

The Varying Phenology and Growth Patterns of *Baptisia bracteata* (Fabaceae) in Reconstructed Prairie

Chris E. Petersen, Sharon M. Bauzys, Felicia A. Speranske, and Barbara A. Petersen
College of DuPage, Glen Ellyn, IL 60137

ABSTRACT

First flowering time and flowering duration of *Baptisia bracteata* Muhl. ex. Ell (cream wild indigo), were examined in the Russell R. Kirt Tallgrass Prairie, Glen Ellyn, IL, during 2008, 2009, and 2011. While some *B. bracteata* delay flowering, most bloom during May, just prior to the blooming period of the taller and more prolific congener, *B. alba*. Both congeners are host to the pre-dispersal seed predator, *Apion rostrum* Say (Apionidae), although the reproductive cycle of the weevil is synchronized to *B. alba*. Factors relating to seed yield and the growth of the rhizomatous *B. bracteata* were also investigated. *B. bracteata* with more shoots, flowers and racemes tended to flower earlier and longer than those with fewer counts, evidence of the importance of plant size to flowering phenology. Still, as indicated by flower count/plant, a larger size was only positively correlated to seeds matured/plant during 2011. Counts of *A. rostrum* showed positive relationships to pods and seeds matured/plant during 2008 and 2011. Mean shoot count/plant was not significantly different between 2008 and 2011 among 39 tracked individuals. Growth was largely limited to smaller individuals while larger individuals sometimes declined in size. Selective pressures favoring larger size may include competition for resources. However, rewards of seeds matured/plant based on a larger inflorescence size, may not be realized every year. Larger plants may be more prone to resource limitations and weevil attacks. Variances in plant sizes can be just explained by age. Alternatively, size plasticity may occur due to changing environmental conditions and reproductive effort from year to year. It remains unknown if low output of mature pods was due to a lack of pollinators. By subsequently having lower seed output, the species may lower its' attractiveness to *A. rostrum*.

INTRODUCTION

One basic principle of life history theory explains that there is a cost to reproduction which is minimized by trade-offs among components of reproductive yield (Sánchez-Humanes, et al. 2011; Williams, 1966). Flowering phenology may be under the influences of trade-offs within a species, e.g., when the timing of first flowering or flowering duration show asynchrony as a response to changing environmental constraints (Elzinga et al., 2007). Larger plants are often found to bloom earlier and longer than smaller plants, presumably to attract pollinators and because they have greater nutrient reserves available for flowering (Bolmgren and Cowan, 2008; Bustamante and Burquez, 2008; Pettersson, 1994). By flowering off-peak, smaller plants may be able to avoid consumers

such as seed predators, but perhaps at the cost of less favorable weather (Albrechtsen, 2000; Evans et al., 1989; Mahoro, 2002; McIntosh, 2002; Mduma et al., 2007).

Baptisia bracteata Muhl. ex. Ell (cream wild indigo; = *B. leucophaea*) is a native tall-grass perennial of the Midwest which shows variance in flowering phenology. At our study site, the reconstructed Russell R. Kirt Prairie, IL, the species blooms in May when a new season of emergent prairie growth has just begun to show (Petersen et al., 1998). Most plants tend to flower at the same time while a few delay. Using data collected during 2008, 2009, and 2011, we investigated factors that could explain the asynchrony. We also examined factors relating to seed yield and the change in size of 39 plants over a 4-year span.

Each *B. bracteata* consists of subterranean rhizomes from which multiple aerial shoots develop to form a concentric cluster measuring up to a half meter in diameter. Racemes along shoots radiate outward from the cluster, exposing conspicuous displays of yellow flowers. Aging flowers along the indeterminate racemes shift from being staminate to carpellate. This shift allows for a degree of self pollination (Haddock and Chaplin, 1982). *Bombus* are the major pollinators. Pods inflate with pollination and can bear over 14 seeds. Unlike the congener, *B. alba* L. (Vent)(white wild indigo) which also grows in the prairie, inflated pods of *B. bracteata* remain attached regardless of seed number, and the ones that fail to mature seeds appear to ripen at the same rate as those that retain seeds. *B. alba* often aborts many to all of its inflated pods in apparent response to environmental extremes and low counts of seeds in pods (Petersen et al., 2011).

At our study site, *B. bracteata* is infested by the pre-dispersal seed predator, *Apion rostrum* Say (Apionidae). The weevil also infests and is more synchronized to pod development of the later blooming *B. alba* (Petersen and Wang, 2006). Overwintering adult weevils oviposit into inflating pods of both congeners. Resulting larvae consume seeds as their only source of nutrition. Maturation is reached by August, and the weevils disperse when pods dehisce or fragment.

METHODS

Reconstruction of the 7.1 ha Russell R. Kirt Tallgrass Prairie began in 1984. Today, the dominant tall grasses are *Andropogon gerardii* Vitman (big bluestem), *Sporobolus heterolepis* Gray (prairie dropseed), and *Sorghastrum nutans* (L.) Nash (Indian grass). Over 100 species of forbs contribute to the flora. The prairie was burned annually until 2006. It has not been burned since.

Sampling methods in 2008, 2009, and 2011 followed the same protocol. A concentric cluster of *B. bracteata*, with shoots being within 10 cm of one another, was assumed to be one individual based on soil excavation of individuals not otherwise included in sampling. Fifty to 51 plants were randomly selected for sampling each year. First and last flowering dates of each *B. bracteata* were recorded along with counts of shoots, racemes, and flowers. When pods matured, they were counted along with their contents of seeds and weevils. If pods had holes from which weevils could escape, *A. rostrum* count/plant was prorated using mean counts from intact pods. Shoot and flower counts per plant pro-

vided alternative measures of plant size. Seeds matured/plant and counts of *A. rostrum*/plant provided measures of reproductive output and weevil infestation, respectively.

All statistical analyses were done using Statistica 6 (Statsoft, 2001). Due to failure in meeting assumptions of parametric testing, relationships between flowering phenology, other reproductive allocations to include seeds matured, and weevil infestation were explored using Spearman Rank Correlation (Zar, 1984). Rhizomatous growth was estimated by comparing the ratio of 2011:2008 shoot counts to 2008 shoot counts using Spearman Rank Correlation.

RESULTS

The first *B. bracteata* flowered on May 11th during 2008 and 2011, and on May 26th during 2009. Plant measurements according to year are presented in Table 1. For individuals, an earlier flowering start, a longer flowering duration, and a higher flowering count/plant were positively correlated for all years, except in 2011 between flowering initiation and duration (Table 2). However, as indicated by flower count/plant, a larger size was only positively correlated to seeds matured/plant during 2011. Plants producing more flowers also tended to show higher shoot counts; but more shoots did not correlate consistently with an earlier time and duration of flowering. It also did not translate to a higher yield of seeds matured. Finally, mean counts of *A. rostrum*/plant were positively correlated to pods and seeds matured per plant in 2008 and 2011, but not in 2009.

Table 1. Summary (mean \pm standard error; n) of variables associated with reproductive yield of *Baptisia bracteata* and infestation by *Apion rostrum* according to year. Flowering time is in reference to the mean date plants flowered after the first *B. bracteata* bloomed.

Variable	Year		
	2008	2009	2011
Time of first flowering	9.6 \pm 0.8 (51)	9.2 \pm 0.8 (50)	14.0 \pm 1.0 (42)
Flowering duration (days)	16.8 \pm 0.6 (51)	17.2 \pm 0.5 (50)	16.5 \pm 1.1 (42)
Shoots/plant	8.0 \pm 1.0 (51)	9.6 \pm 0.9 (50)	10.9 \pm 1.3 (42)
Flowers/plant	114.4 \pm 16.2 (51)	95.1 \pm 11.9 (50)	122.9 \pm 23.8 (42)
Pods matured/plant	9.8 \pm 3.1 (51)	32.3 \pm 6.4 (50)	19.2 \pm 5.9 (42)
Seeds matured/plant	28.1 \pm 16.3 (51)	62.5 \pm 20.6 (50)	8.5 \pm 6.5 (42)
<i>Apion rostrum</i> /plant	10.8 \pm 4.4 (20)	13.6 \pm 4.3 (32)	26.7 \pm 8.3 (24)
% of <i>Baptisia bracteata</i> bearing mature pods	37.3% (51)	80.0% (50)	59.5% (42)

While shoot count among tracked *B. bracteata* did not change significantly from 2008 to 2011 ($t = 1.876$; $df = 38$; $P < 0.068$), plants with fewer shoots accounted for most increases (Figure 1). The ratio in shoot count between 2011 and 2008 was negatively correlated with shoot count in 2008 ($r_s = -0.54$; $P < 0.05$). From 2008 to 2011, 22 plants showed an increase in shoot count, 4 showed no change, while 13 decreased in shoot count.

Table 2. Spearman rank correlation comparing variables of flowering phenology, reproductive yield, and Apion rostrum infestations presented sequentially for years 2008, 2009, and 2011. AC = Counts of Apion rostrum/plant. The AC sample sizes (n's) for 2008, 2009, and 2011, were 20, 32, and 24, respectively. Otherwise, n = 51 for 2008, 50 for 2009, and 42 for 2011. Bold type denotes significance ($P \leq 0.05$).

	FD	SC	FC	PM	SM	AC
Time of first flowering (FF)	-0.85	-0.21	-0.36	<0.00	0.23	-0.33
	-0.55	-0.35	-0.55	-0.28	0.02	-0.17
	-0.23	-0.07	-0.32	<0.00	0.17	-0.08
Flowering duration (FD)		0.13	-0.85	-0.06	-0.20	0.30
		0.36	0.43	0.52	0.20	-0.12
		0.45	0.54	0.39	0.43	0.14
Shoot count/plant (SC)			0.65	0.15	-0.06	0.21
			0.41	0.43	0.10	0.12
			0.42	0.44	0.27	0.51
Flower count/plant (FC)			0.21	<0.00	0.43	
			0.59	0.20	0.31	
			0.48	0.42	0.42	
Pods matured/plant (PM)				0.56	0.52	
				0.52	0.34	
				0.72	0.78	
Seeds matured/plant (SM)					0.56	
					0.25	
					0.43	

DISCUSSION

Flower count per *B. bracteata* provided a better correlating factor to flowering phenology than shoot count/plant. The discrepancy may reflect the additional function of shoots in photosynthesis. Shoot number may vary due to disproportionate allocations of energy to non-reproductive and reproductive structures as a reaction to changing environmental conditions. Regardless, results are consistent with larger *B. bracteata* blooming earlier and longer than those smaller.

Plant size can indicate age. Alternatively, plant size may be influenced by the local environment and changes in reproductive effort from year to another. With larger *B. bracteata* being more likely to become smaller, and smaller individuals larger between 2008 and 2011, such changes in size can function to promote the fitness of a perennial over the course of its lifetime (Salguero-Gómex and Casper, 2010). Larger size may offer competitive benefits to acquisition of resources not investigated in this study. Nevertheless, greater rewards of seeds matured/plant, where plant size is based on flower count, may not be realized every year. Larger plants may also be more prone to resource limitations and attack by consumers like *A. rostrum* (Hainsworth et al., 1984; Ohasi and Yahara, 2000). A longer term study should offer insights in explaining size differences in *B. bracteata*.

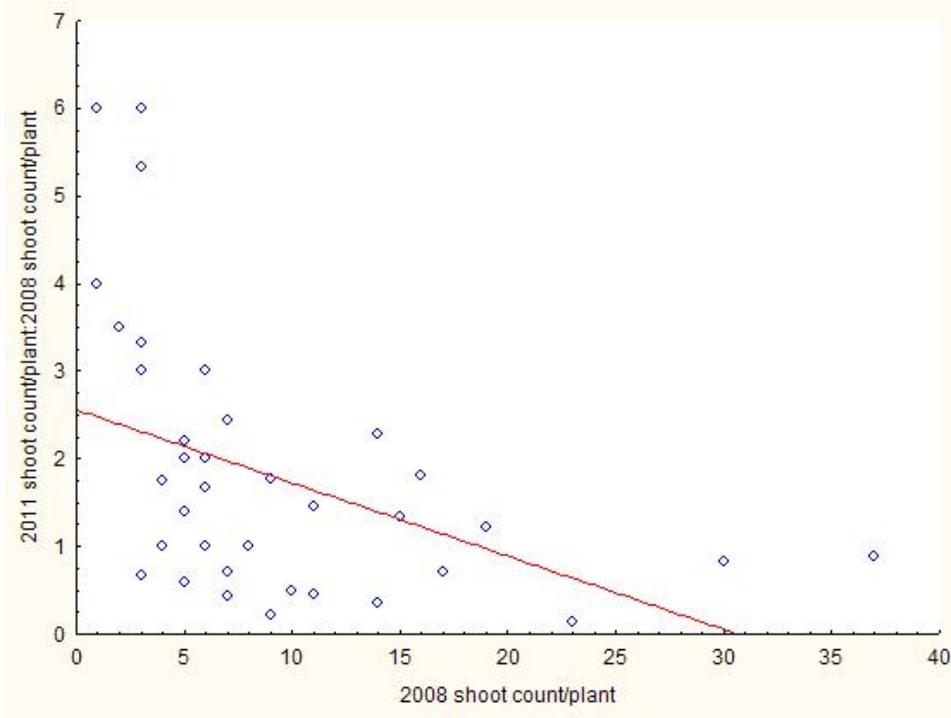


Figure 1. Shoot count ratio of *B. bracteata* comparing years 2011 to 2008, plotted against the 2008 shoot count. Best-fit linear regression line is provided to help visualize trend.

Despite the seemingly prolific flowering by *B. bracteata*, few pods were matured/plant. It remains unknown if pollen limitations are due to a lack of pollinators at the reconstructed site. Mature pods bear seeds. By having a seed output much lower than *B. alba* (Petersen et al., 2007), the species may be less attractive to *A. rostrum* explaining the synchronization of the weevil's reproductive cycle around the taller and more prolific congener.

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