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Multiyear Study of Factors Related to Flowering Phenology and Reproductive Yield of *Baptisia alba* in Northeastern Illinois

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ABSTRACT

Factors related to flowering phenology and the reproductive yield of the white wild indigo, *Baptisia alba* (Fabaceae), were investigated in a multiyear study. The study site was a 7.1 ha reconstructed prairie located in northeastern Illinois. Factors considered were pre-dispersal seed predation by the *Apion rostrum* (Apionidae), pollination, and weather. First flowering time (FFT) and flower duration were measured from 2007-2009, as were components of reproductive yield and pod infestation from 2003-2009. Earlier flowering *B. alba* showed a longer flowering duration and were larger based on racemes/plant. However, only during 2009 did these plants have more inflated pods/flower, an indicator of pollination success, and matured significantly more seeds. Larger *B. alba* tended to produce a higher number of mature seeds, but also tended to attract more weevils. Across years, *A. rostrum* infestation of pods was significantly related to fewer mature seeds/plant. Likewise, warmer departures from local average daily temperature during June-July when pods were developing was associated with reduced seeds matured/flower. Seed development may be sensitive to heat as encountered later in the summer. Escaping the heat of summer can explain why most *B. alba* flower earlier, although at a possible cost of seed depredation. Trends in pod infestation did not indicate that larger, earlier FFT plants saturate *A. rostrum*. A longer flowering duration by these plants may preclude benefits of mass flowering in lowering pod infestation by weevils. Smallness did not appear to have benefits in seeds matured/plant. Later FFT by these plants may be the consequence of needing a longer time to secure resources prior to flowering.

INTRODUCTION

The white wild indigo, *Baptisia alba* L. (Vent.) (= *B. leucantha*), is a widely distributed legume in prairie and open woods of the Midwest (Swink and Wilhelm 1994). The perennial blooms prolifically during late spring, producing a central raceme and often 10 or more satellite racemes. In northeastern Illinois, the location of the current study, most *B. alba* bloom during a two-week period in June. However, some plants bloom much later, beginning after mid July.

This asynchronous flowering is often linked to plant size, with larger plants blooming earlier (Bolmgren and Cowan 2008, Bustamante and Burquez 2008, Pettersson 1994). An earlier first flowering time (FFT) may enable larger plants to bloom longer, exposing plants to more pollinators, but also to pre-dispersal seed predators and the effects of weather (O'Neil 1999). These selective pressures on FFT vary over time and space (Brody 1997, Evans et al. 1989, Kolb et al. 2007, Ollerton and Lack 1990). Thus, the advantage of a particular flowering phenology to a perennial may only be realized over the course of multiple seasons.

In a two-year study of *B. alba*, larger plants with more racemes flowered earlier and tended to yield more mature seeds, although the difference in yield was never significant (Petersen et al. 2010*s*). A hypothesis forwarded by the study was that sporadic reproductive successes related to FFT of plants of varying size are strong enough to select for variable flowering phenology in *B. alba*.

Baptisia alba begins a cycle of reproductive growth as the soil warms during spring and new shoots emerge. *Bombus* are the major pollinators. Pods inflate from flowers that have been pollinated (Haddock and Chaplin 1982). Many, if not all of the pods are aborted as they mature (Petersen and Sleboda 1994). Abortion appears to be selective, targeting pods with fewer seeds. Pre-dispersal seed predation by the weevil, *Apion rostrum* Say (Apionidae), is influential to this loss. Pods mature during August to September, with seeds being dispersed as pods dehisce and fragment. Above ground growth of *B. alba* senesces in autumn.

Apion rostrum is the only known pre-dispersal seed predator of *B. alba* in the prairie under study in this paper, the Russell Kirt Tallgrass Prairie located in northeastern Illinois. Overwintering adults appear first in May on an earlier blooming congener, *Baptisia bracteata* Muhl. ex Ell. and then on *B. alba* (Petersen et al. 2006). The weevils mate and females begin ovipositing eggs within developing pods. After a period of oviposition, the adult weevils disappear, suggesting the species is univoltine. The larvae within pods consume seeds for nutrition, often devouring all within a pod. The adult stage is reached by August, with adults dispersing from opened pods by early autumn. Presumably adults overwinter in the soil since burning does not prevent the subsequent reappearance of the weevils.

In the following study, we investigated how patterns of flowering phenology and reproductive yield shown by *B. alba* are related to seed predation, pollination and weather using data from 2003-2009. We were interested if a long-term study would uncover relationships, unclear from short-term studies, which explain the variable reproductive patterns of the legume.

METHODS

Reconstruction of the 7.1 ha Russell Kirt Tallgrass Prairie was begun in 1984. The prairie was burned entirely each year until 2008, but has since been selectively burned. *B. alba* plants selected for study were from a section of the prairie which was burned in entirety from 2003-2008, and not burned in 2009. The prairie flora is characterized by the graminoids big bluestem (*Andropogon gerardii* Vitman), Indian grass (*Sorghastrum nutans*

(L.) Nash), and prairie dropseed (*Sporobolus heterolepis* Gray), and in excess of 100 species.

Sampling methods were similar for all seven years. *B. alba* were tagged for study as they began to flower. FFT and last flowering time were recorded for years 2007-2009. Common measurements for all years were racemes/plant, flowers/plant, pods inflated/plant (except for 2005), pods ripened/plant, seeds matured/plant, and *A. rostrum*/pod. Mature seed and weevil counts were taken from ripened pods. Five regularly spaced pods/raceme were selected for sampling. If a raceme had fewer than 5 pods, then all of the pods were inspected for seeds and weevils. Racemes/plant provided a measure of plant size and *A. rostrum*/pod a measure of weevil infestation. *Apion rostrum*/plant , evaluated by the product of inflated pods/plant and *A. rostrum*/pod, was used to examine if larger plants attracted more weevils overall. Inflated pods were used instead of mature pods to account for pod, and subsequent weevil, loss prior to ripening. Seeds matured/plant provided a measure of reproductive yield, pods inflated/flower a measure of pollination efficiency, and seeds matured/flower a measure of flower reward to a plant.

Weather data were obtained from O'Hare International Airport (http://www.crh.noaa .gov/) which is located 20km northeast of the site. Data for year 2004 were unavailable. Chosen measurements were departures in daily temperature (DPTR) and precipitation (DPPC) from averages due to the likely influence of these parameters on above-ground growth during March-August, and on pollination activity and seed maturation during June and July.

Despite use of transformations, normality and homogeneity of variance could not be safely assumed with most data within a year or among years. Spearman rank correlation was used to detect relationships among variables. Statistica (StatSoft 2001) was used in all analyses.

RESULTS

Table 1 summarizes parameters of flowering, reproductive yield, and weevil infestation according to year. In most years, *B. alba* experienced substantial pod loss from inflation through ripening resulting in highly variable counts of seeds matured per plant and flower. Years 2005-2007 showed warmer departures from normal (Table 2). This pattern included months June-July with year 2005 being especially dry.

Baptisia alba that flowered earlier, also flowered for a longer duration (Table 3). These plants were larger based on counts of both racemes and flowers. An earlier FFT was significantly related to more seeds matured/plant for years 2007 and 2009, but not for year 2008 when the mean count of weevils/pod was higher. FFT showed contrasting relationships to *A. rostrum*/pod. Only during 2009 was *A. rostrum*/pod significantly related to flowering duration. Pods inflated/flower tended to be negatively correlated to FFT, significantly so for 2009. No significant correlations were found between flowering duration and pods inflated/flower. Rewards of seeds matured per flower appeared only during 2009 when earlier flowering *B. alba* and those flowering for a longer duration produced significantly more seeds.

The relationship between seeds matured/plant and racemes/plant was always positive and significantly so in 4 of the 7 years (Table 4). Count of seeds matured/plant showed a contrasting relationship to *A. rostrum*/pod. Correlation coefficients between seeds matured/plant and pods inflated/flower were always positive but only significantly so in 3 of 6 years where data were available. While *B. alba* with more racemes tended to attract more weevils, the levels of infestation/pod varied greatly among years.

From 2003-2009, warmer departure from average June-July temperatures was associated with reduced seeds matured/flower (Table 5). Seeds matured/plant were negatively correlated to the count of *A. rostrum*/pod, and seeds matured/flower were positively linked to racemes/plant and seeds matured/plant.

DISCUSSION

The hypothesis that earlier FFT by *B. alba* helps in securing pollinators received marginal support. As an indicator of pollination activity the ratio of pods inflated/flower, though always negatively correlated to FFT, was only significantly so during 2009. Findings did not support that larger, earlier flowering plants can saturate pod infestation by *A. rostrum* as two years of three failed to show an expected positive relationship between FFT and *A. rostrum*/pod. When considering a longer flowering duration, these plants may only function to attract and retain ovipositing weevils.

Reward in seed yield by earlier flowering, longer flowering, and generally larger *B. alba* only occurs during the occasional seasons when weather is especially favorable to reproductive growth. The negative relationship between seeds matured/flower and June/July DPTR may indicate why most *B. alba* flower earlier. A higher reward in seeds matured/flower is unlikely to occur later in the season. The adverse effect of extreme weather on seed yield has been observed among other legumes (Evans et al. 1989, Mduma et al. 2007, Siemens and Johnson 1995, Young et al. 2007).

Although later flowering plants may avoid more intense predator pressures by *A. rostrum* during some years, the reward in seed yield is yet to be seen. Smaller *B. alba* may be younger or otherwise limited in above-ground growth, and lacking in the nutritional reserves to bloom earlier. More extreme temperatures as the season progresses may limit any benefit in seed yield to a later FFT and explain the shorter flowering duration. The fitness of these late bloomers may be maximized by reproducing to a lesser degree than not at all.

Pre-dispersal predation should be expected to reduce seed yield in *B. alba* that has one flowering episode per season. Data from across seasons indicate *A. rostrum* has a major negative effect on seed yield of *B. alba*. However, the weevil's selective role in affecting the flowering time of *B. alba* is not clear. *A. rostrum* is known to be a major seed predator of other *Baptisia* species, including those growing in warmer climates (Evans et al. 1989, Haddock and Chaplin 1982, Horn and Hanula 2004). The weevil's ability to adapt to congeneric hosts seems evident. Hence in northeastern Illinois, *A. rostrum* should synchronize its oviposition time with pod formation of its two hosts, *B. alba* and *B. bracteata*. The observation that *B. alba* with later FFT were also infested demonstrates the plasticity the weevil shows in oviposition period. Even among the few *B. alba* that flowered late, positive pod infestation is proof that there were a few ovipositing weevils to take advantage of these plants.

The major selective determinant on flowering time and duration of *B. alba* appears to be weather. Limited sampling seasons may have prevented reaching conclusions on how weather at different times of the growing season can affect the reproductive phenology of the legume. Continued study should further elucidate determinants affecting flowering phenology of *B. alba*.

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Table 1. Summary (mean ± standard error; n) of flowering phenology, growth parameters, and *Apion rostrum*/pod for *Baptisia alba*. The sample size which is enclosed in parentheses, is provided next to the first parameter listed for a year and applies to remaining measurements unless otherwise noted. Symbols: FFT = first flowering time.

Parameter	Year						
	2003	2004	2005	2006	2007	2008	2009
FFT					11.6 ± 1.3(63)	15.7 ± 1.5(61)	13.8 ± 1.2(91)
Flowering duration					17.8 ± 0.7	16.1 ± 0.8	19.4 ± 0.8
Racemes/plant	3.0 ± 0.7(38)	4.1 ± 0.3(38)	2.8 ± 0.2(40)	3.4 ± 0.4(40)	3.9 ± 0.3	3.2 ± 0.3	3.9 ± 0.3
Flowers/plant	134.0 ± 13.5	101.7 ± 10.0	70.5 ± 6.6	74.7 ± 6.8	71.1 ± 7.6	57.9 ± 5.8	88.2 ± 6.7
Pods inflated/plant	50.8 ± 6.2	53.6 ± 7.7		39.4 ± 4.6	44.2 ± 6.4	27.8 ± 3.2	60.0 ± 4.8
Pods matured/plant	9.7 ± 2.9	47.4 ± 7.3	2.2 ± 0.9	10.2 ± 1.5	9.3 ± 3.4	0.7 ± 0.3	31.0 ± 3.2
Seeds matured/plant	37.7 ± 14.9	366.0 ± 64.2	3.3 ± 2.0	19.3 ± 4.3	30.8 ± 13.5	2.7 ± 2.0	228.1 ± 36.3
A. rostrum/pod	1.9 ± 0.3(15)	1.5 ± 0.2(37)	2.7 ± 0.4(14)	3.9 ± 0.2(35)	2.9 ± 0.25(39)	3.4 ± 0.4(11)	2.42 ± 0.22
Inflated pods/flower	0.40 ± 0.04	0.72 ± 0.16		0.52 ± 0.03	0.59 ± 0.03	0.52 ± 0.02	0.66 ± 0.02
Seeds matured/flower	0.33 ± 0.15	4.8 ± 1.4	0.03 ± 0.02	0.22 ± 0.07	0.24 ± 0.07	0.08 ± 0.07	1.96 ± 0.25

Table 2. Select local weather measurements by year taken from O'Hare International Airport, IL. Symbols: DPTR = departure from average daily temperature; and DPPC = departure from average daily precipitation.

Measurement	Year					
	2003	2005	2006	2007	2008	2009
March-August DPTR (°C)	-4.3	10.8	13.1	15.9	0.3	-2.7
March-August DPPC (cm)	0.12	-11.29	-0.79	3.33	0.65	5.52
June-July DPTR (°C)	-2.00	4.61	1.83	1.94	1.83	-2.50
June-July DPPC (cm)	-1.18	-4.43	0.61	-0.99	1.80	1.57

Table 3. Spearman rank correlation comparing first flowering time (FFT) and flowering duration to variable of plant reproductive yield and pod infestation by *Apion rostrum* for years 2007-2009. Subscripts in parentheses beside correlation coefficients indicate sample sizes deviating from the rest. Symbol: *denotes significance ($P \leq 0.05$).

Parameter	First Flowering Time			Flowering duration		
	2007	2008	2009	2007	2008	2009
Flowering duration	*-0.53	*-0.73	*-0.88			
Racemes/plant	*-0.46	*-0.50	*-0.68	*0.61	*0.64	*0.72
Flowers/plant	*-0.53	*-0.45	*-0.69	*0.76	*0.58	*0.77
Seeds matured/plant	0.13	0.01	*-0.62	0.22	0.24	*0.63
Apion rostrum/pod	*0.32$_{(39)}$	0.22$_{(11)}$	*-0.61	0.17$_{(39)}$	-0.14$_{(11)}$	*0.60
Pods inflated/flower	-0.07	-0.08	*-0.25	0.15	0.23	0.13
Seeds matured/flower	0.18	0.02	*-0.51	0.16	0.23	*0.49
Sample size by year	63	61	91	63	61	91

Table 4. Spearman rank correlation comparing variables of plant reproductive yield and pod infestation by *Apion rostrum* for years 2003-2009. Subscripts in parentheses beside correlation coefficients indicate sample sizes deviating from the rest. Symbol: *denotes significance ($P \leq 0.05$).

Variable 1	Year						
Variable 2	2003	2004	2005	2006	2007	2008	2009
Seeds matured/plant							
Racemes/plant	0.10	*0.42	0.18	*0.37	*0.27	0.04	*0.89
Flowers/plant	0.29	*0.34	0.28	*0.48	*0.27	0.16	*0.76
Apion rostrum/pod	*0.50$_{(15)}$	*-0.50$_{(37)}$	-0.08$_{(14)}$	-0.23$_{(35)}$	-0.08$_{(39)}$	-0.35$_{(11)}$	*0.75
Pods inflated/flower	*0.49	*0.44		0.23	0.13	0.41	*0.38
Racemes/plant							
Flowers/plant	*0.75	*0.70	*0.83	*0.90	*0.83	*0.85	*0.93
Apion rostrum/pod	-0.44	-0.03	0.17	<0.01	0.22	-0.50	*0.63
Apion rostrum/plant	0.28	*0.56	0.17	*0.68	*0.46	0.34	*0.79
Sample size by year	38	38	40	40	63	61	91

Table 5. Spearman rank correlation of yearly *Baptisia alba* averages of reproductive yield and pod infestation by *Apion rostrum*, and local select weather patterns from 2003-2009 measured at O'Hare International Airport, IL. Weather data from year 2004 are missing. All n = 7 except for correlations involving weather measurements where n = 6. Symbols: *Denotes significance ($P \leq 0.05$); DPTR = departure from average monthly temperature; and DPPC = departure from average monthly precipitation.

Parameter	Racemes/plant	Seeds matured/plant	*Apion rostrum*/pod	Pods inflated/flower	Seeds matured/flower
Racemes/plant		*0.86	-0.68	0.35	*0.89
Seeds matured/plant			*-0.79	0.64	*0.96
Apion rostrum/pod				-0.41	-0.71
Pods inflated/flower					0.64
March-August DPTR	0.49	-0.37	0.71	0.36	-0.43
March-August DPPC	0.49	0.54	-0.20	0.82	0.71
June/July DPTR	-0.52	-0.67	0.41	-0.05	*-0.81
June/July DPPC	-0.09	-0.09	0.43	0.41	0.20