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A Two-Year Study of the Reproductive Phenology of *Baptisia alba* (Fabaceae)

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ABSTRACT

Baptisia alba L. (Vent.)(Fabaceae), is a native of tallgrass prairie that exhibits asynchronous flowering. The two-year study of *B. alba* was conducted during 2007 and 2008 in a re-created prairie in northeastern Illinois with the objective of identifying factors related to the flowering phenology of *B. alba*. Prescribed burning was conducted during early spring of both years, except a portion of the site was not burned in 2008. The flowering period of *B. alba* began and ended about 10 days later in 2008 than 2007, with the reproductive activity of the pre-dispersal seed predator *Apion rostrum* Say (Apionidae) following suit. Reproductive yield varied across years, including two years prior to the study. In 2008, *B. alba* from the burned area flowered for a longer duration, produced more racemes, flowers, and mature seeds than those in the unburned area. However, it was not known if these differences were attributed to burning. Common trends over the two-year study included the timing of first flowering being negatively related to flowering duration, flowering synchrony, raceme number/plant, and inflorescence size. Likewise, flowering duration showed positive relationships to plant size and inflorescence size. The count of seeds matured/plant was negatively correlated to flowering synchrony although the correlation was only significant in 2007. The count of seeds matured/plant was positively correlated to the count of racemes/plant in 2008, and to inflorescence size for both years. Larger plants tended to flower earlier and for a longer duration. Higher flowering synchrony among these plants suggests an advantage to this flowering phenology, although the benefit in seeds matured/plant was not clearly demonstrated in this study. A longer term study is required to test if sporadic, but ongoing reproductive successes among plants of various sizes can explain the variable flowering phenology of *B. alba*.

INTRODUCTION

The timing and duration of flowering are under multiple abiotic and biotic controls that vary within and across seasons. Patterns of precipitation and temperature provide abiotic controls (Bustamante and Burquez 2008, Evans et al. 1989), while biotic controls include the presence of pollinators and absence of seed predators and grazers (Evans et al. 1989, Mahoro 2002, Mendez and Diaz 2001, Pettersson 1994, Pilson 2000). Evolutionary theory predicts that the flowering phenology of a plant affects fitness. A perennial species may show a varied flowering pattern influenced by growth conditions, competition, and consumer pressures across seasons (Inouye et al. 2002).

Plant size is often a determining factor in the timing of flowering. Within a species, larger plant size has been associated with greater flower production, earlier flowering, and extended flowering period presumably because largeness confers a greater nutritional capacity to support reproduction (Bolmgren and Cowan 2008, Bustamante and Burquez 2008, McIntosh 2002, Pettersson 1994). However, greater seed yield of larger plants may not be assured by factors such as aberrant weather which can cause premature fruit abortion and the attraction of consumers such as seed predators (Mduma et al. 2007).

We examined flowering phenology of the legume, *Baptisia alba* (L.) Vent (=*B. leucantha* Torrey & Grey), within a re-created tallgrass prairie in northeastern Illinois. This perennial has been found to show asynchronous flowering where most flowering occurs during a two week period beginning in May and proceeding into June (Petersen et al. 2008). However, a few individuals, which tend to be smaller in size and possibly younger, bloom later for a shorter period of time.

The yearly growth cycle of *B. alba* begins with the emergence of a new shoot after the ground thaws during spring (Petersen and Sleboda 1994). By early May flowering has begun with *Bombus* species being the major pollinators. The plants produce a main stem with a racemous inflorescence, and often secondary racemes which number 2 to over 10. Plant height at the tip of the central raceme commonly exceeds one meter. Pods inflate from the pollinated flowers shortly after flowers fade. The pods, which may contain over 30 ovules, mature by August. Seeds are dispersed as pods detach or dehisce by fall. Frequently many, or all, initially inflated pods abort prior to ripening. Abortion appears selective, favoring those pods having fewer seeds (Petersen and Sleboda 1994). Factors linked to pod abortion include pre-dispersal predation by *Apion rostrum* Say (Apionidae) and weather conditions. *B. alba* dies back to the ground with the approach of winter.

This study was conducted over a two year period to investigate factors related to flowering phenology of *B. alba* within evolutionary and ecological contexts. These factors were plant size, inflorescence size, reproductive yield, pre-dispersal seed predation by *A. rostrum*, and fire. As a measure of reproductive yield, seeds matured/plant provided a means to investigate the advantages of certain parameters of flowering phenology, including the time of first flowering, flowering duration, and flowering synchrony.

METHODS

The study site was the Russell Kirt Tallgrass Prairie located on the main campus of College of DuPage, in DuPage County, Illinois. The 7.1 hectare plot encloses two marshes and a retention pond, each about a half hectare in area (Figure 1). Re-construction of the mesic prairie began in 1984. The common grasses are big bluestem (*Andropogon gerardii* Vitman), prairie dropseed (*Sporobolus heterolepis* Gray), and Indian grass (*Sorghastrum nutans* (L.) Nash). *B. alba*, one of more than a hundred species of forbs (Kirt 1996), selected for this study were located around the north marsh. Historically, the prairie has been burned annually during early spring. The entire study site was burned during 2007, but only the south side of the north marsh was burned during 2008.

Methodology was the same for both years except that the area under study was expanded in 2008 to increase the sample size of *B. alba*. Sampling began with the first individual *B. alba* that flowered. This plant, along with the succession of others that followed, was tagged for continued observation through the maturation of pods and seeds. Recorded from each plant were first and last flowering dates, and counts of racemes, flowers, inflated pods, ripened pods, seeds matured per plant, and *A. rostrum*/ripened pod. Counts of seeds matured and weevils were taken from five ripened pods sampled from each raceme of a plant. The most basal and most distal pods were sampled along with three pods located between. If a raceme had fewer than five pods, all pods were sampled. Seeds matured/plant were estimated using the product of the mean count of seeds matured/pod and the count of ripened pods. The count of racemes/plant was used as a measure of plant size, the count of seeds matured/plant was used as measure of reproductive yield, and the count of weevils/pod provided a measure of infestation.

The first appearance and final disappearance of overwintered adult *A. rostrum* was monitored on *B. alba* through visual observations. The visual observations of plants were during the morning, afternoon, or evening to take into account varied activity over the course of a day.

Flowering synchrony (X) was measured following the procedure of Augspurger (1983) using the equation:

$$X_i = (1/(n-1))(1/f_i)\sum_{j=1}^{n} ej \neq i$$

where $\sum ej \neq i$ is the number of days in which individuals i and j overlap in flowering, f_i is the number of days individual i flowered, and n is the number of individual plants in the sample. A synchrony of 1 indicates a plant is fully in synchrony with flowering of all other individuals while a value of 0 indicates no synchrony in flowering.

All statistical summarization was done using Statistica (StatSoft 2001). Nonparametric tests were used due to non-normal distribution of data even with transformations. Mann-Whitney U tests were used to determine statistical differences between years, and for 2008, between areas burned and not burned. The Chi-square goodness of fitness test was used to test for differences in the number of plants with ripened pods between years in burned areas, and between the burned and unburned areas in 2008. Relationships among flowering and reproductive yield components were explored using Spearman rank correlation. Significance was determined at $P \leq 0.05$.

RESULTS

Flowering by *B. alba* began and ceased later in 2008 than in 2007 (Table 1). The reproductive activity of *A. rostrum* partly followed the development of *B. alba* with early activity of the weevil being directed to the congener, *B. bracteata* Muhl. ex. Ell. that also grows in the prairie. Table 2 provides a summary of flowering phenology and growth parameters of *B. alba* according to year, and for 2008, to burn treatment. Flowering duration was significantly longer in 2008 than 2007, and for year 2008 in the burned area than in the area not burned (Tables 3 and 4). In all comparisons, flower synchrony did not vary significantly.

Initial reproductive yield/plant in burned areas was greater in 2008 than in 2007, although this did not lead to greater numbers of pods ripened and seeds matured (Tables 2 and 3). The difference in the relative numbers of plants bearing ripened pods between years was also non-significant ($\chi^2 = 0.29$, $P = 0.593$). Median count of *A. rostrum*/pod was not high enough to be significant and explain the losses in "mature" yield. *B. alba* in the burned area for year 2008, showed a higher reproductive output than individuals in the area unburned in all categories, though counts of *A. rostrum*/pod were not higher in the unburned area (Table 4). Where the prairie was burned in 2008, plants flowered longer and produced more racemes, flowers, inflated pods, and mature seeds. In addition, the counts of pods ripened/plant and seeds matured/plant were significantly higher, and proportionately more plants were able to produce ripened pods ($\chi^2 = 15.76$, $P < 0.001$).

The timing of first flowering was negatively correlated to flowering duration, flowering synchrony, count of racemes/plant, and count of flowers/plant, although not significantly in the burned area during 2008 (Table 5). Correlations to *A. rostrum*/pod were conflicting between years, with a negative correlation to first flowering in 2007, and a positive correlation in 2008. Flowering duration showed positive relationships to counts of racemes/plant and flowers/plant during 2008 with significance achieved except in the burned area. Negative correlations were found between seeds matured/plant and flowering synchrony, although the correlation was significant only during 2007. Across the study area, the count of seeds matured/plant was positively correlated to the count of racemes/plant in 2008 and to the count of flowers/plant in both years.

DISCUSSION

Larger *B. alba* may have the nutritional reserves to flower earlier and for a longer duration. Higher flowering synchrony may suggest an advantage to this flowering phenology. However, benefit in the form of seeds matured/plant was not clearly demonstrated in this study. The parameters of reproductive yield, particularly pods ripened/plant and seeds matured/plant, were inconsistent between years, between burn treatments in 2008, and compared to earlier years (Petersen et al. 2006, Petersen and Wang 2007). Pre-dispersal seed predation by *A. rostrum* may partially explain patterns. Counts (mean ± standard error (n)) of seeds matured/plant have ranged to a high of 386 ± 66.2 (36) in 2004 when the count of *A. rostrum*/pod was lowest at 1.47 ± 0.14 (36). However, the highest count of *A. rostrum* of 3.91 ± 0.16 (35) was recorded in 2006 when the count of seeds matured/plant was measured at 19.3 ± 4.3 (35). The variability in the timing of flowering and reproductive yield shown by *B. alba* suggests that factors including, but not limited to, pre-dispersal seed predation, are affecting the overall reproductive phenology of the plant. Weather has been linked to pod and seed loss, and to changes in the timing of flowering of legumes (Evans et al. 1989, Mduma et al. 2007, Siemens and Johnson 1995).

We have just begun to examine the effects of fire on the legume. Besides being important to the maintenance of tallgrass prairie by removing competing woody vegetation, fire affects flowering, species richness, and ecological succession (Copeland et al. 2002, Howe 1995). Burning removes over-shading senescent growth and darkens the earth, thereby increasing exposure to sunlight and warming the soil faster in spring (Hulbert 1988). These effects could promote earlier above-ground growth and the sequestering of nutrient reserves needed for *B. alba* to flower for a longer period of time, resulting in larger plants, more flowers, and higher seed yield/plant. However, the greater reproductive productivity of *B. alba* in the burned area could also be indicative of a unique genetic collection of plants, larger plants, older plants, and/or local growth conditions within the prairie. Continued study is required to scrutinize the effects of burning.

In their multi-year study, Haddock and Chaplin (1982) reported that despite *B. alba* initiating a relatively large number of seeds, nearly all were destroyed prior to dispersal except during one year when a large seed crop was observed. The authors explained this large seed crop as resulting from a lower than average population of pre-dispersal seed predators. It may be that sporadic, but ongoing reproductive successes are strong enough to select for variable flowering phenology of this perennial. A longer-term study is needed to test this hypothesis.

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Table 1. Dates of flowering initiation, flowering termination, and appearance of *Apion rostrum* on *Baptisia alba* according to year.

Event	2007	2008
Date first individual began to flower	May 20th	June 1st
Date last individual began to flower	July 2nd	July 10th
Date last individual ceased to flower	July 14th	July 26th
First appearance of *Apion rostrum*	May 2nd	May 22nd
Last appearance of *Apion rostrum*	June 26th	July 28th

Table 2. Summary (mean ± standard error) of growth parameters of *Baptisia alba* and infestation of pods by *Apion rostrum* during the years of 2007 and 2008. The entire study site was burned in 2007. Data are partitioned according to burn treatment for the year 2008. Date of flower initiation is based on days after when the first plant flowered for a particular year.

Growth Parameter	Year 2007	Year 2008		
		All plants	In burned area	In area not burned
Sample size	63	80	21	59
Number of plants with ripened pods	39 (61.9%)	23 (31.9%)	15 (71.4%)	8 (13.6%)
Flower initiation	10.3 ± 1.2	12.7 ± 1.2	7.0 ± 0.7	14.7 ± 1.5
Flowering duration/plant	17.7 ± 0.7	18.5 ± 0.8	25.1 ± 1.1	16.2 ± 0.8
Synchrony of flowering	0.544 ± 0.030	0.520 ± 0.019	0.587 ± 0.015	0.501 ± 0.025
Racemes/plant	3.85 ± 0.32	3.74 ± 0.26	5.48 ± 0.41	0.61 ± 0.32
Flowers/plant	71.2 ± 7.6	71.9 ± 6.0	116.7 ± 11.4	55.9 ± 5.9
Inflated pods/plant	44.4 ± 6.4	33.4 ± 3.3	54.4 ± 7.2	25.9 ± 3.2
Ripened pods/plant	9.30 ± 3.42	1.78 ± 0.52	5.05 ± 1.67	0.61 ± 0.32
Seeds matured/plant	30.8 ± 13.5	5.1 ± 2.0	11.9 ± 4.8	2.7 ±2.1
Apion rostrum/pod	2.87 ± 0.25[a]	3.39 ± 0.29[b]	3.43 ± 0.35[c]	3.33 ± 0.55[d]

[a] denotes n = 39, [b] denotes n = 24, [c] denotes n = 15, and [d] denotes n = 9.

Table 3. Mann-Whitney rank comparison of plant growth parameters and infestation of pods by Apion rostrum between years 2007 and 2008 in burned areas. n = 63 for 2007 and n= 21 for 2008, except for the count of Apion rostrum/pod/plant where n = 39 for 2007 and n = 15 for 2008.

Growth parameter	U	P
Flowering duration	229.3	<0.001
Synchrony of flowering	576	0.377
Count of racemes/plant	365.5	0.002
Count of flowers/plant	308	<0.001
Count of inflated pods/plant	463.5	0.041
Count of ripened pods/plant	611.5	0.606
Count of seeds matured/plant	595	0.492
Count of Apion rostrum/pod	225.5	0.196

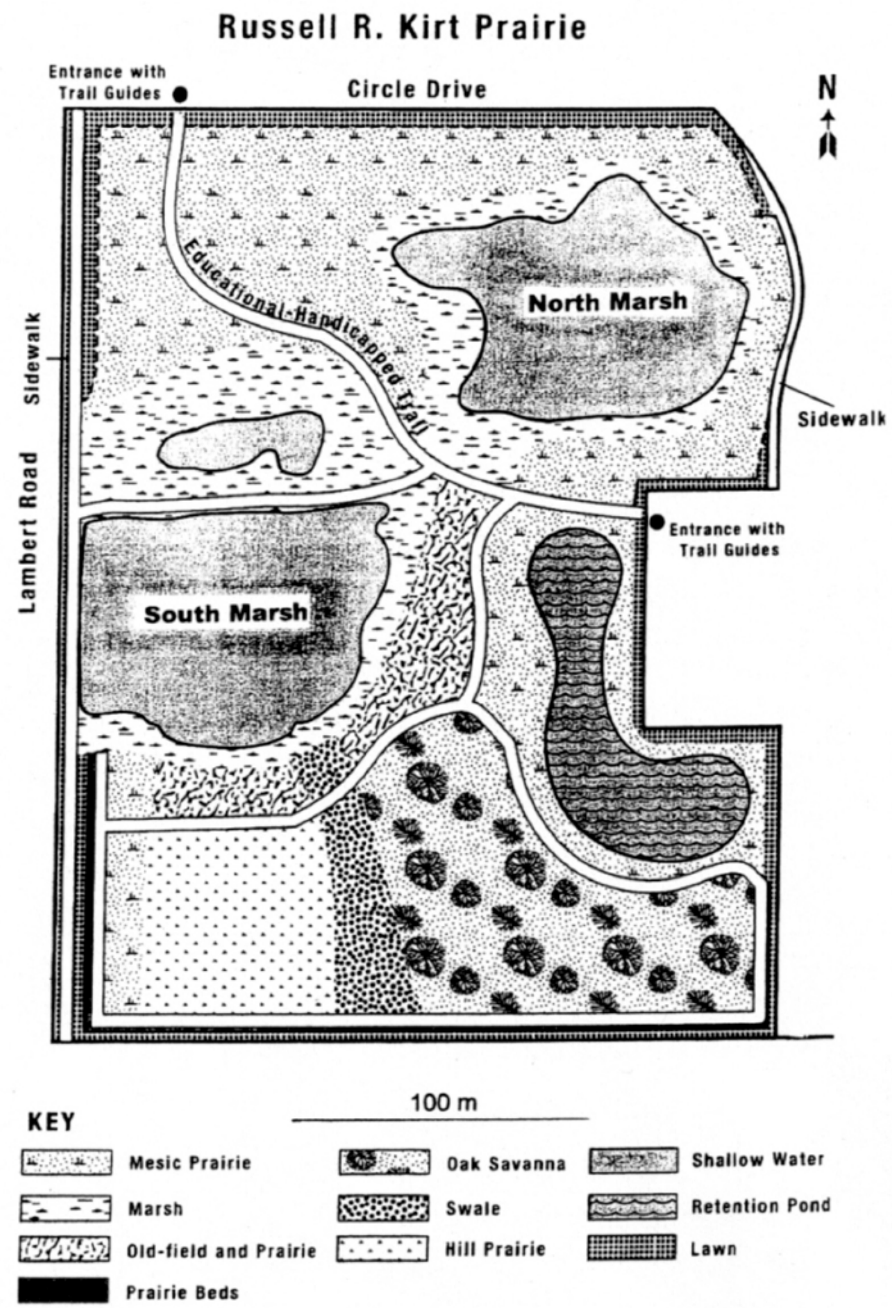
Table 4. Mann-Whitney (U) rank comparison of plant growth parameters and infestation of pods by *Apion rostrum* between burned and unburned areas during 2008. n = 21 for the burned area and n = 59 for the unburned area, except for the count of *Apion rostrum*/pod/plant where n = 15 for the burned area and n = 9 for the unburned area.

Growth parameter	U	P
Flowering duration	164.5	<0.001
Synchrony of flowering	596	0.797
Count of racemes/plant	274	<0.001
Count of flowers/plant	221	<0.001
Count of pods inflated/plant	286	<0.001
Count of pods matured/plant	246	<0.001
Count of seeds matured/plant	328	<0.002
Count of *Apion rostrum*/pod	53.5	0.400

Table 5. Spearman rank correlation showing relationships between flower phenology and growth characteristics of *Baptisia alba*. Date of flower initiation is based on days after when the first plant flowered for a particular year. *Significant (P ≤ 0.05).

Growth parameter	Timing of first flowering	Flowering duration	Flowering synchrony	Count of seeds matured/plant
2007 – [a]denotes n = 39, otherwise n = 63				
Flower duration	*-0.518			
Flowering synchrony	*-0.297	*-0.371		
Count of seeds matured/plant	0.129	0.235	*-0.289	
Count of racemes/plant	*-0.543	*0.669	-0.011	0.226
Count of flowers/plant	*-0.532	*0.756	-0.095	*0.271
Count of *Apion rostrum*/pod	*-0.319[a]	0.152[a]	0.274[a]	-0.080[a]
2008 - [a]denotes n = 24, otherwise n = 80				
Flower duration	*-0.643			
Flowering synchrony	*-0.363	-0.031		
Count of seeds matured/plant	-0.098	*0.434	-0.124	
Count of racemes/plant	*-0.520	*0.696	0.050	*0.315
Count of flowers/plant	*-0.448	*0.661	-0.020	*0.384
Count of *Apion rostrum*/pod	*0.407[a]	-0.013[a]	0.161[a]	*-0.478[a]
2008 – burned area, [a]denotes n = 15, otherwise n = 21				
Flower duration	-0.343			
Flowering synchrony	-0.344	*0.968		
Count of seeds matured/plant	-0.105	0.222	-0.311	
Count of racemes/plant	*-0.445	0.431	-0.420	0
Count of flowers/plant	-0.369	0.361	-0.351	0.070
Count of *Apion rostrum*/pod	*0.636[a]	-0.091[a]	0.128[a]	-0.364[a]
2008 – are not burned - [a]denotes n = 9, otherwise n = 59				
Flower duration	*-0.712			
Flowering synchrony	*-0.494	0.181		
Count of seeds matured/plant	0.051	0.251	-0.113	
Count of racemes/plant	*-0.479	*0.641	0.164	0.199
Count of flowers/plant	*-0.389	*0.567	0.031	0.251
Count of *Apion rostrum*/pod	0.120[a]	-0.111[a]	0.451	*-0.730

Figure 1. Map of the study site. *Baptisia alba* selected for study were located around the North Marsh, distributed in mesic prairie to the south up to the Educational-Handicapped Trail, north, and west of this marsh.



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