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Short-term Response of Old-field Plant Communities to Fire and Disturbance

Abstract.—We examined the mechanisms that cause short-term changes in old-field plant communities in the 1st yr following two different disturbances: tilling and burning. In particular, we wanted to determine whether short-term changes in plant community structure following disturbance were more strongly influenced by interspecific differences in growth rates or interspecific differences in germination and establishment ability. Because the density of annual plants varied more across treatments than plant size, we concluded that differences in germination and establishment were important causes of community change in the 1st yr following disturbance. Thus, a more detailed mechanistic understanding of the factors influencing germination and establishment will be necessary to understand community patterns in this old-field system.

Introduction

The causes of the sequential changes in species composition and abundance associated with secondary succession are still poorly understood (*see* Huston and Smith, 1987; Walker and Chapin, 1987; Tilman, 1988). The initial stages of succession might be most strongly influenced by species differences in dispersal rates, germination strategies, and establishment ability or by species differences in growth rates rather than by the outcome of competitive interactions among species if competitive interactions take longer than a single growing season to complete (Tilman, 1988). Thus, the dominant species during the initial stage of succession may either be the species that arrive, germinate and establish in high numbers or those species that achieve a high initial biomass due to high growth rates in early-successional environments. Because there may be trade-offs between establishment ability, maximal growth rate in open habitats and competitive ability, these early successional species may be replaced over time by species that are poorer colonists or that grow more slowly, yet are superior competitors.

At Cedar Creek Natural History Area in Minnesota, fields abandoned from agriculture undergo succession towards an open savannah (Inouye *et al.*, 1987a; Tilman, 1988). In addition, portions of fields at Cedar Creek may occasionally go through succession in response to gopher activity (Tilman, 1983; Inouye *et al.*, 1987b) and fire (Tester, 1989). In this study we examine the effect of two experimental manipulations, burning and tilling, on the 1st-yr community in two fields of different ages, in order to determine whether changes in community composition are due to differences in establishment ability or are caused by differences in growth rates.

Methods

The experiment was conducted in the spring and summer of 1989 at the Cedar Creek Natural History Area in E-central Minnesota in a field that was abandoned from agriculture in 1968 (Field A in Tilman, 1987). A portion of this field has been fenced to keep out above- and belowground mammalian herbivores and half of the fenced area was disked in 1982 (Tilman, 1987). Thus, in 1989, part of the field was disked 21 yr previously and part of the field had been disked 7 yr earlier. In both the 7-yr and 21-yr areas we set up 36 plots, each 2 m by 2 m, in a six by six grid with 1.5 m between each plot. Plots were either (1) roto-tilled, (2) burned, or (3) left unmanipulated as a reference. Each treatment was randomly assigned to 12 replicate plots in each grid. Each plot was roto-tilled twice and ranked to remove biomass twice on 10–12 May 1989. Plots were burned on 10 May 1989.

We estimated percent cover of species in one half of each plot (2 m^2) on 21 August 1989 to the nearest 1%. Species with cover of <1% were assigned a cover of 0.5%. When we sampled percent cover in the 21-yr field we did not distinguish between *Euphorbia glyptosperma* and *E. supina*, so percent cover for *Euphorbia* represents both species combined. In order to estimate plant density of some of the important species, we counted the number of *Ambrosia artemisiifolia* in a 0.5 by 2 m strip in each plot and we counted the number of *Lespedeza capitata, Euphorbia glyptosperma, E. supina* and

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TABLE 1.—Mean percent cover and the number of plots where present (in parentheses, max = 12) in the 7-yr and 21-yr fields for the most common species and litter, bare ground, and mosses and lichens. Values in the same row that share a letter are not significantly different at P = 0.05 (Duncan's Multiple Range test)

	Reference	Burned	Tilled
7-yr field			
Agropyron repens	3.7^{a} (11)	0.8^{b} (12)	0.1^{b} (12)
Lespedeza capitata	2.4^{a} (11)	1.9^{ab} (11)	0.2^{b} (4)
Ambrosia artemisiifolia	1.6^{a} (12)	8.0^{b} (12)	35.6^{c} (12)
Cyperus filiculmis	1.5^{a} (10)	1.3^{a} (10)	0.5^{a} (6)
C. schweinitzii	1.5^{a} (6)	6.8^{a} (9)	4.5^{a} (8)
Cenchrus longispinus	1.1^{a} (7)	0.6^{a} (6)	3.9^{b} (12)
Polygonum convolvulus	0.9^{ab} (9)	0.3^{b} (7)	1.5^{a} (12)
Euphorbia glyptosperma	0.6^{a} (10)	2.4^{b} (12)	0.7^{a} (11)
Bare ground	5.3^{a} (12)	7.8^{a} (12)	49.9^{b} (12)
Litter	30.4^{a} (12)	2.5^{b} (12)	0.5^{b} (12)
Moss and lichens	30.5^{a} (12)	64.7^{b} (12)	0.5^{a} (12)
21-yr field			
Agropyron repens	4.2^{a} (12)	1.8^{b} (12)	0.1^{c} (7)
Ambrosia artemisiifolia	3.2^{a} (12)	6.2^{a} (12)	42.8^{b} (12)
Poa pratensis	2.5^{a} (10)	1.3^{b} (10)	0.0^{c} (0)
Euphorbia sp.	1.4^{ab} (7)	1.8^{a} (11)	0.1^{b} (7)
Polygonum convolvulus	0.2^{a} (5)	0.4^{a} (8)	1.3^{b} (12)
Bare ground	12.1^{a} (12)	17.1^{a} (12)	51.4^{b} (12)
Litter	68.8^{a} (12)	11.9^{b} (12)	0.5^{b} (12)
Mosses and lichens	1.5^{a} (12)	50.9^{b} (12)	0.5^{a} (12)

Polygonum convolvulus in each 4 m^2. To get a non-destructive estimate of plant size, we measured the maximum height of five (if possible) *Ambrosia artemisiifolia* and *Lespedeza capitata* in each plot and the maximum diameter (measured as the maximum total spread) of five (if possible) *Euphorbia glyptosperma* and *E. supina* in each plot on 7 September 1989. We moved through each plot in a specified order and sampled the first five plants that we encountered. We chose to measure the height of *A. artemisiifolia* and *L. capitata* and diameter of the two *Euphorbia* species because of the upright growth form of the former two species and the prostrate growth form of the latter two.

We used Spearman rank correlations to examine the effect of litter cover on the density of *Euphorbia glyptosperma* in the 7-yr and 21-yr fields and *E. supina* in the 21-yr field (*E. supina* was absent in the 7-yr field). In order to examine the overall effect of litter on the density of species in this genus we combined the results of these three correlations to determine an overall significance level following the approach outlined in McGinley *et al.* (1990).

RESULTS AND DISCUSSION

Natural and anthropogenic disturbances can have profound effects on the structure of plant communities (*e.g.*, Platt, 1975; Loucks *et al.*, 1985; Pickett and White, 1985; Pickett *et al.*, 1989). Disturbance is important in determining community structure in old fields (*e.g.*, Tilman, 1983; Armesto and Pickett, 1985; McConnaughay and Bazzaz, 1987; Goldberg and Gross, 1988; Carson and Pickett, 1990). At Cedar Creek, species responded differently to fire and tilling. In the 7-yr field, the two dominant perennials, *Agropyron repens* and *Lespedeza capitata*, were almost completely eliminated from the tilled plots (Table 1). *Ambrosia artemisiifolia* increased significantly in both burned and tilled plots and had its highest cover in the tilled plots (Table 1). *Polygonum convolvulus* had significantly higher cover in the tilled than burned plots (Table 1). *Euphorbia glyptosperma* had significantly higher cover in the burned plots, but its cover did not differ significantly between reference and tilled plots.

TABLE 2A.—The density (no./M^2) of *Ambrosia artemisiifolia, Polygonum convolvulus*, and *Euphorbia glyptosperma* and *E. supina* in reference, burned and tilled plots in the 7- and 21-yr fields. Values in a row that share a letter are not significantly different at P = 0.05 (Duncan's Multiple Range test)

	Reference	Burned	Tilled
7-yr field			
Ambrosia artemisiifolia	5.58^{a}	28.25^{b}	43.33^{c}
Polygonum convolvulus	3.08^{a}	1.73^{a}	11.17^{b}
Euphorbia glyptosperma	1.64^{a}	13.72^{b}	3.29^{a}
E. supina	0.00^{a}	0.00^{a}	0.00^{a}
21-yr field			
Ambrosia artemissifolia	11.17^{a}	25.08^{b}	54.66^{c}
Polygonum convolvulus	0.54^{a}	1.58^{a}	9.50^{b}
Euphorbia glyptosperma	0.42^{a}	7.16^{b}	1.00^{a}
E. supina	2.29^{a}	2.45^{a}	4.47^{a}

In the 21-yr field, the cover of the perennial grasses *Agropyron repens* and *Poa pratensis* declined in both the burned and the tilled plots, while the cover of *A. artemisiifolia* increased dramatically in tilled plots (Table 1). Again, the *Euphorbia* species had their highest cover in the burned plots and *Polygonum convolvulus* had its highest cover in the tilled plots (Table 1).

Were differences in cover of individual species among the three treatments due to differences in growth rates in response to changes in environmental conditions or were they due to differences in establishment ability in the different environments? *Ambrosia artemisiifolia* had a seven-fold increase in density between the reference and tilled plots in the 7-yr field and a five-fold increase in density in the 21-yr field (Table 2a). Although plants were significantly taller in the tilled plots than in the reference plots (1.28 times taller in 7-yr field and 1.24 times taller in the 21-yr field, Table 2b), these differences were slight compared to the differences in density between treatments. In addition, because

TABLE 2B.—Mean plant size (either maximum height or diameter) for plants in reference, burned and tilled plots in the 7- and 21-yr fields. Values in the same row that share a letter are not significantly different at P = 0.05 (Duncan's Multiple Range test)

	Reference	Burned	Tilled
7-yr field			
		Maximum plant height (cm)	
Ambrosia artemissifolia	32.48^{a}	31.05^{a}	41.85^{b}
Lespedeza capitata	50.79^{a}	47.38^{a}	42.80^{a}
		Maximum plant diameter (cm)	
Euphorbia glyptosperma	12.60^{a}	11.12^{a}	10.45^{a}
E. supina	—	—	—
21-yr field			
		Maximum plant height (cm)	
Ambrosia artemisiifolia	36.25^{a}	35.01^{a}	44.88^{b}
Lespedeza capitata	—	—	—
		Maximum plant diameter (cm)	
Euphorbia glyptosperma	13.83^{a}	13.72^{a}	10.30^{a}
E. supina	14.36^{a}	19.66^{b}	12.43^{a}

of the upright growth form in these plants, changes in height may have no influence on the cover of this species. Thus, the increase in cover of *A. artemisiifolia* was due more to changes in density than changes in plant size. The density of *Euphorbia glyptosperma* was eight times greater in burned plots than in reference plots in the 7-yr field and it was 17 times greater in the burned plots than it was in the reference plots in the 21-year field (Table 2a). The maximum diameter of these plants did not differ significantly between treatments (Table 2b). The density of *Polygonum convolvulus* was over three times greater in tilled plots than in reference plots in the 7-yr field and 17 times greater in the 21-yr field (Table 2a). Thus, changes in cover of these species result from differences in establishment ability rather than differences in plant size caused by differences in growth rates.

In contrast, differences in growth rates may be responsible for changes in cover in *Euphorbia supina*, which was no more abundant in the burned plots than in the reference plots of the 21-yr field (Table 2a). However, plants were 1.4 times larger in the burned plots than in the reference plots (Table 2b), suggesting that this species increased in cover in burned plots because individuals grew to a larger size in burned habitats than they could in the other two habitats.

Litter has been observed to influence seedling germination and establishment (reviewed by Facelli and Pickett, 1991). At Cedar Creek, burning decreased the proportion of ground that was covered by litter (Table 1). The density of the annuals *Euphorbia glyptosperma* and *E. supina* in the untilled plots (reference and burned) decreased as the cover of litter, mosses, and lichens in those plots increased (Spearman rank correlations: *E. glyptosperma*, 7-yr field, $r_s = -0.47$, $n = 24$ plots, $P = 0.019$; 21-yr field, $r_s = -0.1$, $n = 24$, $P = 0.65$; and *E. supina*, 21-yr field, $r_s = -0.24$, $n = 24$ plots, $P = 0.26$; combined-$Z = 2.24$, $P < 0.02$). Because *Euphorbia* has a short spreading growth form, it is unable to successfully germinate and establish when it is covered by a layer of litter because it would be difficult for the seedling to break through the litter to reach light. Gross (1984) showed that seedling growth form was important in determining whether plants could establish in dense litter and that small seeded species with spreading growth forms were unable to establish in dense litter. Thus, *Euphorbia* established more successfully in the burned plots because the litter layer was reduced.

Other species of annuals responded to changes in the biotic environment. The cover of the dominant perennials was reduced by both disturbances (Table 1), which may have increased the availability of both above- and belowground resources. The density of *Ambrosia artemisiifolia* and *Polygonum convolvulus* was strongly influenced by the cover of the dominant perennials; the density of these two species decreased as the combined cover of the two most dominant perennial plants (*Agropyron repens* and *Lespedeza capitata* in the 7-yr field and *A. repens* and *Poa pratensis* in the 21-yr field) increased (Spearman rank correlations: *Ambrosia artemisiifolia* 7-yr field, $r_s = -0.81$, $n = 36$ plots, $P < 0.001$ and 21-yr field, $r_s = -0.79$, $n = 36$ plots, $P < 0.001$ and *Polygonum convolvulus* 7-yr field, $r_s = -0.51$, $n = 36$ plots, $P = 0.013$ and 21-yr field, $r_s = -0.66$, $n = 36$ plots, $P < 0.001$). Thus, the density of *A. artemisiifolia* and *P. convolvulus* may have increased in both the burned and tilled plots in response to an increase in resource availability because competition with perennials was reduced by the disturbances.

Perennials may have been unable to establish from seed in the tilled plots because they were outcompeted by seedlings of annuals. When grown from seed alone in pots, *Ambrosia artemisiifolia* achieved greater biomass and height than perennials such as *Agropyron repens* and *Poa pratensis* at all soil nitrogen levels (Tilman, 1986), which may allow them to outcompete seedlings of the perennials. In an old field in Michigan, *Ambrosia artemisiifolia* was competitively dominant to *Agropyron repens* and two other perennials (Miller and Werner, 1987), and the presence of perennials had no effect on the biomass accumulation of *Ambrosia artemisiifolia*. It is possible that competition between perennials such as *Agropyron repens* and annuals such as *Ambrosia artemisiifolia* is asymmetric; the annual may be the superior competitor when competing against seedlings of perennials and the inferior competitor when competing against adult plants.

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LITERATURE CITED

ARMESTO, J. J. AND S. T. A. PICKETT. 1985. Experiments on disturbance in old-field plant communities: impact on species richness and abundance. *Ecology*, 66:230–240.

CARSON, W. P. AND S. T. A. PICKETT. 1990. Role of resources and disturbance in the organization of an old-field plant community. *Ecology*, 69:984–994.

FACELLI, J. M. AND S. T. A. PICKETT. 1991. Plant litter: its dynamics and effects on plant community structure. *Bot. Rev.*, 57:1–32.

GOLDBERG, D. E. AND K. L. GROSS. 1988. Disturbance regimes of midsuccessional old-fields. *Ecology*, 68:1211–1223.

GROSS, K. G. 1984. 'Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *J. Ecol.*, 72:369–387.

HUSTON, M. AND T. SMITH. 1987. Plant succession: life history and competition. *Am. Nat.*, 130: 168–198.

INOUYE, R. S., M. A. STILWELL AND K. C. ZINNELL. 1987a. Old field succession on a Minnesota sand plain. *Ecology*, 68:12–26.

———, N. J. HUNTLY, D. TILMAN AND J. R. TESTER. 1987b. Pocket gophers, vegetation, and soil nitrogen along a successional sere in east central Minnesota. *Oecologia*, 72:178–184.

LOUCKS, O. L., M. L. PLUMB-MENTJES AND D. ROGERS. 1985. Gap processes and large-scale disturbances in sand prairies, p. 71–83. *In:* S.T.A. Pickett and P. S. White (eds.). The ecology of natural disturbance and patch dynamics. Academic Press, Orlando.

MCCONNAUGHAY, K. D. M. AND F. A. BAZZAZ. 1987. The relationship between gap size and performance of several colonizing annuals. *Ecology*, 68:411–416.

MCGINLEY, M. A., C. C. SMITH, P. F. ELLIOTT AND J. J. HIGGINS. 1990. Morphological constraints on seed mass in lodgepole pine. *Funct. Ecol.*, 4:183–192.

MILLER, T. E. AND P. A. WERNER. 1987. Competitive effects and responses between plant species in a first-year old-field community. *Ecology*, 68:1201–1210.

PICKETT, S. T. A. AND P. S. WHITE. Patch dynamics: a synthesis, p. 371–384. *In:* S. T. A. Pickett and P. S. White (eds.). The ecology of natural disturbance and patch dynamics. Academic Press, Orlando.

———, J. KOLASA, J. J. ARMESTO AND S. L. COLLINS. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos*, 54:129–136.

PLATT, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. *Ecol. Mon.*, 45:285–305.

TESTER, J. R. 1989. Effects of fire frequency on oak savannah in east-central Minnesota. *Bull. Torrey Bot. Club.*, 116:134–144.

TILMAN, D. 1983. Plant succession and gopher disturbance along an experimental gradient. *Oecologia*, 60:285–292.

———. 1986. Nitrogen-limited growth in plants from different successional stages. *Ecology*, 67: 555–563.

———. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecol. Monogr.*, 57:189–214.

———. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, N.J. 360 p.

WALKER, L. R. AND F. S. CHAPIN III. 1987. Interactions among processes controlling successional change. *Oikos*, 50:131–135.

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