

## The Effect of Burning and Insect Herbivory on Seed Production of Two Prairie Forbs

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**ABSTRACT** — The effect of burning on the reproductive success of prairie forbs is poorly understood, and the combined effect of burning and insect herbivory on these forbs has not been studied. We investigated the effects of burning and insect herbivory on seed production in *Ratibida pinnata* (Asteraceae) and *Monarda fistulosa* (Lamiaceae). *R. pinnata* is dependent upon seed production for recruitment and tends to be over-represented in the seed bank, while *M. fistulosa*, which tends to be under-represented in the seed bank, is rhizomatous and can propagate itself vegetatively. Burning produced a significant reduction in seed production in *Monarda* but not in *Ratibida*. Seed reduction in *Monarda* was due to a reduction in plant parts, particularly numbers of stems and numbers of inflorescences per stem. Insect infestation in *Monarda* reduced seed production by 33% but did not affect the fecundity of *Ratibida*. The rate of insect infestation of *Ratibida* was higher in the burned than the unburned area. In addition, fire and infestation interacted in *Ratibida* to produce larger seeds. The latter findings indicate the importance of considering plant-insect interactions when studying the effects of fire on vegetation.

The effect of fire on survivorship, reproduction, and recruitment of native and introduced grasses has been studied extensively (Kucera and Koelling 1964, Zimmerman and Kucera 1977, Risser et al. 1981). However, detailed data are lacking for most forbs. Knapp (1984) reported that fire reduced seed production in *Vernonia baldwinii* (western ironweed), but most reports of how fire affects forbs have noted only general responses, e.g., an increase or decrease in density or flowering activity (Kucera and Koelling 1964, Zimmerman and Kucera 1977, Pemble et al. 1978, Wright and Bailey 1982).

In addition to its effects on plants, burning also can produce changes in insect abundance (Nagel 1973, Knutson and Campbell 1976, Evans 1984). This may have important consequences for the vegetation. For example, changes in the reproductive success of prairie plants following a fire could be mediated by changes in the behavior or population size of pollinators and/or seed predators.

The purpose of this study was to compare the effect of a prescribed burn on the seed production and floral herbivory in grayheaded prairie coneflower, *Ratibida pinnata* (Asteraceae), and wild bergamot, *Monarda fistulosa* (Lamiaceae). Both species were categorized as "modal species" by Havercamp and Whitney (1983) in their study of forbs associated with the tall-grass prairie. Modal species are those typically found on but not restricted to prairies. However, the two species differ in several important attributes. *Monarda* exhibits vegetative growth while *Ratibida* does not, and compared to *Ratibida*, *Monarda* plants flower for a shorter period of time and produce fewer seeds (Havercamp and Whitney 1983). In fact, a discriminant analysis performed by Havercamp and Whitney (1983) showed considerable differentiation between the two species,

with *Ratibida* grouped more with the "weedy" than the "modal" species. In a study of the seed bank in a tall-grass prairie, *Ratibida* was found to be significantly over-represented in the seed bank while *Monarda* was found to be significantly under-represented (Johnson and Anderson 1986). Based on their findings, Johnson and Anderson (1986) termed *R. pinnata* an "agressive and weedy" species. Because *Ratibida* is more dependent upon seed production for recruitment than *Monarda*, we hypothesized that if fire affected sexual reproduction in these species, it was more likely to have an adverse effect on *Monarda* than on the more weedy *Ratibida*.

#### STUDY SITE

We conducted our study in a 3-ha patch of rolling grassland at the Macalester College field station, the Katharine Ordway Natural History Area, in Inver Grove Heights, Dakota County, Minnesota. Soils at Ordway are part of the Esterville-Wadena-Hubbard association and are characterized as coarse to medium textured, dark, prairie-type soils which are usually well drained (Arneman 1963). Dominant grasses in the study are *Andropogon gerardii* (big bluestem), *Schizachyrium scoparium* (little bluestem), *Sorghastrum nutans* (Indian grass), *Spartina pectinata* (prairie cordgrass), *Poa pratensis* (Kentucky bluegrass), and *Agrostis alba* (redtop). Forbs are abundant including *Ratibida pinnata*, *Liatris aspera* (rough blazing star), *Asclepias tuberosa* (butterfly weed), *Petalostemon purpureum* (purple prairie clover), *Solidago rigida* (stiff goldenrod), *S. speciosa* (showy goldenrod), *S. canadensis* (Canada goldenrod), *Aster azureus* (azure aster), and *Monarda fistulosa*. Prior to the study, the grassland had not been burned for four years.

#### STUDY ORGANISMS

*Monarda fistulosa* L. (Lamiaceae) is an aromatic, rhizomatous, herbaceous perennial common in prairies although it commonly grows in woody habitats as well (Gleason and Cronquist 1963). Its range extends from Quebec to British Columbia south to Georgia and Arizona (Gleason and Cronquist 1963). Plants are 30-135 cm tall and produce dense glomerules of sessile flowers at the end of branched stems. At Ordway, plants emerge in late April and flower in mid-July and early August. A microlepidopteran larva (superfamily: Pyralidoidea) infests inflorescences in late August and September and feeds on the developing seeds.

*Ratibida pinnata* (Vent.) Barnh. (Asteraceae), is a tall (0.5-1.5 m), herbaceous, prairie perennial. Its range, central and north central United States, matches much more closely that of the original tall-grass prairie than does that of *M. fistulosa* (Gleason and Cronquist 1963). At Ordway plants emerge in late April and flower from mid-July through mid-September. A microlepidopteran larva (family Gelechiidae) infests the inflorescences and feeds inside the receptacle.

#### MATERIALS AND METHODS

*Monarda fistulosa*. In August 1984, we set up four adjacent areas in which *M. fistulosa* was abundant, each consisting of three plots (5x5 m), and recorded

stem and inflorescence densities for each plot. Eight randomly chosen plots (two in each area) were burned on 5 May 1985; the remaining four were not burned and served as a control. In late August 1985, stem and inflorescence densities were again recorded. The effect of burning on density and inflorescence production was assessed by an analysis of covariance, in which the 1984 values of the variables were used as covariates to correct for differences due to plot effects rather than treatment effects. In September 1985, inflorescences (5-15 depending on inflorescence density) were randomly collected (a total of 38 from burned plots, 40 from unburned plots). In the laboratory, the diameter of each inflorescence was measured and the number of flowers in the head counted. From one half of each inflorescence, ten flowers were randomly inspected for evidence of seed predation by moth larvae. The fate of ovules was divided into three categories: seed eaten by predator, seed present, or ovule aborted. Potential seed production in the absence of predators was estimated by multiplying the number of flowers in the head times four (four nutlets per flower in *M. fistulosa*) and subtracting the number of aborted ovules. From the other half of each inflorescence, all seeds were weighed in groups of five, then germinated in groups of 25 on moist filter paper in a petri dish in the dark at a constant temperature of 30° C and relative humidity of 50-80%.

*Ratibida pinnata*. A separate 0.5-ha portion of the grassland was burned on 5 May 1986. In late August, 24 flowering stems in the burned area and 24 flowering stems in an immediately adjacent unburned area were collected. The 48 stems were dried, separated into leaves, stems, and inflorescences, and weighed. In addition to these stems, a total of 33 plants in the burned area and 40 from the unburned area were randomly selected and measured: number of stems per plant, number of heads per stem, and height above ground of each head. The heads of these selected plants were collected and taken to the laboratory where they were measured (length and width) and dissected to determine if they had been infested by a gelechiid larva. Measurements of *Ratibida* plants were not made prior to the burn and thus it was not possible to correct for possible plot effects. Additional dry (ripe) heads from the burned and unburned areas were collected in late September and measured and dissected in the same way. Seed number and mass (in groups of 40 seeds) were made for the heads collected in late September. After measurement and dissection, heads were kept in the dark at 7° C for six months and then 25 seeds from 10 heads from each of the four groups (burned-uninfested, burned-infested, unburned-uninfested, unburned-infested), were tested for viability using the tetrazolium test (Colbry et al. 1961).

Statistical comparisons were made with t-tests, analysis of covariance, and two-way analysis of variance. All error measurements provided in this paper are standard deviations.

## RESULTS

*Monarda fistulosa*. In 1984, before the plots were burned, there was no difference between plots in the densities of stems or inflorescences or in the number of inflorescences per stem (Table 1). In 1985, all of these variables declined; however, the reduction in the burned plots was significantly greater than that

Table 1. *Monarda* stem and inflorescence density for burned and unburned plots.

Variable	Year	Burned		Unburned		P
Stem density	1984	74.4	± 65.7	51.3	± 57.8	NS
	1985	10.4	± 8.9	23.8	± 15.1	.05
Inflorescence density	1984	292.4	± 285.5	162.5	± 175.9	NS
	1985	14.9	± 12.0	59.8	± 32.1	.01
Number of inflorescences per stem	1984	3.45	± 0.85	3.04	± 0.46	NS
	1985	1.29	± 0.57	2.71	± 0.73	.01

Stem sample sizes (for number of inflorescences per stem) were: 1984, burned — 585; 1984, unburned — 205; 1985, burned — 84; 1985, unburned — 94.

All statistical comparisons made with analysis of covariance.

in the control plots (Table 1). Inflorescences from both treatments did not differ in diameter nor in the number of flowers per head (Table 2). Seed reduction due to infestation did not differ between burned and unburned plots, nor was there a significant plot difference in the rate of ovule abortion nor in mean estimated fecundity of inflorescences (Table 2). When the effect of burning on the number of inflorescences per stem was taken into account, stems in unburned plots produced significantly more seeds than stems in burned plots ( $B = 272 \pm 195$  seeds/stem,  $n = 38$ ;  $U = 528 \pm 326$  seeds/stems,  $n = 40$ ;  $t = 4.20$ ,  $P < 0.001$ ). When the decrease in stem density between treatments was taken into account, calculated fecundity for burned plots was further reduced ( $B = 4744 \pm 4071$  seeds/plot,  $n = 38$ ;  $U = 11,772 \pm 7894$  seeds/plot,  $n = 40$ ;  $t = 4.90$ ,  $P < 0.001$ ). Neither mean seed mass nor rate of germination differed between treatments (Table 2).

*Ratibida pinnata*. Plants in the burned and unburned areas did not differ in the total biomass allocated to stems, leaves, or inflorescences, nor in the number of stems per plant, number of inflorescences per stem, nor number of inflorescences per plant (Table 3).

Compared to those in the unburned area, flower heads in the burned area were closer to the ground, longer, and wider (Table 3). Infested and uninfested heads differed in length but did not differ in width nor in height about ground (Table 4).

Seed production per head was not affected either by burning (Table 3) or by infestation (Table 4). Seed mass was unaffected by burning (Table 3); however, infested heads produced heavier seeds than uninfested heads (Table 4). Moreover, there was a significant interaction between burning and infestation with respect to seed mass ( $F = 15.91$ ,  $P < .001$ ). Specifically, infestation had a significant effect on seed mass in the burned area ( $I = 18.9 \pm 6.2$  mg,  $n = 30$ ;  $U = 15.0 \pm 4.3$  mg,  $n = 30$ ;  $t = 2.83$ ,  $P < 0.01$ ) while it had no effect in the unburned area ( $I = 18.1 \pm 4.9$  mg,  $n = 30$ ;  $U = 17.1 \pm 6.6$ ,  $n = 30$ ;  $t = .667$ ,  $P > 0.50$ ).

Heads in the burned and unburned area did not differ in the number of

Table 2. Plant attributes for *Monarda fistulosa* in burned and unburned plots. All statistical comparisons were made with the t-test.

Variable	n	Burned	n	Unburned	P
Inflorescence diameter (cm)	38	1.37 ± 0.37	40	1.27 ± 0.36	NS
No. flowers per inflorescence	38	68.8 ± 31.5	40	68.4 ± 31.5	NS
Estimated no. seeds per inflorescence	38	198 ± 141	40	189 ± 114	NS
Seed mass (mg)	50	1.13 ± .447	40	1.03 ± .316	NS
% Ovules aborted	38	35.3%	40	34.3%	NS
% Seeds eaten	38	31.8%	40	36.0%	NS
% Seeds germinated	100	56.4%	100	55.8%	NS

fully developed embryos per sample of 25 ( $B = 11.1 \pm 3.5$ ,  $n = 10$ ;  $U = 11.4 \pm 6.1$ ,  $n = 10$ ;  $F = 0.03$ ,  $P > 0.8$ ) or in the number of viable seeds per sample ( $B = 3.0 \pm 3.5$ ,  $n = 10$ ;  $U = 2.05 \pm 3.03$ ,  $n = 10$ ;  $F = 0.86$ ,  $P > 0.3$ ). Infested and uninfested heads likewise did not differ either in number of fully developed embryos ( $I = 12.3 \pm 3.5$ ,  $n = 10$ ;  $U = 10.2 \pm 6.0$ ,  $n = 10$ ;  $F = 1.69$ ,  $P > 0.2$ ) or number of viable seeds ( $I = 3.1 \pm 3.7$ ,  $n = 10$ ;  $U = 2.0 \pm 2.8$ ,  $n = 10$ ;  $F = 1.05$ ,  $P > 0.3$ ).

Percent infestation by gelichiid larvae was higher in the burned than in the unburned area ( $B = 24.6\%$ ,  $n = 211$ ;  $U = 16.1\%$ ,  $n = 217$ ;  $t = 2.19$ ,  $P < 0.05$ ).

#### DISCUSSION

Our findings confirmed our prediction that fire would be more detrimental to the reproductive effort of *Monarda* than to *Ratibida*, which is more dependent upon seed production for recruitment. Thus, as would be expected of a weedy species, *Ratibida* is able to maintain a high level of seed production under variable conditions. The fact that stem density in *Monarda*, as well as its seed production, was significantly reduced by burning suggests that in the original tall-grass prairie *Monarda* may have been restricted to areas protected from frequent burning. For example, commonly found in woody habitats elsewhere in its range, *Monarda* may have persisted in the prairie along the edges of gallery forests. (The first author, Mark Davis, has seen *Monarda* growing in this habitat at Konza Prairie.) On the other hand, because it can spread vegetatively, an initial decline in *Monarda* density may be compensated in subsequent years by vegetative growth.

The significant reduction in reproductive effort in *Monarda* following burning was due exclusively to a reduction in the number of plant parts (stems and

Table 3. *Ratibida* plant attributes from burned and unburned plots.

Variable	n	Burned	n	Unburned	P
Biomass (g)					
Stems	24	4.46 ± .209	24	5.24 ± .215	NS
Leaves	24	1.71 ± .748	24	1.74 ± .762	NS
Inflorescences	24	1.10 ± .640	24	1.24 ± .551	NS
No. stems per plant	33	1.39 ± .86	40	1.25 ± .74	NS
No. inflorescences per stem	46	4.59 ± 1.78	50	4.36 ± 2.99	NS
No. inflorescences per plant	33	6.37 ± 5.17	40	5.45 ± 4.53	NS
Mean inflorescence height above ground (cm)	211	111.3 ± 14.9	217	120.0 ± 15.7	.001
Inflorescence Size					
Length (mm)	206	14.4 ± 2.2	187	14.1 ± 2.2	.05
Width (mm)	206	11.9 ± 1.4	188	11.5 ± 1.4	.01
No. seeds per inflorescence	38	269 ± 49	39	275 ± 49	NS
Seed mass (mg)	60	16.9 ± 2.5	60	17.5 ± 2.3	NS

Statistical comparisons of inflorescence size, seed mass, and number of seeds per inflorescence were made with a 2-way analysis of variance (burned/unburned x infested/uninfested). Other comparisons were made with a t-test.

Table 4. *Ratibida* plant attributes for infested and uninfested individuals.

Variable	n	Infested	n	Uninfested	P
Inflorescence height above ground (cm)	86	114.0 ± 16.7	342	116.1 ± 15.7	NS
Inflorescence Size					
Length (mm)	84	13.6 ± 2.2	309	14.4 ± 2.2	.001
Width (mm)	84	11.6 ± 1.6	310	11.7 ± 1.3	NS
No. seeds per inflorescence	37	264 ± 43	40	280 ± 53	NS
Seed mass (g)	60	18.4 ± 2.3	60	16.0 ± 2.1	.001

All statistical comparisons were made with a 2-way analysis of variance (burned/unburned x infested/uninfested).

inflorescences). The size of plant parts (inflorescences and seeds) and viability of seeds was not affected. Similar results were obtained for *Vernonia baldwinii* (Asteraceae), a prairie forb which also exhibited reduced seed production after a spring burn (Knapp 1984). Based on our study, we are unable to determine the cause for the reduction in plant parts. Knapp (1984) suggested that vigorous growth of grasses following fire may have contributed to the lower seed production in *V. baldwinii* through competition for resources such as light, water, and nutrients. In our study area, big bluestem, *Andropogon gerardii*, experienced a marked increase in height (20%), biomass (10%), and flowering (600%) following burning, which may have accounted for some of the suppression of growth in *Monarda*. The fact that *Monarda* stem density in the control plots declined by 50% indicates that forb densities in prairie habitats can vary markedly from year to year even in the absence of fire.

Although seed predation by Pyralidoidea larvae significantly reduced seed output in *Monarda*, the gelechiid larvae did not reduce seed output, development, or viability in *Ratibida*, primarily because they feed on the receptacle of the inflorescence and not the seeds themselves. The size of uninfested inflorescences on infested *Ratibida* plants did not differ from that of inflorescences on uninfested plants. Thus infestation had no negative effect at either the level of the inflorescence or the individual plant.

We do not know why the infestation rate by the gelechiid larvae was higher in the burned area nor how fire and infestation interacted to produce significantly larger seeds in *Ratibida*. In this study, larger seeds did not mean more viable seeds; however, it is possible that seedlings from larger seeds might grow faster and experience a competitive advantage over those from smaller seeds (Stanton 1984). In any case, the interaction between fire and floral herbivory that we documented indicates that plant-insect interactions need to be assessed when investigating fire effects on vegetation.

The importance of seed production in ongoing recruitment of prairie forbs is poorly understood. Perennial forb species characteristic of the closed tall-grass prairie tend to be long lived, and seedling establishment is a rare event (Anderson 1946, Christiansen and Landers, 1966). For these species and for species like *Monarda* that can spread by vegetative propagation, major annual fluctuations in seed production produced by fire or insects may be much less important than for species like *Ratibida* which are short-lived and depend upon recruitment by seed.

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