SUCCESSION IN OLD-FIELD PLANT COMMUNITIES:
EFFECTS OF CONTRASTING TYPES
OF NUTRIENT ENRICHMENT

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Abstract. We investigated the effects of monthly nutrient applications on succession in two old-field plant communities. Succession was monitored for 3 yr in 1-yr (younger) and 4-yr (older) experimental plots. Three 0.1-ha plots in each old field were treated with sludge, three with fertilizer, and two were left as untreated controls.

In the younger community, herbaceous perennials and winter annuals replaced summer annuals by the 3rd yr of succession in control plots. Summer annuals, however, dominated enriched plots throughout the study. Species richness was significantly higher in enriched plots than in control plots during the 1st yr, but was significantly lower than control plots thereafter. Annual aboveground net primary productivity (ANPP) was significantly greater in enriched plots than in controls in the 1st yr, but the converse occurred in the 3rd yr. The type of nutrient enrichment affected ANPP; sludge plots had significantly lower ANPP than fertilizer plots in the 1st and 3rd yr.

In the older community, two summer annuals and a biennial displaced dominant perennial grasses in enriched plots. In contrast to the younger community, ANPP was consistently greater in nutrient-enriched plots than in controls, and nutrient enrichment did not alter species richness. The type of nutrient enrichment affected the older community in an opposite manner from the younger community; sludge plots had significantly greater ANPP than fertilizer plots in the 3rd yr. We concluded that the age and physiognomy of the old-field community, the type of nutrients applied, and the duration of enrichment, each influenced the course of succession; responses observed in the 1st yr of enrichment were not indicative of later trends.

Key words: fertilizer; nutrient enrichment; old fields; plant life histories; sludge; species richness; succession; summer annual; winter annual.

INTRODUCTION

This 3-yr study examined the effects of monthly application of two types of nutrients (fertilizer and sewage sludge) on two old-field plant communities with different age, physiognomy, and species composition. By using contrasting communities, we investigated how each responded to identical rates of nutrient application. Also, by comparing two types of nutrient enrichment (differing predominantly in their forms of nitrogen: organic vs. urea nitrogen), we determined how these different nitrogen forms affected succession. In this study, we focused only on the producer trophic level. The effects of heavy metals in the sludge applied to these fields have been reported elsewhere (Anderson et al. 1982, Anderson and Barrett 1982, Maly and Barrett 1984, Kruse and Barrett 1985).

The disposal of sewage sludge is a major environmental problem (Culliney and Pimentel 1986). An applied objective of this study was to evaluate old fields as potential sludge disposal sites. Previous studies have examined the effects of sludge on agricultural (e.g., Kelling et al. 1977a, b) and forest (e.g., Sopper and Kerr 1979) communities. Few studies, however, have investigated the effects of sludge on intermediate stages of succession such as old fields. Nitrogen fertilization of old fields increased the production of leaf material, which released nitrogen rapidly when decomposing (e.g., Vitousek 1983). The rapid release of nutrients from enriched sites in an ecologically safe form (e.g., N2) potentially could make old fields ideal communities for processing sewage waste products.

Nutrient enrichment experiments using old-field communities also provide an opportunity to test ecological theory about the role of resource availability for early plant community development. Nutrient amounts vary temporally and spatially in old-field plant communities (Robertson and Vitousek 1981, Tilman...
lived herbaceous and woody species. Tilman's experiments, however, were conducted on a variety of abandoned and disturbed fields already several years into secondary succession and differing in soil type and soil chemistry. It remains unclear if Tilman's findings relate directly to most younger nutrient-enriched old-field communities because early and late successional plant species differ in life histories (Pickett 1976, Bazzaz 1979), growth rates (Grime 1979), and their ability to assimilate different resources (Chapin 1980, Tilman 1986a). Thus, there is need to conduct an array of nutrient-enrichment experiments on early successional communities differing in soil type, age, physiognomy, and species composition to elucidate mechanisms of plant community development. This study addresses the following questions:

1) Does nutrient enrichment alter the relative abundances of summer annuals, winter annuals, biennials, and perennials for younger and older communities and within each year?
2) Does nutrient enrichment significantly affect seasonal patterns of aboveground standing crop biomass and annual aboveground net primary productivity?
3) Does nutrient enrichment significantly affect the seasonal pattern of species richness?

MATERIALS AND METHODS
Study site and experimental design
This study was conducted at the Miami University Ecology Research Center located near Oxford, Ohio, USA (39°30' N, 84°44' W). The soil is a Xenia silt-loam over limestone bedrock (Ohio Department of Natural Resources 1978). Soil pH (X ± se) was 5.1 ± 1.1 in the younger community and 5.6 ± 1.2 in the older community (mean of 24 soil samples for each community taken in July 1978). Two 0.8-ha old fields in the first (younger community) and fourth (older community) years of secondary succession (Fig. 1) each were subdivided into eight 0.1-ha plots and enclosed with sheets of 0.95 mm (20-gauge) galvanized steel to restrict stocked small-mammal populations (Anderson and Barrett 1982, Maly and Barrett 1984).

The younger field was plowed, disked, and a commercial fertilizer (12-12-12 N-P-K) applied at 336 kg·ha⁻¹·yr⁻¹ in October 1977. Winter wheat (Triticum aestivum var. Ranger) was sown at a rate of 22.6 kg/ha on 25 October 1977. Since no herbicides were applied and the wheat was not harvested, this agricultural community underwent secondary succession in 1978 and was similar floristically to the 1-yr-old fields described by Sweringa and Wilson (1972). Nutrient enrichment (sludge and fertilizer) commenced in May of the 1st yr of succession (1978) and continued for 3 yr. The older community was plowed and disked in early spring 1975. On 26 April 1975, each 0.1-ha plot was

FIG. 1. Aerial photograph (August 1978) of the 16 0.1-ha plots depicting the experimental design; F denotes fertilizer-treated, S denotes sludge-treated, and C denotes untreated control plots. The older old field had been out of cultivation 3 yr longer than the younger old field.
planted with seeds of a mixture of grasses consisting of 6.8 kg *Festuca elatior*, 11.3 kg *Poa pratensis* (perennials), and 4.5 kg *Secale* sp. (annual) (see Stueck and Barrett 1978 for details). Hence, we established a perennial pasture-type community (e.g., Mellinger and McNaughton 1975); these plots thus began secondary succession in 1975. Experimental enrichment commenced in May of the 4th yr of secondary succession (1978) and continued for 3 yr.

Treatments were assigned to experimental plots in a completely randomized design within both the younger and older fields (Fig. 1). Three replicate plots of each community type were treated with dried sludge, three with commercial fertilizer, and two were left as untreated controls. Cyclone hand-operated seeders were used to apply sludge and fertilizer homogeneously at monthly intervals (May–September). The sludge was Milorganite (6-2-0 N-P-K), a heat-dried aerobically digested sludge, and it was applied to each 0.1-ha sludge plot at recommended annual rates of 8960 kg ha⁻¹ year⁻¹ (Shea and Stockton 1975) divided equally between months. This represented an annual N addition of 538 kg/ha and P addition of 179 kg/ha. Details regarding the nutrient and heavy metal content of Milorganite have been previously reported (Furr et al. 1976, Anderson et al. 1982, Maly and Barrett 1984, Kruse and Barrett 1985). The alternative type of nutrient enrichment was urea-phosphate fertilizer (34-11-0 N-P-K) applied at the rate of 1570 kg ha⁻¹ year⁻¹ divided equally between months. This represented an annual addition of N at 534 kg/ha and of P at 173 kg/ha.

Upon land application, Milorganite contained primarily organic N (≥90%; Milwaukee Sewage Commission, Milwaukee, Wisconsin). This organic N is water insoluble and not immediately available for plant uptake. Only 40–50% of the organic N is mineralized during the first growing season (Magdoff and Amadon 1980, Parker and Sommers 1983, Fox and Axley 1985). Urea, however, is water soluble and rapidly available for plant uptake (Ting 1982).

**Vegetation analysis**

Vegetation was sampled at monthly intervals from April through October in 1978–1980. Aboveground plant biomass was harvested from four randomly selected 0.25 m² circular quadrats in each plot on each sampling date. Quadrats were located at least 2 m from enclosure walls to reduce edge effects. Standing vegetation was clipped at ground level, sorted to species, oven dried at 80°C for 72 h and weighed to the nearest 0.1 g.

Aboveground net primary productivity (grams per square metre per day) was computed by summing the increment of new plant biomass for each species between each monthly sampling date (Poole 1974). Mean productivity values were obtained by averaging values obtained from replicate plots. Annual aboveground net primary productivity (grams per square metre per year) for each plot was estimated by summing the peak biomass of each species (Malone 1968).

Species richness was the total number of plant species found within the four 0.25-m² quadrats per plot for each sampling date. Richness was expressed as the mean number of species per square metre for each treatment. Nomenclature follows Weishaupt (1971).

**Statistical analyses**

Community composition was defined by the vector \( P_i = (P_{i1}, P_{i2}, P_{i3}, P_{i4}) \), where \( P_{ij} \) is the relative abundance of summer annuals, winter annuals, biennials, and perennials. A single-factor MANOVA and Wilks’ criterion were used to determine whether \( P_i \) differed significantly among treatments. Since relative abundances sum to one (and thus are linearly dependent), the MANOVA was performed on the total number of vectors \( (P_{ij}) \) minus one (Morin 1983). Relative abundances were transformed angularly before analysis.

We used an ANOVA (General Linear Models [GLM]) and a Duncan’s Multiple Range Test to determine significant treatment differences in annual aboveground net primary productivity of the dominant plant species (Allen 1982). All tests (including the MANOVA) were based on three replicate plots each for the fertilizer and sludge treatments and two replicate plots for the controls. Data were log₁₀ transformed to reduce heteroscedasticity. ANOVA (GLM) and Duncan’s Multiple Range Tests were also used to determine significant treatment differences in annual aboveground NPP and species richness. Annual aboveground NPP data were log₁₀ transformed to eliminate a possible mean–variance relationship.

**Results and Discussion**

**Community composition and primary productivity**

In the younger community, *Ambrosia artemisiifolia, Chenopodium album, Cirsium arvense, Trifolium pratense, Setaria faberi,* and *Triticum aestivum* dominated both enriched and control plots in 1978 (Table 1). Annual aboveground net primary productivity (ANPP) of *A. artemisiifolia* and *S. faberi* was significantly higher in enriched plots than controls in 1978. In 1979 and 1980, species composition diverged between enriched and control plots. ANPP of *Aster pilosus, Potentilla norvegica, Trifolium pratense, Daucus carota, and Erigeron annuus* was significantly higher in control plots in 1979 (Table 1). *Aster pilosus* and *E. annuus* also had significantly greater ANPP values in control plots in 1980, whereas *Cirsium arvense* had significantly less ANPP. Conversely, *A. artemisiifolia* had significantly higher ANPP in enriched plots in 1979, and *Polygonum persicaria* and *S. faberi* had significantly greater ANPP in both 1979 and 1980. The type of nutrient enrichment (sewage sludge or fertilizer) affected species composition little throughout the study.
with the exception that productivity of *Ambrosia artemisiifolia* and *Chenopodium album* was significantly greater in fertilizer than sludge plots in 1978 and 1979, respectively, and *Ambrosia trifida* was significantly greater in fertilizer plots in 1979 and 1980.

Seasonal aboveground net primary productivity in the younger community was significantly higher in fertilizer plots than in either sludge or control plots during 1978 (Fig. 2). Total ANPP in the younger community (Table 1) also differed significantly between treatments (1978), with fertilizer plots exhibiting the greatest total productivity followed by the sludge plots. Seasonal aboveground NPP was greater for enriched plots only in July 1979 (Fig. 2), whereas total ANPP was not significantly different between treatments. By 1980, control plots had significantly greater NPP than sludge plots in July and significantly greater productivity than all enriched plots in April and October. Total ANPP for control plots was significantly greater than sludge plots, but not fertilizer plots (Table 1).

These unexpected results reflected the contrasting life histories and phenologies of the plants found in enriched vs. control plots in the younger community (Tables 1 and 2). The life histories of species in the control plots allowed temporal partitioning of the growing season, which did not occur in enriched plots. Specifically, the high productivity in July and October in control plots correlated with mid- and late-season peaks in the production of a winter annual (*Erigeron annuus*) and a herbaceous perennial (*Aster pilosus*),

### Table 2. Mean percent annual ANPP for summer annuals, winter annuals, biennials, and perennials in the younger field. Means for plots treated with fertilizer (F) and sludge (S) are based on three replicates; controls (C) are based on two replicates.

<table>
<thead>
<tr>
<th>Year</th>
<th>Life history*</th>
<th>Treatment</th>
<th>F</th>
<th>S</th>
<th>C</th>
<th>ANOVA</th>
<th>MANOVA</th>
</tr>
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<tbody>
<tr>
<td>1978</td>
<td>Summer annual</td>
<td>F</td>
<td>90.0</td>
<td>87.9</td>
<td>69.7</td>
<td>.023</td>
<td>.227</td>
</tr>
<tr>
<td></td>
<td></td>
<td>S</td>
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<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>C</td>
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<td>0.7</td>
<td>0.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Perennial</td>
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<td>11.4</td>
<td>29.8</td>
<td>.039</td>
<td></td>
</tr>
<tr>
<td>1979</td>
<td>Summer annual</td>
<td>F</td>
<td>68.8</td>
<td>74.1</td>
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<td>.049</td>
</tr>
<tr>
<td></td>
<td></td>
<td>S</td>
<td>1.1</td>
<td>0.2</td>
<td>7.6</td>
<td>.102</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>C</td>
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<td>24.0</td>
<td>.026</td>
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<tr>
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<td>58.7</td>
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<td></td>
</tr>
<tr>
<td>1980</td>
<td>Summer annual</td>
<td>F</td>
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<td>.002</td>
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<td></td>
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<td>22.8</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>C</td>
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<td>9.7</td>
<td>6.4</td>
<td>.007</td>
<td></td>
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<td>Perennial</td>
<td>22.4</td>
<td>41.9</td>
<td>64.3</td>
<td>.007</td>
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</tr>
</tbody>
</table>

* Species included in each category are identified in Table 1.
† The ANOVA column indicates levels of significance from univariate tests for effects of each treatment on life history type. The MANOVA gives conservative levels of significance (F, Wilks’ criterion) for simultaneous differences among all treatments within each year for life history types.
respectively. These seasonal peaks are typical for these two species in this region (Hopkins and Wilson 1974). Summer annuals, which dominated enriched plots, declined in NPP after their peak in August (Fig. 2).

Relative abundances of summer annuals, winter annuals, biennials, and perennials in the younger community were not significantly different between treatments in 1978 (Table 2). In 1979, however, treatments diverged significantly ($P < .05$) and by 1980 contrasted sharply ($P < .01$, Table 2). Summer annuals dominated or shared dominance in enriched plots, whereas winter annuals and perennials dominated control plots (Tables 1 and 2).

In the older community, Dactylis glomerata, Festuca elatior, Phalaris arundinacea, Poa pratensis, and Solidago canadensis dominated both enriched and control plots in 1978 (Table 3). Also, ANPP of $F$. elatior and $P$. pratensis was significantly higher in enriched plots than control plots in 1978. In 1979 and 1980, several new species established in enriched plots. Ambrosia artemisiifolia, Setaria faberii, Barbarea vulgaris, and $S$. canadensis shared dominance in enriched plots in 1980, whereas $F$. elatior, $P$. pratensis, and $S$. canadensis maintained dominance in control plots. ANPP of $S$. faberii was significantly higher in enriched plots than in control plots in 1979 and 1980. Sludge and fertilizer plots seldom differed in composition with the exception of $F$. elatior and $A$. artemisiifolia, which had greater ANPP in fertilizer plots in 1978 and in 1979 and 1980, respectively.

The older community contrasted with the younger in that enriched plots exhibited significantly greater

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**Fig. 2.** Net primary productivity in the younger and older plant communities. Arrows (**) indicate dates of nutrient enrichment. Significant differences between treatments within a sampling date are indicated by different letters ($P < .05$, ** = $P < .01$).
Table 3. Mean annual aboveground net primary productivity (ANPP, g·m⁻²·yr⁻¹) of dominant plant species in the older (4-yr) old-field community.* Means for plots treated with fertilizer (F) and sludge (S) are based on three replicates; controls (C) are based on two replicates.

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Life history†</th>
<th>1978</th>
<th>1979</th>
<th>1980</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>S</td>
<td>C</td>
<td>F</td>
</tr>
<tr>
<td>Ambrosia artemisiifolia</td>
<td>SA</td>
<td>0+</td>
<td>0+</td>
<td>0+</td>
</tr>
<tr>
<td>Barbaraea vulgaris</td>
<td>B</td>
<td>0+</td>
<td>0+</td>
<td>0+</td>
</tr>
<tr>
<td>Dactylis glomerata</td>
<td>P</td>
<td>105+</td>
<td>48+</td>
<td>36+</td>
</tr>
<tr>
<td>Festuca elatior</td>
<td>P</td>
<td>350+</td>
<td>177+</td>
<td>125</td>
</tr>
<tr>
<td>Phalaris arundinacea</td>
<td>P</td>
<td>270+</td>
<td>200+</td>
<td>128</td>
</tr>
<tr>
<td>Poa pratensis</td>
<td>P</td>
<td>120+</td>
<td>100+</td>
<td>75+</td>
</tr>
<tr>
<td>Polygonum persicaria</td>
<td>SA</td>
<td>0+</td>
<td>0+</td>
<td>0+</td>
</tr>
<tr>
<td>Setaria faberii</td>
<td>SA</td>
<td>11+</td>
<td>13+</td>
<td>0+</td>
</tr>
<tr>
<td>Solidago canadensis</td>
<td>P</td>
<td>120+</td>
<td>112+</td>
<td>21+</td>
</tr>
<tr>
<td>Vernonia altissima</td>
<td>P</td>
<td>0+</td>
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<td>Total</td>
<td>1124+</td>
<td>747+</td>
<td>465</td>
<td>1407+</td>
</tr>
</tbody>
</table>

* Means with the same letter (within years and rows) are not significantly different (P > .05) as determined by ANOVA (GLM) and Duncan’s Multiple Range Test. Only species with ANPP > 20 g·m⁻²·yr⁻¹ during any year of the study are included.
† P = perennial; B = biennial; SA = summer annual.

NPP (both seasonal and annual) than control plots throughout the study (Fig. 2, Table 3). Fertilizer plots produced significantly more than sludge plots in 1978; however, sludge plots produced significantly more than fertilizer plots in 1980 (Table 3). Since the nitrogen in sludge is mineralized slowly, residual nitrogen from 1978 and 1979 increased nitrogen levels in 1980 and, consequently, annual productivity (Kelling et al. 1977b, Magdoff and Amadon 1980). This slow mineralization rate probably accounted for the lower levels of seasonal and annual NPP in sludge plots relative to fertilizer plots in 1978 for both the younger and older communities. Overall, in contrast to species composition, the effect of nutrient enrichment on biomass and NPP depended not only on the duration of enrichment, but also on the type of nutrient enrichment and on the community type.

Life histories were not significantly different (P > .05) between treatments during the study in the older community (Table 4), even though several summer annuals increased significantly in ANPP in enriched plots. Species including Barbaraea vulgaris, Polygonum persicaria, and S. canadensis had high rates of ANPP but were patchily distributed within and between plots making community-level comparisons difficult.

Overall, enrichment shifted relative abundances towards summer annuals and away from perennials for both the younger and older plant communities. Previous old-field enrichment studies, however, have found that perennials were favored by nutrient enrichment (e.g., Bakelaar and Odum 1978, Pratt 1984, Tilman 1984).

One might argue that a toxic property of the fertilizer or sludge caused the changes in species composition. We think this unlikely because: (1) the number of species in an old field the fertilizer would have had to affect in a similar manner was large (see Reed 1977); (2) nutrients were applied at monthly intervals, and single applications were of relatively small amounts; (3) nutrients as potential toxicants in sludge are released over a period of several months (Ryan et al. 1973); (4) under field conditions the heavy metals in sludge rarely reach levels that are toxic to plants (Kelling et al. 1977a, Soon et al. 1980); and (5) toxic effects attributed solely to urea-phosphate fertilizer were unlikely because changes in fertilizer and sludge plots were nearly identical.

**Community richness**

Species richness in enriched plots of the younger community was significantly greater than in control plots on several dates during the 1978 growing season (Fig. 3). Conversely, control plots exhibited significantly greater species richness than enriched plots thereafter; this is consistent with previous findings for old-field communities (Mellinger and McNaughton 1975, Bakelaar and Odum 1978, Pratt 1984). In the older community, however, no significant differences in species richness were found (Fig. 3).

In the younger community, increased rates of NPP by Ambrosia artemisiifolia, Cirsium arvense, Setaria faberii, and Polygonum persicaria resulted in a dense canopy (W. Carson, personal observation, and Fig. 1) that shaded out plants of lower stature. Conversely, the canopy did not close on control plots, where greater species richness occurred. Armesto and Pickett (1985) found that dense canopies in old fields reduce species richness in the subcanopy. Tilman (1984, 1987) found that nutrient enrichment greatly enhanced this effect.

In the older community, species richness did not change in enriched plots. In the control plots, Festuca elatior and Poa pratensis dominated and formed a thick mat, which promoted low species richness. Within enriched plots, two summer annuals and a biennial established during the experiment, but we observed no significant change in species richness (Fig. 3). Again,
Table 4. Mean percent annual ANPP for summer annuals, biennials, and perennials in the older community. Means for plots treated with fertilizer (F) and sludge (S) are based on three replicates; controls (C) are based on two replicates.

<table>
<thead>
<tr>
<th>Year</th>
<th>Life history*</th>
<th>Treatment</th>
<th>ANOVA</th>
<th>MANOVA</th>
</tr>
</thead>
<tbody>
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<td></td>
<td></td>
<td>F</td>
<td>S</td>
<td>C</td>
</tr>
<tr>
<td>1978</td>
<td>Summer annual</td>
<td>5.6</td>
<td>2.5</td>
<td>2.3</td>
</tr>
<tr>
<td></td>
<td>Biennial</td>
<td>0.2</td>
<td>0.2</td>
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</tr>
<tr>
<td></td>
<td>Perennial</td>
<td>94.2</td>
<td>97.3</td>
<td>97.7</td>
</tr>
<tr>
<td>1979</td>
<td>Summer annual</td>
<td>41.1</td>
<td>12.3</td>
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</tr>
<tr>
<td></td>
<td>Biennial</td>
<td>4.4</td>
<td>5.0</td>
<td>1.6</td>
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<td></td>
<td>Perennial</td>
<td>54.5</td>
<td>83.8</td>
<td>98.4</td>
</tr>
<tr>
<td>1980</td>
<td>Summer annual</td>
<td>58.2</td>
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<td></td>
<td>Biennial</td>
<td>14.8</td>
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<tr>
<td></td>
<td>Perennial</td>
<td>27.0</td>
<td>54.0</td>
<td>97.0</td>
</tr>
</tbody>
</table>

* Species included in each category are identified in Table 3.
† The ANOVA column indicates levels of significance from univariate tests for effects of each treatment on life history type. The MANOVA gives conservative levels of significance (F, Wilks’ criterion) for simultaneous differences among all treatments within a year for life history types.

The effect of enrichment on a community-level parameter (i.e., species richness) differed depending on duration of enrichment and community type. Type of nutrients apparently had little effect on species richness.

Mechanisms of species replacement and persistence

Three years of nutrient enrichment altered species composition in both the younger and older communities; summer annuals replaced (older community) or excluded (younger community) perennials. Typically,
herbaceous perennials and winter annuals suppress or replace summer annuals during the 2nd and 3rd yr of secondary succession by preempting resources, especially nutrients (Raynal and Bazzaz 1975, Peterson and Bazzaz 1978, Bazzaz 1979). In our study, resource preemption apparently occurred in the control plots of the younger community where summer annuals were suppressed and/or replaced mainly by Erigeron annuus and Aster pilosus during the 2nd yr of succession. In enriched plots, however, nutrient preemption probably did not occur because summer annuals persisted.

Tilman (1987) found that nitrogen fertilization played a major role in determining plant community composition, species richness, and successional dynamics in old-field communities in Minnesota. Our results are generally consistent with the theory of plant competition for limiting resources developed by Tilman (1982, 1985, 1986a) that old-field plants compete for resources such as nitrogen along gradients, and that each species is a superior competitor at a different point along the gradient. Miller and Werner (1987) also suggest that all the species in an old-field community are limited by and competing for the same resource or resources resulting in a hierarchy of species' competitive ability.

In the older field, enrichment resulted in the establishment of two summer annuals with high relative growth rates, high nutrient absorption rates, and high photosynthetic rates (Bazzaz 1979, Grime 1979, Tilman 1986a); these traits are well adapted to fertile environments (Chapin 1980). Grime (1979) predicted that such summer annuals could exploit environments already occupied by perennial species. We found that nutrient enrichment resulted in the establishment of highly productive species within both community types. Their establishment resulted in communities that resembled earlier stages of secondary succession characterized by annual species.

Interestingly, new species often do not become dominant where nutrient subsidies are discontinued after one growing season (Mellinger and McNaughton 1975, Reed 1977, Bakelaar and Odum 1978, Pratt 1984). We observed community divergence in the younger field and species establishment in the older field during the 2nd and 3rd yr of continuous nutrient enrichment. Thus, nutrient enrichment experiments should be designed to evaluate competitive effects on a long-term basis. Our results indicate that altering resource levels on a continuous basis can change the initial trajectory or pathway of secondary succession.

Disturbance and herbivory have also been found to be important regulatory mechanisms in old-field communities (e.g., Armento and Pickett 1985). Huston and Smith (1987) noted that small-scale disturbances regularly open up new space and mediate competition. We did not observe any small-scale disturbances, however, that would explain plant community changes or treatment differences found during this 3-yr study.

Herbivorous small mammals have been found to be primarily responsible for plant community changes in nutrient-enriched plots (e.g., Tilman 1983). Although meadow voles (Microtus pennsylvanicus), an important small-mammal herbivore in old-field communities (e.g., Golley 1960), were equally stocked (five adult pairs) in each enclosure during June of each year (Anderson and Barrett 1982, Maly and Barrett 1984), no consistent differences in small-mammal population dynamics were found between treatments or between community types that would explain plant community changes attributed to nutrient enrichment.

In summary, nutrient enrichment in old-field communities resulted in the establishment of summer annuals that exhibit high relative growth rates, high nutrient absorption rates, and high photosynthetic rates (Bazzaz 1979, Grime 1979, Tilman 1986a). Thus, these nutrient-enriched plots were dominated by competitive and ruderal species well adapted to habitats of high fertility (Grime 1977, Chapin 1980).

Resource management implications

An objective of this investigation was to determine if old fields were suitable sites for sludge disposal, especially since land application as a means of disposal has received much attention (e.g., Sopper and Kerr 1979). Sludges from communities with minimal amounts of industrial chemicals and other materials can be used effectively as fertilizer for crop production (e.g., Pahren et al. 1979, Pahren 1980, Jacobs 1981). Sludges from municipalities with large amounts of industrial chemicals, however, are unsuitable for crop application because of the potential for bioaccumulation of heavy metals into human food chains (see e.g., Culliney and Pimentel 1986 and references therein). Sludge application to forest communities also poses problems (e.g., Sopper and Kerr 1979) mainly because it often releases nitrate nitrogen to ground water in excess of United States Environmental Protection Agency (EPA) standards (Hook and Kardos 1978, Burton and Hook 1979).

Applying dried sludge to intermediate stages of succession (e.g., old fields) may represent an ecologically safer means of sewage waste disposal because (1) nitrate leaching was within EPA standards in an old-field site (Hook and Kardos 1978); (2) heavy metal accumulation in small mammals did not affect their reproduction and survivorship within our old-field plots (Anderson et al. 1982, Maly and Barrett 1984); and (3) health hazards from biological pathogens can be minimized by applying dried sludge (Wallis et al. 1984).

Our data suggest that old fields deserve consideration as potential disposal sites because plant species with high rates of growth and nutrient assimilation dominated or persisted in sludge plots. Thus, nitrate input from sludge may be more rapidly assimilated and temporarily stored in living and dead biomass in old fields than in later successional stages. For example, Foster
et al. (1980) found that summer annuals, especially *Ambrosia artemisiifolia*, could greatly reduce nitrate levels in an old-field community by taking up and storing nitrogen during early succession. They speculated that most of the nitrogen taken up is probably readily available to plants in subsequent years.

It could be argued that old fields are not as appropriate as forests for sludge disposal because of low biomass storage per energy flow (B/E) relative to forests (Odum 1969). Storage, however, may not be the key to effective use of natural ecosystems for disposal of sewage wastes. Sludge applied to old fields is rapidly decomposed, mineralized, and either recycled (see above) or released, primarily in ecologically safe gaseous form (primarily N2; Haynes and Sherlock 1986). Applying sludge to old fields reduces leaching of nitrate nitrogen because early successional plant species are highly adapted to efficiently taking up large amounts of nutrients (see Introduction). Also, leaching losses of nitrate nitrogen are further minimized by applying sludge in a dried form, as we did in our study. This slows release of nitrate nitrogen and times its release to periods when moisture is available (see Haynes 1986) for plant growth and nitrogen uptake. An additional advantage of applying dried sludge is that it can be stored during winter and applied during the growing season using large mechanized equipment. Because of the high rates of assimilation, decomposition, and denitrification in old fields, more sludge probably can be processed per unit time in this manner than can be stored in living and dead plant biomass in forests and periodically harvested. Also, application of sludge to forests is invariably done by spray irrigation (e.g., Sopper and Kardos 1973. Sopper and Kerr 1979), which maximizes the potential for leaching losses of nutrients (see above). Thus high rates of processing and safe release of nutrients may make early successional stages optimal sites for sludge disposal.

Additional research is needed to evaluate critically the effects of nutrient enrichment on rates of assimilation, decomposition, and denitrification before major sludge disposal decisions are made. Also, potential is great for increasing ecological understanding from these and related studies. For example, changes in plant species composition may enhance or retard nitrate leaching. Investigations of the timing and amount of nutrient enrichment, therefore, may lead to methods of manipulating plant community composition such that leaching losses are minimized. Tests of ecological theory should be incorporated into such studies both to increase ecological understanding and potentially to provide long-term solutions to important environmental problems (see Barrett 1985, 1987).

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