

Removal experiments to test mechanisms of plant succession in oldfields*

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Abstract

We investigated the effects of total (TR) or partial (PR) removal of the above-ground biomass of the dominant species on early successional trends in two oldfields in central New Jersey, USA. Our objective was to assess the occurrence of facilitation, tolerance, or inhibition as mechanisms of species replacement in the fields studied. In a 2nd-yr oldfield dominated by *Ambrosia artemisiifolia*, floristic composition and distribution of species cover changed markedly between the 2nd and the 3rd yr, regardless of the removal treatment. In both TR and PR plots and in control plots dominance shifted from an annual (*A. artemisiifolia*) to a biennial (*Erigeron annuus*). This indicates that the presence of the annual dominant is not necessary to promote this successional replacement, and therefore facilitation can be ruled out. Most species present in the 3rd-yr community were late summer and fall invaders which were not initially present. In a 7-yr oldfield dominated by *Solidago canadensis*, a clonal perennial, very little change in the distribution of species cover could be detected between years. Overall physiognomy remained the same, but there was a gradual change in floristic composition. In this field, TR and PR treatments enhanced vegetational change by allowing the increase in cover of suppressed understory species. Both inhibition and tolerance mechanisms may be involved in the pattern of vegetational change in this field. Finally, we stress that the mechanisms of species replacement operating in early secondary succession are dependent on structural and life history characteristics of the species assemblage on a particular site.

Introduction

A most important feature of secondary succession is the process of species replacement with time

(Clements, 1916; Gleason, 1926). Successional theory should, therefore, account for the mechanisms by which one species replaces another during succession. Connell & Slatyer (1977) proposed three possible ways in which structural changes could take place within a community: (1) facilitation, (2) tolerance and (3) inhibition. Although the three were originally presented as alternative and testable successional models, they are now considered as three hypotheses on specific successional mechanisms that could operate individually, or simultaneously, at different points in successional time or in different plant communities (Hils & Vankat, 1980; Turner, 1983a, b; Quinn & Dunham, 1983; Peet *et*

* Nomenclature follows Gleason & Cronquist (1963)

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al., 1983; Escarré *et al.*, 1983).

Different predictions of successional pattern are derived from each one of Connell & Slatyer's (1977) models, which can be used to assess the mechanisms of species replacement in a given plant community. Thus, if facilitation of a later successional species by an earlier species or group of species occurs (e.g., Werner & Harbeck, 1982; McDonnell & Stiles, 1983; Turner, 1983a), removal of the earlier species will arrest successional change. On the other hand, if a tolerance mechanism operates, both pioneer and later successional species will be present at the initiation of succession, but with time, climax species will replace early successional ones (Egler, 1954; Hils & Vankat, 1980; Pickett, 1982). Finally, according to the inhibition mechanism, early colonizers inhibit further invasion and establishment of later successional species, and species replacement will only occur by natural death of early colonists. If this is the case, removal of early successional species will enhance vegetational change. Disturbance experiments, such as the removal of some important components of the community to study the subsequent structural changes, have proved of great value in understanding community dynamics and succession in marine and terrestrial environments (Allen & Forman, 1976; Abul-Fatih & Bazzaz, 1976; Sousa, 1980; Hils & Vankat, 1980; Turner, 1983b).

Our objective was to evaluate the relative contribution of facilitation, tolerance and inhibition mechanisms to successional change in two oldfields in central New Jersey, USA. The basis for acceptance or rejection of a given mechanism of species replacement for the fields studied was the comparison of the observed year-to-year trend with the patterns predicted above. A 2-yr-old field dominated by the annual species *Ambrosia artemisiifolia*, and a 7-yr-old field dominated by the clonal perennial *Solidago canadensis* were selected for this study. These fields were disturbed in spring by removing all or part of the above-ground biomass of the dominants. The effects of removal of the dominant species on successional change were followed during two subsequent growing seasons.

Study sites

The two oldfields used in this study were fallow

fields of approximately 1 ha each, located within the boundaries of the William L. Hutcheson Memorial Forest, 14 km west of New Brunswick, New Jersey, USA. Information on characteristics of the soils and climate of the area are provided by McDonnell & Stiles (1983) and Armesto & Pickett (1985).

In spring 1981, the 2nd-yr oldfield (the 'younger' field) had 80–90% cover of *Ambrosia artemisiifolia* and much lower cover values of *Raphanus raphanistrum*, *Allium vineale*, and *Barbarea vulgaris*. Only one stratum of vegetation, about 30 cm tall, was distinguishable in this field. The 7th-yr oldfield (the 'older' field) had 70–90% cover of *Solidago canadensis*, which formed a continuous, species-poor overstory, nearly 1 m tall in June 1981. Less abundant species in the overstory were *Solidago rugosa* and *Asclepias syriaca*. This field had, in addition, a sparse understory which included several rosette-forming and low stature (less than 30 cm tall) herbs, such as *Raphanus raphanistrum*, *Galium aparine*, *Cerastium arvense* and *Oxalis stricta*.

Methods

Experimental design and sampling

Two removal treatments were applied to 1.5 × 0.5 m plots in each field: (1) In June 1981, the dominant species were almost totally removed by clipping the plants between 5 and 10 cm above ground level using grass clippers (TR treatment). Between 80–90% of the total above-ground biomass was removed by this method in each field. (2) A second group of plots was subjected to a partial removal treatment (PR treatment) which was necessarily different in the two fields because of their diverse vertical structures. In the 7-yr-old field the PR treatment consisted of clipping all stems of *S. canadensis* at 25 cm above ground, resulting in the removal of 60–75% of the above-ground biomass. In the younger field, this treatment consisted of clipping *A. artemisiifolia* from five roughly circular patches of 10 cm diameter, located regularly within the plots. Between 50–60% of the total above-ground biomass was removed by this treatment. Ten plots per treatment, and 10 undisturbed plots that served as controls throughout the experi-

ment, were distributed in a latin square design over an area of 10×15 m in each field. Plots were sampled once before treatment (June 1981), and then at monthly intervals during the 1981 growing season (July–September). All plots were sampled again once (younger field) or twice (older field) during the 1982 growing season. Cover of all species was estimated visually with the aid of a rectangular wooden frame (1×0.25 m), subdivided into 5% cover sections. This frame was placed in the center of each plot for cover estimations. All plots were separated from one another by 0.5 m wide strips of unmanipulated vegetation that served as access paths.

Analysis of data

Average cover data for all species per treatment were used to determine rates and magnitudes of vegetational change during the growing season, and between years. We inferred qualitative and quantitative changes in community structure through time using two indices: (1) Sørensen's community coefficient (Greig-Smith, 1983), defined as

$$CC = 2c/a + b,$$

where a is the number of species in community A or at time A, b is the number of species in community B or at time B, and c is the number of species in common. (2) The percent similarity index (PS) of Whittaker (1975), defined as

$$PS = 2 \text{ Sum} (\min x_i, y_i) / \text{Sum} (x_i + y_i)$$

where x_i and y_i are the percent cover of species i in communities x and y or at times x and y , and $(\min x_i, y_i)$ is the lower cover value for each species common to both communities or times.

Two types of comparisons were made. First the three groups of plots (TR, PR and control), sampled at different times during 1981–82, were compared with each of their pretreatment (June 1981) communities. This comparison is referred to as 'similarity to the pretreatment community', and assesses cumulative changes in floristic composition (CC) or distribution of species cover (PS), since pretreatment sampling. The second comparison is between manipulated (TR and PR) plots and control plots at different times during the two growing seasons. This comparison is referred to as 'similarity to controls,' and indicates year-to-year differences from control plots. The significance of the observed differences in CC or PS values among

sampling dates, or among the three groups of plots (TR, PR, and control) were assessed using a two-way ANOVA (Sokal & Rohlf, 1969). In comparing seasonal and year-to-year trends among treatments, values for June 1981 (pre-treatment sampling) were excluded.

Detrended Correspondence Analysis (Hill & Gauch, 1980; Gauch, 1982) was also used to detect differences in community structure between manipulated plots and control plots. This multivariate technique provides a graphic representation of the variation in community structure among plots within and between treatments. Each field was ordinated separately, and the degree of segregation of disturbed and control plots on the two first ordination axes was compared between dates during one growing season.

Results

Floristic similarity to the pretreatment community

In the 7-yr-old field (the older field), similarity in floristic composition (CC) to June 1981 decreases gradually in both disturbed and control plots, to a minimum between 50 and 60% in 1982 (Fig. 1A).

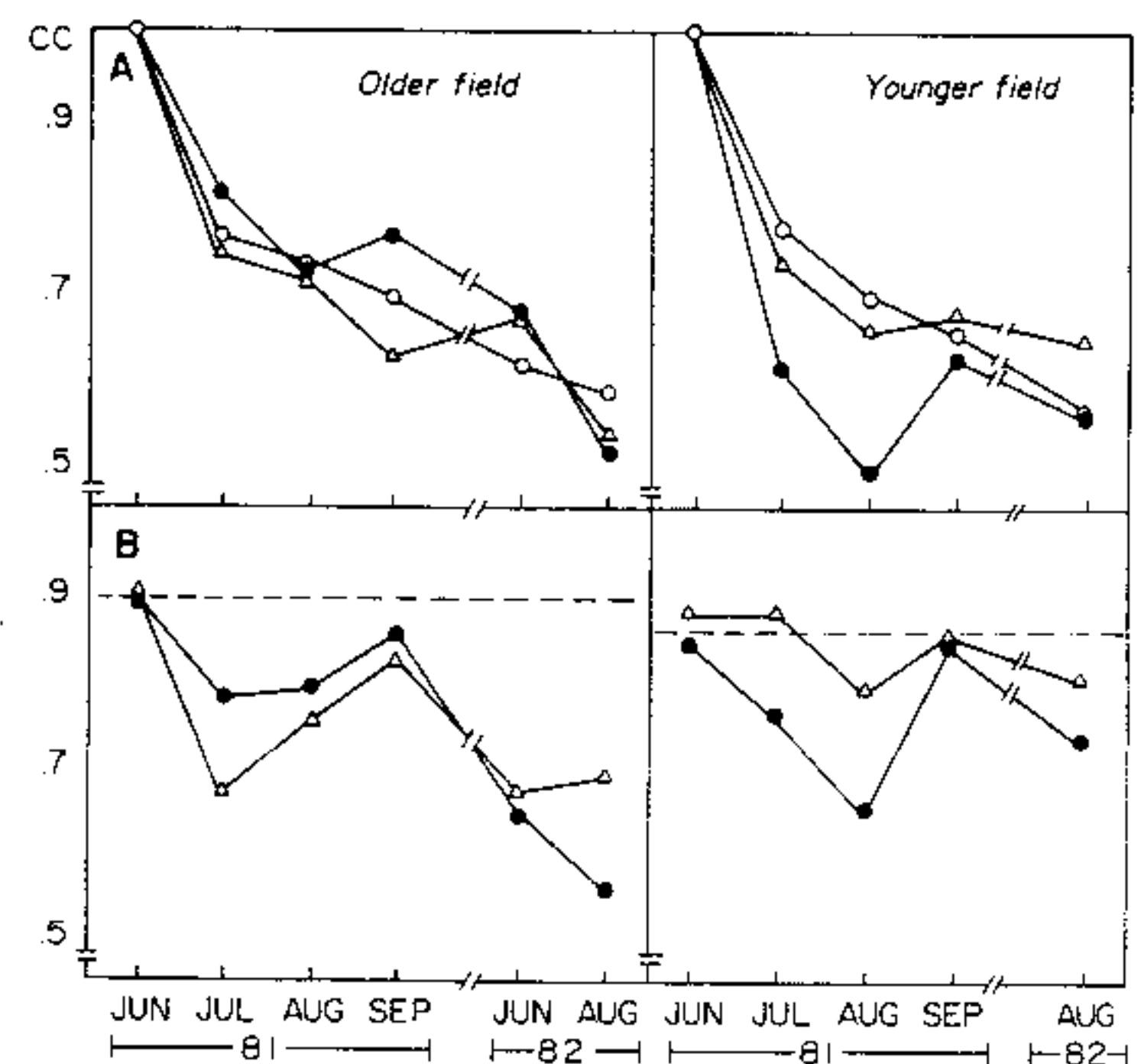


Fig. 1. A-top row: Floristic similarity (CC) between manipulated and control plots, and each of their pretreatment (June 1981) communities in two oldfields. ● = total removal of the dominant species, △ = partial removal of the dominant species, and ○ = control plots. B-bottom row: Floristic similarity, before (June 1981) and after treatment, between treatment (symbols as in A) and control plots in two oldfields. The dashed line indicates average pretreatment similarity between control and treated plots.

The largest drop in similarity occurs between June and July, regardless of the treatment. This trend of decreasing similarity in all plots is highly significant ($F=100$, $p<0.001$). Although there is some fluctuation in PR and TR plots above or below the similarity value of control plots, the overall trend of decreasing floristic similarity to June 1981 is not significantly ($F=1.01$, $p>0.05$) affected by the removal treatments.

The 2-yr-old field (the younger field) also shows a gradual decrease in floristic similarity to the pretreatment community, both over the first season and continuing into the second year (Fig. 1A). This trend is significant in all plots ($F = 14.2$, $p<0.001$). While PR plots follow the same pattern seen in undisturbed plots during the two growing seasons, TR plots, where *Ambrosia artemisiifolia* was totally removed, show the largest and fastest decrease in floristic similarity to June 1981, especially between July and August (Fig. 1). This trend is significantly different from that of control and PR plots ($F=4.54$, $p<0.05$). In September, however, control and TR plots tend to converge, and they show the same decrease in similarity the following season.

Floristic similarity to controls

When the species composition of PR and TR plots in the older field, before and after disturbance are compared to that of control plots (Fig. 1B), similarity decreases in both types of plots the first and second month after treatment. Subsequently, in September, both treatments recover to near predisturbance levels, followed by a second marked drop in floristic similarity in 1982. In August 1982, PR plots are 20% and TR plots 35% less similar to control plots than they were before treatment. Thus, in the older field, there are significant differences within the first season and between years ($F=6.06$, $p<0.025$), but no significant differences between the two removal treatments.

The situation is different in the younger field (Fig. 1B). Here, TR and PR plots show some decrease in floristic similarity to control plots after treatment, but there are no statistically significant differences between treatments or among sampling dates. Thus, in the younger field, all plots have roughly the same similarity to control plots both before and after disturbance and in both seasons.

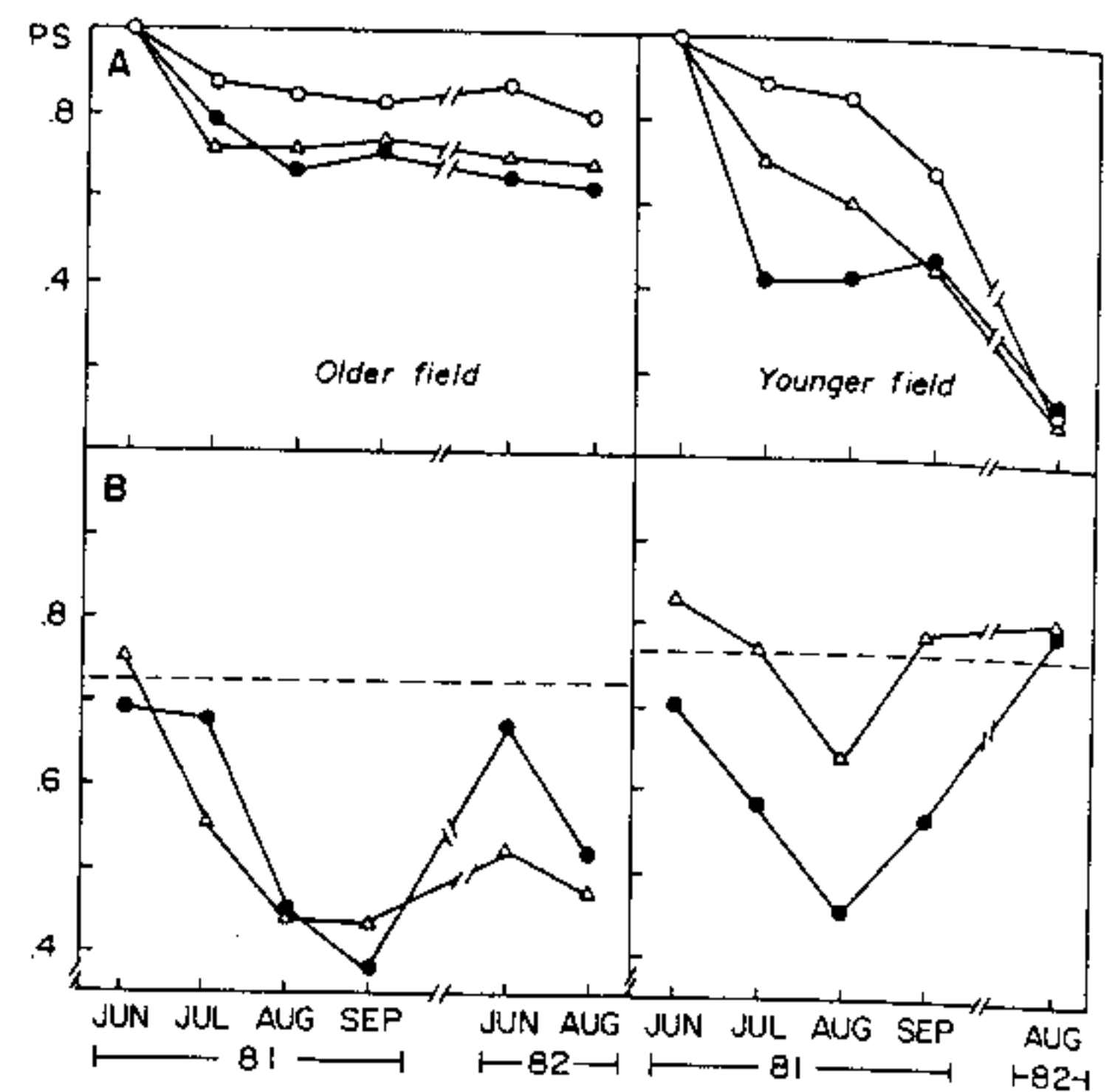


Fig. 2. A-top row: Similarity of species cover (PS) between manipulated and control plots, and each of their pretreatment (June 1981) communities in two oldfields. ● = total removal of the dominant species, ▲ = partial removal of the dominant species, and ○ = control plots. B-bottom row: Similarity of species cover, before (June 1981) and after treatment, between treatment (symbols as in A) and control plots in two oldfields. The dashed line indicates average pretreatment similarity between control and treated plots.

Similarity of species cover to the pretreatment community

Changes in the PS index, when comparing disturbed and control plots to their respective June 1981 communities reveal a marked and significant ($F=13.04$, $p<0.001$) drop in similarity in the younger field over the two growing seasons (Fig. 2A). The similarity in vegetation structure between August 1982 and June 1981 is about 10% in all plots. In contrast, similarities to the pretreatment community in the older field remain above 60% for manipulated plots and above 80% for control plots (Fig. 2A). The effects of removal of the dominant species can be seen in the larger decrease in similarity to predisturbance conditions in TR and PR plots than in control plots of both fields during the first season. In the younger field, the decrease in similarity is more pronounced in TR plots, intermediate in PR plots and more gradual in control plots between July and August (Fig. 2A). These trends of decreasing similarity are significantly

different from one another ($F=15.7$, $p<0.005$). Nonetheless, disturbed and control plots tend to converge (become less dissimilar) in September, and they all have the same low similarity to their predisturbance communities in 1982. On the other hand, TR and PR plots in the older field are always about 10–20% less similar to their predisturbance communities than are control plots in 1981 and 1982 (Fig. 2A), which results in a significant difference between the year-to-year trends of manipulated and control plots ($F=25.5$, $p<0.001$).

Similarity of species cover to controls

In both fields, similarity of manipulated plots to control plots, measured by the PS index, is highest before removal, decreases one month after removal, and tends to increase in late summer and in the following growing season (Fig. 2B). Since the differences between control and manipulated plots calculated by the PS index are greatly influenced by the cover values of the dominant species, which were clipped in each field, we examined the trends in similarity excluding the dominant from the calculations. For the older field, there is no difference between TR and PR treatments (Fig. 2B; $F=1.0$, $p>0.25$). Nevertheless, there are still significant differences among dates in the similarity of both removal treatments to control plots ($F=18.2$, $p<0.005$), as shown by the marked drop in similarity in August and September 1981, and then again, to about 50%, in August 1982. This PS value is 20–30% less than the pretreatment value (Fig. 2B). In the younger field, the largest decrease in similarity occurs in August, 2 months after disturbance, in both TR and PR plots (Fig. 2B). This decrease is less pronounced in PR plots; there are, however, no significant differences between treatments or among sampling dates in this field. One year after treatment, manipulated plots in the younger field had 80% similarity to control plots, more or less the same similarity that they had before the treatments.

Ordinations

Results of Detrended Correspondence Analysis of treated and undisturbed plots reveal trends consistent with those presented above. Although it was expected that sample points corresponding to each

of the removal plots would tend to separate more clearly along the first ordination axis (presumably reflecting treatment differences), this only occurred in the older field (Fig. 3A). In the younger field, disturbed samples tend to diverge from one another in more than one direction, indicating that the treatments interact with an unknown factor or factors, probably related to environmental heterogeneity within the field, leading to unpredictable differences in vegetation structure. Despite this problem, separation of TR from control plots in the older fields is evident in the progression from June (predisturbance sampling) to September (Fig. 3A). PR plots also tend to fall outside the range of control plots although to a lesser extent. Most of the spread of samples in this field is unidirectional, associated with the first ordination axis which ex-

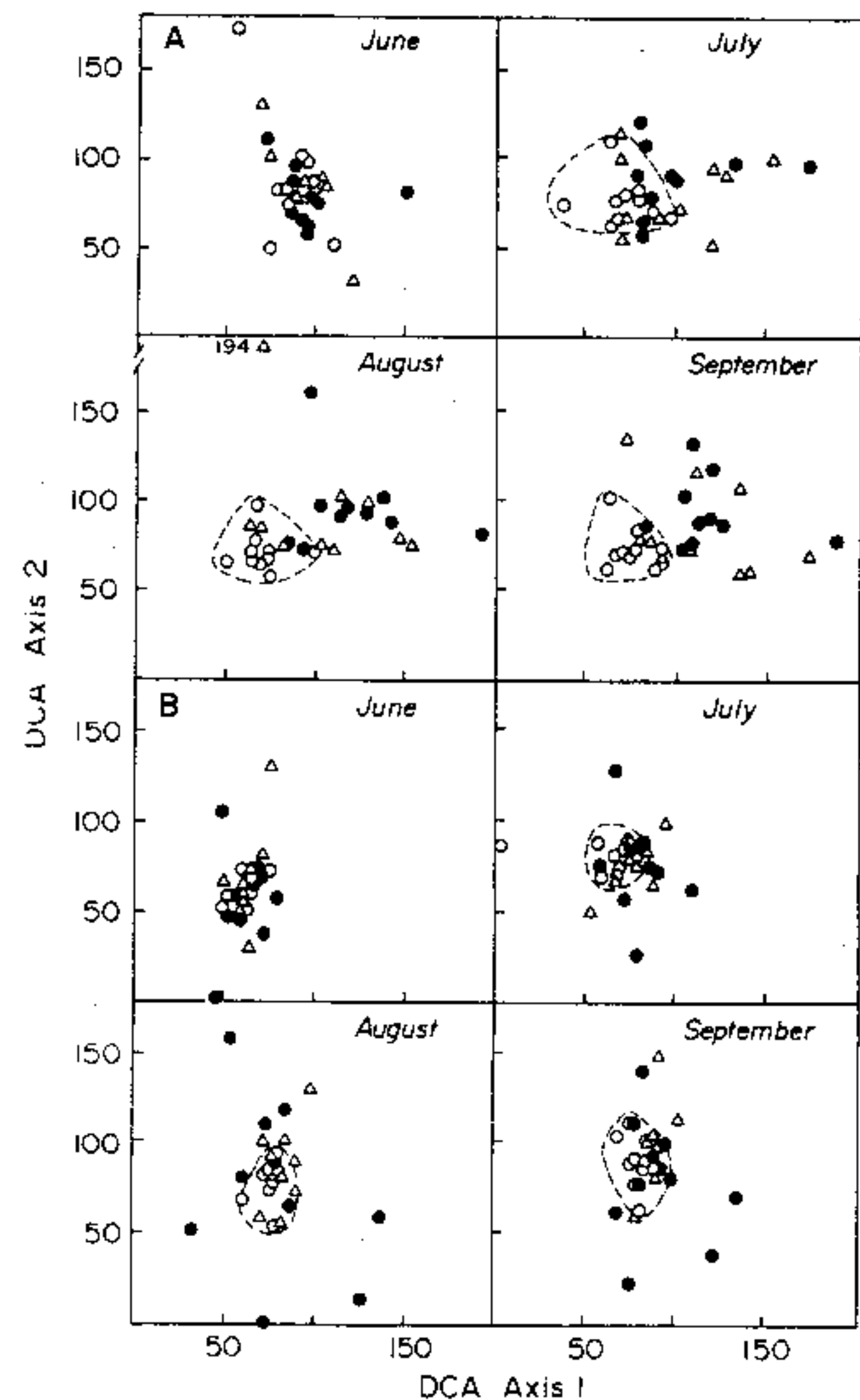


Fig. 3. Results of a Detrended Correspondence Analysis for two oldfields, showing the variation in vegetation structure before (June) and after treatment among plots where the dominant species was totally (●) or partially (△) removed, as compared to unmanipulated plots (○). The dotted line encloses the values for control plots. A-top four panels: older field. B-bottom four panels: younger field.

plains 36% of the variation. It should be noted that the divergence along both axes is greater for TR and PR than for control samples on all dates (Fig. 3A).

In the younger field, separation of undisturbed plots from PR or TR treatments is less clear (Fig. 3B). In this field some disturbed plots tend to spread widely on the second, as well as on the first ordination axis. This great spread indicates greater heterogeneity in community structure among disturbed plots at all dates in this field than in the older field. The divergence in disturbed samples is in marked contrast, however, to the tight clustering of control plots (Fig. 3B). In July and August, TR plots are spread in all directions, but generally away from control plots. A greater overlap in the positions of PR and control plots is observed on all dates.

Discussion

Secondary succession involves qualitative (floristic) and quantitative (species cover) changes in the vegetation of a site over long periods of time (from decades to hundreds of years). Long-term trends, however, are nothing more than the summation of small changes occurring seasonally as well as year to year (Bornkamm, 1981; Jukola-Sulonen, 1983). Moreover, the same mechanisms of change may operate at different times during succession (Pickett, Collins & Armesto, in prep.). We have studied the magnitudes and rates of change in species composition, and distribution of species cover, during two growing seasons in two early successional fields of different ages, occurring within 100 m of one another. We also compared the effects on the overall successional pattern of removal, partial or total, of the dominant species in each field.

Results show that, from June 1981 to August 1982, there is a major change in species composition and dominance in a 2-yr-old field, producing a 90% decrease in similarity according to the PS index, and a 45% decrease according to the CC (Fig. 1, 2). A comparable decrease in similarity in early oldfield succession has been documented by Bornkamm (1981). Between the 2nd and the 3rd year of succession, dominance shifts from a summer annual, *Ambrosia artemisiifolia*, to a winter annual *Erigeron annuus* (Armesto, 1984). *Ambrosia* is en-

tirely absent from the 3rd-yr community. This dramatic decline has also been documented by Lewis (1972) and Pickett (1982). The exclusion of *Ambrosia* can be explained by the effects of chemical inhibitors from winter annuals on the germination of this species (Bazzaz, 1979; Raynal & Bazzaz, 1975), or by autotoxicity (Raynal & Bazzaz, 1975; Jackson & Willemsen, 1976). Some kind of allelopathy seems plausible in this case given the complete absence of the species from the 3rd-yr field, and the fact that it often reappears later in succession (Pickett, 1982). However, the real importance of allelopathic effects on successional change still remains controversial (Keever, 1983). Pre-emption of available resources by winter annuals is probably a more direct, but also more site specific, mechanism leading to the exclusion of *Ambrosia* (Raynal & Bazzaz, 1975; Keever, 1979).

Removal of the above-ground biomass of the second year dominant in the younger field causes a transient deflection in the seasonal trend of vegetational change in TR and PR plots, as compared to the seasonal trend in undisturbed plots (Fig. 1, 2). However, this effect is not statistically significant for either CC or PS, and disturbed plots tend to converge with control plots in late summer. The structural convergence of control and disturbed plots in late summer is not so much due to recovery of *Ambrosia*, as it is due to the die back of this species, documented in control plots (Armesto & Pickett, 1985). In the third year, when *Ambrosia artemisiifolia* is no longer present, all plots support a similar community (Fig. 2), regardless of the treatment in the previous year. The convergence of 3rd-yr samples occurs despite the fact that, during the first season after disturbance, plots from which *Ambrosia* was removed diverged in several directions from control plots, as illustrated by the results of the ordination (Fig. 3).

The successional pattern described above is not consistent with a 'facilitation' mechanism of succession, according to which the presence of the early successional dominant (i.e., *Ambrosia*) is needed for the transition to the next stage (Connell & Slatyer, 1977). If this were the case, the 3rd-yr community should be different in plots where *Ambrosia* was removed. Since the same vegetation developed in manipulated and control plots after 1 yr, we conclude that the presence of a large cover of *Ambrosia* is not required for the development of

that community. Analysis of species responses to the removal of *Ambrosia* shows that species which are abundant in the 3rd year (e.g., *Erigeron annuus*, *Daucus carota*, *Potentilla simplex*, Armesto & Pickett, 1985) invade the plots in late summer and fall during the 2nd year, that is, when *Ambrosia* is at the end of its annual life cycle.

The marked decrease in floristic similarity from June 1981 to August 1982 in the younger field (Fig. 1) indicates that some species that were absent in the beginning of the 2nd year are present in the 3rd year (Armesto, 1984). This illustrates that recruitment of additional species is a feature of successional change in this field. Thus, 'relay floristics' (Egler, 1954), rather than 'initial floristics' or tolerance, better describes this specific phase of early succession. Most likely, these new species are recruited from seeds, dispersed into the field or present in the soil, because they are predominantly annuals and biennials (e.g. *Barbarea vulgaris*, *Erigeron annuus*, *Oenothera biennis*).

Compared to the younger field, the distribution of species cover in the older field seems highly stable from year to year. The PS value between the community of June 1981 and that of August 1982 is 80% for control plots (Fig. 2). In terms of floristic composition, however, there is a significant change between the 7th and the 8th year (Fig. 1). These data suggest that some species can invade the field, but their abundances remain relatively low, presumably due to suppression by the dense overstory of *Solidago canadensis* (Armesto & Pickett, 1985).

The successional change in the older field is best described by the 'inhibition' mechanism (Connell & Slatyer, 1977). Although some species are able to germinate, or spread vegetatively into *S. canadensis*-dominated vegetation, their growth is inhibited. Partial or total removal of the canopy provides resources, e.g. additional light and soil moisture (Armesto & Pickett, 1985; Platt & Weis, 1977) to allow the invaders to increase in cover (Armesto, 1984). This increase might be significant in enhancing the chances of invaders to compete successfully with *S. canadensis* for a place in the canopy. At the same time, a large increase in bird-dispersed species such as *Rubus* (Armesto & Pickett, unpubl.) might accelerate the input of bird-dispersed propagules in the manner suggested by McDonnell & Stiles (1983). The spread of disturbed

sample points only along one axis of the ordination (Fig. 3) suggests that the direction of community changes is similar in all disturbed plots, i.e., they are colonized by a similar species assemblage.

The removal of *S. canadensis* from the older field has a marked influence on subsequent community development relative to the high stability of control plots. TR and PR plots show a pronounced drop in their similarity to control plots after removal, in terms of both CC and PS values (Fig. 2). Furthermore, according to the PS index, control plots are more similar to June 1981 than either PR or TR plots after 1 yr (Fig. 2). The CC, however, shows a roughly equal decrease in floristic similarity to June 1981 in all plots, regardless of treatment. Consequently, even in the absence of disturbance, species composition tends to change gradually between the 7th and 8th year. In the older field a majority of species is recruited in spring or in late summer and fall (Armesto & Pickett, 1985). These species either die off, or persist with very low cover values in the absence of disturbance. Hence, PS remains fairly high from year to year, although the CC shows a significant decline. This result suggests that passive tolerance, i.e., persistence and slow growth of herbs under the canopy, may also be involved, together with inhibition, as mechanisms of successional changes in this field. Removal of the canopy of *S. canadensis* has a positive effect on both recruitment of fall species, which begins earlier than in control plots, and on growth in cover of spring colonizers whose cover increases significantly over values for control plots in some species (see also Armesto & Pickett, 1985).

Fields dominated by *Solidago canadensis* seem to represent a widespread and long-lasting stage in early secondary succession in eastern North America (Bard, 1952; Mellinger, 1972; Werner *et al.*, 1980; Messina, 1982; Keever, 1983). Reports of 10–20 yr duration of the *Solidago* stage are not uncommon (Keever, 1983), and *Solidago* species may become dominant as early as the 5th year. The rapid and concerted clonal spread of this species (Smith & Palmer, 1976) together with its growth in height, which leads to the establishment of a dense 1.5 m tall canopy, explain the important role of *Solidago* in controlling many early successional communities (Mellinger, 1972; Keever, 1983).

Undisturbed plots show little change between the 7th and the 8th year, as measured by the PS index

(Fig. 2). It can be hypothesized that the establishment of dominance by *S. canadensis* prevents major successional turnover from year to year. The fact that floristic composition changes significantly in the same period (Fig. 1) suggests that the potential for a change in community structure exists, but only when the canopy of *S. canadensis* is removed can this change take place. Remarkable structural changes in oldfields dominated by *S. canadensis* following defoliation by host-specific beetle species of the genus *Trirhabda* (Messina & Root, 1980; Messina, 1982) suggest that natural agents may promote this change. Consistent with this idea, McBrien *et al.* (1983) have reported a decrease in cover of *S. canadensis* from 70 to 1% within 1 yr following heavy defoliation and suggest that insect outbreaks causing this damage may not be uncommon. Acceleration of successional change due to the action of herbivores such as grazers has also been documented in marine intertidal systems (Sousa, 1980; Turner, 1983b; Lubchenko, 1983). Other processes that may also promote successional change in *Solidago*-dominated vegetation could be simultaneous death of clonal populations or unusually dry years causing a thinning of the overstorey.

Conclusion

The oldfields studied illustrate two early successional stages where different mechanisms can lead to species replacement and transition to a subsequent successional stage. In the younger field, replacement of the dominant occurs as a consequence of the die back of *Ambrosia artemisiifolia*, the dominant summer annual, and its replacement by winter annuals. The presence of *Ambrosia*, and probably any other summer annual, is not necessary for this change to take place. In the older field, the reduction in resource levels (i.e., light, soil moisture) that results from the establishment of a closed canopy of *S. canadensis* apparently inhibits vegetational change, in spite of the continuous invasion by some species through propagule dispersal. Structural changes in this vegetation are probably caused by openings in the canopy, due to herbivory or senescence of clones. This leads to an increase in abundance of a different species assemblage and, thereby, to successional turnover. Thus, which mechanisms of species replacement operate at a

particular time and place in succession depends largely on (1) the life history and growth form of the dominant species of the site (e.g., annual vs. perennial life cycle, canopy-forming vs. understory species, clonal vs. nonclonal, etc.), (2) the life history characteristics, dispersal mode and growth form of potential occupants of the site, (3) the probability of occurrence of natural disturbance, and (4) the magnitude and timing of that disturbance. The contrast in the results of comparisons between years in the younger and older fields, and the different patterns of change following disturbance in each field, illustrate the multiplicity of mechanisms operating in early secondary succession.

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