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ROLE OF RESOURCES AND DISTURBANCE IN THE ORGANIZATION OF AN OLD-FIELD PLANT COMMUNITY[1]

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Abstract. The roles of disturbance and resource availability in influencing species richness and plant abundance were examined by conducting a factorial experiment for 2 yr in an old field in New Jersey, USA, dominated by goldenrods (*Solidago* spp.). Replicate plots were treated by (1) adding macronutrients, (2) adding water, (3) tying back tall herbs to increase light to ground layer species, and (4) creating gaps in the vegetation by disturbing the soil with a hand trowel early in the growing season.

Nutrient additions increased the cover of the herbaceous canopy and enhanced the dominance of *Solidago* spp. Water additions also increased canopy cover during the second growing season, a year with low seasonal rainfall. Light enrichment as a consequence of canopy manipulations resulted in the competitive release of subcanopy species, primarily *Fragaria virginiana*. Other subcanopy dominants were limited by different resources; *Hieracium pratense* responded most strongly to water and *Rumex acetosella* to nutrients. These differences in limiting resources may be responsible for the continued coexistence of these three subcanopy species. Additionally, we observed marked seasonal and yearly fluctuations in the severity of resource limitation which might serve to favor different species in this community at different times.

Species richness was decreased by light enrichment alone, whereas light with irrigation interacted to increase species richness. Nutrient additions had little direct effect on species richness. A single small disturbance at the beginning of the growing season had little impact on species richness or abundance. Relative to the influence of resources, small-scale disturbance plays only a minor role in this community. Our results suggest that nonequilibrium organization of old-field communities can occur via a shifting resource base in the absence of natural disturbances.

Key words: competition; disturbance; drought; gap; light; nutrients; old field; Solidago canadensis; *species richness; subcanopy; succession; water.*

INTRODUCTION

Both resources and disturbance influence plant community composition and structure (e.g., Connell 1978, Tilman 1982, Pickett and White 1985). Resources vary widely in space, creating a mosaic that may favor different plant species in different places (Tilman 1982, Gibson 1986). Plant distributions have been correlated with several resources, especially nutrients (e.g., Snaydon 1962, Tilman 1987, Gibson 1988*a*), although few studies have elucidated cause and effect (Gibson 1988*a*). Disturbance creates gaps in plant communities, providing space for establishment (Platt 1975, Armesto and Pickett 1985, McConnaughay and Bazzaz 1987). Because disturbance is assumed to release resources (Rabinowitz and Rapp 1985), disturbance may be tightly coupled with resource variability. Together, disturbance and resource patchiness may promote plant coexistence and spatial heterogeneity in plant communities.

Both resources and disturbance may play an important role in old-field communities. Nutrients, especially nitrogen, can alter both the dominance of plants and species composition (e.g., Mellinger and McNaughton 1975, Bakelaar and Odum 1978, Tilman 1984, 1987, Carson and Barrett 1988). Few field studies, however, have investigated experimentally the role of other resources (e.g., light and water), perhaps because nitrogen is generally considered the most limiting resource in terrestrial plant communities (Tilman 1984, Chapin and Shaver 1985). In experimental studies in grassland (Gibson 1988*b*) and tundra (Chapin and Shaver 1985), however, resources besides nutrients limited plant growth and altered plant distribution. We define a limiting resource as one that when added, results in an increase in plant cover or biomass (Tilman 1982).

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Disturbance can be an important factor in plant coexistence. Several studies in old-field communities found that small disturbances release resources that favor subordinate species (Armesto and Pickett 1985, 1986, Goldberg 1987, McConnaughay and Bazzaz 1987). But recently Goldberg and Gross (1988) have challenged the importance of fine-scale disturbance in old-field communities. They found that peripheral vegetation rapidly encroached upon gaps created by natural disturbances. Thus, gaps did not provide a sanctuary for suppressed or later successional plants.

We examined the role of resources and small-scale disturbance in old-field plant community organization. We asked two questions: (1) do resources, disturbance, or their interaction account for plant abundance and distribution in an old-field community; and (2) are different species limited by different resources or combinations of resources?

MATERIAL AND METHODS

Study site and experimental design

We conducted this study at the William L. Hutcheson Memorial Forest (HMF) located 14 km west of New Brunswick, New Jersey, USA. The climate is subcontinental with a mean annual rainfall of 115 cm distributed evenly through the year (Robichaud and Buell 1973). The soil is derived from the Brunswick red shale formation and is a well-drained loam (Ugolini 1964). The study site was an 8-yr-old *Solidago*-dominated old field. The herbaceous canopy was dominated by *Solidago canadensis* and *Aster pilosus*. Four other common *Solidago* species, in decreasing order of abundance, were *S. graminifolia*, *S. juncea*, *S. rugosa*, and *S. nemoralis*. The subcanopy was dominated by *Fragaria virginiana*, *Hieracium pratense*, and *Rumex acetosella* (nomenclature follows Gleason and Cronquist 1963). All of these species are clonal perennials.

We laid out 160 1.0 × 0.5 m experimental plots within this old field. We incorporated four treatments: increased nutrients (Nu), increased water (W), increased light (L), and a soil disturbance (D), into a random block, factorial design with all resource treatment plots placed at least 2.5 m apart. This resulted in 16 treatment combinations (NuW, WL, NuWL, etc.) each replicated 10 times and randomly allocated to 1 of 10 blocks. Each main addition treatment (i.e., Nu, W, L, D) was thus replicated 80 times. Percent cover of each species was estimated with the aid of a sampling frame that was subdivided into eight sections, each equal to 12.5% cover (Armesto and Pickett 1985). Percent cover values could exceed 100% whenever plots contained multiple vegetation layers (Armesto and Pickett 1985). Percent cover was recorded in early June, mid-July, and mid-September of 1985 and 1986. Nutrient and water additions began prior to the first plant sample in 1985, whereas the light enrichment began immediately after the first plant sample in 1985. This was necessary because soil resources had to be applied in early spring when limitation was likely. Because light treatments required manipulating the canopy plants above a certain height (see section below), this treatment could not begin until mid-June.

Resource and disturbance manipulations

In our increased nutrient treatment, we applied fertilizer (Agway Turfood Special Fertilizer NPK, 10-6-4) in equal amounts on 18 May, 9 July, and 30 August 1985 and 25 April, 13 June, and 18 August 1986, for an annual total of 270 kg/ha nitrogen, 126 kg/ha phosphorus, and 84 kg/ha potassium. This application rate is moderate relative to previous enrichment studies (e.g., Mellinger and McNaughton 1975, Bakelaar and Odum 1978, Pratt 1984). Dates varied to avoid applications during dry periods, thus preventing toxic effects to the plants. Approximately 80% of the nitrogen was applied in soluble form as ammonium and nitrate nitrogen. The remaining 20% of the nitrogen was applied in slow release form to allow for an increased nitrogen supply throughout the study.

In our increased water treatment, we applied ≈22 mm of water per plot at ≈4-d intervals or 4 d following a rainfall (>15 mm precipitation). The intent was to ameliorate water stress, not to apply some arbitrary total amount. Water was applied via a hose with a fine sprinkler attachment to avoid physically damaging plants. We applied a total of 374 mm of water in 1985 (a year with high seasonal rainfall) and 440 mm of water in 1986 (a drought year). The irrigation treatments began in early April and extended through mid-September in both years.

To increase light to the subcanopy, we attached nylon twine to corner stakes of each plot and pulled tall plants (>20 cm) beyond each plot perimeter, without disturbing plant roots (Gibson 1988*b*). This treament did not injure manipulated plants. Light treatments began on 15 June 1985, after the first vegetation sample in early June, and continued throughout the study.

We disturbed the vegetation and soil once, at the outset of the study, on 1 May 1985. A hand trowel was used to overturn and expose soil throughout ≈70% of each plot to a depth of 10 cm, thereby opening up space for plant establishment. We made every attempt to keep our disturbance as uniform as possible among replicate plots. At the time of the disturbance, shoots of *Solidago canadensis* were ≈10 cm high. Our disturbance disrupted the early growth of the dominant species by severing shoots, roots, and rhizomes and thus creating a gap in the vegetation. A few individuals of *S. canadensis* remained undisturbed in each plot. These gaps were large relative to those commonly found in old-field communities (W. Carson, *personal observation*, Goldberg and Gross 1988).

Monitoring environmental change

We measured photosynthetically active radiation both above and below the canopy using a PAR sensor

(Lambda Instruments) on clear days between 1200 and 1300 on 14 September 1985 and 4 August 1986. Mean values (percent of ambient light reaching the subcanopy) were determined by randomly placing the sensor at 10 spots, 10 cm above the soil surface in each plot. Five alternating blocks of the 10 blocks were randomly sampled in 1985; however, all blocks were sampled in 1986.

We calculated soil moisture (gravimetrically) for the top 10 cm of the soil on 4 August 1985 and 4 June 1986. Samples were taken earlier in 1986 to coincide with a drought. Five alternating blocks were randomly chosen for collecting soil moisture samples, 48 h after an irrigation treatment. Each sample was dried for 24 h at 105°C. Rainfall was recorded daily ≈200 m from our study site.

Soil fertility, including nitrate nitrogen, ammonium nitrogen, phosphorus, potassium, calcium, magnesium, and pH, was analyzed for each plot in late September 1986 by the Rutgers University Soil Testing Laboratory. Concentrations of calcium, magnesium, phosphorus, and potassium were determined using the techniques developed for the acid, low organic matter, low cation exchange capacity soils found locally, including those at HMF (Nelson et al. 1953). Inorganic nitrogen (nitrate and ammonium) was determined colorimetrically following extraction of the soil with 0.5 mol/L NaCl at a 5:1 solution : soil volumetric ratio for 30 min with continuous shaking.

Statistical analyses

We used a factorial analysis of variance for a random block design to determine significant main effects (nutrients, water, light, and disturbance) and to identify significant interactions (Sokal and Rohlf 1981). Percent cover values for individual species, soil moisture, and light were angularly transformed before analysis. Angular transformations could not be used in tests involving canopy and subcanopy cover values because some replicate plots exceeded 100% cover. For these plots, for species richness and soil nutrients, log transformations did not change the interpretation of the data and thus raw data were used in the final analysis. All comparisons were made between treatments within a sampling date. Disturbance did not significantly affect any response variable in 1986; thus, we included disturbance replicates with the other treatment combinations for analysis of 1986 data. Therefore, each resource manipulation had 20 replicates in 1986.

RESULTS

Environmental factors

Tying back the canopy resulted in 75 and 92% of ambient light reaching the subcanopy in 1985 and 1986, respectively. In the unmanipulated plots, only 23 and 24% of ambient light reached the subcanopy in 1985 and 1986, respectively ($n = 40$, $P < .001$ for both 1985 and 1986 for treatment within years). No other treatment or treatment combination had a significant effect on light penetration reaching the subcanopy in 1985. By 1986, however, both the nutrient and water addition plots had significantly less light reaching the subcanopy than those without these additions (Nu = 34% light penetration, no Nu = 14%, $P < .001$; W = 28%, no W = 19.5%, $P < .01$). Because there were no significant interactions, it can be concluded that these resources were independent in their effect on light penetration to the subcanopy. Light reaching the subcanopy in the NuW plots was only 8% of ambient. Because disturbance did not significantly affect light penetration or any other environmental variable measured, values are not presented. Disturbance, however, may have altered environmental variables earlier in the season, before we completed our measurements.

Rainfall for the growing season (April–October) of 1985 was 11.9% higher (30.7 cm) than the mean of 27.5 cm (NOAA 1982). We compared values obtained at the study site to mean values from the nearby New Brunswick climate station for the period 1951–1980. Rainfall for the period June–August was 34.4% higher than the mean for this period (16.8 cm) even though July rainfall was 2.5 cm (23%) below the monthly mean. In 1986 (a drought year), however, rainfall for the growing season was 14.3% below normal and for June to August was 18.4% below normal (NOAA 1982).

Irrigated plots had significantly higher percent soil moisture in both years compared to nonirrigated plots (W = 18.7%, no W = 15.1% in 1985, $P < .001$; W = 12.1%, no W = 6.0% in 1986, $P < .001$). Both light and nutrient additions resulted in significantly decreased soil moisture in 1985 (Nu = 16.0%, no Nu = 17.8%, $P < .001$; L = 16.3%, no L = 17.5%, $P < .001$) but these treatments had no effect on soil moisture in 1986, the drought year (Nu = 9.0%, no Nu = 9.2%, $P > .05$; L = 9.0%, no L = 9.2%, $P > .05$). There were no significant interactions in either year.

Nutrient plots had significantly higher levels of ammonium nitrogen, P, and K, but significantly lower levels of Mg and Ca, than nonnutrient treatments by the end of the study (Table 1). Nutrient levels in treated plots were within the range found naturally on these soils (H. Motto, Rutgers University Soil Testing Laboratory, *personal communication*). Nutrient plots also tended to have lower pH. Irrigation affected fertility, but much less dramatically than nutrient additions. Irrigated plots had significantly lower ammonium nitrogen and potassium levels but significantly higher Mg and Ca levels. Irrigated plots had a slightly higher pH. Only potassium levels were altered in light treatments.

Community responses to manipulations

We divided this community into a canopy and a subcanopy because of the different growth forms (rosette vs. tall species) which dominated the two layers.

TABLE 1. Soil nutrient concentrations and pH values ($\bar{X}$ ± SD) in late September 1986. (Means with different letters are significantly different at $P < .01$.)

	Nutrient (Nu) treatments		Water (W) treatments		Light (L) treatments	
	Nu	No Nu	W	No W	L	No L
pH	4.59 ± 0.15	5.15 ± 0.14	5.03 ± 0.16	4.85 ± 0.12	4.92 ± 0.15	4.98 ± 0.13
			Nutrient concentration (kg/ha)			
NO_3-N	12.2^a	11.9^a	12.7^a	11.7^a	11.9^a	12.2^a
NH_4^+-N	14.8^a	9.1^b	10.5^a	13.3^b	12.8^a	11.1^a
P	86.1^a	28.7^b	56.1^a	58.6^a	59.1^a	55.6^a
K	213.3^a	165.1^b	174.5^a	204.0^b	172.0^a	206.5^b
Mg	121.0^a	161.6^b	153.5^a	129.1^b	137.9^a	144.7^a
Ca	1097.1^a	1235.0^b	1236.4^a	1095.7^b	1150.8^a	1181.2^a

This also allowed us to assess the effects of the light treatment.

The canopy.—The canopy layer responded rapidly to increased nutrients (Fig. 1A). We applied nutrients in mid-May and thereafter these plots had significantly greater canopy cover than the nonnutrient plots. Water was apparently not limiting to the canopy layer in 1985; however, water and nutrients limited plant cover in 1986 (Fig. 1A, B). There were no significant interactions among treatments in either year, thus, when more than one resource significantly increased plant cover, the effects of the resources together were approximately additive (e.g., Fig. 1C, June and July). Disturbance significantly decreased canopy cover throughout 1985 but differences were not significant in 1986 (Fig. 1D).

The subcanopy.—The subcanopy was limited by nutrients until July 1986 when water became the most limiting resource (Fig. 2A, B). Water limited the subcanopy more than the canopy. Specifically, there was a mid- and late-season limitation in 1985 and 1986, respectively, in the subcanopy (July 1985; September 1986; Fig. 2B) that did not occur in the canopy (Fig. 1B). The subcanopy responded rapidly to increased light with plant cover peaking in September in both

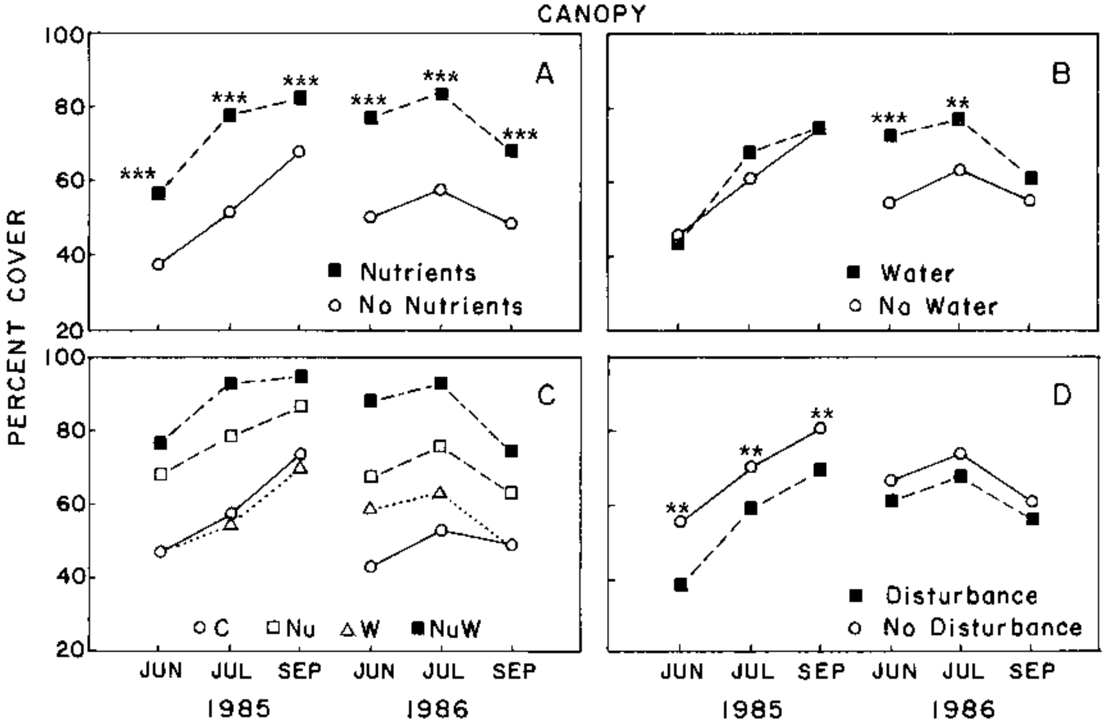

FIG. 1. The response of the canopy layer to (A) increased nutrients, (B) increased water, (C) increased water and nutrients, and (D) disturbance. Nu = nutrients, W = water, NuW = nutrients + water, and C = no nutrients or water. Significant differences between treatments and within a date are indicated by asterisks (** $P < .01$, *** $P < .001$).

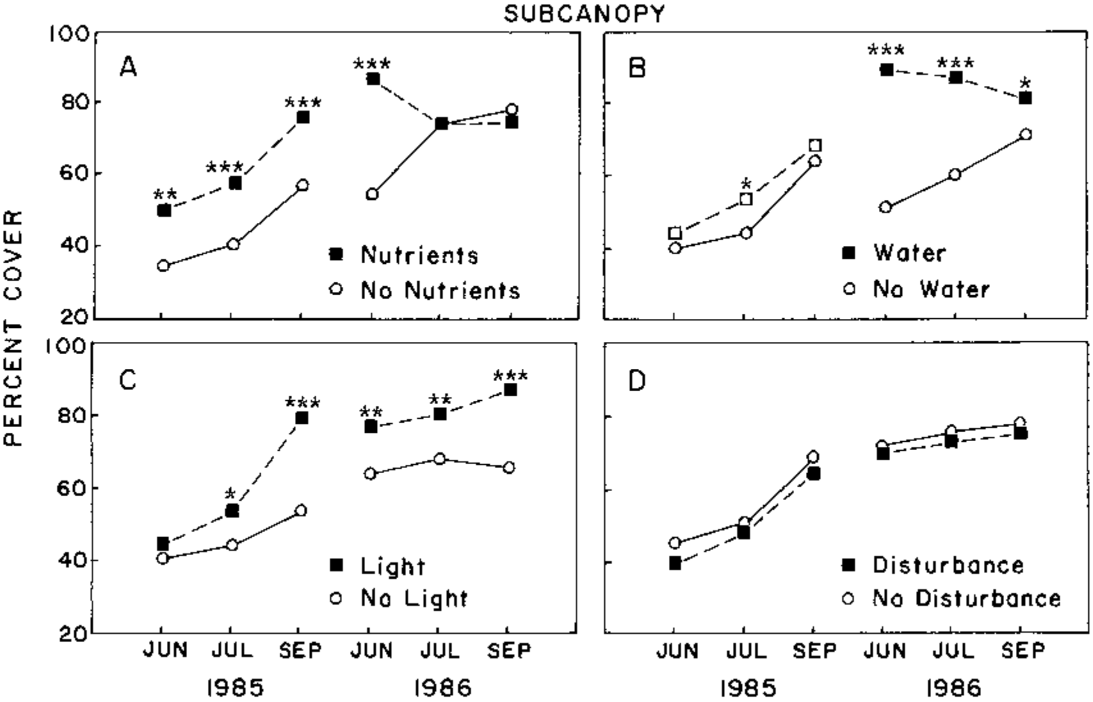

FIG. 2. The response of the subcanopy layer to (A) increased nutrients, (B) increased water, (C) increased light, and (D) disturbance. Significant differences between treatments and within a date are indicated by asterisks (* $P < .05$, ** $P < .01$, *** $P < .001$).

1985 and 1986 (Fig. 2C). Disturbance had little effect on the subcanopy (Fig. 2D); however, this response depended upon the presence or absence of nutrients (Fig. 3). Disturbance alone slightly depressed subcanopy cover but disturbance and nutrients together interacted significantly to increase cover in 1985. This was the only significant interaction among the resource and disturbance manipulations for the subcanopy.

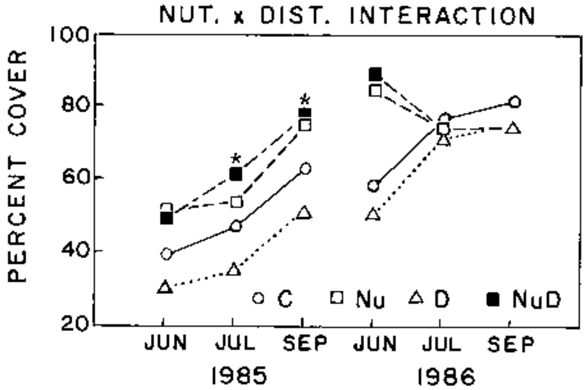

FIG. 3. The effect of the interaction of nutrients and disturbance on the cover of the subcanopy. Nu = nutrients, D = disturbance, NuD = nutrients + disturbance, and C = no nutrients or disturbance. Significant interactions for a given date are indicated by an asterisk (* $P < .05$).

The primary resource or resource combinations that limited subcanopy cover changed seasonally (Fig. 4) and reflected the additive nature (since there were no significant interactions) of the effect of the individual resources on plant cover. Light became the primary limiting resource in September 1985 and September 1986 (Figs. 2C and 4). In contrast, nutrients and water were the primary limiting resources in June 1986 (Figs. 2A, B, and 4). When nutrients and water were plentiful, light became more limiting (i.e., the NuWL treatment > NuW treatment in June 1986). Water became the primary limiting resource in July 1986 (Figs. 2B and 4). Nutrients alone were apparently not limiting in July or September (Figs. 2A and 4).

Although the subcanopy community was altered by each resource, annuals, biennials, and woody vines were only affected by nutrients. Nutrients increased the cover of woody vines (fourfold in July 1986 [Fig. 5]). Annuals and biennials were grouped for analysis since they were not abundant and were patchily distributed. Nutrients often doubled the cover of this group during the study although actual differences were quite small (Fig. 5). No other treatment had any significant effect on these or any other growth forms.

Species richness

Nutrient plots had higher species richness in the beginning of the study, but these differences were small and did not persist (Fig. 6A). There was a significant

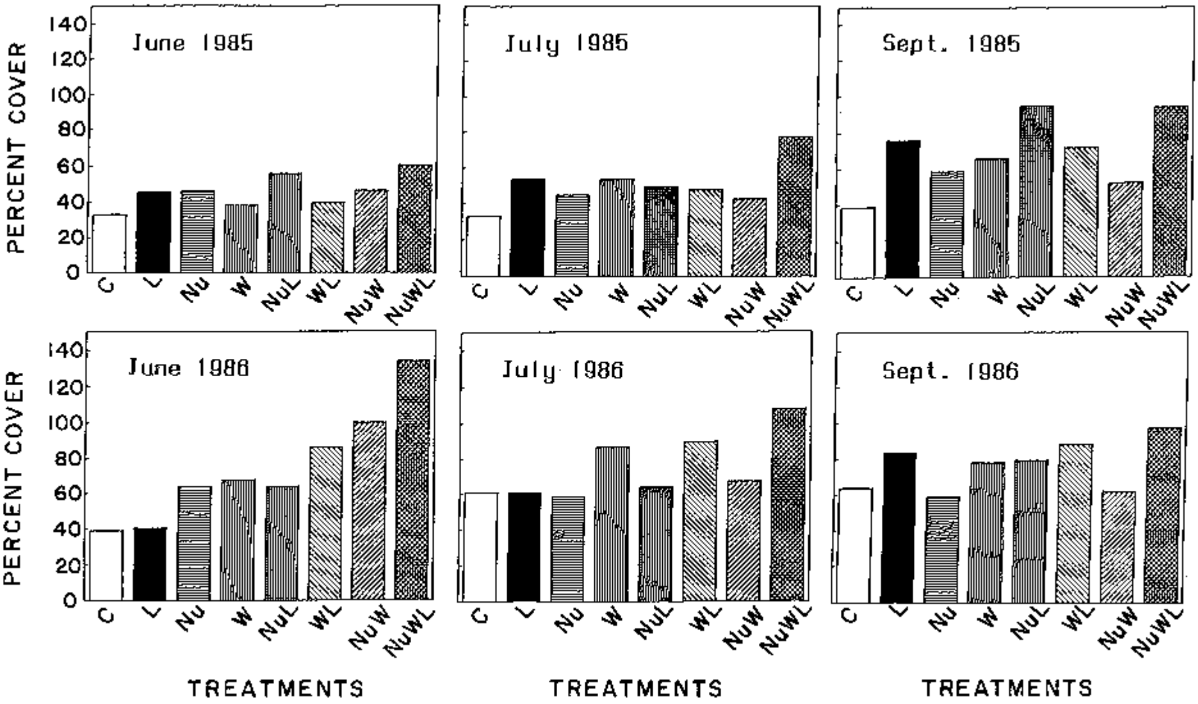

FIG. 4. The response of the subcanopy layer to the eight different resource treatments in 1985 and 1986.

light × water interaction that influenced species richness in both years (Fig. 6B). Increased light in the presence of water increased species richness but increased light alone decreased species richness. Disturbance had no effect on species richness (Fig. 6C).

Species responses to manipulations

There were no significant interactions among resources regarding individual taxa. *Solidago canadensis*, the dominant canopy species, was limited by nutrients throughout the study (Fig. 7A). Water limited the cover of *S. canadensis* only during 1986 and the greatest cover of *S. canadensis* occurred in the NuW treatment where the effects of nutrients and water were additive (Fig. 7B, C). Disturbance significantly decreased the cover of *S. canadensis* in June 1985, but had no effect thereafter (Fig. 7D). Cover by other *Solidago* spp. was spatially highly variable, so we combined *S. graminifolia, S. juncea, S. nemoralis* and *S. rugosa* for analysis (Fig. 8A–C). Nutrients limited this group, whereas no other treatment had a significant effect. *Aster pilosus*, the second most abundant canopy species after *S. canadensis*, was apparently not limited by either nutrients or water (Fig. 9A, B), or by a combination of these resources. Disturbance, however, significantly reduced the cover of *A. pilosus* throughout the 1st yr (Fig. 9C). The percent cover of *A. pilosus* was much lower in 1986 than 1985. Declines of this magnitude and timing have been observed previously in the absence of resource manipulation (Pickett 1982).

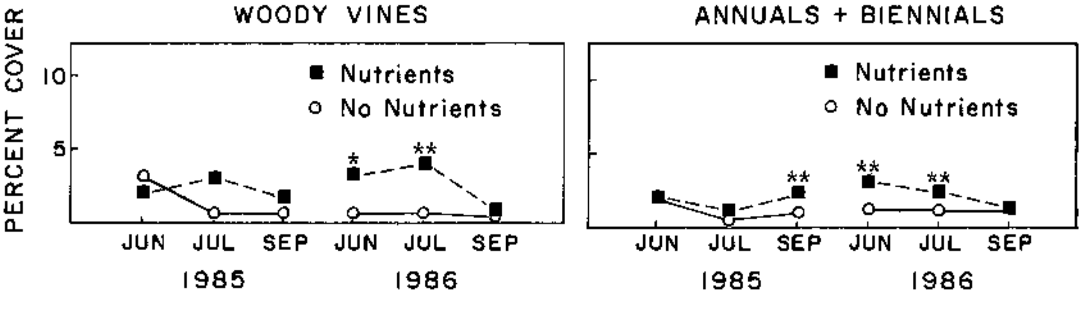

FIG. 5. The effect of nutrients on woody vines and annuals and biennials. Significant differences between treatments and within a date are indicated by asterisks (* $P < .05$, ** $P < .01$).

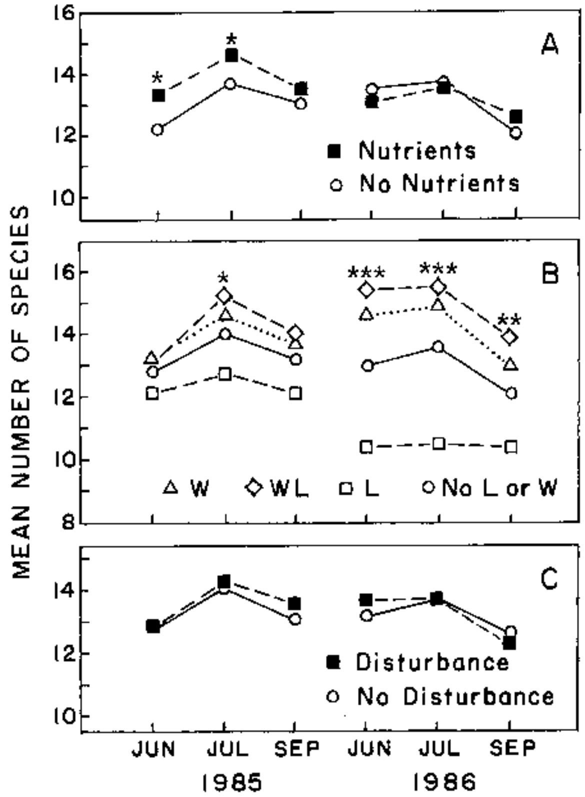

FIG. 6. The effects of (A) increased nutrients, (B) increased water and light, and (C) disturbance on species richness (mean number of species per 1.0 × 0.5 m plot). For (A) and (C) significant differences between treatments and within a date are indicated by asterisks. For (B), significant interactions for a given date are indicated by asterisks (* $P < .05$, ** $P < .01$, *** $P < .001$).

In the subcanopy, disturbance did not significantly alter the abundance of any dominant species (Figs. 10D, 11D, and 12D). Nutrients significantly limited the cover of *Rumex acetosella* (Fig. 10A). Light increased cover of *R. acetosella* only slightly in July and September of 1985 and water had no effect, even during 1986 (Fig. 10B, C). Water, however, was the primary limiting resource for *Hieracium pratense* (Fig. 11B). *H. pratense* recovered quickly upon the resumption of higher rainfall in late August and returned to control levels by September (Fig. 11B). Nutrients significantly increased the cover of *H. pratense* only in June 1986 (Fig. 11A); otherwise, nutrients either had no impact on cover (1985) or indirectly contributed to a decrease in cover (July and September 1986, Fig. 11A). Increased light had little effect on *H. pratense* (Fig. 11C). Light and water limited the cover of *Fragaria virginiana,* although light was more often limiting (Fig. 12B, C); nutrients significantly increased cover only on the first sample date (Fig. 12A).

DISCUSSION

The role of resources in the canopy

The dominant canopy species were limited primarily by nutrients (see also Mellinger and McNaughton 1975, Bakelaar and Odum 1978, Pratt 1984) and secondarily by water (*Solidago canadensis*) in the drought year. There have been few irrigation studies in mesic habitats and this study demonstrates the importance of water as a limiting factor. Although light manipulations primarily affected the subcanopy species, we did find that the basal rosettes of the canopy species *S. juncea* had significantly greater cover in the light treatments but only in September 1985 (light = 5.2% cover, no light = 0.5% cover, $P < .01$). Similarly, the rosettes of the canopy species *Aster pilosus* were limited by light in September 1986 (light = 13.3% cover, no light = 9.8% cover; $P < .05$). *Solidago juncea* as well as *S. nemoralis* and *A. pilosus* form basal rosettes, unlike the other *Solidago* spp. Thus, preemption of light by canopy species may limit these species (see also Armesto and Pickett 1985).

The role of resources in the subcanopy

Mechanisms producing the plant spatial patchiness consistently observed in old fields (e.g., Allen and Forman 1976, Hils and Vankat 1982) have rarely been demonstrated. Because different resources limited the three dominant subcanopy species, resource heterogeneity provides a possible explanation for both the patchy distribution of these species and their coexistence. *Rumex acetosella* did well in nutrient treatments even though a dense canopy decreased light in these plots. *Fragaria virginiana,* however, was reduced in such sites through preemption of light by the canopy. Thus, it may be restricted to relatively nutrient-poor sites where light is more abundant. *Hieracium pratense* is restricted to patches of greater relative soil moisture. This finding is consistent with the spatial distribution of this species in pastures (Thomas and Dale 1976). *H. pratense* did poorly in the nutrient treatment, perhaps due to the lower soil moisture in these sites or more likely the rapid spread of competing species (Hay and Ouellette 1959, Reader and Watt 1981). Thus, microhabitat segregation in this community may be partially based on the fact that different species are limited by different resources. Similarly, Tilman (1987) concluded that spatially variable nitrogen supply rates accounted for plant patchiness in old fields in Minnesota. Also, Chapin and Shaver (1985) found that different resources limited different species in a tundra community, partially explaining plant distribution patterns. In contrast, Miller and Werner (1987) found no evidence for microhabitat segregation in a 1st-yr old field in Michigan. First-year old fields often have high dominance by a single species (e.g., *Ambrosia* spp.; Abul-Fatih and Bazzaz 1979, Pickett 1982, Miller and Werner 1987) in conditions with little microhabitat

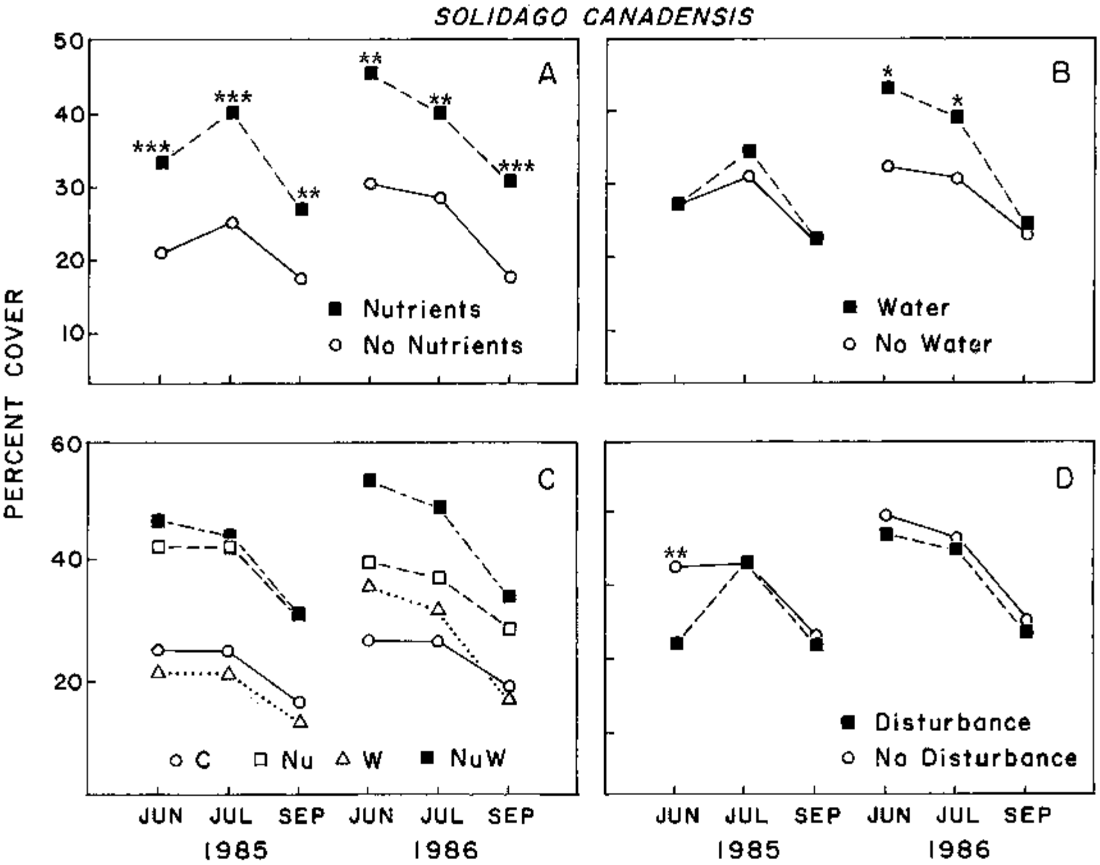

FIG. 7. The effects of (A) increased nutrients, (B) increased water, (C) increased nutrients + water, and (D) disturbance on the cover of *Solidago canadensis.* Nu = nutrients, W = water, NuW = nutrients + water, C = no nutrients or water. Significant differences between treatments and within a date are indicated by asterisks (* $P < .05$, ** $P < .01$, *** $P < .001$).

differentiation. Thus, species interactions may change through succession: initially a few successful species compete for the same resources (Miller and Werner 1987), while later many species partition different resource patches or parts of gradients (Bazzaz 1975, Austin and Austin 1980, Chapin and Shaver 1985, Tilman 1987).

Subcanopy species interacted more strongly with canopy species than with each other. For example, the canopy reduced light and soil moisture which altered the abundance of the subcanopy species (see also Armesto and Pickett 1985). Furthermore, at the same site, Allen and Forman (1976) found that removal of either subcanopy dominant (*F. virginiana* or *H. pratense*) had no reciprocal effect nor an effect on any canopy species. When Allen and Forman (1976) removed *A. pilosus,* however, the canopy dominant, both *F. virginiana* and *H. pratense* increased significantly in abundance. Thus, our data and theirs revealed that competition was primarily asymmetrical where canopy species reduced the abundance of subcanopy species.

We documented major seasonal and yearly variation in resource limitation. Yearly rainfall fluctuations are common in this area. Deviations from the mean >30% for 3- and 6-mo periods have occurred >50 times since 1900 (R. Harnack, Department of Meteorology, Rutgers University, *personal communication*). Consequently, a suitable patch for a species early in the season or in a wet year may be less suitable later in the same season or in a dry year. Thus, no species can obtain a clear long-term advantage. This may provide a further mechanism for maintaining plant coexistence and spatial heterogeneity. For example, van der Maarel (1981) found that yearly fluctuations in rainfall alternately favored different species in a grassland. Chapin and Shaver (1985) suggested that relative abundances of tundra species varied due to yearly changes in environmental conditions. This suggests a nonequilibrium mechanism for plant coexistence which does not rely upon periodic disturbance as previously argued (Pickett 1980). This nonequilibrium coexistence conflicts with Tilman's equilibrium model of community organization even though resource competition remains important (Tilman 1982, 1985). Tilman's model re-

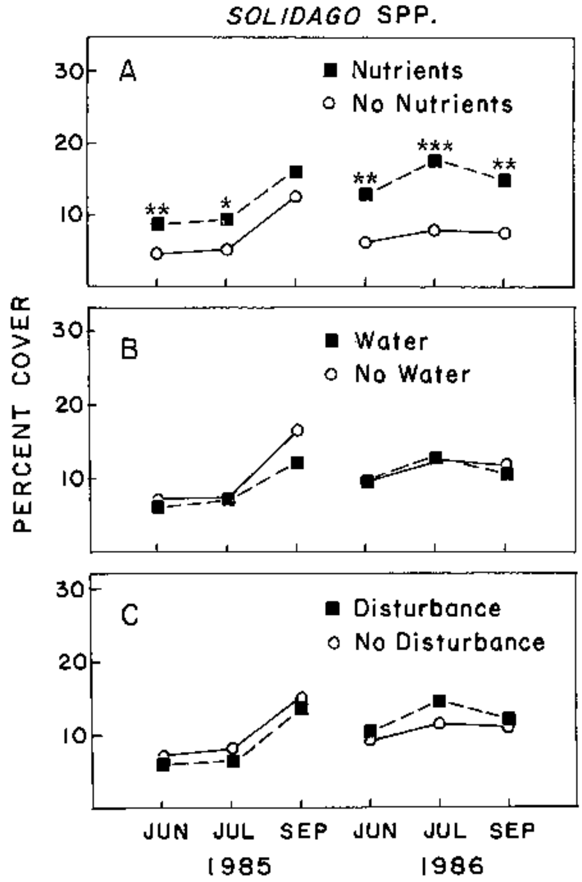

FIG. 8. The effect of (A) increased nutrients, (B) increased water, and (C) disturbance on the cover of *Solidago* spp. Species included are *S. graminifolia, S. juncea, S. nemoralis*, and *S. rugosa*. Significant differences between treatments and within a date are indicated by asterisks (* $P < .05$, ** $P < .01$, *** $P < .001$).

quires that patches in the community reach a competitive equilibrium based on the assumption that the "rate of change in resource availabilities is slow relative to the rate of competitive displacement" (Tilman 1985). We documented rapid seasonal and yearly changes in resource availability and limitation, making such an equilibrium unlikely. Rapid variation in resource availability would most likely violate another assumption of this model, specifically that "resource consumption equal resource supply" (Tilman 1985) since resource supply would be changing rapidly.

Resources and coexistence of life-forms

Species richness during this 2-yr study was influenced primarily by the interaction of water and light. Previous studies have shown that nutrient enrichment usually causes decreases in species richness (e.g., Bakelaar and Odum 1978, Silvertown 1980, Carson and Barrett 1988) probably by increasing the rate of thinning (e.g., Harper 1977) thus speeding competitive exclusion (e.g., Tilman 1982). In this study, however, nutrients had no direct effect. Under high nutrient conditions, light has generally been proposed as the limiting factor that causes decreases in species richness (e.g., Carson and Barrett 1988). One would predict, that at low levels of nutrients, light would be less limiting and species richness would be higher. We found, however, that under high light conditions, low soil moisture caused declines in species richness, but when moisture was adequate, shading caused declines in species richness (Fig. 7). Nutrients may enhance this effect by increasing plant biomass and thereby increasing water uptake and decreasing light penetration to the subcanopy. Thus, nutrients most likely reduce species richness by reducing both light and water levels. This is contrary to some generalizations that compe-

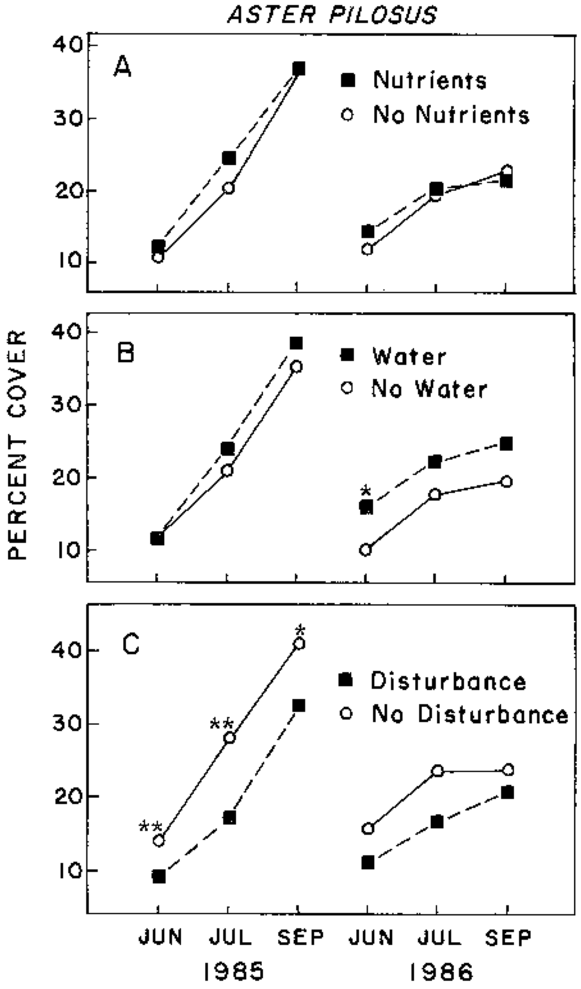

FIG. 9. The effect of (A) increased nutrients, (B) increased water, and (C) disturbance on the cover of *Aster pilosus*. This is the only species that disturbance had a major impact on. Significant differences between treatments and within a date are indicated by asterisks (* $P < .05$, ** $P < .01$, *** $P < .001$).

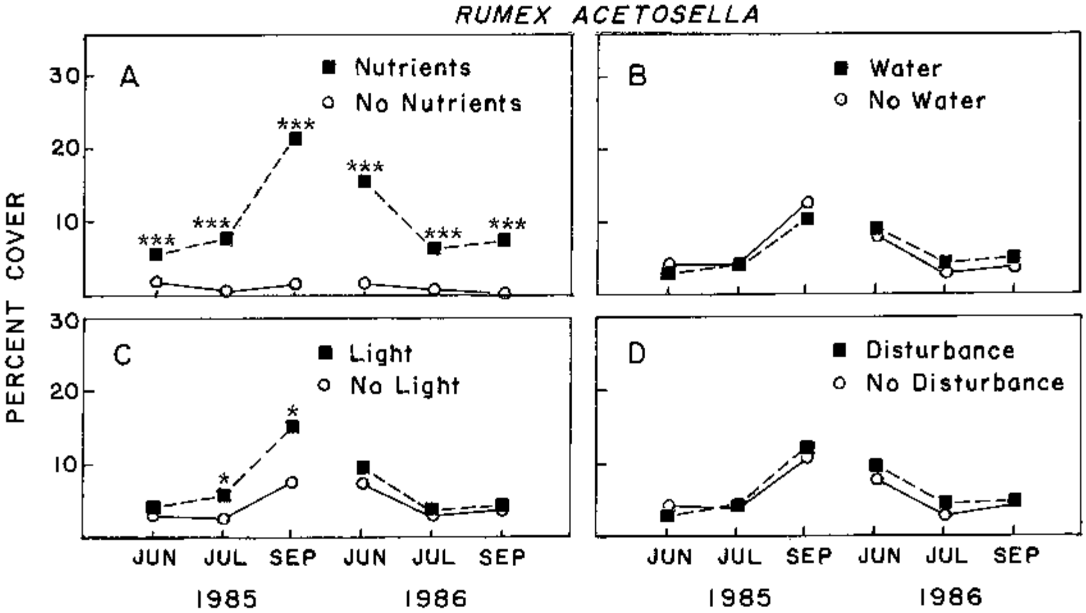

FIG. 10. The effect of (A) increased nutrients, (B) increased water, (C) increased light, and (D) disturbance on the cover of *Rumex acetosella*. Significant differences between treatments and within a date are indicated by asterisks (* $P < .05$, ** $P < .01$, *** $P < .001$).

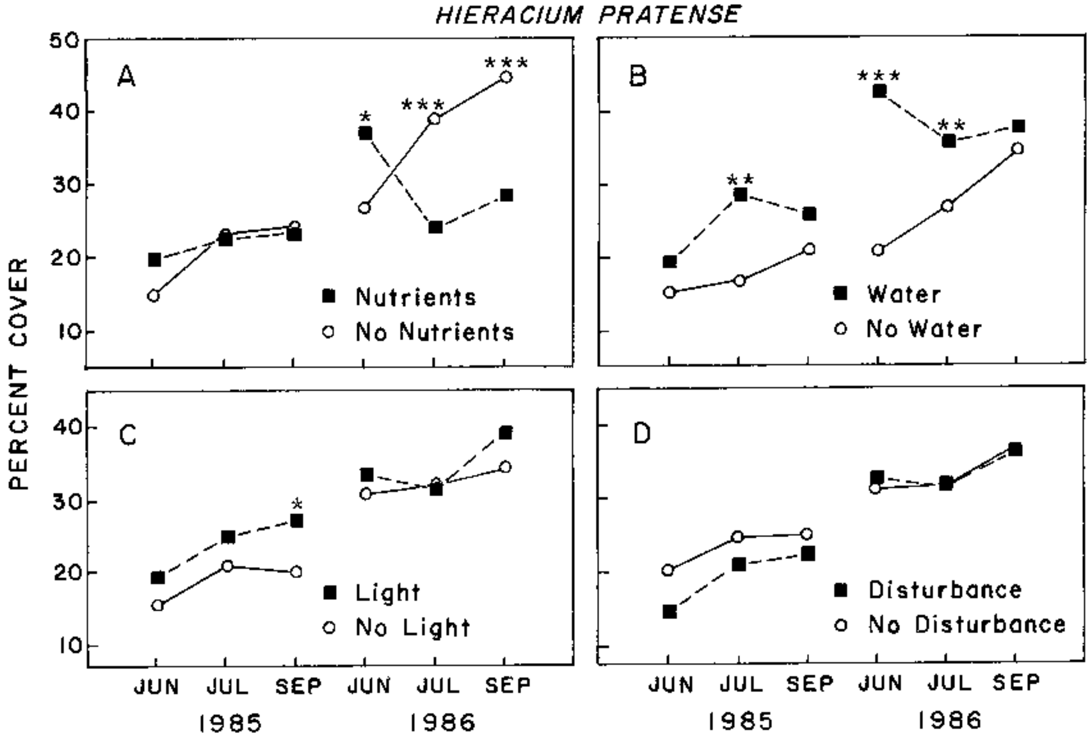

FIG. 11. The effect of (A) increased nutrients, (B) increased water, (C) increased light, and (D) disturbance on the cover of *Hieracium pratense*. Significant differences between treatments and within a date are indicated by asterisks (* $P < .05$, ** $P < .01$, *** $P < .001$).

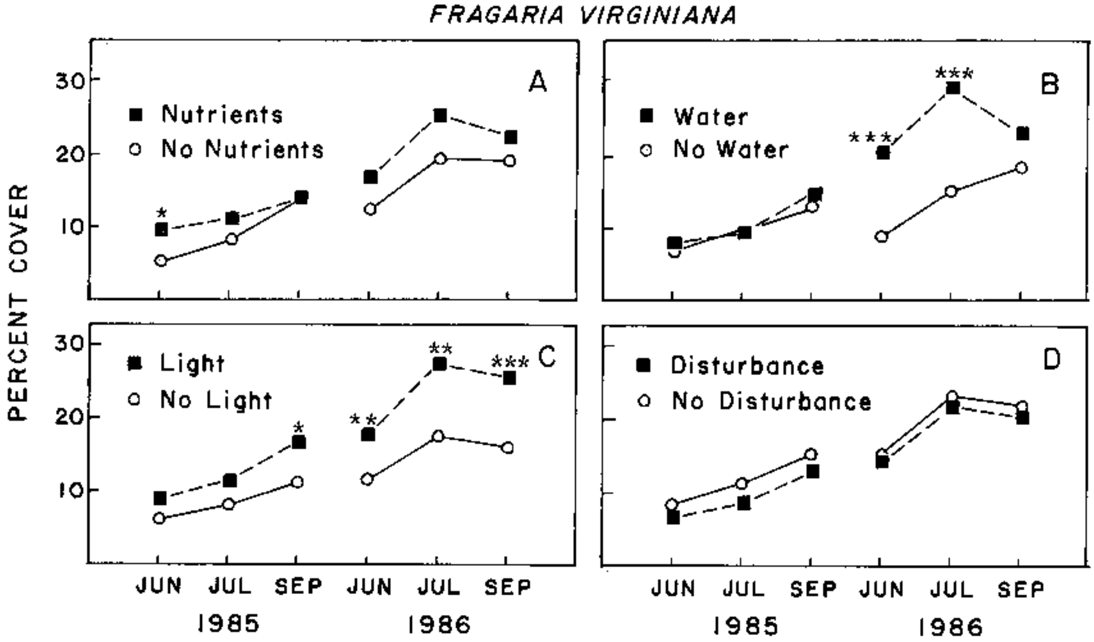

FIG. 12. The effect of (A) increased nutrients, (B) increased water, (C) increased light, and (D) disturbance on the cover of *Fragaria virginiana*. Significant differences between treatments and within a date are indicated by asterisks (* $P < .05$, ** $P < .01$, *** $P < .001$).

tition for nutrients alone is the primary factor that controls species composition in plant communities (Bradshaw 1969, Tilman 1982; but see Huston and Smith 1987). Our study suggests that light, nutrients, and water all play a role in organizing communities and that these resources are shifting regularly within the community.

Resource manipulations also change the abundance of specific growth forms. Nutrient-rich sites may be patches where annual species (e.g., *Ambrosia artemisiifolia*) can displace (Carson and Barrett 1988) or coexist with perennial vegetation (Fig. 5). Additionally, woody vines (e.g., *Lonicera japonica*) may establish on these sites, subsequently dominating large portions of old fields (Pickett 1982).

The role of disturbance

Natural gaps in old fields are created by woodchucks (*Marmota monax*), pheasants (*Phasinus colchicus*), meadow voles (*Microtus pennsylvanicus*), and moles (*Scalopus aquaticus*) (Goldberg and Gross 1988). Disturbances create gaps which usually increase space and resources within communities providing opportunities for colonization and establishment (e.g., Pickett and White 1985). Natural disturbances in this community were small, usually <0.5 m^2. We mimicked disturbances at this scale and saw little response. Armesto and Pickett (1985) found that the effect of a canopy disturbance depended upon the life histories of the resident species. Perennial species that spread vegetatively via rhizomes can respond rapidly to disturbance. For example, the cover of *Solidago canadensis* rapidly returned to control levels. Moderate disturbances may not seriously affect such perennial species and thus provide only a very brief window for establishment of fugitive or later successional species. *Aster pilosus* was most affected by the disturbance, yet it was virtually unaffected by the resource manipulations. Disturbance may limit the abundance of this species, perhaps by reducing its competitiveness relative to *Solidago canadensis*.

Disturbance and nutrients interacted to increase cover relative to nutrient or disturbance treatments alone. Thus, upon gap creation, certain populations may increase, but only if an adequate nutrient supply allows these populations to rapidly take advantage of the newly opened space. In fact, some mammalian disturbances are most common on nutrient-rich sites (Tilman 1983).

It has generally been assumed that small disturbances release significant resources (Rabinowitz and Rapp 1985); however, we obtained strong responses with resource enrichments but virtually no response with disturbance. Our disturbance created a large gap when compared to natural disturbances in old fields (Goldberg and Gross 1988) and the timing and nature (soil disturbance) of the disturbance should have been optimal for early successional summer annuals (Bazzaz 1979). Nonetheless, since there was little response, either insufficient resources were released (Rabinowitz and

Rapp 1985) or they were quickly assimilated by resident perennial vegetation. Our study investigated a single disturbance event at a single point in time. Disturbances that are more frequent, occur in a different season, or create a larger gap, may have a much different impact. For example, McBrien et al. (1983) found that a major outbreak of a phytophagous beetle severely reduced the canopy cover of *Solidago canadensis,* resulting in a dramatic increase of the subcanopy dominant *Fragaria virginiana.* Nonetheless, our study suggests that relative to resources, small disturbances do not play a central role in intermediate-aged old-field communities. Furthermore, Goldberg and Gross (1988) concluded that gaps in mid-successional old fields in Michigan were too rare and small for successful plant establishment. (See Rabinowitz and Rapp 1985, and Rapp and Rabinowitz 1985 for similar results for prairies.) Some studies that have reported significant effects of disturbances in old fields either simulated large, rare disturbances (e.g., Armesto and Pickett 1985, 1986) or artificially increased resource levels along with the disturbance (e.g., McConnaughay and Bazzaz 1987).

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