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Dynamics of associations between plants in ten old fields during 31 years of succession

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Summary

1. The pattern of significant associations between plants was examined in ten old fields during 31 years of succession by calculating rank correlations for species pairs in each old field during each sample year. Three hypotheses were tested concerning the dynamics of species interactions through succession, and correspondence was explored between the pattern of association and published results from field and glasshouse experiments.

2. The proportion, number and level of significance of associations between plants all declined with time. Annuals and biennials had a higher portion of significant associations and more positive associations than perennial species. Plant species involved in many significant associations and implicated as actively interacting with other species were generally neither native nor the most abundant.

3. Seventy per cent of the species analysed in the present study that had also been used in field and glasshouse experiments demonstrating competition reported in the literature, were involved in significant and repeated negative pairwise associations. However, only 33% of species used in field and glasshouse experiments demonstrating allelopathy showed such correspondence. Grasses may be major inhibitory species because they were involved in many significant negative plant associations although they did not achieve high abundance in these old fields.

4. *Lonicera japonica* and *Rosa multiflora* were woody species involved in many negative associations and may play major roles by inhibiting later successional species.

5. Investigations into the role of species interactions during succession may focus productively on those relatively few species that are strongly associated. The timing and the consequences of these associations may illumunate how interaction mechanisms such as competition and alleopathy structure successions.

Key-words: association analysis, Buell succession study, competition and allelopathy, life forms

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Introduction

The role and importance of species interactions in determining community processes has been debated for decades (Egler 1954; Thompson 1982). Debate concerning the role of species interactions has been central in successional theory as well (Pickett & McDonnell 1989) and several models of succession have implicitly assumed that plant–plant interactions were of primary importance in determining successional patterns (Clements 1916; Connell & Slatyer 1977; Tilman 1985). The experimental investigation of the role of plant–plant interactions during succession, however, has been of short duration and focused on only a few species (Hils & Vankat 1982; Armesto & Pickett 1986).

To examine the role and importance of plant–plant interactions in succession more fully, we explore all associations among plant species in ten old fields during 31 years of succession. The focus will be on species pairs that have repeated significant associations, and may therefore be interacting. This is done because the role of species interactions in succession may be a function of the individual species that are interacting (Gleason 1926; Myster & Pickett 1988) and not a composite of species found on the site (Clements 1916). In addition, the following three hypotheses will be tested by comparison with the pattern of association between plants.

Hypothesis 1. During succession there is an increase in the proportion, number and significance level of associations between species (O'Connor & Aarssen 1987). This prediction is made because of the increase in the number of species interactions and in the intensity of interactions found with successional time in some seres (Bazzaz 1979; Parrish & Bazzaz 1982).

Hypothesis 2. Significant associations should be less common among annuals and biennials than among perennials. Early-successional species have broader niches than later species and may interact with less frequency (Bazzaz 1975; Pickett & Bazzaz 1978; Parrish & Bazzaz 1982).

Hypothesis 3. It is abundant, native old-field species that are most involved in significant associations during succession. Abundant species may be functionally dominant (Pickett 1982; Crawley 1986) and interacting. Native species may have developed specific interactions with other species during their evolution (Marks 1983).

Competition and allelopathy are mechanisms of plant–plant interaction that have been demonstrated in field and glasshouse experiments. However, these mechanisms, if they occur, may do so only during part of a succession. Also, species involved in these interactions may be present for longer periods than the interaction persists (Pickett 1982; Keever 1983). Correspondence between pattern of association between species in the field and the outcome of experiments from field and glasshouse reported in the literature will be explored to determine if mechanisms shown in controlled experiments are reflected in real successions.

Woody plants, under-investigated experimentally, eventually dominate old fields in the eastern USA (Keever 1983; Myster & Pickett 1992). The mechanisms regulating woody-plant populations in old fields were a central guiding question in establishing the long-term succession study that we analyse (Buell *et al.* 1971), and the encouragement of woody species by thinning treatments (Armesto & Pickett 1985) shows that woody species do interact with other old-field plants. In addition, trees in old fields have a non-random, clumped spatial distribution (Myster & Pickett 1992) which implies that species interactions between them are common (Greig-Smith 1983). Possible interactions involving woody and herbaceous species are explored using association analysis.

Study site and methods

The study site, William L. Hutcheson Memorial Forest Center (HMF), is located approximately 1 km east of East Millstone, Somerset County, New Jersey, USA (40°30′N, 74°34′W). HMF includes ten old fields (The Buell–Small Succession Study [BSS]; Buell *et al.* 1971; Pickett 1982; Myster & Pickett 1988, 1989) which have been sampled in late July every year since abandonment in 1958. Each of the ten old fields contains 48 permanent, 2·0-m × 0·5-m plots arranged in a grid. The percentage of the surface area of each plot covered by each species was visually estimated with the aid of a sampling frame during each sample period. Plant nomenclature follows Gleason & Cronquist (1963).

ASSOCIATIONS BETWEEN SPECIES

Association analysis was used as a diagnostic tool to illuminate possible species interactions (Kershaw 1959; Turkington, Cavers & Aarssen 1977). A Spearman rank-correlation coefficient (Ludwig & Reynolds 1988), a measure of association and covariation, was computed between each species pair in each of the 217 old-field-years (an old-field-year = data sampled in one old field in 1 year) of the BSS. This coefficient is a non-parametric test (Ludwig & Reynolds 1988) based on ranks of percentage cover rather than on the percentage cover values themselves which did not fit a normal distribution. In addition, this analysis on ranks does not give undue weight to extreme values (Greig-Smith 1983). The species used in the association analysis were those found in at least 10 of the 48 plots in any one old-field-year and plots with zeros for both species were not used in the computation (Ludwig & Reynolds 1988). This study includes 92% of the species present and 95% of the total cover of all old fields over the entire span of the BSS study. If significant associations are not evenly distributed among species, old fields or years, then they may be clumped between certain species pairs. In those cases, the clumping pattern implicates interaction between the species because it reduces the confounding influences of old-field habitat, vegetation patch and year of sampling. The focus on the pattern of clumping between species also reduces the possible need to adjust the significance level due to the large number of computations.

To summarize the data, all significant associations (+ and ++ for positive, − and = for negative) for all ten old fields are presented in 6-year periods: years 1–6, 7–12, 13–18, 19–24 and 25–31 (see Appendices). These generally represent periods of dominance for differing life-form groups (Pickett 1982; Myster & Pickett 1992). These tables contain all significant pairwise associations between species in all ten old fields and each of 6 years, so 60 significant associations are possible in each plant–plant cell of the Appendices and multiple entries are common. A species had to be in at least 10 associations with other plant species in a period over all 10 old-fields to be included in the Appendices. Because fields were abandoned in different years (Myster & Pickett 1989), fewer than 10 old-fields were sampled in later years, and species involved in fewer than 10 associations are included in Appendices 3–5. The minimum limit of associations was adjusted to be proportional to the number of fields missing. Both species and plot ordination has been performed on the BSS data previously and has revealed a close relationship between species composition, variance in abundance and last crop planted before abandonment (Myster & Pickett 1988, 1990). To test statistically for differences between association type, repeated-measures analysis (Hand & Taylor 1987) was performed on PCA ordination (SAS 1985) scores of association type percentages. Analysis of variance was not performed because it would confound time with group effects.

Analysis of pattern cannot unambiguously show mechanism (Greig-Smith 1983), and a significant positive or negative association has three interpretations: (i) both of the associating species could have similar or dissimilar environmental requirements; (ii) other species could be affecting both associating species and the effects could be indirect (Farrell 1991); or (iii) species are interacting directly (Greig-Smith 1983). The last interpretation is implicated by a repeated pattern of association between the same species in many old fields and over successional time. Because environmental variables change through time and are also likely to differ between old fields, in this case interaction of species could not be due only to similar or dissimilar environmental requirements. Effects of third species, if present, should be shown in the pattern of association of species groups.

Lastly, correspondance was explored between published studies in the ecological literature investigating species interactions between old-field plant species found in the BSS and the generated association pattern. No field experiments were done by the authors directly to compare with interactions suggested by the pattern analysis.

Results

HYPOTHESIS 1

There was a mixture of significant positive, significant negative and non-significant associations over time (Appendices 1–5). The associations were not evenly distributed between all species and were clumped, so certain species may have been actively interacting while most were not. The proportion of species showing significant positive and negative associations compared to those showing no significant associations declined with time, as shown by repeated-measures analysis of PCA scores using these proportions (Table 1; $F = 4{\cdot}02$, $P < 0{\cdot}03$). In addition, the raw number of significant associations and the strength of significance both declined with time (Table 2). This does not support the contention

Table 1. Proportion of plant species pairs that showed no significant association, significant positive association and significant negative association through succession in the old-field permanent plots at Hutcheson Memorial Forest, New Jersey

	Association sign (%)		
Year	Positive	Negative	None
1	7	16	77
2	7	18	75
3	8	15	77
4	8	15	77
5	9	14	77
6	8	17	75
7	11	17	72
8	14	13	73
9	10	14	76
10	13	16	71
11	12	15	73
12	14	18	68
13	16	10	74
14	12	10	78
15	13	7	80
16	14	8	78
17	15	8	77
18	15	9	76
19	9	7	84
20	10	6	84
21	7	6	87
22	8	9	83
23	6	7	87
24	7	8	85
25	6	6	88
26	8	4	88
27	8	2	90
28	5	5	90
29	6	5	89
30	6	3	91
31	7	4	89

Table 2. The raw number of significant associations and strength of significance of Spearman coefficients between plant species found in the BSS plots (2·0-m × 0·5-m permanent plots in 10 old-field sites in New Jersey)

		% significant at	
Years	Number of associations	$P = 0{\cdot}01$	$P = 0{\cdot}001$
1–6	147	71	29
7–12	118	73	27
13–18	57	75	25
19–24	52	75	25
25–31	39	76	24

that plant–plant interactions are more common or increase in strength later in succession (Bazzaz 1979; Pickett & Bazzaz 1978; Parrish & Bazzaz 1982) assuming interactions require consistent association.

HYPOTHESIS 2

The rejection of hypothesis 1 may be due in part to the response of species of similar life history, because short-lived species appear earlier in the sere than longer-lived species. In relation to perennial plant species, annuals and biennials had a higher proportion of significant associations compared to non-significant associations and relatively more significant positive associations compared to significant negative associations (Table 3). This could suggest that interactions in general and positive interactions in particular involving annuals and biennials are more common than interactions involving perennials.

HYPOTHESIS 3

The most abundant species in the BSS and the most obvious successional sequence includes the annuals *Ambrosia artemisiifolia* and *Digitaria sanguinalis*; the herbaceous perennials *Erigeron annuus*, *Plantago lanceolata*, *Chrysanthemum leucanthemum*, *Trifolium pratense*, *Hieracium pratense*, *Poa pratensis* and *Poa compressa*; and woody perennials *Rhus glabra* and *Lonicera japonica* (Pickett 1982). However, the pattern of species association (see Appendices) suggests a very different successional sequence of species that may interact strongly in the BSS old fields: the biennial *Daucus carota*; the herbaceous perennials *Dactylis glomerata*, *Oxalis stricta*, *Plantago lanceolata*, *Plantago rugelii*, *Hieracium pratense*, *Fragaria virginiana* and *Solidago juncea*; and the woody perennials *Lonicera japonica* and *Rosa multiflora*.

Table 3. Percentage of plant species pairs that showed significant positive association, significant negative association and no association for species of the four major life-form groups during old-field succession in permanent plots at Hutcheson Memorial Forest, New Jersey

Association type	Annuals	Biennials	Perennials Herbaceous	Perennials Woody
Positive	11	12	4	5
Negative	6	7	6	8
None	83	81	90	87

Most of the species in both the sequence defined by abundance and the sequence defined by association are not native to the site. Introduced species comprise 60% of the total species in early BSS succession and that percentage decreases as succession proceeds (Pickett 1982). Also later in succession, native species form a larger proportion of significant associations than introduced species (Table 4).

CORRESPONDENCE OF PUBLISHED EXPERIMENTS WITH ASSOCIATION ANALYSIS

Demonstration in the field and glasshouse of species interactions creates the possibility that those same species may interact during real successions. Therefore, we searched the ecological literature (top 20 journals 1965–present), aided by computer data focusing on published experiments involving old-field plant species, and looked for correspondence between those results and the pattern of association.

The following species show negative associations and have been shown to interact in allelopathic inhibition experiments: *Erigeron annuus* inhibiting *Ambrosia artemisiifolia* (Numata, Kobayahi & Ohga 1973 and Appendix 1), and *Agropyron repens* inhibiting many old-field species (Rice 1979; Duke 1985 and Appendix 1). Alternatively, the following species do not show significant negative associations in the BSS succession but have been shown to interact in allelopathic inhibition experiments: *Solidago canadensis* (Smith 1969), *Aster pilosus* inhibiting *Ambrosia artemisiifolia* and *A. artemisiifolia* inhibiting *Convolvulus sepium* (Quinn 1974).

The following species show negative associations

Table 4. Percentage of plant species pairs that showed significant positive association, significant negative association and no association for native vs. introduced species in permanent plots in old fields at Hutcheson Memorial Forest, New Jersey

	Years 1–6	7–12	13–18	19–24	25–31
Native species					
Positive association	6	10	15	6	6
Negative association	7	3	7	6	3
No association	87	87	78	88	91
Introduced species					
Positive association	5	10	7	3	2
Negative association	9	5	7	3	1
No association	86	85	86	94	97

and have been shown to interact in plant–plant competition experiments: *Agropyron repens* with *Oxalis stricta* (Hamilton & Buchholtz 1955 and Appendix 1), *Poa pratensis* with *Hieracium pratense* (Appendices 2 and 3) and *Trifolium pratense* (Appendix 2), the grasses *Agropyron repens* and *Dactylis glomerata* with *Rumex actosella* (Appendix 2) and *Poa pratensis* with *Plantago lanceolata* (Appendix 2; all in Sagar & Harper 1961). Alternatively, in spite of field evidence for plant–plant competition in the following species, they do not show significant negative associations: *Ambrosia artemisiifolia* with *Agropyron repens* and *Agropyron repens* with *Plantago lanceolota* (Miller & Werner 1987), *Solidago graminifolia* with *Solidago canadensis* (Putwain & Harper 1970) and *Solidago canadensis* with other old-field species (Armesto & Pickett 1986; Werner, Bradbury & Gross 1980). Based on our comprehensive search of the ecological literature, we conclude that of old-field and glasshouse experiments demonstrating competition and sharing species found in our data set, 70% of those studies showed significant and repeated negative associations between the same species. However, that was true in only 33% of old-field and glasshouse experiments demonstrating allelopathy.

The pattern of positive associations show *Daucus carota* forming many strong positive associations with other species (Appendix 2). In addition, the presence of *Daucus* is facilitated by *Aster* spp. (Allen & Forman 1976) and other old-field species (Dale 1974). However, positive associations are rare in the BSS for grasses and legumes compared to other areas (Aarssen, Turkington & Cavers 1979). Also, *Dactylis* probably does not form facilitative relationships with weed species before abandonment (Vengris 1953) because there were no positive associations between *Dactylis* and BSS old-field species after abandonment.

WOODY AND HERBACEOUS ASSOCIATIONS

Significant associations involving woody species were not present until period 3 (Appendix 3) when woody species first become prominent in the BSS (Myster & Pickett 1992). These woody species were involved in repeated significant associations of the same sign in a time period: *Lonicera japonica* had negative associations with *Fragaria virginiana*, *Hieracium pratense* and *Solidago juncea* (Appendix 3); *Parthenocissus quinquefolia* had positive associations with *Solidago graminifolia* (Appendix 3) and *Rhus radicans* (Appendix 4); *Juniperus virginiana* had a negative association with *Solidago juncea* (Appendix 4); *Parthenocissus* had a negative association with *Solidago rugosa* (Appendix 4); *Rosa multiflora* had negative associations with *Fragaria virginiana*, *Solidago graminifolia* and *Solidago juncea* (Appendix 4) and *Juniperus virginiana* had a positive association with *Rhus radicans* (Appendix 5).

The following pairs of herbaceous species showed repeated significant associations of the same sign: *Oxalis stricta* and *Convolvulus sepium* in periods 1 and 2 (+ association), *Solanum carolinense* and *Convolvulus sepium* in periods 1 and 2 (+), *Oxalis stricta* and *Daucus carota* in periods 1 and 2 (+), *Aster pilosus* and *Hieracium pratense* in periods 2 and 3 (+), *Poa pratensis* and *Hieracium pratense* in periods 2 and 3 (−), *Achillea millefolium* and *Fragaria virginiana* in periods 2, 4 and 5 (+), *Achillea millefolium* and *Hieracium pratense* in periods 2 and 5 (+), *Achillea millefolium* and *Solidago juncea* in periods 4 and 5 (+), *Fragaria virginiana* and *Hieracium pratense* in periods 3, 4 and 5 (+) and *Lonicera japonica* and *Solidago juncea* in periods 3 and 4 (−). In addition, these species showed repeated significance with an alternation of sign, therefore implying that interactions may change sign with time: *Trifolium pratense* and *Solanum carolinense* between periods 1 and 2, *Oxalis stricta* and *Trifolium pratense* between periods 1 and 2, *Daucus carota* and *Hieracium pratense* between periods 2 and 4 and *Solidago graminifolia* and *Parthenocissus quinquefolia* between periods 3 and 4.

Discussion

Early old-field succession at HMF includes canopy species, limited by nutrients and water, overtopping subcanopy species limited primarily by light (Carson & Pickett 1990). Canopy species reduce the abundance of subcanopy species, and subcanopy species interact more strongly with canopy species than with each other (Carson & Pickett 1990). The dynamics of BSS species associations and, by implication, species interactions reflect this changing structure of HMF old fields during succession. Of frequently associated species, canopy species showed negative associations and subcanopy species showed positive associations. The dominant negatively interacting species, *Lonicera* and *Rosa*, form or are a part of the canopy which shades out other species (Pickett 1982). The many negative associations involving *Dactylis* imply that it is a strong competitor (Kershaw 1959). *Dactylis* is implicated as a key species because it persists in the BSS old fields for 5 years after abandonment, inhibits annuals and biennials, and alters successional pathways for up to 8 years after abandonment (Myster & Pickett 1988, 1990). Species that form many positive associations (*Fragaria*, *Oxalis*, *Hieracium*) are subcanopy species which may persist by dividing resources. These species possess great variation in growth form and reproductive mode (Gleason & Cronquist 1963). Such niche differentiation is also seen in *Daucus*. The stout taproot of *Daucus* may allow it to share resources with herbs that have more superficial root systems.

Patterns of association suggest that species interactions change through succession. This may be due in part to changes in nutrient gradients (Thompson 1982; Tilman 1988) during BSS succession (Pickett 1982). Initially a few successful species may compete for the same resources, while later many species partition different resource patches or parts of gradients (Bazzaz 1975; Carson & Pickett 1990). Therefore, the strength of interaction would decrease with time, as was shown in the decline during succession in the number of significant associations and the strength of those associations.

The proportionately greater number of significant associations for annuals and biennials compared to perennial species is consistent with broader niches in early successional plants compared to later succession (Parrish & Bazzaz 1982). Also, diversity increases in the BSS (Pickett 1982) as niches become narrower and there is more niche partitioning (Bazzaz 1975; Carson & Pickett 1990). Perhaps because later invading species are limited to unoccupied areas, negative associations between invading and established species and positive associations between later invading species are common.

The dominance of introduced non-native species, especially in early BSS succession, agrees well with studies at other sites (Denslow 1985). Many of these introduced species are also important in defining successional pathways. In the first 7 years, the BSS succession is characterized by the variation in abundance of *Dactylis glomerata*, in the next 6 years by the variation in abundance of *Hieracium pratense* and in the next 9 years by the variation in abundance of *Rosa multiflora* and *Toxicodendron radicans* (Myster & Pickett 1990).

There is a closer correspondence between the pattern of association and experiments showing competitive interactions than between the pattern and experiments showing allelopathic interactions (cf. Keever 1983). However, competition may be easier to establish than allelopathy because allelopathic mechanisms may be specific to both site and species (Williamson 1990).

The dynamics of species interactions during succession have been modelled by Connell & Slatyer (1977); the validity of these models remains an important question (Farrell 1991). The pattern of association is different from what might be expected if the single net effect (Connell, Nobel & Slatyer 1987) models of inhibition, facilitation or tolerance described this succession totally. However, the passive-tolerance model which explains successional patterns as the meshing of life-history patterns (Pickett, Collins & Armesto 1987; Myster & Pickett 1988) is best supported by the pattern of plant associations. Most species were not significantly associated with many other species (Armesto & Pickett 1986). In addition, the tolerance model many become even more representative of the BSS as succession proceeds, because less-significant associations were seen with time.

It may be most reasonable to view these models as interactions between individual species instead of describing groups of species or entire successional seres (Pickett, Collins & Armesto 1987; Farrell 1991). In that case, our results imply further complexity because many early successional species change in sign of association with different later successional species and members of the same early successional assemblage do not show the same sign of association with later species. Our results do not support models that predict that all plants interact strongly during succession and that those interactions structure their communities (Clements 1916). Instead, we argue that succession is a species-specific and individualistic process (Myster & Pickett 1988).

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References

Aarssen, L.W., Turkington, R. & Cavers, P.B. (1979) Neighbour relationships in grass-legume communities. II. Temporal stability and community evolution. *Canadian Journal of Botany*, **57**, 2695–2703.

Allen, E.B. & Forman, R.T.T. (1976) Plant species removals and old-field community structure and stability. *Ecology*, **57**, 1233–1243.

Armesto, J.J. & Pickett, S.T.A (1985) Experiments on disturbance in old-field plant communities: impact on species richness and abundance. *Ecology*, **66**, 230–240.

Armesto, J.J. & Pickett, S.T.A. (1986) Removal experiments to test mechanisms of plant succession in old-fields. *Vegetatio*, **66**, 85–93.

Bazzaz, F.A. (1975) Plant species diversity in old-field successional ecosystems in southern illinois. *Ecology*, **56**, 485–488.

Bazzaz, F.A. (1979) The physiological ecology of plant succession. *Annual Review of Ecology and Systematics*, **10**, 351–371.

Buell, M.F., Buell, H.F., Small, J.A. & Siccama, T.G. (1971) Invasion of trees and secondary succession on the New Jersey Piedmont. *Bulletin of the Torrey Botanical Club*, **98**, 67–74.

Carson, W.P. & Pickett, S.T.A. (1990) Role of resources and disturbance in the organization of an old-field plant community. *Ecology*, **71**, 226–238.

Clements, F.E. (1916) Plant succession: an analysis of the development of vegetation. *Carnegie Institution of Washington, Publication* **242**.

Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, **111**, 1119–1144.

Connell, J.H., Noble, I.R. & Slatyer, R.O. (1987) On the mechanisms producing successional change. *Oikos*, **50**, 136–137.

Crawley, M.J. (1986) *Plant Ecology*. Blackwell Scientific Publications. Oxford.

Dale, H.M. (1974) The biology of Canadian weeds. 5. *Daucus carota*. *Canadian Journal of Plant Science*, **54**, 673–685.

Denslow, J.S. (1985) Disturbance-mediated coexistance of species. *The Ecology of Natural Disturbance and Patch Dynamics* (eds S.T.A. Pickett & P.S. White), pp. 307–323. Academic Press, New York.

Duke, S.O. (1985) *Weed Physiology*, Vol. I. *Reproduction and Ecophysiology*. CRC Press, Boca Raton, Fla.

Egler, F.E. (1954) Vegetation science concepts. 1.Initial floristic composition a factor in old-field vegetation development. *Vegetatio*, **4**, 412–417.

Farrell, T.M. (1991) Models and mechanisms of succession: an example from a rocky intertidal community. *Ecological Monographs*, **61**, 95–113.

Gleason, H.A. (1926) The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club*, **53**, 7–26.

Gleason, H.A. & Cronquist, A. (1963) *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*. D. Van Nostrand, New York.

Greig-Smith, P. (1983) *Quantitative Plant Ecology*. University of California Press, Berkeley and Los Angeles.

Hamilton, K.C. & Buchholtz, K.P. (1955) Effect of rhizomes of quackgrass (*Agropyron repens*) and shading on the seedling development of weedy species. *Ecology*, **36**, 304–308.

Hand, D.J. & Taylor, C.C. (1987) *Multivariate Analysis of Variance and Repeated Measures*. Chapman and Hall, New York.

Hils, M.H. & Vankat, J.L. (1982) Species removals from a first-year old-field community. *Ecology*, **63**, 705–711.

Keever, C. (1983) A retrospective view of old-field succession after 35 years. *American Midland Naturalist*, **110**, 397–404.

Kershaw, K.A. (1959) An investigation of the structure of a grassland community. II. The pattern of *Dactylis glomerata*, *Lolium perenne* and *Trifolium repens*. *Journal of Ecology*, **47**, 31–53.

Ludwig, J.A. & Reynolds, J.F. (1988) *Statistical Ecology*. John Wiley, New York.

Marks, P.L. (1983) On the origin of the field plants of the northeastern United States. *American Naturalist*, **122**, 210–228.

Miller, T.E. & Werner, P.A. (1987) Competitive effects and responses between plant species in a first-year old-field community. *Ecology*, **68**, 1201–1210.

Myster, R.W. & Pickett, S.T.A. (1988) Individualistic patterns of annuals and biennials in early successional old-fields. *Vegetatio*, **78**, 53–60.

Myster, R.W. & Pickett, S.T.A. (1989) The Buell successional study at Hutcheson Memorial Forest. *Permanent Plotter*, **3**, 2–3. (Published as part of the Newsletter of the Vegetation Section, Ecological Society of America. Tempe, Arizona.)

Myster, R.W. & Pickett, S.T.A. (1990) Initial conditions, history and successional pathway in ten contrasting old fields. *American Midland Naturalist*, **124**, 125–133.

Myster, R.W. & Pickett, S.T.A. (1992) Effects of palatability and dispersal mode on spatial patterns of tree seedlings in old fields. *Bulletin of the Torrey Botanical Club*, **119**, 125–132.

Numata, M., Kobayashi, A. & Ohga, N. (1973) Studies on allelopathic substances concerning the formation of the urban flora. *Fundamental Studies in the Characteristics of Urban Ecosystems* (ed. M. Numata), pp. 59–64. Yokomona, Tokoyo.

O'Connor, I. & Aarssen, L.W. (1987) Species association patterns in abandoned sand quarries. *Vegetatio*, **73**, 101–109.

Parrish, J.A.D. & Bazzaz, F.A. (1982) Niche responses of early and late successional tree seedlings on three resource gradients. *Bulletin of the Torrey Botanical Club*, **109**, 451–456.

Pickett, S.T.A. (1982) Population patterns through twenty years of old-field succession. *Vegetatio*, **49**, 45–59.

Pickett, S.T.A. & Bazzaz, F.A. (1978) Organization of an assemblage of early successional species on a soil moisture gradient. *Ecology*, **59**, 1248–1255.

Pickett, S.T.A., Collins, S.L. & Armesto, J.J. (1987) Models, mechanisms and pathways of succession. *Botanical Review*, **53**, 335–371.

Pickett, S.T.A. & McDonnell, M.J. (1989) Changing perspectives in community dynamics: A theory of successional forces. *Trends in Ecology and Evolution*, **4**, 241–245.

Putwain, P.D. & Harper, J.L. (1970) Studies in the dynamics of plant populations. III. The influence of associated species on populations of *Rumex acetosella* and *R. acetosa* in grasslands. *Journal of Ecology*, **58**, 251–264.

Quinn, J.A. (1974) *Convolvulus sepium* in old-field succession on the New Jersey Piedmont. *Bulletin of the Torrey Botanical Club*, **101**, 89–95.

Rice, E.L. (1979) Allelopathy — an update. *Botanical Review*, **45**, 15–109.

Sagar, G.R. & Harper, J.L. (1961) Controlled interferences with natural populations of *Plantago lanceolata*, *P. major* and *P. media*. *Weed Research*, **1**, 163–176.

SAS (1985) *SAS User's Guide: Statistics*, Version 5 edn. SAS Institute, Cary, N.C.

Smith, A.P. (1969) *The effect of goldenrod and asters on germination and growth of old-field herbs*. MS thesis, Duke University, Durham, N.C.

Thompson, J.N. (1982) *Interaction and Coevolution*. John Wiley, New York.

Tilman, D. (1985) The resource ratio hypothesis of succession. *American Naturalist*, **125**, 827–852.

Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, N.J.

Turkington, R.A., Cavers, P.B. & Aarssen, L.W. (1977) Neighbor relationships in grass-legume communities. I. interspecific contacts in four grassland communities. *Canadian Journal of Botany*, **55**, 2701–2711.

Vengris, J. (1953) Weed populations as related to certain cultivated crops in the Connecticut River Valley, Mass. *Weeds*, **2**, 125–134.

Werner, P.A., Bradbury, I.K. & Gross, R.S. (1980) The biology of Canadian weeds. 45. *Solidago canadensis* L. *Canadian Journal of Plant Science*, **60**, 1393–1409.

Williamson, G.B. (1990) Allelopathy, Koch's postulates, and the neck riddle. *Perspectives on Plant Competition* (eds J.B. Grace & D. Tilman), pp. 143–162. Academic Press, New York.

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Appendices

Significance level of Spearman coefficients between plant species found in the BSS plots (2·0-m × 0·5-m permanent plots in the old fields in New Jersey). A single + or − refers to an association of strength 0·05 > P > 0·01 and ++ or = refers to 0·01 > P > 0·001. All significant pairwise associations in all fields are shown; 60 symbols are possible in each cell and multiple entries are common.

Appendix 1. Years 1–6

Species number and name	Species number of associating species																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1 *Acalypha rhomboidea*																	
2 *Agropyron repens*	−−																
3 *Ambrosia artemisiifolia*	+=	++															
4 *Aster ericoides*																	
5 *Aster pilosus*		−−	−														
6 *Barbarea vulgaris*	++	−	−														
7 *Convolvulus sepium*	−		+−			++											
8 *Dactylis glomerata*		−−− ==		−−−		−											
9 *Daucus carota*								−									
10 *Erigeron annuus*			== +−		−−		+	−−	−								
11 *Hieracium pratense*		++			+					−= +							
12 *Lychnis alba*			+−			+ + ++		−									
13 *Oxalis stricta*	++	−=	−−	−	+	+ + +	+ + ++	=−−	+ + +	+	−	++					
14 *Plantago lanceolata*			++	== +			+−	−−	−	++	+	+	++				
15 *Plantago rugelii*	+	−	−−−	++		−	−	−−	+	+ + +=			+ + −	+ + +=			
16 *Rumex acetosella*		== −	+	+	+=			== −			=		++ ++ + +	−− +=	+		
17 *Solanum carolinense*	+				++		++			++−	−		++				
18 *Trifolium pratense*			=	−			+		++	−+− ==			== −−	+−	+ −−		−−

Appendix 2. Years 7−12

Species number and name	Species number of associating species														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1 *Achillea millefolium*															
2 *Ambrosia artemisiifolia*															
3 *Aster ericoides*															
4 *Aster pilosus*	+	+													
5 *Convolvulus sepium*	−	++ −		++ +											
6 *Daucus carota*	++		++ +−	++ + + −	++										
7 *Fragaria virginiana*	++			++ −−		−−									
8 *Hieracium pratense*	++ +		++ −−−−	++ ++ + +	++−	−−	−−−								
9 *Oxalis stricta*		+	+	+	++	++ +		−							
10 *Plantago lanceolata*	++		+	+−		++ ++		+	−						
11 *Plantago rugelii*			+	+ +	+−	++ + ==									
12 *Poa pratensis*		=		−−− =				−−− −		==					
13 *Rumex acetosella*			− +	++	−	−					++	−			
14 *Solanum carolinense*				+	++ ++	++−		+							
15 *Solidago nemoralis*			+	−−	+	++ +− =	−−	−							
16 *Trifolium pratense*		+	−−		+			+−− −−−	++		−−	−−−		++ +	

Appendix 3. Years 13–18

Species number and name	Species number of associating species									
	1	2	3	4	5	6	7	8	9	10
1 *Achillea millefolium*										
2 *Aster pilosus*										
3 *Convolvulus sepium*		++								
4 *Fragaria virginiana*	+	++	+							
5 *Hieracium pratense*	++ +−	++ + + +		++ + +						
6 *Lonicera japonica*		−	−	== − − −	− − −					
7 *Oxalis stricta*				+						
8 *Parthenocissus quinquefolia*		+		++						
9 *Poa pratensis*		−	++	==	− − − −	−				
10 *Solidago graminifolia*			+	+	==		+	++ + +	+ +	
11 *Solidago juncea*	+	−	−	−	−	− − − =	+			

Appendix 4. Years 19–24

Species number and name	Species number of associating species												
	1	2	3	4	5	6	7	8	9	10	11	12	13
1 *Achillea millefolium*													
2 *Daucus carota*													
3 *Fragaria virginiana*	++ +	+											
4 *Hieracium pratense*		++	++ ++										
5 *Juniperus virginiana*			–										
6 *Lonicera japonica*		+ – = =			–								
7 *Parthenocissus quinquefolia*			–		+								
8 *Poa compressa*			– –										
9 *Rhus glabra*		+											
10 *Rhus radicans*							++	+					
11 *Rosa multiflora*			– – – – –		–		+	–					
12 *Solidago graminifolia*			+				= =				– – –		
13 *Solidago juncea*	++ ++				– – –	= =		+	+	–	– – – –		
14 *Solidago rugosa*							– – –			+	–		

Appendix 5. Years 25–31

Species number and name	Species number of associating species													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 *Achillea millefolium*														
2 *Apocynum cannabinum*														
3 *Fragaria virginiana*	++ +	+−												
4 *Hieracium pratense*	+		++ ++											
5 *Juniperus virginiana*	−			−										
6 *Lonicera japonica*	−		+											
7 *Parthenocissus quinquefolia*			+−											
8 *Poa compressa*														
9 *Rhus radicans*	−				++									
10 *Rosa multiflora*					−	+−	+		−					
11 *Solidago canadensis*								+	−		−			
12 *Solidago graminifolia*								+		−	+			
13 *Solidago juncea*	++											+		
14 *Solidago rugosa*			=				==	+	+−−			+		
15 *Solidago serotina*										−−				==