

## Response of *Zizia aurea* to Seasonal Mowing and Fire in a Restored Prairie

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**ABSTRACT.**—*Zizia aurea* (L.) Koch (Apiaceae) planted in a tallgrass restoration near Viola, Wisconsin, declined in numbers in randomly assigned plots left unburned or burned in May (41 to 9 and 63 to 30 individuals, respectively), but tripled in numbers in plots burned in August (72 to 209). Fire intensity varied widely, with a nine-fold range in May (86–782 kW/m) and a 49-fold range in August (58–2831 kW/m). In the August burn treatment, *Z. aurea* was most common in plots experiencing intense fires that cleared most or all ground litter. These same plots harbored 95% of the *Z. aurea* that flowered in 1996. A separate mowing experiment removed grass canopies to 10 cm, while leaving litter intact. *Zizia aurea* numbers did not change in plots mowed in May (76 to 77 individuals), but doubled in plots mowed in August (66 to 121). *Zizia aurea* is strongly favored by fire that simulates the timing of summer lightning fires thought to be common throughout grasslands and savannas of central North America before European settlement.

### INTRODUCTION

In ecological communities a few species are abundant whereas the vast majority are uncommon or rare (Preston, 1948, 1962; Magurran, 1988), and are variously referred to as satellite, interstitial or simply subdominant (Glenn and Collins, 1990; Howe, 1994a). In effect, competitive dominants relegate the greater majority of species to greatly restricted realized niches (Vandermeer, 1972). Suppression of dominant species increases biodiversity as competitively “saturated” communities admit species that can take advantage of space or resources once occupied by dominants (*see* Huston, 1979, 1994; Cornell and Lawton, 1992), thereby allowing a portion of the subdominant flora to persist which would otherwise be excluded.

In wet and mesic tallgrass prairies of central North America, the perennial forb *Zizia aurea* starts growth early in the spring and flowers in May and June; seeds are shed in autumn and germinate the next spring after exposure to cold, moist winter soil (Rock, 1981, Mohlenbrock, 1986; Swink and Wilhelm, 1994, pers. obs.). This species should be negatively affected by a spring burn or mowing that destroys shoots during a time of normally vigorous growth; it should be favored by prescribed burning or mowing in July or August that removes canopies of dominant competitors or reduces accumulated litter. Here I test the hypothesis that suppression of dominant species through burning or mowing during the midgrowing season favors *Z. aurea*.

### METHODS

*Zizia aurea* was one of 20 grasses and forbs planted in 60, 9 × 9 m plots in a wet-mesic sandy loam near Viola (43°32'N, 90°20'W), Wisconsin in late June and early July 1990. Planting procedures were adapted from Rock (1981). Pre-existing pasture vegetation of Eurasian grasses had been sprayed with contact herbicide (Roundup, Monsanto) in August 1988, and the vegetation was burned 2 wk later. In November 1988 the field was plowed

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before the ground froze. From May 1989 through June 1990, the field was spot-sprayed with Roundup and periodically disced. On 6–7 July 1990 seeds mixed with damp sand were broadcast in each  $9 \times 9$  m plot from one of 60 individually measured and weighed bags of six grasses (*Agropyron trachycaulum* (Link) Malte, *Andropogon gerardi* Vitman, *Andropogon scoparius* Michx., *Elymus virginicus* L., *Panicum virgatum* L., *Phalaris arundinacea* L.), and 12 forbs (*Allium cernuum* Roth, *Aquilegia canadensis* L., *Aster laevis* L., *Monarda fistulosa* L., *Oenothera biennis* L., *Penstemon digitalis* Nutt., *Ratibida pinnata* (Vent.) Barnh., *Rudbeckia hirta* L., *Solidago rigida* L., *Verbena hastata* L., *Zizia aurea*). All plots were raked and rolled, after which two dicots (*Achillea millefolium* L., *Heuchera richardsonii* R.Br.) with seeds  $< 0.2$  mg were broadcast on the surface (minute seeds do not germinate if buried). Future fire lanes 2.5 m wide were similarly broadcast seeded, raked and rolled with *Fescue eliator* to separate the plots. To avoid catastrophic seedling loss in the event of unfavorable conditions, seeds were not damp/cold stratified, resulting in emergence of species with extended dormancy (including *Z. aurea*) in 1991 and later. To avoid dominance due to different sowing densities, seeds of all species were sown at  $50/\text{m}^2$  for a total of 1000 seeds/ $\text{m}^2$ . Originally selected as a predictable early forb on such soils, *Z. aurea* presents an opportunity that is not offered by other species, most of which are too aggressively clonal to be individually counted, or too scarce to be statistically analyzed.

In 1993, 24 of the 60 plots were burned in April in anticipation of the start of seasonal burn cycles, but uncommonly heavy rains and 1–4 cm standing water in July and August prevented the 24 summer burns. The 24 plots burned in April 1993 were later assigned to a mowing experiment. The burning experiment discussed below concerns the remaining  $36 \times 9 \times 9$  m plots. On 24 April 1994 all 60 plots and surrounding areas were burned by an intense anthropogenic wildfire which reduced all vegetation and litter (100%) to ash. This fire delayed seasonal burning and mowing treatments until 1995.

Seasonal treatments commenced in 1995. On 18 May, 12 randomly picked  $9 \times 9$  m plots were burned; on 19–21 August, 12 additional randomly picked plots were burned. Flame height was recorded  $> 1$  m from the edge at five times during each burn (which lasted 3–5 min/ $9 \times 9$  m plot) for calculation of fire intensity (Johnson, 1992), and area burned per plot was estimated as a measure of fire effect. Twelve plots remained unburned and unmowed in 1995 and thereafter. Of 24 mowed plots, 12 were mowed to 10 cm on 20 May 1995 and 12 more were mowed to 10 cm on 22 August 1995.

All species planted appeared by 1992, with a dominance of *Phalaris arundinacea* ( $> 95\%$  by cover from 1992–1996) which was favored by exceptionally heavy rains at planting time in June and July 1990. This aggressive  $C_3$  grass is native to Eurasian and North American wetlands and wet prairies (Sampson, 1921; Curtis, 1959; Galatowitsch and van der Valk, 1996; Mergliano and Lesica, 1998), and formed the matrix with which *Zizia aurea* interacted. *Phalaris arundinacea* flowers in May and June and seeds in late June and July.

*Zizia aurea* plants were censused before and after seasonal burns. In each  $9 \times 9$  m plot, a 1 m border was excluded from sampling to minimize obvious edge effects, leaving  $64 \text{ m}^2/\text{plot}$  for sampling. On 25 May 1993, 5+ wk after 24 plots were burned in the first aborted burn cycle attempt, *Z. aurea* plants were counted in each plot. Counts were not made after the 1994 wildfire or 1995 prescribed fires. On 2–3 June 1996, the season following May and August burns, *Z. aurea* was again counted. In these counts, all plants that could be identified (canopies  $< 4 \text{ cm}^2$  to  $> 10,000 \text{ cm}^2$ ) were included. On 4 June, litter depth and *Phalaris arundinacea* height were measured in 8 randomly assigned sampling points per plot ( $N = 480$  for all fire and mowing treatments). On 15 June 1996, flowering *Z. aurea* were censused in all plots.

Burn and mowing treatments were analyzed separately to avoid confounding treatment

TABLE 1.—Total abundance of *Z. aurea* in June 1996 in 64 m<sup>2</sup> plots burned in May 1995 (N = 12), August 1995 (N = 12) or left unburned in 1995 (N = 12), as compared with pre-burn counts in May 1993

Time of 1995 burn	Preburn 1993	Postburn 1996
May burn	63	30
August burn	72	209
Not burned	41	9

$$^1 \chi^2 = 81.98, 2 \text{ df}, P < 0.0001$$

effects with the different pre-experimental burn histories of the 24 mowed plots as compared with the 36 spring burn, summer burn and unburned plots (*see above*).

### RESULTS

*Fire behavior.*—Fire behavior differed among treatments. Flame height ranged from 0.6 to 1.6 m in the May 1995 burns, but a mean of 1.3 m applied to most of the 12 plots burned. Less than 20% of the ground remained covered by  $\geq 1$  cm litter, indicating a basically uniform burn often observed in dormant-season and spring burns in dry weather (*e.g.*, Howe, 1995). A shorthand estimate of fire intensity is  $I = 259.83 L^{2.174}$  (Johnson, 1992), where  $L$  is flame height. For May 1995 this index yields extremes of 86–782 kW/m, with a mean of 460 kW/m. In contrast, flame height in August 1995 ranged from 0.5–3.0 m, indicating wide variation in intensity (58–2831 kW/m, with a mean  $\pm$  SE of  $742 \pm 207$  kW/m). Litter moistened by intermittent rains throughout August undoubtedly contributed to this variation in fire intensity, and to much more ground covered by at least 1 cm litter (4–95%, with a mean of  $63 \pm 11\%$ ) after August than May burns in 1995. Unburned and mowed plots remained 100% covered by litter.

*Response to fire season.*—Burn season affected presence, abundance and density. In 1996 *Zizia aurea* occurred in 10 of 12 plots burned in August 1995, six burned in May, and four left unburned ( $X^2 = 6.17, 2 \text{ df}, P < 0.05$ ). Preburn data in 1993 showed that this species was no more likely to occur in plots later burned in August than in others ( $P > 0.60$ ). Burn season also influenced total abundance (Table 1). *Zizia aurea* numbers dropped by half after May burns, almost tripled after August burns, and all but disappeared without burns. The mean density of *Z. aurea* was greater after August burns ( $17.4 \pm 8.0$  SE/plot) than after May burns ( $2.5 \pm 0.8$ ) or no burns ( $0.8 \pm 0.4$ ;  $F_{2,33} = 3.909, P < 0.05$ ).

Most *Zizia aurea* did not flower in 1996. A total of 37 plants did flower in burn treatments; of these 35 (of a total of 209) were in plots burned in August, while 0 of 30 and two of nine flowered in plots burned in May or left unburned, respectively. A  $\chi^2$  comparison of total plants and those that flowered suggested that fewer flowered in the latter two treatments than would be expected by their numbers in the plots ( $\chi^2 = 5.14, 2 \text{ df } P < 0.1$ ), a test compromised by the small number of individuals in unburned plots. Excluding unburned plots, a comparison of numbers flowering or not after May and August burns showed that this difference in distributions was unlikely by chance ( $\chi^2 = 4.93, 1 \text{ df}, P < 0.05$ ).

High fire intensities may encourage *Zizia aurea*. August fire intensity in 1995 had been higher in the six plots with more than one *Z. aurea* ( $1164 \pm 331$  kW/m) than in those with 0 or 1 ( $321 \pm 86$  kW/m;  $t = 2.459, 5.7 \text{ df}, P = 0.05$ ) in June 1996. Likewise, the ground remaining covered by  $\geq 1$  cm litter after 1995 fires had been substantially less in

TABLE 2.—Mean ( $\pm$  SE) canopy height of matrix grasses and litter depth on 3 June 1996 in 64 m<sup>2</sup> plots burned in May 1995 (N = 12), August 1995 (N = 12) or left unburned in 1995 (N = 12). Values for each plot are means from eight random sampling points; shown are means and standard errors of those averaged values<sup>1</sup>

Time of 1995 burn	Canopy height (cm)	Litter depth (cm)
May burn	55 $\pm$ 3 <sup>a</sup>	11 $\pm$ 1 <sup>a</sup>
August burn	66 $\pm$ 5 <sup>b</sup>	4 $\pm$ 2 <sup>b</sup>
Not burned	43 $\pm$ 3 <sup>c</sup>	15 $\pm$ 1 <sup>c</sup>

<sup>1</sup> Canopy heights differ (ANOVA,  $F_{2,33} = 10.75$ ,  $P < 0.001$ ), as does litter depth (ANOVA,  $F_{2,33} = 21.64$ ,  $P < 0.001$ ). Means in the same column with different subscripts differ in *a posteriori* Tukey tests at least at the  $P < 0.05$  level

plots with more than one *Z. aurea* ( $36 \pm 14\%$ ) in 1996 than in those with zero or one ( $89 \pm 3\%$ ;  $t = -3.58$ , 5.4 df,  $P < 0.025$ ). In the 1996 census 134 of the 209 *Z. aurea* plants (64%) in the plots burned in August 1995 were in two plots which each had maximal fire intensities of nearly 3000 kW/m, and  $\leq 4\%$  of the ground remaining covered by litter after fire. All individuals that flowered in 1996 after August 1995 burns were in these two plots. Forty-one additional *Z. aurea* (20%) were in another plot in which mean fire intensity had been moderate (422 kW/m) in August 1995, but less than 20% of the ground remained covered by litter after fire.

*Response to mowing season.*—Mowed plots shared an April 1993 burn that those in burn treatments did not, so they are strictly comparable with each other but not with other treatments (*i.e.*, they were not included in the same ANOVA as burn treatments). In 1996, the 12 plots mowed in May 1995 had a total of 77 *Zizia aurea*; in May 1993 (5+ wk after the April 1993 fires) 76 were counted. In 1996, the 12 plots mowed in August 1996 had 121 *Z. aurea*; in May 1993 (after the April 1993 fires), 66 were counted. Spring mowing did not affect population size; August mowing doubled it ( $\chi^2 = 7.14$ , 1 df,  $P < 0.01$ ).

Twenty-four of 121 *Zizia aurea* flowered in plots mowed in August, whereas five of 77 flowered in plots mowed in May. Time of mowing had a significant effect on flowering ( $\chi^2 = 5.14$ , 1 df,  $P < 0.025$ ). As in burn treatments, flowering plants were 0.2–1.0 m high; nonflowering plants were 0.1–0.4 m high.

*Canopy height and litter depth.*—Candidates for suppression of *Zizia aurea* are growing canopies of the dominant grass (> 95%) *Phalaris arundinacea* in the spring, mature canopies in the summer and litter from the previous (or earlier) seasons. Both canopy height and litter depth differed by burn treatment (Table 2). Grass canopies of plots mowed the previous May ( $45 \pm 2$  cm) and August ( $40 \pm 1$  cm) also differed ( $F = 9.16$ , 1,22 df,  $P < 0.01$ ), as did litter depth in the same plots ( $11 \pm 1$  cm and  $7 \pm 1$  cm, respectively;  $F = 24.41$ , 1,22 df,  $P < 0.001$ ). Spearman rank correlations show that *Zizia* numbers decreased as litter depth increased in plots burned in August ( $r_s = -0.81$ ,  $P < 0.005$ ) or May ( $r_s = -0.52$ ,  $P < 0.05$ ). Unburned and mowing treatments lacked sufficient variation of litter depth or *Z. aurea* plants for such correlations.

#### DISCUSSION

Suppression of most species by a few dominants in terrestrial communities has general consequences for habitat occupancy of the majority of species (Preston, 1948, 1962; Magurran, 1988; Howe, 1994a). *Zizia aurea* is a subdominant tallgrass prairie species which,

while conspicuous and widespread, is unlikely to be abundant, dominant, or an important contributor to community structure. Like the 80–95% of species in tallgrass prairie communities that share subdominant status, it responds positively to suppression of dominant species. It differs from most subdominants in this experiment in being common enough to be statistically evaluated, distinctive even as a small ( $< 4 \text{ cm}^2$  canopy) plant, and not clonal.

Reduction of shade by living canopies or accumulated litter allows colonization, establishment from the seed bank, or encourages growth of repressed plants (Knapp and Seastedt, 1986; Huston, 1994; Howe, 1995). Clear differences in both canopy height and litter depth in different burn treatments indicate both effects on growth of dominant species and effects on potential seedling and shoot emergence of subdominant species (Knapp and Seastedt, 1986). The result of suppression of dominants in highly interactive saturated communities (*sensu* Cornell and Lawton, 1992) is creation of less interactive unsaturated communities that admit additional species. As a species which characteristically grows vigorously in early spring and flowers and sets seed in early summer, *Zizia aurea* is not expected to fare well under destructive disturbance by fire or mowing in May, but could benefit from reduction of shade from dominant species that overtop it by midsummer.

*Response to fire season.*—Fire season should affect early- and late-flowering species differently (Neiland and Curtis, 1956; Howe, 1994a; also *see* Hulbert, 1969, 1986, 1988). Anthropogenic fire in autumn or spring removes litter, allowing the soil to warm earlier in the spring than in unburned plots, thereby favoring aggressive  $C_4$  grasses and forbs. Spring fires also destroy shoots and impede root growth and reproduction in early-emerging species, while summer fires suppress late-emerging species by destroying shoots during their period of maximum growth.

Indirect effects are also important (*see* Cornell and Lawton, 1992; McNaughton 1993; Howe, 1994a; Anderson and Briske, 1995). For subdominants like *Zizia aurea*, temporary suppression of any dominants—of whatever phenology—may favor germination or growth of seedlings or repressed plants. Most species respond less to suppression of particular competitors than to any factor that reduces shade. Ultimately, suppression of dominance by grazing, fire, cutting or other factors permits recruitment of less competitive species that would otherwise be excluded by dominants.

Summer fires ignite tallgrass vegetation easily when litter accumulates for more than a season (Bragg, 1982; Steuter, 1987; Biondini *et al.*, 1989; Glenn-Lewin *et al.*, 1990; Howe, 1995), but summer burns are more variable in intensity and effect than dormant-season burns. In this study, spring fires showed a ninefold range in intensity; summer fires a 49-fold range. In this and other experiments at this site (Howe, 1995) the least intense and most intense grass fires occurred in July or August, not in March, April or May. This heterogeneity in intensity of summer fires should ultimately create heterogeneity in effects, favoring higher species richness after summer than after spring burns.

Canopy removal should have different effects on *Zizia aurea* fortunes in May than August. The benefit of clearing canopies and removing litter lasts 3–6 wk after a spring burn, by which time dominant grasses reclaim the canopy. A few *Z. aurea* capable of surviving injury from spring burns then persist in a repressed state in the shade. Comparison of preburn and postburn censuses indicate that the population dropped by half after spring fire, due in part to mortality of plants injured or killed outright by the fires. Slow regrowth of dominant vegetation after August fires gives species capable of rapid recovery far less shade from dominant canopies or litter until the following June, supporting a much healthier and expanding *Z. aurea* population. In this case increased emergence and growth associated with August fires are expected to be augmented by a recruitment from new seeds, since 35 of 37 (95%) of *Z. aurea* that flowered did so after these summer burns. New recruits should

appear after successive burn cycles. Judging from the profusion of forb seedlings and juveniles in June of 1996 in plots burned the previous August, *Zizia aurea* is one of many opportunists that responds to summer fires (see Glenn-Lewin *et al.*, 1990; Howe, 1995).

Fire behavior provided additional insights. Uniform burns of moderate intensity removed almost all litter from plots burned in May, but *Zizia aurea* populations dropped by half. On the other hand, August fires of high intensities ( $> 1000$  kW/m) which removed equivalent litter encouraged *Z. aurea*, and plots with the highest intensities of August fire ( $\geq 3000$  kW/m) harbored the highest densities and greatest proportion of flowering plants. Summer fire intensity sufficient to remove most litter strongly favors *Z. aurea*, whereas spring fire of similar intensity with similar effect on litter does not.

*Response to mowing season.*—Litter removal was not the sole advantage of summer burns to *Zizia aurea*, because plots mowed instead of burned supported sizable populations with canopy removal but with no litter removal. Populations sampled in 1993 remained unchanged after mowing in May 1995, and five of 77 (6%) flowered in 1996. *Zizia aurea* doubled in abundance after August 1995 mowing over counts in 1993, and 24 of 121 (20%) plants flowered. The fact that 83% of the *Z. aurea* flowering in the mowing experiment were in plots mowed in August indicated the advantage of removing summer canopies of dominants even if litter remained intact. I hypothesize that *Z. aurea* did better after mowings than burns in May because most individual plants were small enough to escape damage by mowing at 10 cm, whereas burns killed or damaged most or all shoots.

Damage undoubtedly occurs to shoots of this and similar species of low stature during fires or mowing in August, but such damage is incidental to the annual photosynthetic budget if unburned plants would otherwise be buried under dense 1.5–3.0 m canopies of dominant grasses. A reasonable hypothesis is that resprouts of many species in a defoliated environment add more photosynthate to storage for the next season than spent shoots shaded by much taller vegetation.

*Implications for conservation and restoration.*—If suppression of dominants by growing-season fire or grazing favors subdominants and therefore enhances biodiversity, the common management practices of prescribed burns in autumn or spring and protection from grazing almost certainly accentuate dominance of  $C_4$  grasses substantially taller than  $C_3$  *Phalaris arundinacea*, suppress subdominants and decrease diversity (Howe, 1994a, b, 1995; Huston, 1994; Anderson and Briske, 1995). The issue of fire season is particularly important because natural fires in existing drier grasslands and savannas normally start from ignition of dry grass or trees struck by lightning in July and August (Komarek, 1964, 1968; Vogl, 1974; Bragg, 1982; Higgins, 1984; fossil records of growing-season fire in Baker *et al.*, 1996). Autumn or spring fires maintain grassland diversity at one level by suppressing woody succession (Leach and Givnish, 1996), but at another level they are likely to reduce diversity of subdominants by increasing dominance of large  $C_4$  grasses and clonal late-season forbs (Howe, 1994a, b, 1995). *Zizia aurea* is not a threatened species, but as a sparsely distributed subdominant of small stature it is part of a community of 200–300 subdominant grasses and forbs that may well suffer from anthropogenically enhanced dominance of large  $C_4$  grasses, or benefit from their suppression (Howe, 1994a). The fortunes of such “satellite,” “interstitial,” or subdominant species are important for plant biodiversity, because they comprise 80–95% of it.

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