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PLANT SPECIES REMOVALS AND OLD-FIELD COMMUNITY STRUCTURE AND STABILITY[1]

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Abstract. The roles of species abundance, community structure, and competitive relationships in community recovery following stress were studied by separately removing species in June in three 6-yr-old fields at Hutcheson Memorial Forest, New Jersey. Percent cover of remaining species was measured in September.

In 9 of 17 species removals there was high community recovery, mainly due to one remaining species which increased significantly; 8 removals resulted in low community recovery. Abundant species replaced species removed. Only one remaining species, *Potentilla simplex*, increased regardless of treatment; the responses of others were highly dependent on the particular species removed, emphasizing the importance of species interactions. Reciprocal removals for a species pair produced unrelated responses.

Community recovery correlated inversely with cover of species removed. However, the order of species according to cover differed from the order of amounts of community recovery, indicating that species rank by abundance may be an inadequate measure of relative importance of a species in the community. High community recovery correlated with vertical stratification (bilayered with a dense ground layer), horizontal patchiness (many low diversity patches), abundance of rapid vegetatively reproducing species, and differential species interactions. Species diversity changed negligibly following removal of a species.

It is concluded that community recovery from a stress and the effects of species extinction are dependent on (a) community structure and (b) species composition.

Key words: Community recovery; community structure; competition; diversity; dominance; extinction; perturbation; species removal; stability; New Jersey.

INTRODUCTION

Importance of a species in the community is usually defined by a measure of its abundance in the community. Dayton (1975) and Paine (1974), however, have shown that ecological importance of a species may be disproportionate to its abundance in intertidal communities, where importance refers to the impact or influence a species may have in a community. With species removal techniques they were able to determine interrelating roles of species in different trophic levels, and consequently conclude that high abundance does not necessarily mean high importance.

Daubenmire (1968) suggested that dominants are those species whose removal would cause the greatest readjustment in the ecosystem. Plant species removal studies have primarily removed groups of species. Putwain and Harper (1970) removed all grasses in hill grasslands and observed increased vegetative and seedling growth of *Rumex acetosa*. But when they removed the forbs, there was no effect on *Rumex*, and only the grasses increased. Removal of grasses from fields resulted in increased germination and vegetative growth of three *Plantago* species (Sagar and Harper 1961). Removal of annual species from first-year successional fields produced a surge of growth by the perennials (Fleet 1970, Keever 1950). Dominant grasses in South Carolina old fields interfere with forbs, as evidenced by increased herbaceous productivity upon removal of grasses (Pinder 1975).

Perturbations on ecosystems may cause selective destruction of species; for example, after selective logging the forest composition changes (Sander and Clark 1971, Trimble 1971). Shrub communities under rights-of-way for power lines have been maintained in equilibrium by selectively inhibiting tree species with herbicides (Niering and Goodwin 1974). Selective feeding on oaks, by gypsy moth, has produced stands in which red maple is becoming more abundant (Collins 1961, Campbell and Valentine 1972). Experimental sulfur dioxide stresses at 1 ppm favored grasses over forbs (Cocking 1973).

The competitive relationships between removed and remaining species have been further elucidated in studies involving extraction of only one species. Elimination of ragweed by the herbicide 2,4-D enabled other annual species and grasses to increase in New Jersey (Lewis 1973). The chestnut blight eliminated the dominant species, *Castanea dentata* (chestnut) from many forests of eastern North America, permitting the second and third dominants of the original forest, oak and hickory, to become first and second dominants in present forests (Keever 1950, Good 1968). Dayton (1975) removed *Hedo-*

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phyllum, the dominant algal species of an intertidal zone; the obligate understory species were replaced by fugitive species in the resulting community. Single species removals are informative because, as Dayton (1975) and Paine (1974) point out, nonlinear relationships of species abundance to importance in the community can be discerned.

The concept of community and ecosystem stability includes time of persistence, but may or may not include response to an acute stress (Margalef 1968, MacArthur 1955, Hurd et al. 1971, Cocking 1973, May 1973, Mellinger and McNaughton 1975). We believe stability should be measured in terms of a stress, since measurements of time of persistence will often fall in an interval between acute stresses. Therefore we define stability as that property of a biological system which tends to maintain the system, when stressed, in its original equilibrium or regular oscillation condition. High stability implies persistence in the face of both normal environmental variations, such as diurnal changes, seasonal changes, low level stochastic changes, and uncommon environmental variations, such as a rare flood, hurricane, fire, air pollution buildup or heavy pesticide application. Such uncommon variations applied to the community or ecosystem, whether natural or human induced, are here defined as stresses or perturbations. Thus removal of a dominant species is a stress on the community.

Stability (Hurd and Wolf 1974) is described operationally as the resistance of a community or ecosystem to stress, plus its recovery from stress. Resistance includes time from stress application to initiation of deflection (movement away from the original equilibrium or regular oscillation condition), rate of deflection, and amplitude of deflection. Resistance *per se* was not studied, since the investigator removed species completely, irrespective of community characteristics and other species present. Recovery includes rate of return (movement back toward the original condition), amount of return, time required to reach the original condition, and time for damping oscillation. An overall measure of recovery was used as the difference between control and treated plots at end of experiments.

Recovery is used to refer to the changes in the community following deflection, while response refers to changes at the species level following deflection. Importance is the impact or influence a species has in the community, and is measured in two ways for comparison: (1) dominance and (2) amount of community recovery following its removal. Dominance is the relative amount of a species in the community and is measured here by percent cover. Abundance is used in the general sense of plentifulness and as equivalent to dominance.

The objectives of this study were to determine: (a) if the relationship between abundance of removed species and community recovery is linear, (b) whether community recovery patterns vary with community structure, and (c) if there are patterns of response of individual competing species to the removal of a single species.

The Study Area

Dominant plant species and the uncommon species as a group were separately removed from three old field communities differing structurally and compositionally. Those three 6-yr-old fields, designated upper, middle and lower, are located at the William L. Hutcheson Memorial Forest (Small 1973), Somerset County, on the New Jersey Piedmont. The fields are relatively flat on an incline averaging $\approx 5\%$.

New Jersey has hot, humid summers and fairly mild winters with temperatures varying from an average of 23.5°C for summer months to −1.0°C in winter months. Precipitation averages 115 cm/yr, with monthly averages somewhat higher in summer than in winter (Biel 1958). The summer of 1974, when the study was done, had near average temperature and precipitation except for a 3-wk dry period in July.

The soil is loam derived from the Brunswick red shale formation, except for some clay loam in the lower field (Ugolini 1964). Soil moisture was measured by weight seven times throughout the year and no significant difference was found between the upper and middle fields. The lower field was significantly wetter from October to May, with standing water during much of the spring, but not significantly different from the other fields during June to August. Soil nutrients were analyzed by the Rutgers Soil Testing Laboratory. The lower field is somewhat higher in phosphorus and potassium and lower in magnesium concentration than other fields. Available nitrogen and organic matter are similar in all fields, with slightly higher cation exchange capacity in the lower field. There was no significant difference in pH among the fields.

Methods

In each of the 1-ha fields an area of ≈ 280 m^2 was staked out to accommodate 80 or 90 one m^2 plots, for a total of 260 plots in the study. Each plot was surrounded by a 5 cm unsampled edge, and plots were separated by an additional 60 cm wide pathway. In each field the dominant species and the uncommon species as a group were removed from 10 replicate plots.

The dominant species were those that were $\geq 5\%$ cover; uncommon species were $< 5\%$. *Convolvulus* was slightly less than 5% at the outset, but was pulled with the dominants because it was expected to increase.

There were five such treatments (species removals) in the upper field, five in the middle, and four in the lower (Table 1), with three types of controls in each. The locations of the treatment and control plots, were assigned at random over the staked-out area of each field. The staked-out areas were chosen on the basis of relative homogeneity and representativeness of the vegetation. A few plots which would be obvious statistical outliers (Miller 1966) were reassigned to another spot. Discarded plots had clumps of *Rosa multiflora* or *Solidago rugosa*, or bare patches caused by animal activity.

Two treatments were genus removals because of vegetatively intergrading pairs of species: *Aster pilosus* and *Aster dumosus* in the upper and middle fields, and two unidentified species of *Carex* in the lower field. Uncommon species were pulled as a group since their removal separately probably would result in unmeasurably small changes in the community in one growing season.

Three types of controls were included. Since pulling plants causes changes in the soil and litter, (1) 10 plots in each field were punctured with holes to simulate the holes made by removing species, (2) 10 plots were clipped at ground level at the beginning of the experiment for aboveground biomass, and (3) 10 plots were left undisturbed until the end of the experiment.

Percent cover was estimated 23 May–5 June in all plots before treatments. To improve accuracy, each 1-m^2 plot was divided into quarters, and cover data from the quarters were averaged for the plot. Plants were pulled, rather than clipped, to remove major roots, to keep soil and litter disturbance to a minimum, and to decrease regrowth and possible competitive effects of roots on other species. Fleet (1970) showed that removing roots produces greater recovery by the community than clipping. Large plants were extracted by cutting around the base with a knife. The holes left, about 1–3 cm in diameter and 1–2 cm deep, were filled with surface soil from adjoining fields and were patted flat.

Small plants, almost exclusively seedlings with little root development, were hand pulled. No soil was needed to fill in holes, because the disturbance was minimal. All aboveground plant parts were ovendried at 95°C for 48 h. To minimize edge effects, the removals were extended 5 cm beyond the edges of the plots.

The holes treatment required making 248 large holes per plot in the upper area, 71 large and 13 small holes in the middle, and 47 large and 45 small holes in the lower. These figures represent the average densities of large and small plants in the field plots. Large holes were cut with a knife and filled with soil; small ones were made by inserting the knife tip 1–2 cm into the soil.

Treatments were done in the upper field 5–15 June, in the middle field 15–23 June, and in the lower field 24 June–1 July. Post-treatment cover was determined by subtracting the amount removed from the pre-treatment cover. Productivity data of Botkin and Malone (1967) on first-year fields at Hutcheson Memorial Forest indicate that 20% of growth occurs during June. While the upper and lower fields, which were treated first and last, may represent different stages of growth and should be compared with caution, treatments within a field were finished in 7–10 days and are considered comparable.

There was a tendency for removed species to grow back vegetatively from rhizomes or root stocks left in the ground. Regrowth of removed species in each field was clipped at ground level on 20–25 July and 1–5 September, 1 and 2 mo after the first removal. Those plant parts also were dried. Total regrowth of a removed species never exceeded 10% of the original biomass of the species, and since that was based on two clippings, rarely was 5% present at any one time. All removed species had some regrowth, with *Hieracium*, *Fragaria*, *Plantago* and uncommon species reaching 10% of the original biomass. Regrowth was not included in the calculations.

End-of-season percent cover was measured 7–16 September after the last clipping of regrowth, such that regrowth is not part of the final measurements. All plants in plots were then clipped for aboveground biomass 25 September–10 November and stored at –15°C for 1–6 mo until the material was sorted into species and dried. Voucher specimens were deposited in the Chrysler Herbarium, Department of Botany, Rutgers University. Plant nomenclature follows Fernald (1950).

Percent cover and biomass data were subjected to analysis of variance (ANOVA) and analysis of covariance tests (ANCOVA) (Steele and Torrie 1960). ANCOVA adjusted the September treatment means of percent cover to account for the initial June levels, and proved to be a better statistical tool because of some large differences in initial levels of cover between treatment and control within a field. The differences reflect the high vegetation patchiness in 6-yr-old fields. Some significant differences found by ANOVA proved to be artifacts of statistically significant high or low pre-treatment means using ANCOVA. After the September means are adjusted for the June pre-treatment means, ANCOVA allows the assumption that the June means are the same. Unless otherwise stated, the results are based on adjusted percent cover data.

TABLE 1. Species removed in upper, middle, and lower fields. Dominants, plus uncommon species as a group, are the species removed in this study. U = upper field; M = middle field; L = lower field

Dominant species removed	Common name	Height (cm)	Field
Aster dumosus and *A. pilosus*	aster	50–70	U M
Convolvulus sepium	hedge-bindweed	2–100	U M L
Daucus carota	Queen Anne's lace	10–20	U
Fragaria virginiana	strawberry	10–20	U
Hieracium pratense	king devil hawkweed	2–3	U M
Plantago lanceolata	English plantain	10–15	M
Potentilla simplex	old-field-cinquefoil	2–3	M
Aster dumosus	aster	50–70	L
Carex (2 unidentified species)	sedge	40–60	L
Solidago graminifolia	goldenrod	70–100	L
Uncommon species		2–100	U M L

RESULTS

Community structure.—The vegetation of the upper and middle fields was typical of upland 6-yr-old fields on the New Jersey Piedmont (Bard 1952), while the somewhat different vegetation of the lower field correlated with poorer drainage. In the upper field plots, 64 species were found, 79 in the middle, and 87 in the lower (Table 2). Uncommon species were defined as those species having 5% or less cover. Species number (Tables 1 and 2), species composition (Tables 1 and 2 and Fig. 1), dominant species (Fig. 1), and vertical stratification (Table 1) differed in the three fields.

The upper field was dominated by *Hieracium*, *Fragaria* and *Aster*, which formed three layers of vegetation (Table 1 and Fig. 1). *Hieracium* was a flat rosette rarely found higher than 3 cm, except for flower stalks developed in May and June. *Fragaria* grew up between the rosettes to a height of 10–20 cm with less abundant *Daucus* rosettes interspersed. *Aster* formed the canopy at 50–70 cm. Uncommon species were found at all heights. End-of-season cover dominance was shared by *Hieracium*,

TABLE 2. Uncommon species in upper, middle, and lower fields. U = upper field; M = middle field; L = lower field; * = most abundant uncommon species

Acalypha rhomboidea U,M,L	*Hypericum punctatum* L*	*Rhus radicans* U,M,L
Acer rubrum U,M,L	*Juncus tenuis* U,M,L	*Rosa multiflora* U,M,L
Acer saccharinum L	*Juncus* sp. M,L	*Rubus allegheniensis* U,L
Achillea millifolium U,M,L	*Juniperus virginiana* U,L	*Rudbeckia hirta* L
Agrostis alba U,M,L	*Lactuca scariola* M,L	*Rumex acetosella* U*,M*,L*
Agrostis hyemalis U,M,L	*Lactuca canadensis* U	*Rumex crispus* U,M
Allium vineale U,M,L	*Lepidium campestre* U	*Setaria* sp. U,M
Ambrosia artemisiifolia U,M,L	*Linaria vulgaris* U*,M*	*Sisyrinchium montanum* M,L
Andropogon virginicus M	*Lobelia inflata* U,M,L	*Sisyrinchium mucronatum* L
Apocynum cannabinum U,M,L*	*Lonicera japonica* M,L	*Smilax* sp. L
Aster novae-anglii M	*Lychnis alba* U	*Solanum carolinense* U,M,L
Barbarea vulgaris U*,M,L	*Lycopus* sp. M	*Solidago canadensis* U,M,L
Carex sp. U,M	*Lycopus* (2 spp.) L	*Solidago gigantea* U,M,L
Cerastium vulgatum U*,M,L	*Oenothera biennis* U,M,L	*Solidago graminifolia* U,M
Chrysanthemum leucanthemum U,M,L	*Oenothera perennis* L	*Solidago juncea* U,M,L
Cirsium arvense M*	*Onoclea sensibilis* L	*Solidago nemoralis* U,M,L
Cirsium discolor M,L	*Oxalis stricta* U*,M,L	*Solidago rugosa* U,M,L
Cornus amomum U	*Panicum meridionale* U,L	*Taraxacum officinalis* U,M,L
Cornus florida L	*Panicum* (2 spp.) L	*Trifolium agraria* M
Cyperus sp. L	*Penstemon hirsutum* M*	*Trifolium pratense* U
Danthonia spicata L	*Physalis heterophylla* U,M,L	*Trifolium repens* U
Daucus carota M,L	*Physalis* sp. M	*Trifolium* sp. M,L
Dianthus armeria U,M,L	*Plantago lanceolata* U,L	*Verbascum blattaria* U,M
Digitaria sanguinalis U	*Plantago major* U,M,L	*Veronica officinalis* U,M
Equisetum sp. L	*Poa compressa* U,M,L	*Viburnum prunifolium* L
Erigeron annuus U*,M*,L	*Poa pratensis* U,M,L	*Viola lanceolata* L
Eupatorium maculatum M,L	*Polygonum* sp. M,L	*Vitus* sp. M,L
Euphorbia supina U,M	*Potentilla recta* M	1 unidentified forb species U
Fragaria virginiana L	*Potentilla simplex* L*	1 unidentified shrub species U
Fraxinus americana M	*Prunella vulgaris* L	5 unidentified forb species M
Gerardia purpurea L	*Prunus serotina* L	2 unidentified grass species M
Gnaphalium obtusifolium U	*Prunus* sp. U	2 unidentified shrub species M
Hedeomea pulegioides U,M	*Pycnanthemum muticum* L	6 unidentified forb species L
Hieracium florentinum U,M	*Quercus* sp. L	2 unidentified grass species L
Hieracium pratense L*	*Raphanus raphanistrum* U,M,L	2 unidentified shrub species L
Holcus lanatus L	*Rhus glabra* U,M	

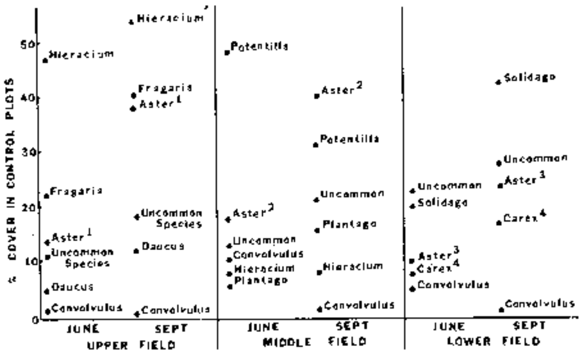

FIG. 1. Percent cover of dominants in the three fields. Values are averages of 10 control plots at beginning and end of experiments. Species with < 5% cover are grouped as uncommon species, and values are sums of the totals for individual species. [1] *Aster dumosus* 0.2%, *A. pilosus* 99.8%. [2] *Aster dumosus* 44%, *A. pilosus* 56%. [3] *Aster dumosus* 100%. [4] Two unidentified species of *Carex*, 42% and 58%.

Fragaria and *Aster* (Fig. 1), but *Aster* was the biomass dominant with *Fragaria* second.

The middle field was essentially bilayered with a ground level and a canopy (Table 1 and Fig. 1). *Potentilla* formed a matrix on the ground with patches of *Hieracium*, smaller patches of *Plantago*, and rosettes of uncommon species, especially *Penstemon* and *Erigeron*. The patchiness of *Hieracium* was striking, with all of the cover often occurring in one half or one quarter of the 1-m^2 plots. The *Aster* canopy was similar to the upper field. The intermediate space between the ground and canopy layers was occupied by a few of the uncommon species such as *Linaria vulgaris* and grass species. Relative biomass and percent cover (Fig. 1) of species correlated well except for *Potentilla*, which was relatively much higher in cover than biomass.

The lower field was quite different in structure, having three tall dominants, *Solidago* (70–100 cm), *Aster* (50–70 cm), and *Carex* (40–60 cm), in that order, from tallest to shortest (Table 1 and Fig. 1). The ground was 40–50% covered with mosses, primarily *Brachythecium* spp., through which rosettes such as *Hieracium* and *Potentilla* grew. The mosses dried out by July and were not studied. The relative orders of species in both biomass and percent cover (Fig. 1) measurements were the same, but *Solidago* was far more dominant in biomass than percent cover.

Community recovery.—Deflection of the communities from control levels, as a result of species removals (Fig. 2), is naturally correlated with abundance of the species removed (Fig. 1). However, only in the case of the first or second dominant of a community was deflection level significantly lower than the control.

Recovery by a community following species removal varied considerably according to the species removed, but in only a few cases did it differ significantly from controls (Fig. 2). Recovery was low for treatments of the first, second and fifth dominants in the upper field, for only the first dominant in the middle field, and for the four dominants in the lower field. Thus, in general, the more abundant a species is when removed, the higher the probability the community will be significantly below controls at end-of-season.

Though community recovery correlated inversely with cover of species removed, the order of species according to cover differed from the order of amounts of community recovery (Fig. 2). This indicates that species rank by abundance may be an inadequate measure of relative importance of a species in the community.

Species removed can be roughly categorized as causing high deflection and little recovery (*Hieracium*, *Fragaria* of upper field; *Potentilla* of middle; uncommon species, *Solidago*, and *Aster* of lower field [Fig. 2]), little deflection and high recovery (*Aster*, *Convolvulus* in upper; all but *Potentilla* in middle; and *Convolvulus*, lower), high deflection and high recovery (uncommon species, upper), and little deflection and little recovery (*Daucus*, upper; *Carex*, lower). The latter two cases should be interpreted with caution because of high variability of both treated and control plots.

Three treatments in the upper field showed total final coverage not significantly different from the controls (Fig. 2), but *Hieracium*, *Fragaria*, and *Daucus* treatments had significantly lower cover. Recovery is indicated by a significantly lower cover of nonremoved species in control plots from remaining species in treated plots (Fig. 2). Therefore, there was little recovery with *Hieracium*, *Fragaria*, and *Daucus* removals. In the *Aster* removal, however, community recovery to control level is indicated by a low level of nonremoved control species compared to the *Aster* removal treatment in September. *Convolvulus* removal means are very similar to the controls. As a species of lower cover in the upper field (Fig. 1), its removal caused a negligible deflection of total cover; since the species declined greatly during the drought in July, no difference from controls is expected.

In the middle field only *Potentilla* removal plots did not recover to control level (Fig. 2). The other treatments indicate either a positive community recovery where cover of nonremoved species in controls is lower than treatments as for *Aster*, uncommon species, *Hieracium*, and *Plantago*, or little change as for the *Convolvulus* removal treatment.

In the lower field the *Convolvulus* removal was similar to the controls, while all other removals

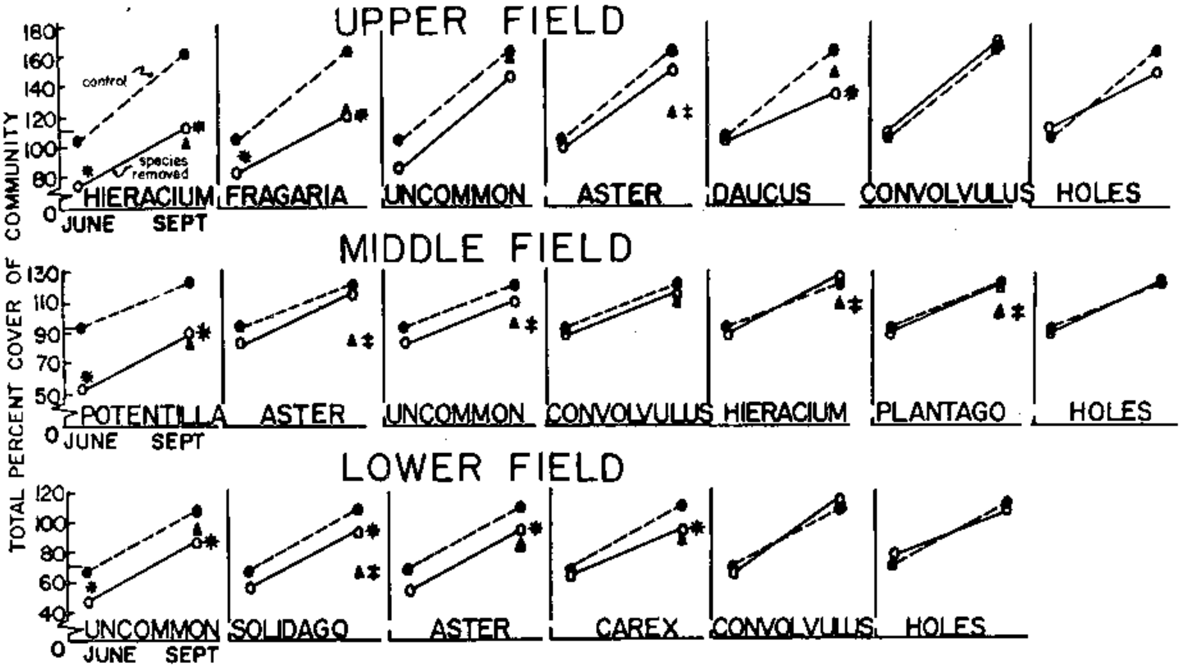

FIG. 2. Effects of species removals on cover of three plant communities. Each graph shows the results of removing the species listed from an old field community. The upper dashed diagonal line is for 10 control plots and the lower solid diagonal line for 10 species removal treatment plots. * indicates cover of treated plots is significantly less than control ($p < .05$). ▲ = cover of nonremoved species in control plots. — on vertical axis is overall average pre-treatment cover for all 80 or 90 plots in a field. ‡ indicates cover of nonremoved species in control plots is significantly different ($p < .05$) from treated plots.

were significantly below controls, regardless of deflection (Fig. 2). There was a low degree of community recovery in the *Solidago* removal treatment, as indicated by low cover of nonremoved species in control plots. In all three fields, the holes treatment caused no significant changes in total plant cover.

Individual species response.—To determine what caused the differing patterns in community recovery at the three sites, species were analyzed individually. The response of each species to a removal is given (Tables 3–5) as increase or decrease over the level of that species in the control plots. The tables can be read both vertically and horizontally. A vertical column lists the responses of each species to a particular treatment. A horizontal row shows the various levels of one species subjected to different treatments. Few species were significantly above or below control level in any treatment. Those responses with or approaching statistical significance ($p < .12$) are marked and are discussed in terms of possible biological significance.

In the upper field, community recovery was significantly lower than the control following three of the species removals, *Hieracium*, *Fragaria* and *Daucus* (Fig. 2). In the first two cases, the low community recovery was due primarily to the loss of the removed species, since in general the remaining species differed little from control and none was significantly below control (first two columns of Table 3). However, in the *Daucus* treatment, one species, *Aster*, was significantly below controls (Table 3), an important reason for the low community recovery. The removal treatments for *Aster* and the uncommon species resulted in high community recovery. In the *Aster* case, two species, *Hieracium* and *Fragaria*, responded by growing faster than controls (Table 3); the reason for the response following removal of uncommon species is because they are relatively low in abundance in September and would be expected to be similar to control.

In the middle field only the *Potentilla* removal had low community recovery (Fig. 2), apparently because no other species increased significantly (first column of Table 4). In four of the five other removals, however, at least one species did increase significantly, and thus community cover returned approximately to control levels.

In the lower field, community recovery was low in four of the five treatments, only reaching control level following removal of *Convolvulus* (Fig. 2). In two of these cases, *Carex* and uncommon species, no species increased significantly (columns in Table 5). In the other two cases, *Solidago* and *Aster* re-

TABLE 3. Response of species to treatments in upper field. Response is the average difference from controls in % cover for each treatment in September (a = $p < .05$; b = $p < .12$ and $> .05$)

	Treatments/species removed							
	Hieracium	*Fragaria*	Uncommon	*Aster*	*Daucus*	*Convolv*	Holes	$LSD_{.05}$
Responses by:								
Hieracium		−0.36	+1.45	+12.64[b]	+0.91	−2.17	−11.05	17.98
Fragaria	+2.29		+4.31	+11.54[b]	−0.36	+2.81	−5.88	15.07
Uncommon	−2.20	−1.19		−3.51	−3.49	+0.52	−1.77	5.99
Aster	−8.87	−7.98	−2.40		−12.53[a]	−5.51	−0.82	10.66
Daucus	−1.41	−1.47	−2.69	+2.17		+0.88	−4.60	8.06
Convolvulus	+0.34	+1.16[a]	+0.23	+0.85	−0.04		−0.02	1.10

movals, there were species that increased significantly, yet not enough to offset the loss of the removed species.

Of the 17 treatments, 8 resulted in low community recovery and 9 in high recovery. All eight treatments resulting in low community recovery appear to be due primarily to the lack of significant response by the remaining species. In one case, a remaining species decreased significantly and in three cases there were species which increased significantly, but not enough to compensate for the loss of the removed species. Of the nine treatments with high community recovery, five are due primarily to a remaining species which increased significantly. In four cases the cover removed was so little that treated and control plots were not significantly different and no remaining species changed significantly.

The patterns of response of a species to a variety of treatments are seen in the rows of Tables 3–5. *Potentilla* (Table 4) was the only one of 10 species that increased regardless of treatment, and no species decreased consistently. Most of the increases in *Potentilla* were significant. The responses of the other nine species were highly dependent on the species removed. Totaling the number of positive and negative responses under species removal treatments, (Tables 3–5) gives an estimate of the consistency of response of species to varying treatments. For *Hieracium*, 8 out of 10 responses were positive, 11 out of 14 for *Convolvulus*, 10 out of 14 for uncommon species, and 4 out of 5 for *Fragaria*. Though most species responses were dependent on the species removed, few responses were significant.

The nonreciprocity of effects of removing two species on each other is evident (Table 4). Removing *Potentilla* allowed no species to increase significantly, yet removing all dominants and the uncommon species enabled *Potentilla* to increase. Similar patterns of nonreciprocity are illustrated by the uncommon species in the lower field, *Convolvulus* in the lower field, *Aster* in the middle field, and *Solidago* in the lower field (Tables 3 and 5).

To determine which of the uncommon species contributed to increases in the different treatments, annuals, perennials and any species with a frequency high enough to allow meaningful statistical analysis were tested for significant deviation from control. In the upper and middle fields no significant differences for species were detected. In the lower field *Oxalis stricta* increased ($p < .10$) where *Aster* and *Solidago* were absent. The annuals were too infrequent for analysis, but the remaining perennials showed a significant increase with the removal of *Aster* and *Solidago.*

The holes treatment in general had little effect (Tables 3–5): species removal evoked a greater response by the community than treating with holes. Holes were no longer visible after the first rain, so this result is not unexpected.

Diversity indices.—Species number was not significantly affected by removals. There was an average of 13.8 species per control plot in September in the upper field, and fluctuations without evident pattern above and below this mean in treated plots. The middle and lower fields showed the same pat-

TABLE 4. Response of species to treatments in middle field. Response, a, and b as in Table 1

	Treatments/species removed							
	Potentilla	*Aster*	Uncommon	*Convolv*	*Hieracium*	*Plantago*	Holes	$LSD_{.05}$
Responses by:								
Potentilla		+22.06[a]	+19.71[a]	+5.73	+15.92[a]	+14.98[a]	+12.60[a]	12.02
Aster	+0.30		+5.37	−6.48	+0.80	+1.80	+1.20	11.71
Uncommon	+4.80	+5.90		+1.80	+6.30	+2.10	+0.85	8.92
Convolvulus	−0.65	+0.79	+0.26		−0.79	+0.31	−0.48	1.61
Hieracium	+0.65	+1.89	+2.47	+1.60		+2.17	+2.81	4.65
Plantago	−2.58	+4.50[b]	−0.98	+2.00	−2.19		−1.00	5.99

TABLE 5. Response of species to treatments in lower field. Response, a, and b as in Table 1

	Treatments/species removed						
	Uncommon	*Solidago*	*Aster*	*Carex*	*Convolv*	Holes	$LSD_{.05}$
Responses by:							
Uncommon		+8.93[b]	+12.70[a]	+7.01	+4.22	+0.05	10.80
Solidago	−0.42		−4.01	−6.21	+2.21	−4.21	8.85
Aster	−2.34	+6.71[b]		−1.61	+1.56	−8.09[a]	7.98
Carex	+0.19	−4.10	−6.58		+0.23	−2.20	8.61
Convolvulus	+0.34	+1.83[a]	+0.95[b]	+0.09		+0.15	1.15

tern, with 17.3 and 22.0 species per control plot respectively. There were too few annuals present in either the control or treated plots for meaningful statistical analysis, which may account for the lack of change in species richness.

The Shannon-Wiener diversity index H' and the equitability index J' (Pielou 1969) were calculated for June and September post-treatment cover data, and treatments were compared by analysis of variance. H' and J' varied according to the species removed, but with no evident pattern. As expected, removal of the uncommon species consistently lowered H' and raised J'. Neither H' nor J' showed a pattern of increase or decrease from June to September, or when correlated with abundance of removed species. Removal of one species from the community caused negligible change in H' and J', while removal of many species caused consistent changes in the indices.

Vertical stratification.—Overall, the highest community recovery was observed in the middle field and lowest recovery in the lower field (Fig. 2). A comparison of the vertical stratification in the three fields reveals some characteristics of community structure which correlate with community recovery.

In the middle field with highest recovery there was a very dense ground layer at 2–3 cm in height (Fig. 1 and Table 1). A canopy layer at 50–70 cm was present but the middle layer at 10–50 cm was very sparse. In the lower field with lowest recovery there was dense vegetation between 3–100 cm, with a poorly developed ground layer. The upper field which overall was intermediate in community recovery (Fig. 2) had a dense ground layer at 2–3 cm, a dense middle layer at 10–50 cm and a less dense canopy at 50–70 cm (Fig. 1 and Table 1).

Community recovery therefore was highest in a bilayered community with a dense ground layer and sparse middle layer, as in the middle field, and lowest in a multilayered community with most cover in the canopy and a sparse ground layer, as in the lower field. Recovery was intermediate when all layers were developed, with increasing cover toward the ground.

DISCUSSION

Plants have different roles in the community which are reflected by the varying responses following species removals. Several factors must determine how individual species and communities respond to removals. Most important may be characteristics of individual species, especially differing abilities to reproduce and fill gaps. However, the results in the three fields may be due not only to characteristics attributable to individual species but also to the community as a whole, because the communities differed in both horizontal and vertical structure. Horizontal structure refers to the degree of patchiness, and vertical structure to the stratification of vegetation. Recovery following removal may be related to community structure.

Vertical stratification.—Daubenmire (1968) suggests that tall plants have a greater effect on the community because of shading and greater utilization of resources. In each of the three plant communities studied, removal of the tall species, *Aster* and *Solidago,* caused the greatest species responses (Tables 3–5). An important question is why the second and third dominants did not always cause the same kinds of changes in each of the communities. Discrepancies might be explained by differences in vertical structure of the communities.

Horizontal patchiness.—Patchiness, largely induced by the vegetative spread of plant species, is quite pronounced by the sixth year of New Jersey old field succession. The variance divided by the mean was > 1 for all dominants in all three fields, indicating patchiness. The degree of patchiness was similar in the fields. However, fields differed in the proportion of monospecific or nearly monospecific patches. Put another way, the amount of overlap of species in different vertical layers or the amount of intermixing of species within patches varied among the fields. Fields with many monospecific patches were left with bare soil patches when those species were removed.

The middle field had the greatest proportion of monospecific or nearly monospecific patches. When *Potentilla,* with a 50% cover overall, was removed in June, many plots were left with > 50% of the ground bare, and only a few individuals of other species in the bare patches. The creation of bare spots influenced the type of response by the community of the middle field. Following removal of *Potentilla* there was no significant response by any other species (Table 4). Those species were able to increase only at the periphery of their patches, which may have been too small and infrequent to fill in gaps in one growing season. However, *Potentilla* was able to invade patches of ground after removal of *Plantago, Hieracium*, *Aster*, and the uncommon species. Thus most of the removals in the middle field resulted in high overall community recovery, because *Potentilla* was able to invade bare patches where there was little or no competition.

In the lower field with lowest overall community recovery, patches appeared more to be species mixtures including two or more canopy species. The removal of a species did not leave large gaps in the canopy and in general, response by remaining species was quite limited. The upper field with intermediate overall recovery had multispecies patches as well as overlapping layers.

Highest community recovery of a field correlated with an abundance of monospecific or near monospecific patches which were invaded when the species were removed. Lowest community recovery correlated with multispecies canopy patches where removals resulted in few large canopy gaps.

An analogy might be made to the forestry practices of selective removal and clearcutting patches. The patches created in the middle field are the "clearcuts," and removal of one layer or of scattered individuals without leaving bare patches in the upper and lower fields is "selective removal." Clear-cutting tends to stimulate plant growth much more than does selective removal (Sander and Clark 1971).

Vegetative reproduction.—Varying responses to removals can be explained by other factors besides community structure. All the species with significant or nearly significant positive responses except perhaps *Aster* (Tables 3–5) can reproduce vegetatively quickly. Autecological studies have been done on some of them.

Kott's (1961) studies on *Hieracium* revealed that the plant has four methods of vegetative reproduction which might enable it to take advantage of open space. Both *Fragaria* and *Potentilla* have aboveground stolons which enhance quick spread. Much of the regrowth of *Fragaria* into plots where it had been removed was by stolons of plants adjacent to the plots. *Plantago* is a weedy species which invades disturbed sites (Stebbins and Baker 1965). The greatest increase of *Plantago* was actually in the pathways between plots which had been disturbed by trampling. *Convolvulus* has a well developed rhizome system and is an agricultural weed (Quinn 1974). In the lower field, the uncommon species which increased included *Oxalis, Hieracium, Potentilla* and other vegetative reproducers.

The lack of increase by *Aster* in the middle and upper fields may be due to high intraspecific competition. Where *Aster* is very abundant, intraspecific competition would be especially strong, as in 6-yr-old fields. Removal of annuals from 1st-year fields enabled *Aster* to increase to a level which it would not normally attain until the 3rd year of succession (Keever 1950). In that study *Aster* was very low in abundance at the beginning of the manipulations and not hampered by interspecific competition.

The lower field was quite different in that *Aster* seedlings were scattered throughout the wet soil in June with $\approx 2\%$ coverage of the total 9% for *Aster*. The positive response by *Aster* to *Solidago* removals may be due to seedling growth. Intraspecific competition of *Aster* in the lower field was lower because of lower abundance, possibly allowing more seedling survival where *Solidago* was absent.

The overall response in the lower field is related to the particular dominants which grew there. *Carex* and *Solidago* did not increase at all. *Solidago*, like *Aster*, had high intraspecific competition at high density. The most active time for growth of *Carex* was in the spring when the ground was wet and flowering occurred.

Species interactions.—The responses to removals by species of a species pair were usually nonreciprocal. That occurred where two species had different abilities to reproduce vegetatively (*Aster* and *Potentilla* of the middle field), where they were pulled from different strata (*Aster* and *Potentilla*, middle; *Solidago* and uncommon species, lower), or where one was patchy and the other scattered (*Hieracium*, *Potentilla*, middle). In each case removing one caused a significant increase in the other, but the reverse was not true.

Dayton (1975) and Paine (1974) provide evidence that some species are important out of proportion to their abundance. The result of plotting abundance of removed species against response in the present study shows that the relationship between different species and the plant community is complex when removals are considered. The most abundant and tallest species exert the strongest influence, but other species are actually less important than their abundance would suggest, as in the case of *Hieracium* in the upper field. Or they may be more important as with *Hieracium* in the middle field. The importance of a species is also dependent on whether it is the removed or remaining species. Community response to *Aster* and *Solidago* removals indicates a high degree of interference, but these species do not contribute to community recovery when others are pulled.

Pinder (1975) showed that productivity of forbs increased three-fold in one growing season when dominant grasses were removed, with the exception of a few minor species. In the present study only one or a few species responded to removals, presumably because only one species at a time was removed. The more specific nature of the responses may be due to a lower abundance of removed material from each plot, but may also point to specific relationships between the removed and responding species, and between the responding and nonresponding species. Some species may be so competitively superior in their response as to prevent others from increasing (Putwain and Harper 1970, Haizel and Harper 1973).

In both Pinder's (1975) and the present study, there were no apparent differences in seedling density in treated and control plots. This is likely because in middle to late June when removals were completed, most species had already passed the part of their life cycle where new germination occurs, and would not be expected to germinate until the following spring.

Caution should be exercised in applying the results of a single growing season study to the long-range effects of species extinctions. The response patterns of slowly responding species, uncommon species separately considered, other native species of the region, and introduced species may be important.

Changes in vegetation composition following selective logging (Sander and Clark 1971; Trimble 1971), the chestnut (*Castanea*) blight (Keever 1953; Good 1968), application of selective herbicides (Niering and Goodwin 1974, Lewis 1973), and gypsy moth defoliation of deciduous forests (Campbell and Valentine 1972) show few consistent patterns, i.e., are relatively unpredictable, and appear to be dependent on many interacting factors. The present study indicates that both community structure (vertical layering and horizontal patchiness) and species composition (reproductive patterns and interspecific interactions) are important in predicting community recovery from a stress. In addition, species removal experiments enhance our understanding of the effects on the landscape of natural or human-caused species extinctions.

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