Comparison of Common Factors Affecting Seed Yield in the Congeners, *Baptisia alba* and *Baptisia bracteata*

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ABSTRACT

This study examined the importance of floral display to pollination and ultimately the size of seed set of Baptisia alba (L.) Vent. and B. bracteata Muhl. ex Ell. (Fabaceae) as to provide evidence that competition for pollinators has influenced reproductive distinctions between the congeners. The congeners partially overlap in flowering period and share common pollinators. The *a priori* assumption was that if the congeners compete, the size of floral display would be a positive predictor of seed matured/plant. As both species are infested by the pre-dispersal seed predator, Apion rostrum Say (Coleoptera: Curculionidae) within the study site, the importance of seed predation as a conflicting variable to seed set of each congener was also studied. The study site was a 7.1 ha, 21year old reconstructed tallgrass prairie located in northeastern Illinois. Individual B. alba produced more flowers, inflated pods, and seeds matured/flower than B. bracteata, but also had a higher mean count of A. rostrum/pod. Flower count/plant and A. rostrum count/pod were significant predictors of seeds matured/plant for B. alba, while only the former was a significant predictor of seeds matured/plant for B. bracteata. Differences in flowering period between the congeners should lessen competition for pollinators. Growth patterns may be adaptations linked to differences in the timing of flowering. The earlier springtime blooming period of *B. bracteata* when the prairie vegetation is emerging and pollinator activity is low, may select for showcasing floral display through a larger flower count/plant and clusters of plants. Height is not critical in the relatively barren landscape. Re-emergence of the prairie flora may select for greater height and multiple racemes in the later blooming period of B. alba, perhaps making B. alba to be more apparent to A. rostrum.

INTRODUCTION

The white wild indigo (*Baptisia alba* [L.] Vent.) and the cream wild indigo (*Baptisia bracteata* Muhl. ex Ell.) are leguminous natives of mesic tallgrass prairie (Ladd 1995, Swink and Wilhelm 1994). Despite their close genetic relationship and the hosting of common pollinators, the congeners differ in stature, number of racemes per plant, and to some extent, flowering period (Haddock and Chaplin 1982). Such differences in morphology and reproductive patterns between flowering congeners have been argued to facilitate co-existence by reducing or eliminating the competitive advantage of one congener over the other (Brown et al. 2002).

In northeastern Illinois and the location of this study, B. alba and B. bracteata bloom during spring when pollinator activity is low (Pearson 1933). Bumblebees (*Bombus* spp.) pollinate both congeners which show overlap in flowering. B. bracteata blooms in May and into early June, while B. alba blooms from late May into the latter half of June. The much larger B. alba has abundant branches that commonly terminate in multiple smaller racemes in addition to a tall central raceme which can extend to 2m. The slender B. bracteata usually produces only a single arching raceme and grows to little more than 0.5m high. Both species have conspicuous flower displays. However, B. alba tends to form less densely populated clumps, with the multiple racemes of each plant projecting above the rejuvenating spring flora. In contrast, B. bracteata forms dense circular clumps of over a dozen individuals with racemes radiating outward (Petersen et al. 2000). The number of ovules per pod averages 35 for B. alba with most producing seeds, and 27 for B. bracteata with only slightly more than half initiating seeds (Haddock and Chaplin 1982). Pollination, subsequent pod and seed development, and maturation follow similar sequences in the congeners. Successful pollination is indicated by pod inflation (Haddock and Chaplin 1982). Pods ripen by early fall as the above-ground tissues senesce and seeds are released as the pods dehisce or fragment. The cycle of new above ground growth and reproduction commences with the return of spring.

Both *B. alba* and *B. bracteata* are infested by the pre-dispersal seed predator, *Apion ros-trum* Say (Coleoptera: Curculionidae) (Petersen 1990, Petersen et al. 2000). Overwintering adult *A. rostrum* appear on plants beginning in late May and during the next month can be observed inserting eggs into inflated pods. Resulting offspring utilize seeds in the pod for their only source of nutrition. The weevils complete development inside the pods by August, dispersing as pods open. A major source of larval mortality is abortion of developing pods, particularly in *B. alba*, which results in the decay of the pods and the developing weevils within them (Petersen and Sleboda 1994, Petersen et al. 1998).

Our study examines the importance of floral display to pollination and ultimately the size of seed set of *B. alba* and *B. bracteata* for evidence that competition for pollinators has influenced the congeners. The *a priori* assumption was that if the congeners compete, the size of floral display would be a positive predictor of seeds matured per plant. We also study the role of seed predation by *A. rostrum* as a conflicting variable influencing seed set.

METHODS

The study was conducted in the 7.1 ha, Russell Kirt Tallgrass Prairie, a 21-year old 7.1 ha reconstruction located on the main campus of College of DuPage, DuPage County, Illinois. Prairie planting began in 1984. Over 150 species of native tallgrass forbs and graminoids, with big bluestem (*Andropogon gerardii* Vitman) and prairie dropseed (*Sporobolus heterolepis* Gray) being the dominant grass species in the prairie (Kirt, 1996) which is burned annually.

The study was conducted over one season of growth during 2004. Plants of *B. alba* and *B. bracteata* were randomly selected for study as they flowered during May and June. *Baptisia alba* and *B. bracteata* were monitored from flowering through seed maturation

and pod ripening to elucidate differences in and the importance of size of floral display to reproductive output. Flowers and pods that inflated were counted on each plant. During August and September as plants began to senesce, five sealed pods were collected from each raceme and sampled for counts of matured seeds and weevils. The most proximal, distal, and three pods spaced evenly between were those sampled. If a raceme had less than five pods, all pods were sampled. Seed yield was computed as the product of the mean count of matured seeds/pod and inflated pods/plant. The degree of weevil infestation was computed as the grand mean count of *A. rostrum*/pod among racemes of a plant.

Flower counts/plant, pods inflated/plant, seeds matured/plant, and *A. rostrum* counts/pod were compared between the congeners using one-way analysis of variance (ANOVA). The ratio of pods inflated/flower and seeds matured/flower provided measures of pollination success and reproductive reward, respectively, per flower produced. Counts of seeds/plant, pods inflated/plant, and weevils/pod were $\log_{10}(x+1)$ transformed prior to analysis to meet normality. The effects of flower count/plant and *A. rostrum* count/pod on $\log_{10}(x+1)$ transformed count of seeds matured/plant were evaluated for each congener using multiple regression. Redundancy of the two independent variables was examined with computations of correlation coefficient and tolerance (where 0 indicated redundancy and 1 independence). Significance was determined at $P \le 0.05$. It was presumed that counts of seeds/plant and weevils/pod would not be collinear from evidence that *A. rostrum* evaluates individual pods as suitable oviposition sites (Petersen and Sleboda 1994). Curculionids are also known to chemically mark fruits as a deterrent to additional oviposition (Kozlowski et al. 1983). All statistical summarization and analyses were done using Statistica (Statsoft 2001).

RESULTS

Plants of *B. alba* produced more flowers ($F_{1,103} = 142.4$, P < 0.001), initiated more inflated pods ($F_{1,102} = 130.4$, P < 0.001), and had more seeds matured per plant ($F_{1,103} = 80.3$, P < 0.001) and flowers ($F_{1,103} = 24.1$, P < 0.001) than *B. bracteata* (Table 1). However, *B. alba* had a higher mean count of *A. rostrum* count/pod than *B. bracteata* ($F_{1,102} = 43.2$, P < 0.001). The ratio of pods inflated/flower did not differ significantly between the congeners ($F_{1,103} = 1.9$, P = 0.167).

Flower count/plant was a positive predictor of seeds matured/plant for both congeners, while *A. rostrum* count/pod was a negative predictor of seeds matured/plant only for *B. alba* (Table 2). Redundancy was not detected for the independent variables with either *B. alba* (r = 0.021, tolerance = 0.999, N = 36) or *B. bracteata* (r = 0.052, tolerance = 0.997, N = 68).

DISCUSSION

Flowering and growth patterns by *B. alba* and *B. bracteata* have sufficient selective value as evidenced by their persistence in the tallgrass environment. Moreover, the positive relationship between flower count/plant and seeds matured/plant indicates the importance of flower display to attracting pollinators, a competitive interaction that would be alleviated by the morphological and reproductive distinctions between *B. alba* and *B. bracteata*. The positive relationship between counts of flowers and seeds matured has also

been shown at the level of flower count/clump of *B. bracteata* (Petersen et al. 2000). A greater stature is not required by *B. bracteata* to attract pollinators when much of the surrounding floral landscape has just begun to reemerge. However, larger inflorescence size per individual as well as per cluster of *B. bracteata* appears to facilitate pollination without attracting higher counts of *A. rostrum*/pod. Clustering can also function to crowd out other plant species as to enable photosynthesis that is required to support the next season's reproductive effort (Harper 1977).

Flower initiation two weeks after that for *B. bracteata* in a rapidly emerging springtime community may select for a larger floral display among multiple racemes of a taller *B. alba*, again explaining the significance of flower count/plant to seeds matured. In addition, being taller and more profusely branched can provide *B. alba* the added leaf area to support photosynthetic needs. The cost of a greater stature of *B. alba* and/or later development than *B. bracteata*, appears to be a greater attraction and subsequent pod infestation by *A. rostrum* at the interspecific level. Where other factors such as nutrition or water stress may also affect seed yield (Brevedan and Egli 2003), increasing pod counts of the seed predator eventually should take a noticeable toll, explaining the significance of counts of *A. rostrum*/pod on seeds matured/pod.

Despite the non-significant difference in pods inflated/flower and the higher levels of pod infestation by *A. rostrum*, seeds matured/pod by *B. alba* was still 3.3 times greater, and seeds matured/plant 14 times greater, than for *B. bracteata*. Perhaps it is the higher number of seeds in pods in addition to the abundance of the pods on plants that draws more weevils to *B. alba*. Lower seed count/pod has been suggested to be an evolved response to counter seed predation in other legumes (Siemens et al. 1992), possibly explaining the lower seed counts/pod and the ratio of seeds initiated/pod ovules in *B. bracteata*. Conversely, *B. alba* may be more vulnerable to *A. rostrum* infestation due to having a later developmental period that more closely coincides to when the weevil is most actively ovipositing. Weevil selection of pods for oviposition, and oviposition activity, as well as the intensity of post-dispersal seed predation, seed viability, and seedling survival, have not been studied for either congener and would provide greater insight into the adaptive dynamics of the legumes in a tallgrass environment. The two congeners are also known to vary in alkaloid composition (Crammer and Turner 1967), a factor which may affect the probability of seed consumption.

The significance of flower display as a predictor of seeds matured/plant is evidence of the importance of inflorescence size to both *Baptisia* species. Interspecific competition for the spring population of *Bombus* may, in part, be reduced by the difference in the flowering times of the congeners. Varying selective pressures resulting from this difference, to include pre-dispersal seed predation by *A. rostrum*, may explain morphological and other reproductive distinctions between the congeners.

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Variable	Plant species				
Variable	Baptisia alba	Baptisia bracteata			
Flower count/plant	$102.1 \pm 10.3 (37)$	17.4 ± 1.07 (68)			
Inflated pod count/plant	54.1 ± 7.9 (37)	8.2 ± 0.8 (68)			
Seeds matured count/plant	386.4 ± 66.2 (36)	27.9 ± 5.3 (68)			
Inflated pod count/flower	0.73 ± 0.16 (37)	0.46 ± 0.03 (68)			
Seeds matured/flower	5.05 ± 1.48 (36)	1.53 ± 0.25 (68)			
Apion rostrum count/pod	1.47 ± 0.14 (36)	0.59 ± 0.06 (68)			

Table 1. Sample mean \pm sample standard error (sample size) of parameters of plant reproductive yield and pod infestation by *Apion rostrum* according to species of *Baptisia*.

Table 2. Summary of multiple regression analyses for counts of seeds matured/plant according to congener of *Baptisia* in relation to flower count/plant and *Apion rostrum* count/pod. Seeds matured/plant were $log_{10}(x + 1)$ prior to each analysis.

Whole model				Flower count/plant		Apion rostrum count/pod			
Species	Р	F	r^2	Ν	Р	t	Р	t	
Baptisia alba									
	< 0.001	16.188	0.704	36	< 0.001	4.318	< 0.001	-3.797	
Baptisia bracteata									
	0.006	5.527	0.145	68	0.003	3.121	0.196	-1.306	