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Phenological patterns in the desert spring ephemeral *Astragalus holmgreniorum* Barneby (Fabaceae)

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Abstract.—Herbaceous perennial species may exhibit winter or summer dormancy, or they may be spring ephemerals with dormancy extending from summer through winter. Herbaceous perennials, and spring ephemerals in particular, are most common in strongly seasonal but relatively mesic temperate environments. Warm deserts are typically dominated by shrubs and annuals that are better adapted to withstand or avoid severe summer heat. *Astragalus holmgreniorum* Barneby (Fabaceae) is a perennial spring ephemeral that has a restricted distribution at the northeastern edge of the Mojave Desert. We explored factors that regulate its phenological development in an observational study at 2 sites over 2 growing seasons. We examined consequences of weather variation in terms of phenological patterns and their effect on survival, growth, and reproductive output. Both seedling emergence and reinitiation of shoot growth occurred in early spring, with timing varying by site and year. Flowering peaked in early April each year regardless of weather variation. Plants ceased aboveground activity as daily maximum temperatures exceeded 30 °C in May. Between-year variation in winter-spring precipitation timing had significant effects on growth, survival, and reproductive output in 2 years with similar above-average total precipitation. Early-season precipitation favored high seedling emergence, whereas midseason precipitation favored increased growth and flowering of adult plants, high fruit set, and high seedling survival, and late-season precipitation favored high seed set. Our study showed that variation in precipitation timing can have major impacts on plant success in a desert environment, even in years with similar above-average total precipitation.

Resumen.—Las especies herbáceas perennes pueden mostrar períodos de inactividad durante el invierno o el verano, o pueden ser efímeras (propias de la primavera) y, por lo tanto, permanecer inactivas desde el verano hasta el invierno. Las plantas perennes herbáceas y, particularmente, las efímeras de primavera son más comunes en ambientes estacionales claramente templados, pero relativamente mésicos. Los desiertos cálidos suelen estar dominados por arbustos y plantas anuales con mayores cualidades adaptativas para resistir o evitar el intenso calor del verano. La *Astragalus holmgreniorum* Barneby (Fabácea) es una planta perenne efímera de primavera, presenta una distribución restringida a la periferia del noreste del desierto de Mojave. En un estudio observacional realizado en dos sitios, durante dos temporadas de crecimiento, exploramos los factores que regulan su desarrollo fenológico. Examinamos las consecuencias de la variación del clima en términos de patrones fenológicos y su efecto en la supervivencia, el crecimiento y el rendimiento reproductivo. Tanto la germinación de las plántulas como la reiniciación del crecimiento de los brotes se produjeron al iniciar la primavera, con variaciones temporales según el sitio y el año. Cada año, la floración alcanzó su punto máximo a principios de abril, independientemente de la variación del clima. Las plantas cesaron su actividad a nivel del suelo cuando las temperaturas diarias alcanzaron los 30 °C en mayo. La variación interanual en el periodo de precipitación durante invierno-primavera tuvo importantes consecuencias en el crecimiento, la supervivencia y el rendimiento reproductivo, en dos años con precipitaciones totales similares por encima del promedio. Las precipitaciones tempranas favorecieron la aparición de plántulas. Mientras que, las precipitaciones de mediados de temporada impulsaron el crecimiento y la floración de las plantas adultas, generaron más frutos y un aumento en la supervivencia de las plántulas. Finalmente, las precipitaciones tardías favorecieron al aumento de la producción de semillas. Nuestro estudio mostró que las variaciones en los períodos de precipitación pueden tener un impacto positivo en las plantas del desierto, incluso en años con una precipitación total similar por encima del promedio.

Different plant life-forms in deserts utilize precipitation in different ways, but most have an opportunistic response to available moisture (Ehleringer 1985). Most woody perennial species experience reduced biological activity or enter dormancy during the summer months (Beatley 1974), but some can utilize both summer and winter precipitation (Ehleringer et al. 1991). Winter annuals, which dominate the flora of warm deserts (Went 1949, Shreve

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and Wiggins 1951, Beatley 1974), most often utilize fall precipitation for germination and complete their reproductive cycle as soon as temperatures warm in the spring. Herbaceous perennials are relatively uncommon in warm deserts, making up <3% of vegetative cover (Beatley 1974). Most herbaceous perennials in this environment germinate or reemerge in response to effective fall or early winter precipitation and are active during winter, which is usually relatively mild. Only a few are spring ephemerals that remain dormant from summer through winter and reinitiate growth in spring. Most of these are geophytes with deep-seated storage organs (Adamson 1939, Noy-Meir 1973). Hemicryptophytes are similar to geophytes, but their perennating buds are at or just below surface level (Adamson 1939, Whittaker and Niering 1964). The soil surface in warm deserts can experience very high summer temperatures, which may explain why the hemicryptophyte life-form is rare in this environment.

Perennial plants of seasonally varying environments have evolved shoot dormancy as a mechanism for surviving periods unfavorable for aboveground growth (Vegis 1964). They become dormant in response to environmental cues that signal the approaching unfavorable season, rather than in direct response to the stressful environment that ensues (Lang et al. 1987, Volaire and Norton 2006). Temperature is the most common cue, though photoperiod is sometimes also implicated (Volaire and Norton 2006, Rohde and Bhalerao 2007, Kamenetsky 2009). Perennial plants in cold winter climates experience dormancy induction in response to cooler temperatures and shorter days, while release from shoot dormancy generally requires winter chilling.

In climates with mild winters and dry summers, shoot dormancy is induced in response to warmer temperatures and longer days. This dormancy induction is distinct from the development of desiccation tolerance, as it occurs even in plants not under water stress (Volaire and Norton 2006). Release from dormancy is less well understood in summer-dormant species (Volaire and Norton 2006). Apparent dormancy may represent quiescence (ecodormancy sensu Lang et al. 1987) under conditions unfavorable for growth, with only the return of favorable conditions in autumn required for growth reinitiation.

For spring ephemerals, induction into dormancy likely follows the pattern for summer-dormant species, but winter chilling is usually required for release. Flowering induction is generally mediated by the same cues that regulate dormancy status (i.e., temperature and photoperiod; King and Heide 2009). Vernalization (winter chilling) commonly preconditions bud meristems to develop into flowers in spring-flowering species, though long days are sometimes also necessary for flowering.

Astragalus holmgreniorum Barneby, a federally listed endangered species restricted to extreme southwestern Utah (USFWS 2001), is a spring ephemeral hemicryptophyte that occurs in a warm desert environment where this life-form is rare. The observational study reported here builds on a 22-year demographic data set that provided the basis for population viability analysis (PVA) for this species (S. Meyer, R. Van Buren, and A. Searle 2015, unpublished report on file at The Nature Conservancy Utah Field Office, Salt Lake City, UT). The demographic data were collected yearly in late spring. Many vital rates were only weakly correlated with total winter-spring precipitation in this analysis, leading us to hypothesize that within-season variation in precipitation and temperature patterns and their effect on phenological development could affect variation in vital rates.

To address this question, we examined phenological patterns and selected vital rates at 2 sites across 2 growing seasons. We hypothesized that variability in timing and magnitude of temperature and precipitation cues would have a direct effect on *A. holmgreniorum* phenology, and that this in turn would affect survival, growth, and reproductive output. The primary questions addressed were (1) How does interannual variation in the timing and magnitude of environmental cues affect phenological patterns, (2) How does interannual variation in phenological pattern affect plant success, and (3) How do site-specific factors interact with environmental cues to mediate both phenological patterns and plant success?

METHODS

Study Species

Astragalus holmgreniorum grows only in warm desert shrub communities along wash

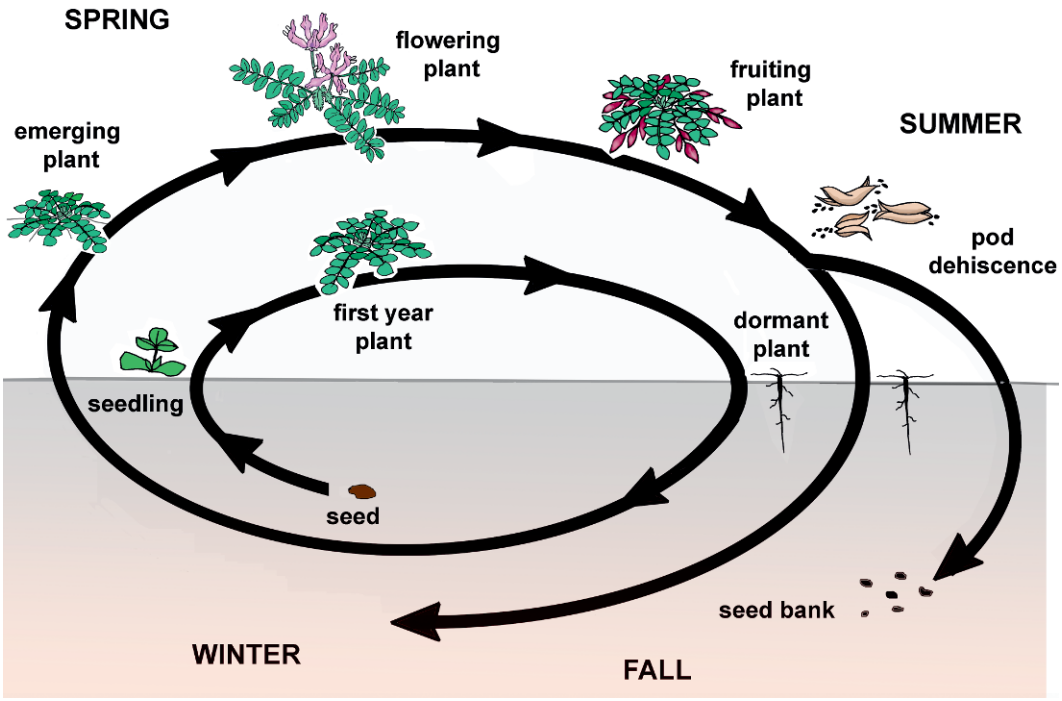

Fig. 1. Schematic diagram of principal phenological transitions in the life cycle of *Astragalus holmgreniorum,* showing the season during which each transition takes place.

skirts and gravelly slopes, primarily within the Virgin Limestone member of the Moenkopi geological formation (Van Buren and Harper 2003, USFWS 2006). It is restricted to the northeastern edge of the Mojave Desert, USA. All known populations occur within 15 km of rapidly expanding metropolitan St. George, Utah.

Astragalus holmgreniorum emerges in late winter, flowers and fruits in spring, and enters dormancy in early summer (Fig. 1). It is a prostrate plant that grows from a taproot topped by a branched caudex that produces basal leaves (Barneby 1980). Flowers are usually produced only on plants that have survived at least one dormant season. Its leathery, 2-chambered pods can contain up to 38 seeds. The seeds are physically dormant at maturity and lose this hard-seededness over a period of 10 or more years in the soil (Searle 2011). Most plants do not survive past their third growing season (Van Buren and Harper 2003). Population viability analysis for this species identified seed production and seed bank persistence as key life history transitions affecting population survival.

Study Sites

Astragalus holmgreniorum occurs as 3 main population centers (State Line, Gardner Well, and Central Valley) and 3 outlier populations (Fig. 2; USFWS 2006). In 2015, 5 sites in the State Line population and 1 site in the Gardner Well population were selected for the phenology study. In 2016 we added 2 sites in the Central Valley population because 4 of the State Line sites had insufficient plant numbers for sampling. In this paper we present only data from the Gardner Well site and from the Atkinville site in the State Line population, which were included in both study years (Table 1). This enabled a statistical examination of between-year trends and also a comparison of 2 sites with different topography and disturbance histories. Data from additional sites (not shown) confirmed the phenological patterns reported here over a broader range of sites.

Climate and Weather Characterization

We used climate and yearly weather data obtained from the PRISM weather interpolator

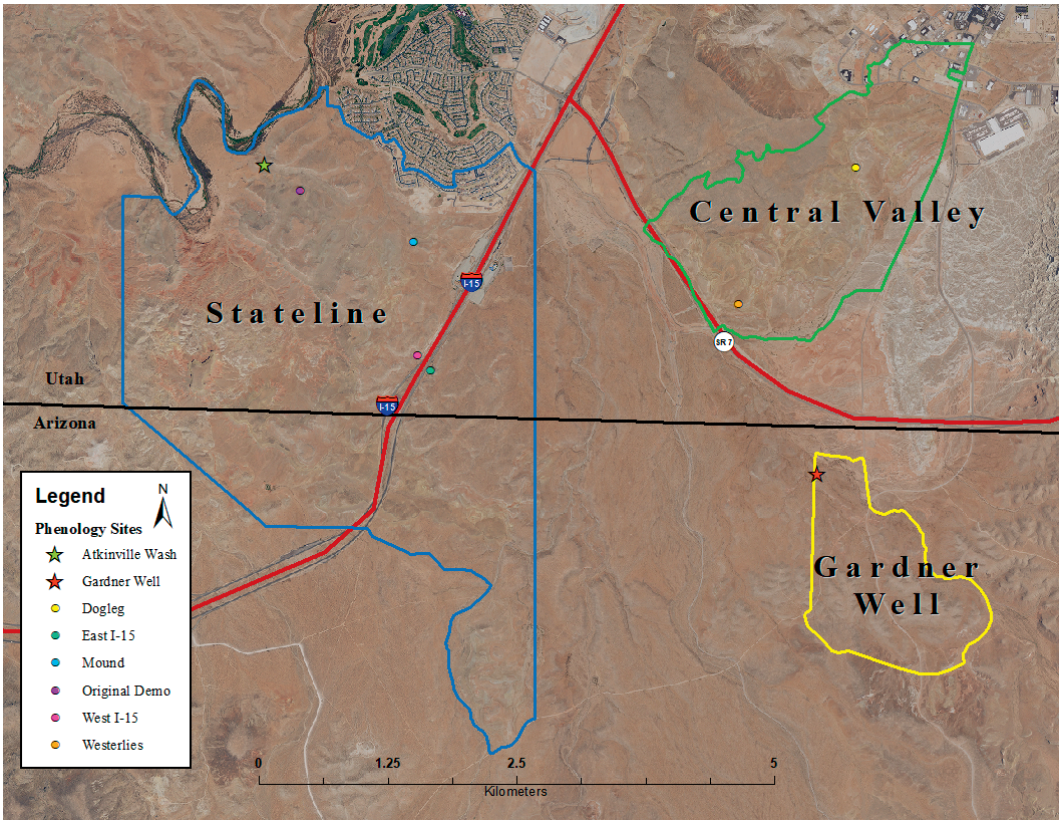

Fig. 2. Map of the main distribution of *Astragalus holmgreniorum*, showing the 3 principal population centers, the principal phenology sampling sites (Atkinville Wash and Gardner Well), and the supplemental phenology sampling sites (sampled only in a single year; data not presented).

(http://prism.oregonstate.edu/explorer/) to examine how weather variation affected observed phenological patterns. The 2 sites had very similar weather. We used interpolated data from the Gardner Well study site (Table 1) in the weather data presentation (Fig. 2). Daily maximum and minimum temperatures were averaged and daily precipitation totals were summed for each week of the study each year (i.e., from 1 November to 31 May).

Phenology Study

Plots for the phenology study at each site were placed in areas where previous demographic studies had shown reasonable plant densities (Van Buren and Harper 2003, Searle 2011). An area 100 m by 20 m was surveyed by marking and numbering all plants in the plot as they emerged. Individual plants were treated as replicates. At each visit, data were taken for newly emerged plants and also for plants that were marked in previous visits.

In situ evaluation was initiated prior to emergence each year. In 2015, sites were visited weekly from 7 February through 4 April (the end of emergence) and continued weekly through 20 June. In 2016, sites were visited weekly from 29 January through 18 March (the end of emergence) and then every other week through 4 June. Because of high emergence in 2016, we haphazardly chose one seedling from each clump of >3 seedlings to track through the season.

At each visit we recorded the following phenological stages: seedling (cotyledons present at first census) or adult (returning from at least one season of dormancy), diameter, number of reproductive stalks and stage of development of each stalk (bud, full flower, post-flowering unfertilized, fruit visibly elongated but green, fruit mature). Flowers were not

Table 1. Location of study sites and numbers of seedling and adult plants tagged and followed at each site in 2015 and 2016.

			2015		2016	
Site	Latitude	Longitude	Seedlings	Adults	Seedlings	Adults
Atkinville	37.021485	−113.638065	34	61	114	106
Gardner Well	36.995842	−113.576990	63	38	168	54

enumerated because of time constraints; a stalk was scored in a phenological stage based on the stage of a majority of flowers on the stalk. Plant mortality was also recorded.

Reproductive Output Study

We also carried out reproductive output studies at Atkinville and Gardner Well. For fruit set, flowers were enumerated on >20 representative individuals that were tagged and evaluated in full flower each year. Fruits on each plant were then counted at the point of fruit maturation when all fruits could be distinguished, but none had disarticulated from the stalks. For seed fill we selected >30 representative ripe, intact fruits at each site each year, and determined number of sound, insect-damaged, and aborted seeds. A subset of sound seeds was evaluated for viability, which always exceeded 95%; only sound seed data were reported. As unfertilized ovules were not counted, fill data are presented as seeds/fruit.

Experimental Design and Statistical Analysis

To examine general phenological patterns, the data are presented graphically as time series. Weekly or biweekly data for each phenological transition are plotted for each site each year. For emergence and survival, data are presented as proportions of the total number of plants evaluated that year at each site. These numbers do not sum to 1 because some plants experience mortality before emergence is complete. Plant size on each date is the mean of all seedlings or all adult plants present on that date. For flowering phenology, data represent the proportion of the total number of stalks that were present in each stage on each date. These numbers also do not sum to 1 because more stalks appeared through time early in flowering, and because some disappeared due to frost, herbivory, and other damage. Fruiting stalks also tend to decrease in apparent number as mature fruits disarticulate from the stalks later in the season.

To examine whether the trends observed in the time-course data were statistically supported, we used SAS 9.4 (Statistical Analysis Institute, Boca Raton, FL). The model for most analyses included site and year independent variables as fixed main effects, as well as the site-by-year interaction. SAS Proc GLM (general linear models) was used for analysis of variance (ANOVA) because of the unbalanced design caused by variable numbers of plants evaluated between sites and years (Table 1). Continuous response variables were transformed as needed to meet the assumptions of ANOVA; untransformed means are reported. SAS Proc Logistic was used for analyzing binary response variables such as survival. Analyses that included continuous independent variables such as emergence date or plant size were performed using linear regression (SAS Proc Reg) when only continuous independent variables were included or analysis of covariance (ANCOVA) in SAS Proc GLM when both categorical (class) and continuous independent variables were included. Response variables from the phenology data set included emergence date, end of season survival, and maximum diameter for both seedlings and adults, as well as proportion of plants flowering, number of flowering stalks per plant, and proportion of flowering stalks that were unfertilized (i.e., stalks on which no flowers set fruit). Date of emergence was enumerated for each individual as the number of weeks post-February 7th each year. Response variables from the reproductive output data set included number of fruits per plant, fruit-to-flower ratio, and number of seeds per fruit.

Results

Weather Patterns

Both years of the study experienced slightly above-average precipitation over the period 1 November to 31 May, and totals for the 2 years were similar (30-year mean: 140 mm; 2015: 152 mm; 2016: 164 mm). Patterns of

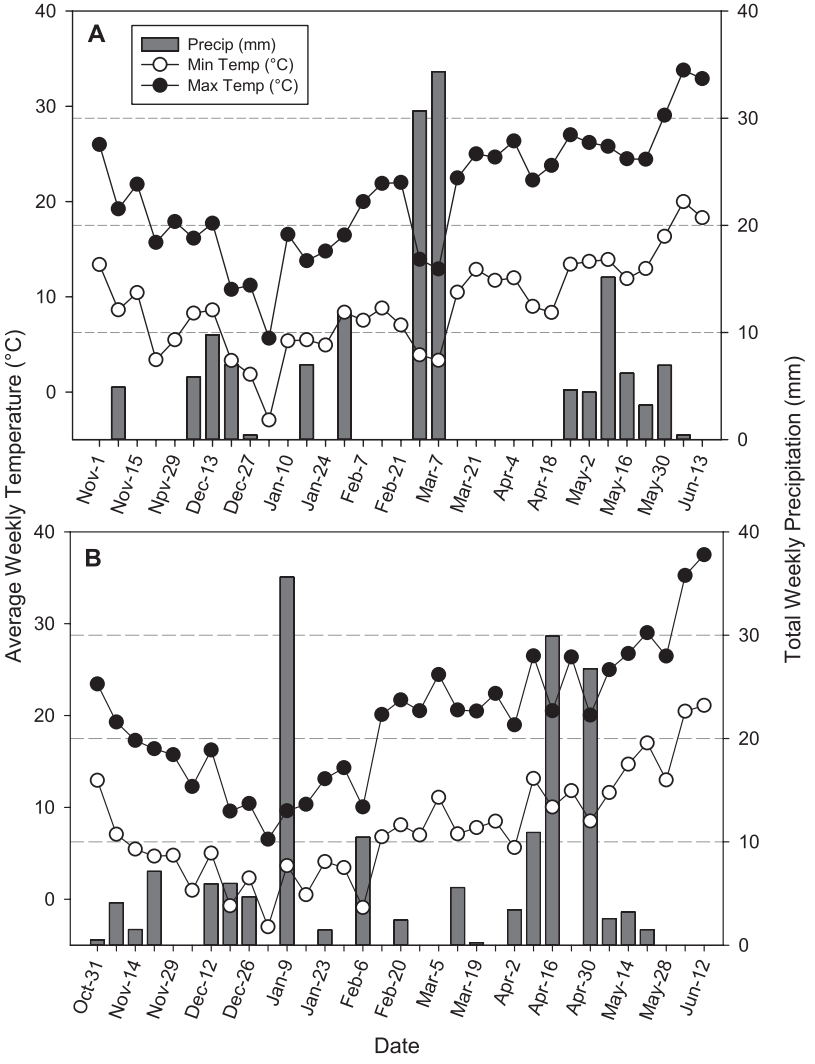

Fig. 3. Weekly total precipitation, mean maximum temperature, and mean minimum temperature during the period 1 November to 14 June for the 2 growing seasons included in the study: **A,** 2014–2015; **B,** 2015–2016. Data are from http://prism.oregonstate.edu/explorer/.

variation in temperature during this period were also similar across years, with the only short-term variation directly associated with storms (Fig. 3). Precipitation patterns through time, however, were very different between the 2 study years. In 2015, there was reasonably frequent precipitation through the winter but no major storms until early March. No additional rainfall was received during the 6-week period following these March storms, and there was little effective late-spring rain. In contrast, in 2016, the first major storm was in early January, and there was little follow-up precipitation through most of the spring, though there was no dry period as long as that observed in 2015. Two major storms then arrived in mid-to-late April 2016.

Emergence

Adults initiated emergence in mid-February 2015 at Atkinville (Fig. 4A), whereas seedling emergence took place in early to mid-March, after the major storms (Fig. 3). In 2016, both seedlings and adults commenced emergence at Atkinville the second week in February, and both showed emergence peaks the following

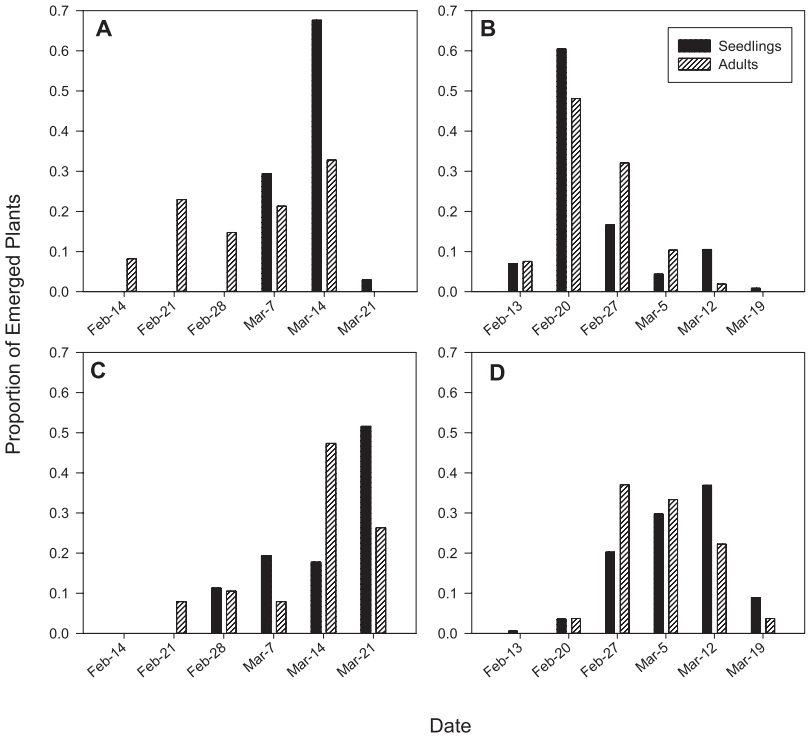

Fig. 4. Time courses of seedling emergence (black bars) and adult plant emergence (hatched bars) plotted by weekly evaluation date: **A,** Atkinville study site in 2015; **B,** Atkinville study site in 2016; **C,** Gardner Well study site in 2015; **D,** Gardner Well study site in 2016.

week as the weather warmed (Fig. 4B). At Gardner Well in 2015, seedling emergence started after the major storms in early March and peaked in late March, while adults started emergence in mid-February and peaked in mid-March (Fig. 4C). In 2016 at Gardner Well, seedlings started emerging 2 weeks earlier than in 2015 and peaked the week of 12 March (Fig. 4D). Adults initiated emergence the week of 20 February with no clear emergence peaks.

As a result of these time-course differences, mean emergence time was 1.4 weeks later for seedlings and 1 week later for adults in 2015 than in 2016, both significant differences (Fig. 5A, B; Table 2). Emergence of both seedlings and adults was also significantly later at Gardner Well than at Atkinville. The difference in mean emergence time between years was much greater at Atkinville (2.3 weeks) than at Gardner Well (0.8 weeks), resulting in a significant year-by-site interaction (Table 2). Seedling emergence times were significantly different between sites only in 2016.

Growing Season Survival

The proportion of evident living seedlings and adult plants dropped dramatically after mid-May in both 2015 and 2016, indicating that a substantial proportion either entered summer dormancy or died during this period (Fig. 6). As it is not possible to distinguish entry into dormancy from death in the field based on a single season of data collection, growing season survival is calculated based on surviving plants prior to this sharp drop.

In both years, seedling growing season mortality was approximately linear through time (Fig. 6), but the mortality rate per week was much higher in 2015 than in 2016 at both sites, so that survival to the end of the growing season was significantly higher in 2016 than in 2015 (Table 2, Fig. 5D). Seedling survival was also significantly higher across years at Gardner Well than at Atkinville Wash. For adult plants, growing season survival was very high across both years (Fig. 6), and there were no significant effects of either year or site (Table 2, Fig. 5C).

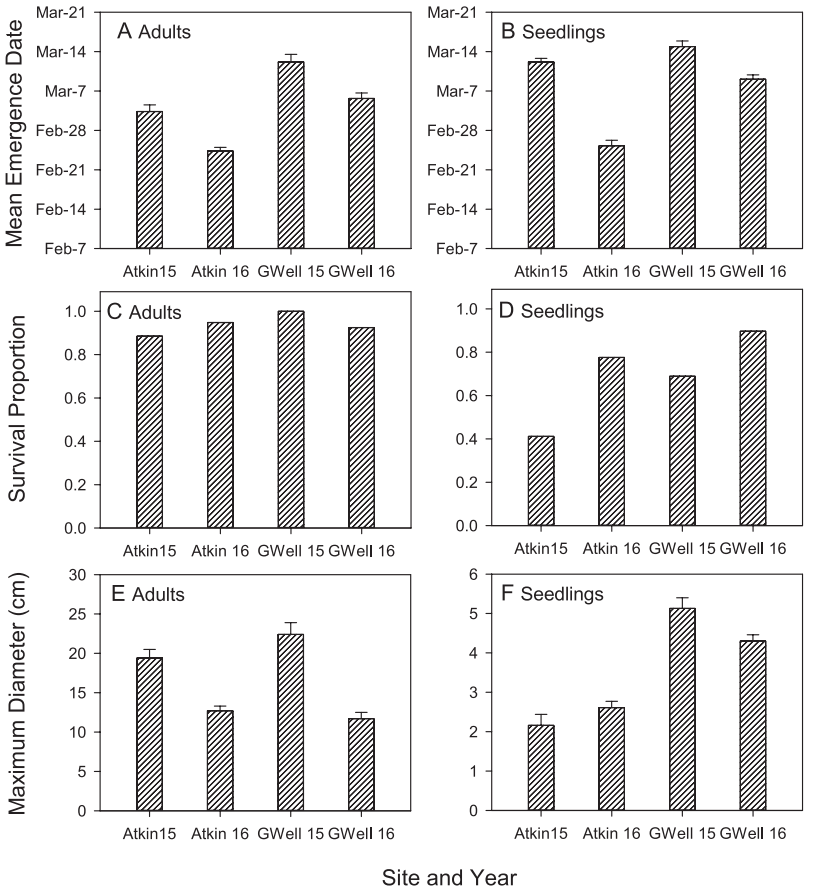

Fig. 5. Mean values for 6 demographic measures at Atkinville and Gardner Well in 2015 and 2016: **A,** mean emergence date of adults; **B,** mean emergence date of seedlings; **C,** proportion of adults surviving; **D,** proportion of seedlings surviving; **E,** mean maximum diameter of adults; **F,** mean maximum diameter of seedlings. Error bars = standard error of the mean. See Table 2 for statistical analysis.

Seedling survival increased with emergence date in an ANCOVA with site, year, and emergence date included as main effects (df = 1,151, $F = 8.71$, $P = 0.004$), but this pattern was only evident in 2015 (emergence date × year interaction: df = 1,151, $F = 5.48$. $P = 0.002$) and primarily at Atkinville (emergence date × site interaction: df = 1,151, $F = 3.31$. $P = 0.070$). This was because seedling survival from later emergence dates was similarly high across sites and years, but Atkinville had reduced seedling survival relative to Gardner Well from earlier emergence dates in 2015 (Fig. 6A, C).

GROWTH.—Adult plants grew significantly larger in 2015 than in 2016 (Table 2, Fig. 5E); maximum diameter occurred in mid-April of both years (Fig. 7). The adult plant growth pattern was similar across years during the first 6 weeks, but in 2015, growth rate increased in response to 2 weeks of substantial precipitation in early March (Figs. 3, 5). This growth response to precipitation was not observed in seedlings (Fig. 5). Adult plants at Gardner Well responded more strongly to the favorable growth conditions in 2015 than those at Atkinville, whereas under less favorable conditions in 2016, there was no significant difference between sites (Table 2, Fig. 5E). Seedling diameter peaked in mid-April and was not significantly different between years (Table 2, Fig. 5F); however, maximum seedling size across years was significantly greater at Gardner Well. After mid-April, both seedlings and adult plants decreased in average diameter due to outer leaf senescence (Fig. 7).

Table 2. Results of analysis of variance for year and site main effects and year × site interactions for 12 demographic response variables. Analyses were conducted using SAS Proc GLM, unless otherwise noted. ns = not significant, α = 0.05.

	Year main effect			Site main effect			Year × site interaction		
Response variable	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Mean seedling emergence date[c]	1, 245	123.2	<0.0001	1, 355	58.48	<0.0001	1, 245	21.76	<0.0001
Mean adult emergence date	1, 255	42.73	<0.0001	1, 255	77.94	<0.0001	1, 255	0.05	ns
Seedling survival probability[a]	1	23.50[b]	<0.0001	1	8.45[b]	0.0037	1	0.62[b]	ns
Adult survival probability[a]	1	0[b]	ns	1	0[b]	ns	1	0.001[b]	ns
Seedling maximum diameter	1, 245	3.43	ns	1, 245	18.87	<0.0001	1, 245	0.06	ns
Adult maximum diameter	1, 255	82.58	<0.0001	1, 255	1.16	ns	1, 255	4.51	0.0347
Flowering probability[a]	1	19.50[b]	<0.0001	1	4.88[b]	0.0271	1	5.95[b]	0.0147
Flowering stalk number	1, 148	48.16	<0.0001	1, 148	0.01	ns	1, 148	0.49	ns
Unfertilized stalk proportion	1, 129	14.25	0.0002	1, 129	17.02	<0.0001	1, 129	0.37	ns
Fruits/flowering plant	1, 108	21.61	<0.0001	1, 108	1.25	ns	1, 108	3.2	ns
Fruits/flower	1, 114	4.49	0.0362	1, 114	1.23	ns	1, 114	11.19	0.0011
Viable seeds/fruit	1, 96	33.22	<0.0001	1, 96	26.41	<0.0001	1, 96	0.12	ns

[a]Analyzed with SAS Proc Logistic
[b]Wald chi-square statistics
[c]Emergence date analyzed as number of weeks post-February 7th

We used ANCOVA to analyze plant diameter with emergence date as a covariate to test whether emergence date had any effect on maximum diameter. Later emergence had a negative effect on adult maximum diameter overall (emergence date main effect: df = 1, 241, $F = 6.93$, $P = 0.009$), but the negative effect was observed only at Atkinville (emergence date × site: df = 1, 241, $F = 4.33$, $P = 0.038$) and most prominently in 2015 (emergence date × year: df = 1, 241, $F = 5.01$, $P = 0.026$). In contrast, later emergence had a net positive effect on seedling size (emergence date main effect: df = 1, 251, $F = 5.50$, $P = 0.020$), but again, this effect was only observed at Atkinville (emergence date × site: df = 1, 241, $F = 4.33$, $P = 0.038$) and especially in 2015 (emergence date × year: df = 1, 251, $F = 5.01$, $P = 0.026$).

Reproduction

Flowering and fruiting phenology was similar across years (Fig. 8). Budding stalks were first observed in mid-March, and plants were in full flower during the first 2 weeks in April. The year 2015 was significantly more favorable than 2016 for all reproductive output response variables except seeds per fruit (Table 2, Fig. 9). The proportion of plants flowering in 2015 was 83%, compared to only 47% in 2016, and the mean number of flowering stalks per plant was much greater. The percentage of unfertilized stalks was also significantly lower in 2015. Plants set over 4 times as many fruits in 2015 as in 2016, and fruit set per flower was 1.5 times higher. In contrast to these results, number of seeds per fruit was significantly higher in 2016 than in 2015.

Plants at Gardner Well were always more successful in terms of reproductive output than plants at Atkinville for those variables for which there was a significant difference (Table 2, Fig. 9). Gardner Well plants had a significantly higher proportion of flowering plants than Atkinville plants, and this effect was much more pronounced in the favorable year (2015; Fig. 9A). Gardner Well plants also had a significantly lower unfertilized stalk percentage (Fig. 9C).

We performed ANCOVA on the flowering data including plant diameter as a covariate. Plant diameter accounted for 42.9% of the variation in flowering proportion (df = 1, 247, $P < 0.0001$) and 58.4% of the variation in

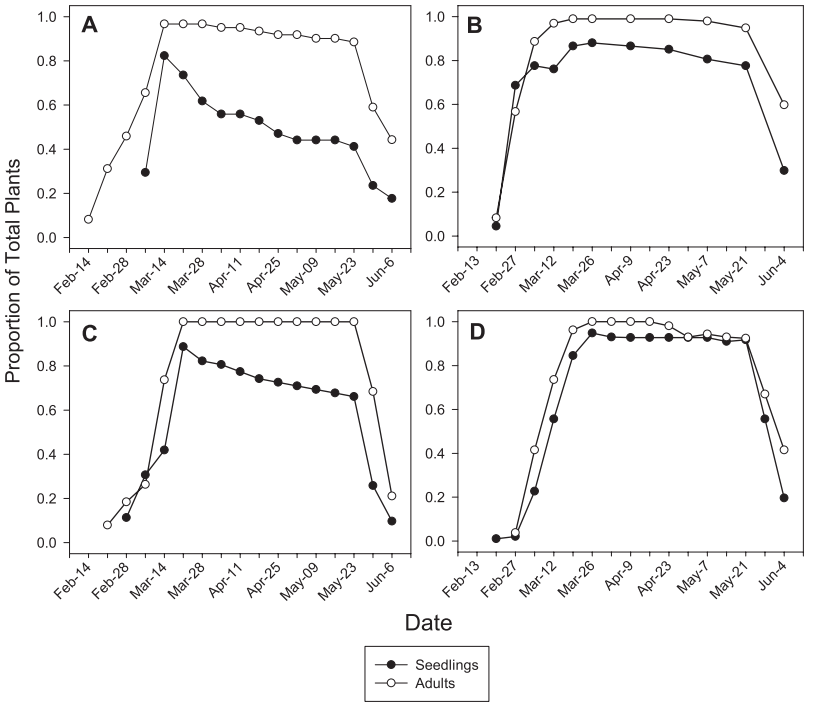

Fig. 6. Time courses of emerged seedlings surviving (black circles) and adult plants surviving (white circles) plotted by evaluation date: **A,** Atkinville study site in 2015; **B,** Atkinville study site in 2016; **C,** Gardner Well study site in 2015; **D,** Gardner Well study site in 2016.

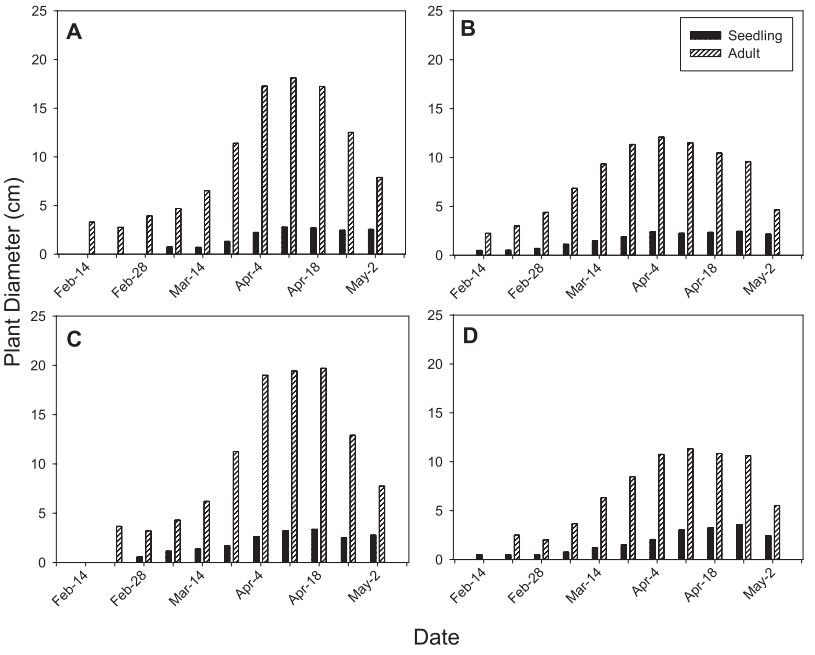

Fig. 7. Time courses of mean plant diameter for seedlings (black bars) and adult plants (hatched bars) plotted by evaluation date: **A,** Atkinville study site in 2015, **B,** Atkinville study site in 2016; **C,** Gardner Well study site in spring 2015; **D,** Gardner Well study site in spring 2016.

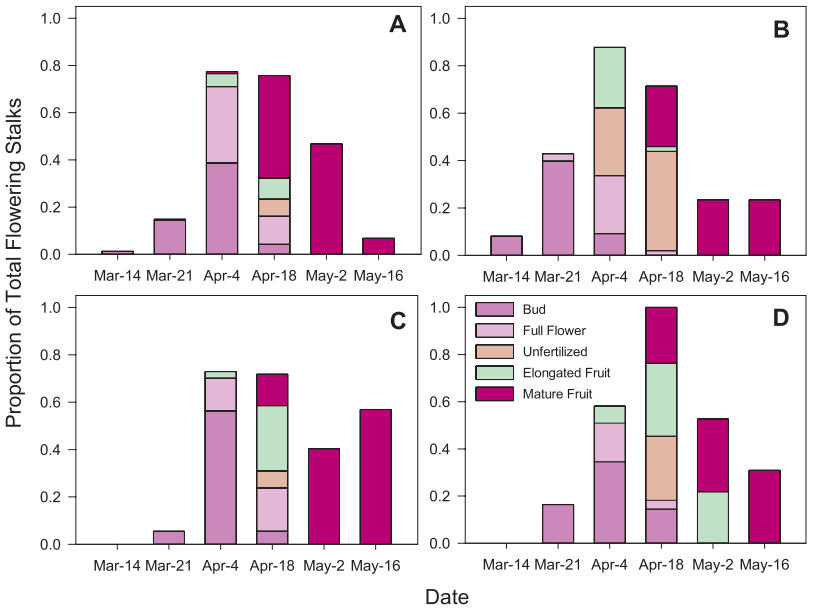

Fig. 8. Time courses for proportion of total flowering stalks that were in the bud, full flower, postflower unfertilized, fruit elongation, and mature fruit phenological stages at each evaluation date: **A,** Atkinville study site in 2015; **B,** Atkinville study site in 2016; **C,** the Gardner Well study site in 2015; **D,** Gardner Well study site in 2016.

number of stalks per plant (df = 1,151, $P < 0.0001$), but even when plant diameter was included as a covariate in these analyses, the differences between sites and years were still significant for flowering proportion (site: Wald $\chi^2 = 6.23$, $P = 0.012$; year: Wald $\chi^2 = 4.41$, $P = 0.036$; site × year interaction: Wald $\chi^2 = 5.37$, $P = 0.020$); and the year main effect was still marginally significant for stalks per plant (df = 1,144, $F = 3.74$, $P = 0.060$). This suggests that differences in flowering success between sites and years were not solely a result of size differences.

Discussion

Environmental Cues and Phenological Transitions

The environmental cues that mediate dormancy induction and release as well as flowering in *A. holmgreniorum* are apparently similar to those that operate in other strongly seasonal environments. Vegetative dormancy induction occurred with the onset of high temperatures regardless of soil moisture status, as documented for summer-dormant grasses (Volaire and Norton 2006). Plant death or dormancy induction occurred as temperatures increased above 30 °C (Figs. 3, 6). This phenological transition occurred at roughly the same time in both years as maximum day length was approaching. A preliminary growth chamber experiment confirmed this result and also demonstrated that longer days alone are neither necessary nor sufficient for dormancy induction (K. Rominger 2016, unpublished data).

Release from shoot dormancy apparently involves a winter chilling cue, as our data showed that plants in the field do not resume shoot activity in response to favorable fall conditions. Geophyte spring ephemerals of more mesic environments can resume root activity in fall (Lapointe and Lerat 2006), but it is not yet known whether this occurs in *A. holmgreniorum.* It is also not clear from field observations whether vernalization is needed for floral initiation or whether time to flowering is governed by a thermal time requirement or by a photoperiod cue.

Effects of Interannual Variation in Precipitation Patterns

This study showed that, even though precipitation and soil moisture status apparently do not directly mediate phenological transitions involving dormancy and flowering,

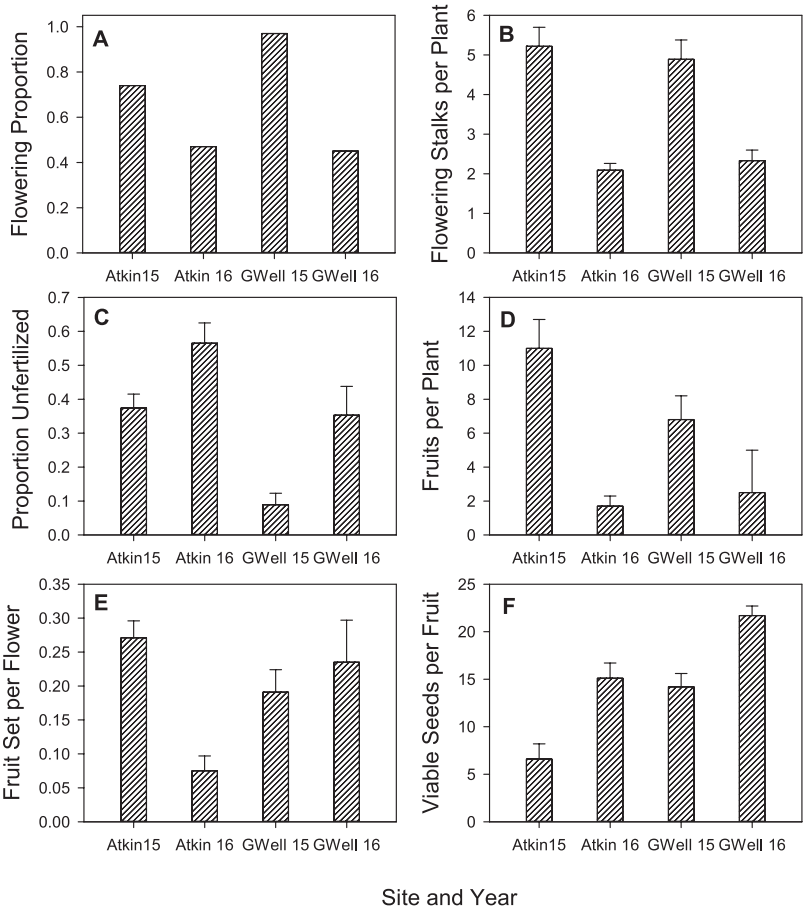

Fig. 9. Mean values for 6 reproductive output measures at Atkinville and Gardner Well in 2015 and 2016: **A,** proportion of adult plants that flowered; **B,** mean number of flowering stalks per flowering plant; **C,** proportion of unfertilized flower stalks; **D,** mean number of fruits per plant; **E,** fruit-to-flower ratio; **F,** mean number of viable seeds per fruit. Error bars = standard error of the mean. See Table 2 for statistical analysis.

precipitation and specifically the timing of precipitation can have a strong impact on the timing of emergence, seedling survival, plant growth, and components of reproductive output. The 2 study years had similar slightly above-average total growing season precipitation, but differences between years in the timing of storms impacted both phenology and plant success.

Emergence phenology for seedlings appeared to be tied more to precipitation than to increasing temperature. In 2015 there was little late-winter rain, but adult plant emergence started as temperatures warmed. Two weeks later, during a major storm, seedling emergence began. When temperatures increased again after the storm, both seedling and adult emergence spiked. This suggests that adult *A. holmgreniorum* plants only need warmer temperatures to emerge, whereas seedlings do not emerge until after a major precipitation pulse. In 2016, a major precipitation event in early January provided an extended period of reasonably high soil moisture. This resulted in earlier seedling emergence relative to 2015 but had little effect on adult emergence. Both adults and seedlings began emerging as temperature increased in mid-February.

Seedling survival, but not adult plant survival, also appeared to be closely tied to precipitation patterns. Low survival of early emerging cohorts in 2015 was probably associated with marginal conditions due to the relatively

dry winter. The 6-week lack of precipitation following the early March storms likely impacted seedlings more strongly than adult plants, which can use deep soil moisture. This resulted in reduced survival of seedlings but not adult plants during spring 2015. In 2016, the January storm facilitated survival of early seedling cohorts, and there were smaller but more frequent storms in mid-spring that may have been more advantageous to shallow-rooted seedlings than larger but less frequent precipitation events.

The early March storms in 2015 led to the development of much larger adult plants that flowered and produced fruit more profusely and also exhibited higher fruit set per flower, likely because of improved pollination related to increased flowering. However, viable seed number per fruit was significantly higher in 2016. A possible explanation for this is that late spring storms in 2016 improved resource conditions during seed filling and resulted in a lower proportion of seeds that aborted due to resource limitation.

We know from our earlier demographic studies that below-average winter-spring precipitation can have a drastic effect on plant success. For example, in extremely dry years (e.g., 2002, 2007), no seedling emergence was observed and survival of dormant plants was also close to zero across the species' range. However, the effect of above-average precipitation was more difficult to predict. This phenology study shows that, in years with adequate precipitation, the timing of storms is as important to different components of plant success as the total amount of precipitation received.

Site Quality Effects on Plant Success

In terms of plant success, the differences between Atkinville and Gardner Well were striking, with Gardner Well plants outperforming Atkinville Wash plants in almost every measure (Figs. 4, 9). Plants at Gardner Well were also either less sensitive to the negative impacts of year quality or able to respond more strongly to favorable conditions. Underlying environmental differences between these 2 sites are more likely than genetic differentiation to explain this performance contrast (King et al. 2012). Slightly later emergence and flowering phenology at Gardner Well were probably due to topography, as the Gardner Well site has a northern exposure with bluffs immediately to the south, while the Atkinville site has a more western exposure, making the Gardner Well site slightly cooler and more mesic overall.

Another plausible explanation for site differences involves the level of anthropogenic disturbance, including urban development, recreational use, and cattle grazing. Atkinville is immediately adjacent to the southern edge of St. George, with a new housing development only a few hundred meters to the north, whereas Gardner Well is not directly adjacent to urban development and consequently receives much less recreational use (Fig. 2). Both areas are permitted for winter grazing by cattle, but the apparent disturbance from grazing is much greater at Atkinville. Cattle have rarely been observed at Gardner Well but are regularly present at Atkinville every winter. Anthropogenic disturbances can affect plant performance through trampling damage to dormant, emerging, or actively growing plants, increases in weedy competition, disruption of the seed bank, and loss of nesting areas and alternate food sources for ground-nesting native bees that ensure reproductive success (V. Tepedino, 2005 unpublished report, USDA–ARS Bee Biology and Systematics Laboratory, Logan, UT).

Phenological Patterns in *Astragalus* Species

Most members of the very large genus *Astragalus* are herbaceous perennials of temperate regions of the northern hemisphere (Barneby 1964). Clear patterns have emerged regarding seasonal dormancy in herbaceous perennial *Astragalus* species. In environments with cold winters and mild summers, the common pattern is winter dormancy—that is, plants emerge in spring and remain active through summer and fall, entering dormancy in late fall or early winter (e.g., *A. tennesseensis*, Baskin et al. 1972). In Mediterranean climates with mild winters and hot, dry summers, plants emerge in fall, remain active through the winter and spring, and then enter summer dormancy (e.g., *A. nitidiflorus*, Martínez-Sánchez et al. 2011). In climates with both cold winters and dry summers, the common pattern is the perennial spring ephemeral life history. Plants emerge in spring and complete their life cycle prior to the onset of summer drought, then persist in the dormant state

through summer, fall, and winter (e.g., *A. lithophyllus,* Shi et al. 2006).

Several spring ephemeral Astragali exhibit another notable dormancy pattern, namely the ability to remain dormant through one or more seasons usually favorable for growth (e.g., *A. microcymbus*, DePrenger-Levin et al. 2013; *A. scaphoides,* Gremer et al. 2010; *A. ampullarioides,* Van Buren and Harper 2003). This pattern, referred to as prolonged or vegetative dormancy, has also been observed in other herbaceous perennials of semiarid steppe environments (e.g., Lesica and Crone 2007), as well as in many other habitats (reviewed by Shefferson 2009). This life history pattern has prompted modeling studies examining whether it represents a bet-hedging strategy (Reintal et al. 2010, Gremer et al. 2012, Gremer and Sala 2013).

The spring ephemeral pattern observed in *A. holmgreniorum* appears to be an adaptation to a climate with cold winters and dry summers, yet the winters in the Mojave Desert where the species occurs are sufficiently mild to permit active shoot growth in other herbaceous perennials that occupy the same habitat, including its congener *A. amphioxys.* This suggests that perhaps *A. holmgreniorum* has retained a life history strategy that reflects a colder climate regime in its historical past. Its occurrence at the northernmost edge of the North American warm desert region supports this idea. We have no evidence that it can escape the effects of unfavorable years through persistent dormancy. Its capacity to persist in the current climate environment in spite of high dormant plant mortality (Van Buren and Harper 2003) probably hinges on other life history features, namely relatively high reproductive output and the ability to form a persistent seed bank (Searle 2011).

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