	Yes	FR
Crataegus douglasii	black hawthorn	shrub	21-Jul	4	N/A	

Continued

Table 4. (*Cont'd*)

Scientific name	Common name	Life form	Date of first mature seed	Duration of mature seed (weeks)	Observed microsite sensitivity (≥2 weeks)	Observed phase variability
Crataegus douglasii	black hawthorn	shrub	21-Jul	4	N/A	
Crepis atribarba	slender hawksbeard	forb	23-Jun	2	N/A	
Crepis intermedia	gray hawksbeard	forb	30-Jun	3	No	
Danthonia unispicata	onespike oatgrass	graminoid	21-Jul	6	N/A	
Delphinium bicolor	larkspur	forb	23-Jun	3	Yes	EM, BU, FL, FR
Dodecatheon conjugens	Bonneville shootingstar	forb	16-Jun	4	Yes	EM, BU, FL, FR
Dodecatheon pulchellum	few flowered shooting star	forb	16-Jun	7	Yes	MS, SE
Draba nemorosa	woods draba	forb	21-Jul	1	N/A	
Elymus glaucus	blue wild rye	graminoid	28-Jul	17	N/A	
Ericameria nauseosa	gray rabbitbrush	shrub	15-Sep	10	Yes	BU, FL
Erigeron compositus	cutleaf daisy	forb	19-May	4	Yes	FL, FR, MS
Erigeron divergens	spreading fleabane	forb	23-Jun	12	Yes	BU, FL, FR, MS, SE
Erigeron pumilus	shaggy fleabane	forb	30-Jun	4	Yes	MS
Erigeron speciosus	aspen fleabane	forb	21-Jul	4	Yes	FR
Eriogonum ovalifolium	cushion buckwheat	forb	14-Jul	5	N/A	
Eriogonum umbellatum	sulphur buckwheat	forb	14-Jul	5	Yes	BU, FL
Festuca campestris	rough fescue	graminoid	30-Jun	7	Yes	EM
Festuca idahoensis	Idaho fescue	graminoid	23-Jun	8	Yes	EM, FL, FR, MS, SE
Fritillaria pudica	yellow bell	forb	30-Jun	5	Yes	EM, BU, FL, FR
Gaillardia aristata	blanket flower	forb	7-Jul	20	Yes	BU, FR, MS, SE
Geranium viscosissimum	sticky geranium	forb	14-Jul	4	Yes	SE
Geum triflorum	prairie smoke	forb	16-Jun	8	Yes	EM, FR, MS, SE
Heterotheca villosa	hairy golden aster	forb	14-Jul	12	Yes	EM, FR, SE
Hieracium scouleri	Scouler's woollyweed	forb	21-Jul	2	Yes	EM, BU, SE
Hydrophyllum capitatum	ball head waterleaf	forb	16-Jun	6	Yes	FL
Koeleria macrantha	June grass	graminoid	7-Jul	9	Yes	EM, BU, FL, FR, MS
Lewisia rediviva	bitterroot	forb	30-Jun	3	Yes	EM, FL, MS
Lithophragma glabrum	smooth fringecup	forb	23-Jun	10	N/A	
Lithophragma parviflorum	smallflower woodland star	forb	16-Jun	11	Yes	EM, BU, FL, FR, SE
Lithospermum ruderale	field gromwell	forb	30-Jun	21	Yes	EM, BU, MS, SE
Lomatium ambiguum	Wyeth's biscuitroot	forb	14-Jul	10	Yes	EM

Continued

Table 4. (Cont'd)

Scientific name	Common name	Life form	Date of first mature seed	Duration of mature seed (weeks)	Observed microsite sensitivity ($\geq$2 weeks)	Observed phase variability
Lomatium triternatum	nine-leaf lomatium	forb	9-Jun	12	Yes	FL, FR, MS
Lupinus argenteus	silvery lupine	forb	7-Jul	2	No	
Lupinus sericeus	silky lupine	forb	30-Jun	3	Yes	EM, BU, FR, FL, MS
Melica bulbosa	oniongrass	graminoid	14-Jul	10	No	
Mertensia oblongifolia	leafy bluebell	forb	14-Jul	3	N/A	
Microseris nutans	nodding microseris	forb	23-Jun	3	N/A	
Microsteris gracilis	pink microsteris	forb	9-Jun	5	Yes	EM, FL, SE
Nemophila breviflora	Great Basin blue-eyes	forb	30-Jun	3	N/A	
Orthocarpus tenuifolius	pink owl clover	forb	7-Jul	7	Yes	FL, FR, MS
Packera cana	woolly groundsel	forb	7-Jul	2	No	
Pedicularis contorta	coil-beaked lousewort	forb	7-Jul	3	N/A	
Penstemon eriantherus	fuzzy tongue penstemon	forb	14-Jul	10	N/A	
Penstemon wilcoxii	Wilcox's penstemon	forb	7-Jul	11	N/A	
Perideridia gairdneri	Gardner's yampah	forb	1-Sep	4	Yes	EM, BU
Phacelia linearis	thread-leaf phacelia	forb	14-Jul	2	Yes	FL, FR

Increased fecundity of exotic plants might be expected due to reduced competition for resources when the exotics emerge earlier and stay green later than native plants. Wolkovich and Cleland (2010) stated that the success of exotic species may be due to (1) temporally vacant niches, (2) being active earlier in the growing season, (3) having wider phenological niches, and/or (4) greater phenological plasticity. Our data support the first three of these statements, and cannot address the fourth as this is a single-year study. Pearson et al. (2012) found that in grasslands of western Montana, top invaders appear to exploit an empty temporal niche. Their study highlighted how exotics emerged earlier, but bolted and flowered later. Our study supports these results, and we also found that exotics had longer periods of total emergence and seed dispersal as well as differences in initiation of phenological phases. Knapp and Kühn (2012) also found that nonnative species in Germany were more likely to flower later than natives.

Research is emerging on quantifying the fitness importance of differing phenology of nonnatives. Godoy and Levine (2014) found that differing phenology conferred fitness advantage via the occupation of vacant niches, and Verdú and Traveset (2005) found early emergence of exotics conferred a fitness advantage. Future research with exotics in our ecoregion might address competition of exotics with natives of the most similar phenology.

Flowering Phenology of Native Plants

Native plants in our study area flowered between March and November. Native short-lived forbs, native perennial forbs, and native shrubs all showed a wide and similar variation in date of first flower and duration of flowering. Native graminoids had a shorter and less-varied flowering window. The temporal staggering of native flowering suggests that species occupy temporal niches. This supports a trait-based community assembly (Ackerly and Cornwell 2007).

When restoring a degraded system, reassembly of a complete flowering regime is important for ecosystem function, so

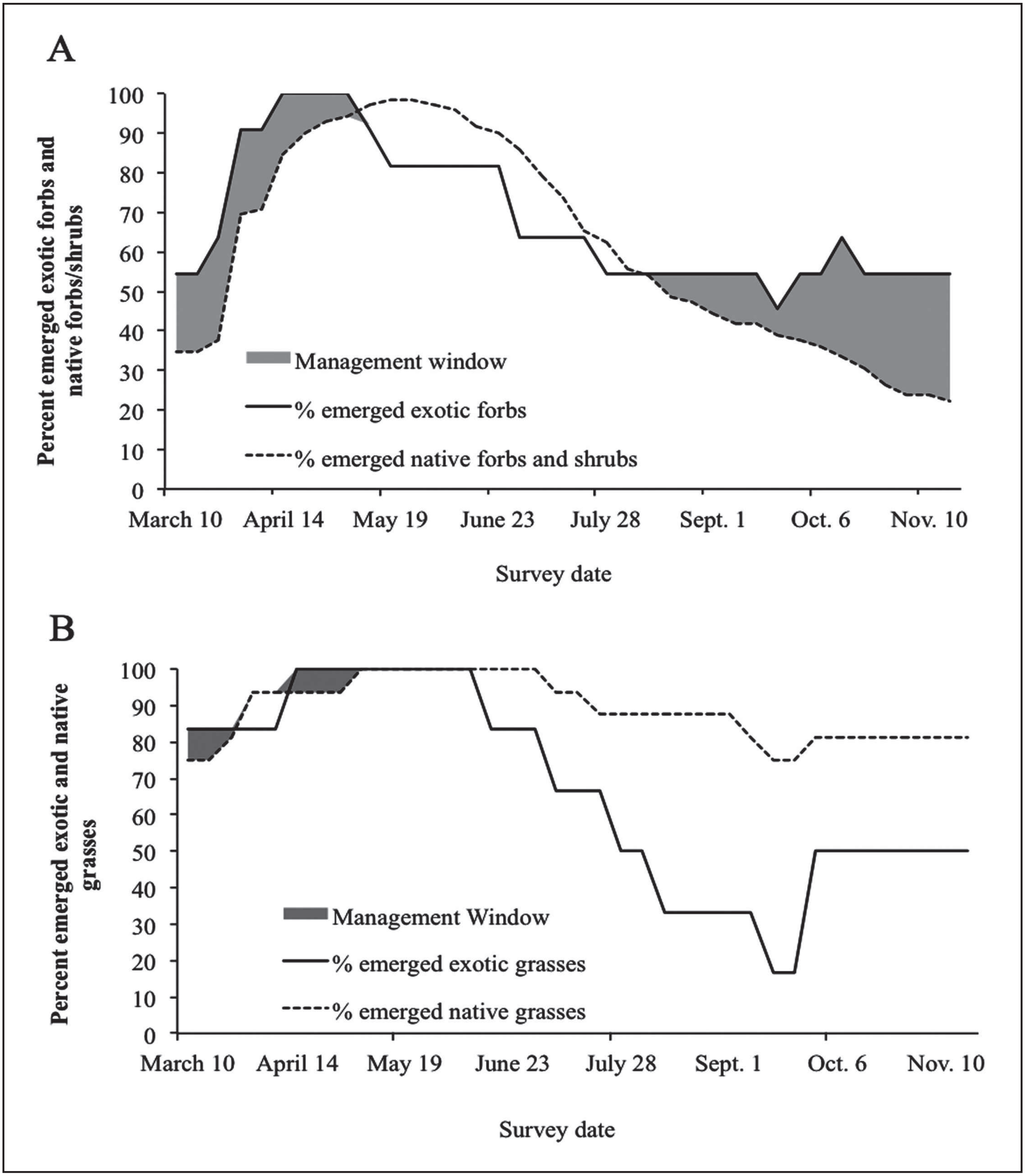

Figure 4. The percent of surveyed forbs and shrubs (A) and grasses (B) emerged at each weekly survey throughout the growing season. The dotted line represents the percent emerged of all surveyed native forbs and shrubs (A) and all surveyed native grasses (B). The solid line represents the percent emerged of all surveyed exotic forbs (A) and all surveyed exotic grasses (B). The "management window" (gray fill) is the period in time when the percent of exotic plants with vegetative growth is greater than the native plants, when control measures are presumed to harm the least number of native species.

attention should be given to capture a community assemblage with this wide span of temporal flowering.

Seed Collection and Genetic Materials

Restoration ecologists often research and consider conditions of origin when choosing seed (Krauss and He 2006; Barnes 2009). We wanted to know the extent of phenological variation across microsites to help us determine the relative importance of seed source for our collection efforts. We supply this information in table form in hope that it can be useful to others (Table 4).

Variables often used to consider seed source include the climatic conditions of rainfall, winter minimum temperatures, summer maximum temperatures, and soil types (Withrow-Robinson and Johnson 2006). However, through this filter our entire area of study would have nearly identical conditions (unpub. data). Microsites within the study area vary in total annual solar radiation, soil moisture, nutrient availability, and soil and air temperatures. Microsites can be important factors for plant establishment and success (Titus and Tsuyuzaki 2003; Dunwiddie and Martin 2016). Since plant phenology can vary with environmental cues, it follows that microsites, with their unique combination of light, temperature, and soil moisture, may also influence phenology. Species with different phenology across microsites may show phenotypic plasticity, or may have evolved genetically unique phenology at that microsite (Rathke and Lacey 1985; Richards et al. 2006). Genetically fixed phenology would retain the phenological patterns of origin, whereas species showing plasticity might adjust phenology to changing environmental cues. Without a common garden study for each species, we are unable to determine which populations have fixed genetic phenology. Consequently, species from the same elevation and climatic condition may prove unfit at another location because species may retain phenology when growing elsewhere (Godoy et al. 2009a). These species with microsite-dependent phenology and fixed genetic responses may require attention to seed source for restoration, even within a local seed collection area.

Selection of seed source to maximize genetic fitness is often approached through provenances or elevation, and on such a scale that a nearby population is considered to have the same climatic conditions (Miller et al. 2011). A common assumption is that sites close together in space and elevation produce similarly adapted species (McKay et al. 2005). We found that for some species, phenology varied up to four weeks between proximal sites. For example, the shrub *Philadelphus lewisii* Pursh. (mock orange) flowered four weeks later at a site that differed by 85-m elevation and 1000-m distance. The late-flowering mock orange grew in the bottom of a steep V-shaped draw and received seasonal and daily shade, while the earlier flowering site was south facing and with many heat-holding rocks. The fact that so many native species show phenological variability suggests that, for this area, topography and insolation may create more specific environmental cues than ecoregion, soil type, geographic distance, or elevation.

In conclusion, we also note that seed collection sometimes occurs only in the late summer or fall. Our data indicate seed collection must occur throughout the entire growing season (starting as early as April) to capture the breadth of native diversity. Additionally, some species have available seed for only a week, so consideration of individual dispersal strategy is important for planning purposes.

Management Windows

Broadleaf herbicide applications in rangelands seek to benefit a desired plant community by suppressing a target exotic forb (Pearson and Ortega 2009). However, nontarget effects on desirable plants within the community and the release of exotic grasses can decrease the benefits of such applications (Ortega and Pearson 2011). For this reason, caution has been urged in the application of herbicides in wildland settings because the herbicide application does not always lead to native species recovery; rather, secondary invaders often occupy the treated area (Mason and French 2007; Rinella et al. 2009; Larson and Larson 2010; Kettenring and Adams 2011).

A range of environmental, physiological, and biochemical factors determine herbicide susceptibility (Monaco et al. 2002), but a prerequisite for foliar herbicide uptake is green leaf tissue (Wang and Liu 2007). One approach for exotic control is to apply herbicides while most natives are dormant (Cleland et al. 2013). However, this could harm susceptible remnant natives in competition with or evolving to compete with exotics in the same niche space (Fargione and Tilman 2005; Funk et al. 2008; Godoy et al. 2009b). To maximize competition with exotics, killing native species that share phenological patterns with the exotics should be avoided. Herbicide applications during the window when only a few natives are active could further reduce the native competition and allow for the establishment of exotics by increasing the empty temporal niche.

Our results indicate no clear window when natives are dormant while exotics are active in our study area. To illustrate, in the period when exotic forb presence was greatest and native forb presence was lowest, 19 of the 72 monitored native forb species were growing in at least one study site (Figure 4). Although this number is substantially lower than the number of species present during peak activity, if one were to apply herbicide in this period these 19 native species, which may be better adapted to tolerate exotic species, could be harmed. Native grass species remained emergent across the growing season; at the lowest points of emergence, 12 of 16 native grass study species were still present with green tissue in at least one study site. Even at one of the most degraded sites, with only 16% native plant cover, native grass and forb species were concurrently emergent with *C. stoebe* and *B. tectorum* from March through November. Removing native species from direct competition at that site could open niche space for exotics. Possibly, management windows could only be identified through careful observation by a manager near the time of herbicide application due to seasonal variability in differences between dormancy of native and exotic plants.

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Daniel L. Mummey earned his BA in microbiology at Eastern Washington University, his MS in soil science at Washington State University, and his PhD in soil science and restoration ecology at the University of Wyoming. After graduating in 2004, he worked as an assistant research professor in the Department of Biological Sciences at the University of Montana, Missoula. Dan's research focuses on how soil structure, soil organisms, and plants determine plant community composition and ecosystem function. In Dan's current role at MPG Ranch, he develops and implements methods to establish healthy native plant communities in disturbed areas.

Lauren Shreading has a BA in biology from the University of Montana. She works in restoration and ecology research at MPG Ranch.

Philip W. Ramsey, PhD, is an ecologist and general manager of MPG Ranch. His research interests are in ecosystem processes and he has published on the influence of management practices on forest soils, factors allowing for the spread of invasive weeds in grasslands, and nutrient flow between rivers and floodplain forests. In addition to research, he oversees the management and operations of MPG Ranch, a 3800-hectare conservation property in western Montana.

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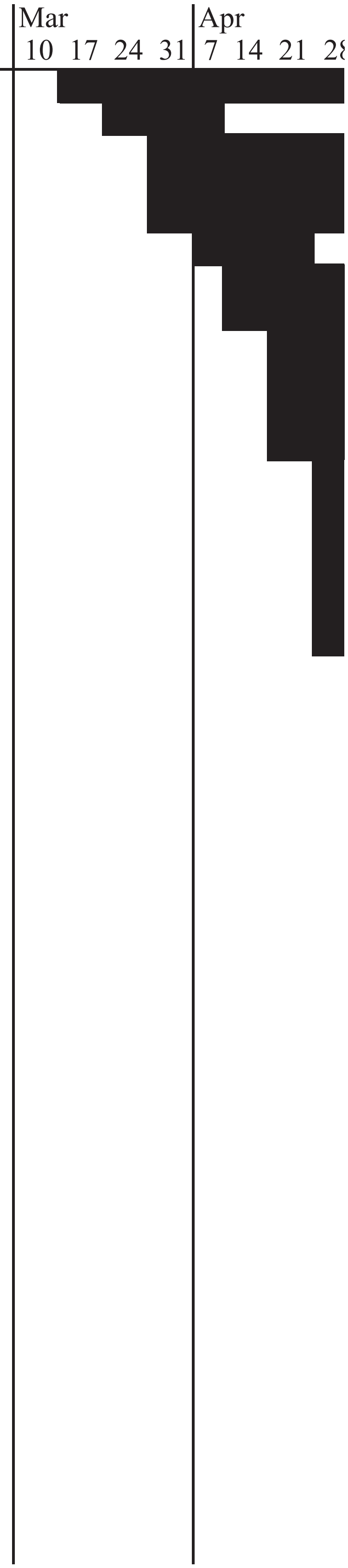
Appendix. Flower duration for each study species by life form.

Perennial Forbs

Native

Scientific name	Common name
Lomatium cous	cous biscuitroot
Ranunculus glaberrimus	sagebrush buttercup
Fritillaria pudica	yellow bell
Lomatium triternatum	nine-leaf lomatium
Dodecatheon conjugens	Bonneville shootingstar
Antennaria dimorpha	low pussy-toes
Erigeron compositus	cutleaf daisy
Hydrophyllum capitatum	ball head waterleaf
Lithophragma parviflorum	smallflower woodland-star
Claytonia lanceolata	lanceleaf springbeauty
Delphinium bicolor	larkspur
Viola nuttallii	Nuttall's violet
Dodecatheon pulchellum	few-flowered shooting star
Erythronium grandiflorum	glacier lily
Geum triflorum	prairie smoke
Lomatium ambiguum	Wyeth's biscuitroot
Lomatium macrocarpum	big seed biscuitroot
Balsamorhiza sagittata	arrowleaf balsamroot
Lithophragma glabrum	smooth fringecup
Antennaria rosea	rosy pussy-toes
Antennaria umbrinella	umber pussytoes
Saxifraga integrifolia	wholeleaf saxifrage
Senecio integerrimus	lambstongue groundsel
Zigadenus venenosus	death camas
Lithospermum ruderale	field gromwell
Arenaria congesta	ballhead sandwort
Lupinus sericeus	silky lupine
Triteleia grandiflora	triteleia
Astragalus inflexus	hairy milkvetch
Astragalus miser	timber milkvetch
Lupinus argenteus	silvery lupine
Penstemon eriantherus	fuzzytongue penstemon
Penstemon wilcoxii	Wilcox's penstemon
Agoseris glauca	false-dandelion
Arnica sororia	twin arnica
Eriogonum ovalifolium	cushion buckwheat
Silene oregana	Oregon campion
Apocynum androsaemifolium	spreading dogbane
Erigeron pumilus	shaggy fleabane
Lewisia rediviva	bitterroot
Microseris nutans	nodding microseris
Eriogonum umbellatum	sulphur buckwheat
Achillea millefolium	western yarrow
Crepis atribarba	slender hawksbeard
Gaillardia aristata	blanket flower
Pedicularis contorta	coil-beaked lousewort



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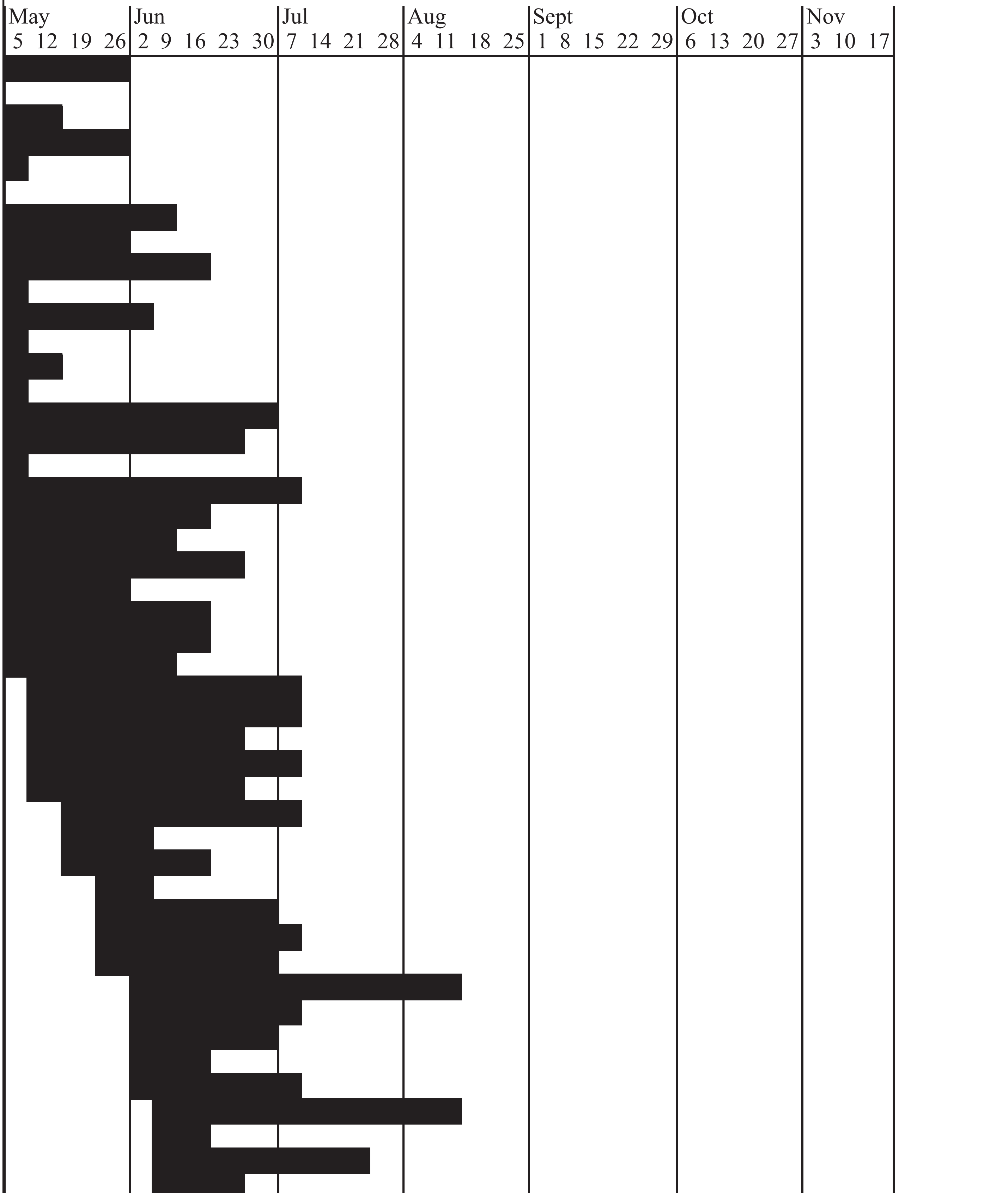
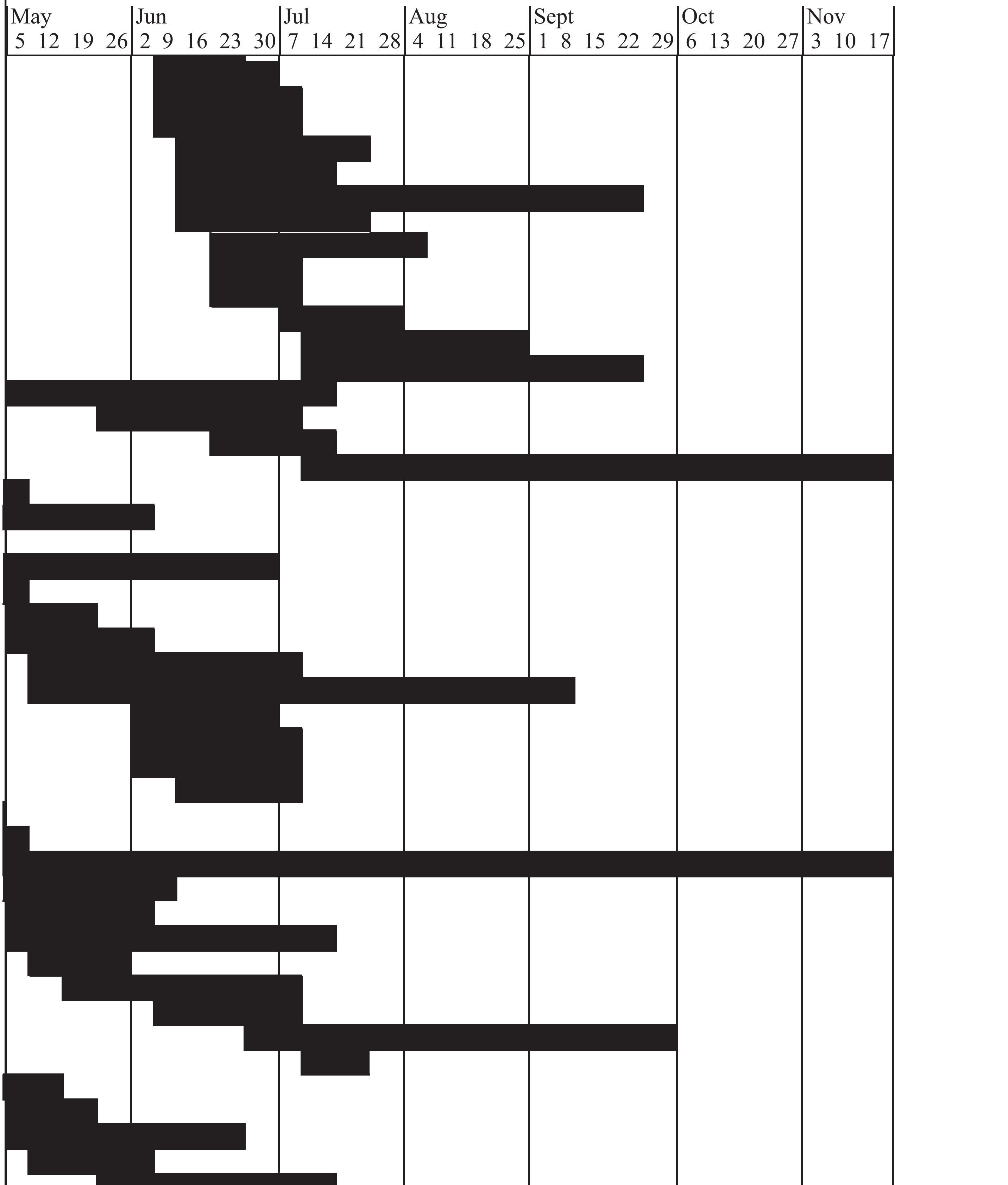


Appendix. (Cont'd)

Group	Origin	Scientific name	Common name	Mar 10	Mar 17	Mar 24	Mar 31	Apr 7	Apr 14	Apr 21	Apr 28
		Potentilla glandulosa	sticky cinquefoil								
		Packera cana	woolly groundsel								
		Agastache urticifolia	giant horsemint								
		Allium cernuum	nodding onion								
		Crepis intermedia	gray hawksbeard								
		Heterotheca villosa	hairy golden aster								
		Campanula rotundifolia	scotch harebell								
		Erigeron speciosus	aspen fleabane								
		Potentilla gracilis	slender cinquefoil								
		Sedum stenopetalum	narrow-petaled stonecrop								
		Hieracium scouleri	Scouler's woollyweed								
		Perideridia gairdneri	Gardner's yampah								
		Solidago missouriensis	Missouri goldenrod								
	Exotic	*Euphorbia esula*	leafy spurge								
	Exotic	*Silene latifolia ssp. alba*	bladder campion								
	Exotic	*Potentilla recta*	sulphur cinquefoil								
	Exotic	*Centaurea stoebe*	spotted knapweed								
Short-lived forbs	Native	*Polemonium micranthum*	littlebells				■	■	■	■	■
Short-lived forbs	Native	*Microsteris gracilis*	pink microsteris				■	■	■	■	■
Short-lived forbs	Native	*Montia linearis*	narrowleaved montia					■	■	■	
Short-lived forbs	Native	*Collinsia parviflora*	blue-eyed Mary						■	■	■
Short-lived forbs	Native	*Nemophila breviflora*	Great Basin blue-eyes								■
Short-lived forbs	Native	*Draba nemorosa*	woods draba								
Short-lived forbs	Native	*Mertensia oblongifolia*	leafy bluebell								
Short-lived forbs	Native	*Phacelia linearis*	thread-leaf phacelia								
Short-lived forbs	Native	*Erigeron divergens*	spreading fleabane								
Short-lived forbs	Native	*Collomia linearis*	narrow-leaved collomia								
Short-lived forbs	Native	*Orthocarpus tenuifolius*	pink owl clover								
Short-lived forbs	Native	*Geranium viscosissimum*	sticky geranium								
Short-lived forbs	Native	*Clarkia pulchella*	pink fairies								
Short-lived forbs	Exotic	*Draba verna*	spring draba				■	■	■	■	■
Short-lived forbs	Exotic	*Holosteum umbellatum*	jagged chickweed				■	■	■	■	■
Short-lived forbs	Exotic	*Erodium cicutarium*	storksbill							■	■
Short-lived forbs	Exotic	*Veronica verna*	vernal speedwell								■
Short-lived forbs	Exotic	*Alyssum alyssoides*	yellow alyssum								
Short-lived forbs	Exotic	*Sisymbrium altissimum*	tumble mustard								
Short-lived forbs	Exotic	*Camelina microcarpa*	little-pod false flax								
Short-lived forbs	Exotic	*Tragopogon dubius*	yellow salsify								
Short-lived forbs	Exotic	*Cynoglossum officinale*	hound's tongue								
Short-lived forbs	Exotic	*Verbascum blattaria*	moth mullein								
Short-lived forbs	Exotic	*Lactuca serriola*	prickly lettuce								
		Carex geyeri	elk sedge								■
		Carex petasata	Liddon's sedge								
		Poa secunda	Sandberg's bluegrass								
		Carex filifolia	threadleaf sedge								
		Koeleria macrantha	June grass								

Appendix. (Cont'd)



Appendix. (Cont'd)

		Scientific name	Common name	Mar 10	Mar 17	Mar 24	Mar 31	Apr 7	Apr 14	Apr 21	Apr 28
Perennial graminoids	Native	*Pseudoroegneria spicata*	bluebunch wheatgrass								
		Festuca campestris	rough fescue								
		Festuca idahoensis	Idaho fescue								
		Stipa occidentalis	western needlegrass								
		Melica bulbosa	oniongrass								
		Bromus carinatus	mountain brome								
		Stipa comata	needle and thread								
		Aristida purpurea	three-awn								
		Danthonia unispicata	onespike oatgrass								
		Bouteloua gracilis	blue grama grass								
		Elymus glaucus	blue wild rye								
	Exotic	*Poa bulbosa*	bulbous blue grass								■
		Poa pratensis	Kentucky bluegrass								
		Agropyron cristatum	crested wheatgrass								
		Thinopyrum intermedium	intermediate wheatgrass								
Shrubs	Native	*Amelanchier alnifolia*	saskatoon								■
		Acer glabrum	Rocky Mountain maple								
		Purshia tridentata	antelope bitterbrush								
		Prunus virginiana	chokecherry								
		Crataegus douglasii	black hawthorn								
		Physocarpus malvaceus	ninebark								
		Philadelphus lewisii	mock orange								
		Symphoricarpos albus	snowberry								
		Chrysothamnus viscidiflorus	green rabbitbrush								
		Ericameria nauseosa	gray rabbitbrush								
		Artemisia dracunculus	wild tarragon								
		Artemisia frigida	fringed sagebrush								
		Artemisia tridentata	big sagebrush								
Annual grasses	Exotic	*Bromus tectorum*	cheatgrass								
		Bromus commutatus	meadow brome-grass								
		Bromus japonicus	Japanese brome								

Appendix. (Cont'd)