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Effects of mowing and fertilization on succession in an old-field plant community

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Summary

1 We studied the effects of five years of mowing and one year of fertilization on the succession in an old-field plant community on a shallow soil over coarse gravel in northern Switzerland.

2 After nine years of succession the vegetation was dominated by the invasive species *Solidago altissima.* Although already a considerable number of woody species were present, annuals and short-lived perennials (especially the invasive *Erigeron annuus*) were still an important component of the vegetation.

3 A canonical correspondence analysis showed that the treatments had significant effects on the overall composition of the vegetation. Fertilization strongly reduced the number of woody species in unmown quadrats, but increased it slightly in mown plots. In contrast, the number of annual species was highest in mown but unfertilized quadrats. Fertilization increased the cover of grasses, especially in mown plots, whereas cover of legumes was not influenced by fertilization, but increased strongly in response to mowing.

4 After five years of annual mowing the cover of the invasive perennial *S. altissima* was only 12% compared with 41% in unmown quadrats. There was a trend for fertilization to reduce the cover of S. altissima in unmown quadrats. The monocarpic *E. annuus* was not influenced significantly by either mowing or fertilization.

5 Addition of fertilizer resulted in a significant reduction of species richness already after one year. This was mainly a consequence of a decrease in the number of annual plants and of woody species. Mowing also reduced the total number of species. However, because mowing increased the evenness of the community, species diversity (H') was not affected.

Keywords: canonical correspondence analysis, diversity, *Erigeron annuus,* invasive species, nutrient effects, *Solidago altissima*

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Introduction

Old-field succession, i.e. the development of the vegetation in abandoned agricultural fields, has frequently been used as a model system for the study of vegetation processes and the fundamental mechanisms driving successions (e. g. Bazzaz 1968; Bakelaar & Odum 1978; Inouye *et al.* 1987; Tilman 1993; Wilson & Tilman 1995). One of the advantages of old-field succession as a model system is that succession proceeds much faster than in most other systems because of the mature soil and the often large seed bank in the soil (Whittaker 1975; Schmidt 1988). Therefore, distinctly different stages can be observed in the course of a few years and causal mechanisms can be studied by manipulative experiments.

The study of old-field successions is also becoming increasingly important because in Europe large areas of agricultural land are taken out of production as part of set-aside programmes (e. g. Greiler & Tscharntke 1990; Heißenhuber *et al.* 1994). In 1990/91 the percentage of the area of abandoned fields in Germany even exceeded the area of all German nature reserves (2.5% compared to 1.7%; Schmidt 1993). Hence, understanding the mechanisms that determine the structure and species composition of successional communities is of crucial importance for predicting changes in vegetation and conservation management (Miles 1987).

The development of the vegetation in an abandoned field presents a typical example of a secondary succession. In a temperate climate, old-field successions proceed generally from communities dominated by fast-growing, short-lived annuals to a vegetation consisting mainly of long-lived woody plants (e.g. Tilman 1988). Important factors influencing the course of secondary successions include the initial composition of the vegetation (Clements 1916; Egler 1954), mainly in form of a seed bank, the composition of neighbouring vegetation that may function as a source of diaspores (Miles 1987), the availability of nutrients (Mellinger & McNaughton 1975; Carson & Barrett 1988; Tilman 1988), and finally, active management measures like cutting, grazing and ploughing (Carson & Pickett 1990; Schmidt 1993).

Effects of experimental nutrient addition on secondary succession have been intensively studied in North America and Europe (Bornkamm & Hennig 1982; Tilman 1987, 1993; Carson & Barrett 1988; Schmidt 1988). Mowing, which involves not only the destruction of biomass, but also the removal of nutrients from the system, has also profound effects on old-field succession (Schmidt 1993).

Dominant species in North American old-field successions like *Solidago* spp. and *Erigeron* spp. (e.g. Bazzaz 1968) frequently play an important role as invasive neophytes also in Europe and can dominate certain stages of secondary successions (Zwölfer 1976; Voser 1983). These species can present a problem for set-aside schemes, if the aim is the development of species-rich communities consisting of native plants with a high value for conservation. Because of their clonal growth and the formation of dense stands some species of *Solidago* may even delay the succession towards a forest for a long time (Werner *et al.* 1980; Schmidt 1993).

This paper presents the results of an experimental study on the effects of five years of mowing and one year of fertilization on the succession in an old-field plant community dominated by the invasive species *Solidago altissima* and *Erigeron annuus.* Treatments were applied in a full factorial design that allowed the study of possible interactions. Specific questions were: (1) Do nutrient addition and mowing alter the relative abundance of functional groups that are typical for different stages of succession (e.g. annuals and woody species) and of trophic specialists like legumes? (2) Do nutrient enrichment and mowing affect the two invasive species? (3) Which effects have the treatments on species diversity?

Material and methods

STUDY SITE

The study was carried out in the nature reserve «Reinacherheide», c. 6 km south of Basel (47° 30' N, 7° 36' E; 280 m a. s. l.). The mean annual temperature in Basel is 9 °C, with a July mean of 18.5 °C and annual precipitation 790 mm (average 1961–1990, Swiss Meteorological Office). The length of the growing season is more than 220 days. At the study site only a thin layer of soil (c. 25 cm) covers a 10-m thick layer of calcareous gravel deposited by the river Birs. The pH of the A_h-horizon (0–25 cm) is 7.0 and that of the C-horizon (> 25 cm) 7.5 (Meyer 1992). The very stony and nutrient-poor soil quickly dries out during periods of low rainfall. The nature reserve was mainly established to protect species-rich dry grassland and dry scrubland, but it also contains some old fields. A detailed description of the flora and vegetation can be found in Moor (1962). Nomenclature follows Binz & Heitz (1990), except for *Solidago altissima* L. (often regarded as *S. canadensis* L., see Meyer & Schmid 1992).

THE EXPERIMENT

The study site was used as an arable field until 1982, when it was last planted with maize, and then abandoned. In the following years the two invasive plant species *Solidago altissima* and *Erigeron annuus* spread over the area. In August 1987 a large project was started to study the effect of mowing and fertilization on the demography of the two invasive species (see e. g. Meyer 1992; Egli 1994; Schmid & Dolt 1994; Wille 1994). This experiment provided also an opportunity to investigate the role of resource availability and disturbance by mowing for community development.

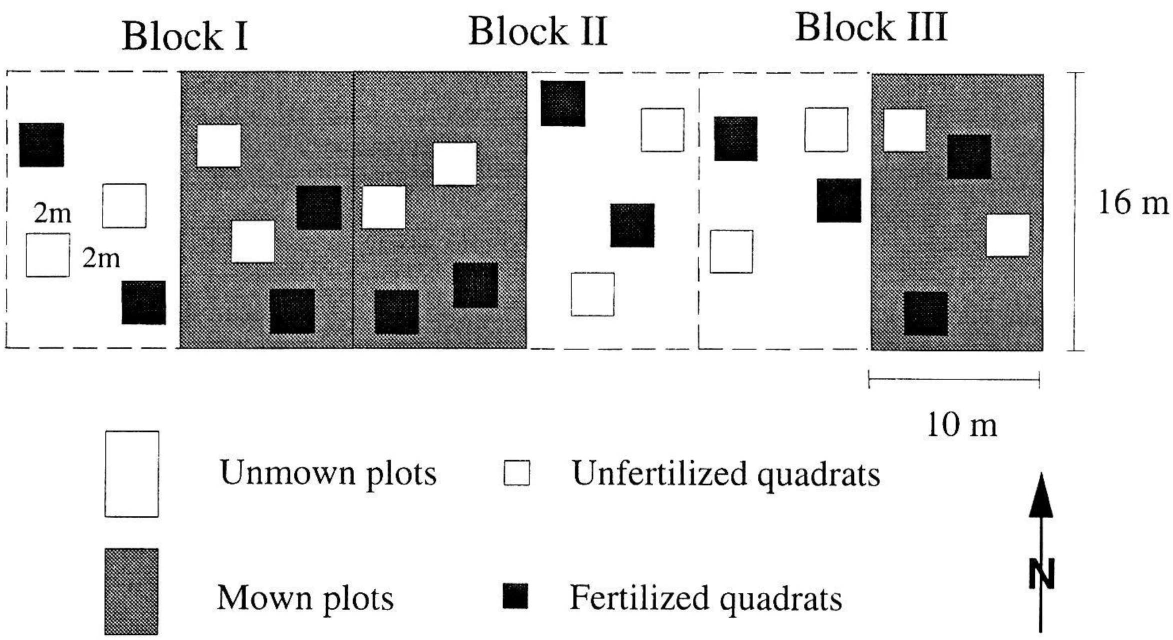

Fig. 1. Sketch of the experimental design of the study in the nature reserve 'Reinacherheide' near Basel. The design was a split-plot with three blocks consisting each of two plots, one of which was mown annually. In each plot four quadrats were established, half of which were fertilized. For the current study the vegetation in two quadrats per plot was analyzed.

The experimental design was a split-plot with three blocks that consisted each of two plots (each 10 m x 16 m, Fig. 1). One plot in each block was mown very short (5 cm) every year at the end of summer (August / September), starting in 1987. In spring 1991 four quadrats (2 m x 2 m) were established in each plot. Half of the quadrats were treated with liquid fertilizer (0.8 g N m^{-2}, 0.3 g P m^{-2}, 0.7 g K m^{-2}) in March, April and May 1991. In addition, solid fertilizer was applied in June 1991 and April 1992 (8 g N m^{-2}, 4 g P m^{-2}, 8 g K m^{-2}). The amount of nitrogen added was equivalent to c. 90 kg N ha^{-1} $year^{-1}$.

To analyze the effect of the treatments on the vegetation, the cover of all species was estimated in two quadrats per plot in June 1992. Cover values > 20 % were estimated to the nearest 5 %, cover values < 20 % to the nearest 1 %. To increase the precision of the estimate a wire quadrat of 1 % of the area of the study quadrats was used as a size reference. Three independent estimates were made and averaged.

DATA ANALYSIS

The data were analysed by analyses of variance. Because of the hierarchical split-plot design the effect of mowing was tested against the residual variance among plots, and the effect of fertilization and the interaction between fertilization and mowing against the residual variance among quadrats. All statistical analyses were carried out with the statistical package Genstat 5 (Payne *et al.* 1987). Overall changes in vegetational composition were analyzed with the two ordination techniques correspondence analysis (CA) and canonical correspondence analysis (CCA, program CANOCO; Ter Braak 1986, 1987). The significance of the ordination axes of the CCA was tested using the Monte Carlo permutation test available in CANOCO (Ter Braak 1987).

Results

After nine years of fallow a species-rich vegetation had developed in the study area. A total of 51 species were found in the study quadrats (total area 48 m^2). The vegetation consisted mainly of species characteristic for grasslands (e. g. *Poa trivialis, Taraxacum officinale, Galium album),* but contained also some typical weeds of arable fields (e. g. *Myosotis arvensis, Pastinaca sativa, Galium aparine),* and waste grounds (Table 1). In addition, species of woodlands (e. g. *Crataegus monogyna, Clematis vitalba, Acer platanoides)* and of forest edges (e. g. *Hypericum perforatum, Origanum vulgare)* occurred. Although large areas covered by dry calcareous grasslands were close (50 m), only two typical species of dry meadows were found frequently *(Euphorbia cyparissias* and *Medicago lupulina),* another *(Plantago media)* was very rare. The two invasive neophytes *Solidago altissima* and *Erigeron annuus* together covered on average more than 47 % of the area of the study quadrats.

There were strong effects of the treatments on the course of succession. The results of analyses of variance showed that different functional groups were influenced in different ways. The number of woody species was significantly lower in mown than in unmown quadrats (0.5 compared with 5.8 species, Table 2a, Fig. 2a). There was, however, a significant interaction between the effects of mowing and fertilization, i. e. the effect of fertilization on the number of woody species depended on the mowing regime. Fertilization strongly reduced the number of trees and shrubs in unmown quadrats (–3.3 species), but increased it slightly in mown plots (+0.4 species). In contrast, the number of annual species was highest in mown, but unfertilized quadrats (Fig. 2b). Fertilization significantly increased the cover of grasses (Fig. 2c), but

Table 1. Frequency (occurrence in 12 study quadrats) of plant species in an old field that had been abandoned since nine years. L, light indicator value; F, moisture indicator value; N, nitrogen indicator value (cf. Ellenberg et al. *1992)*

Species	Frequency	L F N	Species	Frequency	L F N
Erigeron annuus	12	7 6 8	*Achillea millefolium*	2	8 4 5
Poa trivialis	12	6 7 7	*Acer campestre*	2	5 5 6
Taraxacum officinale	12	7 5 7	*Acer pseudoplatanus*	2	4 6 7
Daucus carota	11	8 4 4	*Arrhenatherum elatius*	2	8 5 7
Hypericum perforatum	11	7 4 x	*Dactylis glomerata*	2	7 5 6
Solidago altissima	11	- - -	*Euonymus europaea*	2	6 5 5
Euphorbia cyparissias	10	8 3 3	*Geranium columbinum*	2	7 4 7
Medicago lupulina	10	7 4 x	*Plantago lanceolata*	2	6 x x
Myosotis arvensis	10	6 5 6	*Anthriscus sylvestris*	1	7 5 8
Pastinaca sativa	10	8 4 5	*Carpinus betulus*	1	4 x x
Origanum vulgare	9	7 3 3	*Cerastium brachypetalum*	1	9 3 2
Galium album	8	7 5 x	*Cerastium glomeratum*	1	7 5 5
Crataegus monogyna	7	7 4 3	*Convolvulus arvensis*	1	7 4 x
Crepis taraxacifolia	7	9 4 5	*Cornus sanguinea*	1	7 x x
Verbascum nigrum	7	7 5 7	*Fragaria vesca*	1	7 5 6
Vicia sativa	7	5 x x	*Heracleum sphondylium*	1	7 5 8
Galium aparine	5	7 x 8	*Lonicera xylosteum*	1	5 5 x
Acer platanoides	4	4 x x	*Lotus corniculatus*	1	7 4 3
Clematis vitalba	4	7 5 7	*Picris hieracioides*	1	8 4 4
Geum urbanum	4	4 5 7	*Plantago media*	1	7 4 3
Prunus spinosa	4	7 x x	*Poa pratensis*	1	6 5 6
Senecio erucifolius	4	7 3 4	*Prunus mahaleb*	1	7 3 2
Trifolium pratense	4	7 x x	*Rubus fruticosus agg.*	1	- - -
Bromus sterilis	3	7 4 5	*Scrophularia nodosa*	1	4 6 7
Ligustrum vulgare	3	7 x x	*Trifolium repens*	1	8 x 7
Thlaspi perfoliatum	3	8 4 2			

this effect was much stronger in mown plots (+20% cover) than in unmown plots (+4% cover; significant interaction between mowing and fertilization, s. Table 2b). Legumes were not significantly influenced by fertilization, but reacted very positively to mowing (+13% cover, Fig. 2d).

The statistical analyses indicated significant plot effects for the number of woody species, for the number of annual species, and for the total number of species present, indicating considerable spatial variation in community composition at the scale of the plots (10–20 m). This is either the result of variation in habitat conditions at this scale or the consequence of different distances of the plots to sources of seeds for colonization.

Of special interest was the reaction of the two invasive species *Solidago altissima* and *Erigeron annuus* to the treatments. Mowing in late summer had a strong negative influence on the rhizomatous perennial *S. altissima*. The cover of *Solidago* in mown quadrats was only 12% compared with 41% in unmown quadrats (Fig. 3, Table 3). The effect of fertilization was not significant, but there was a trend for fertilization to reduce the cover of *Solidago* in unmown quadrats.

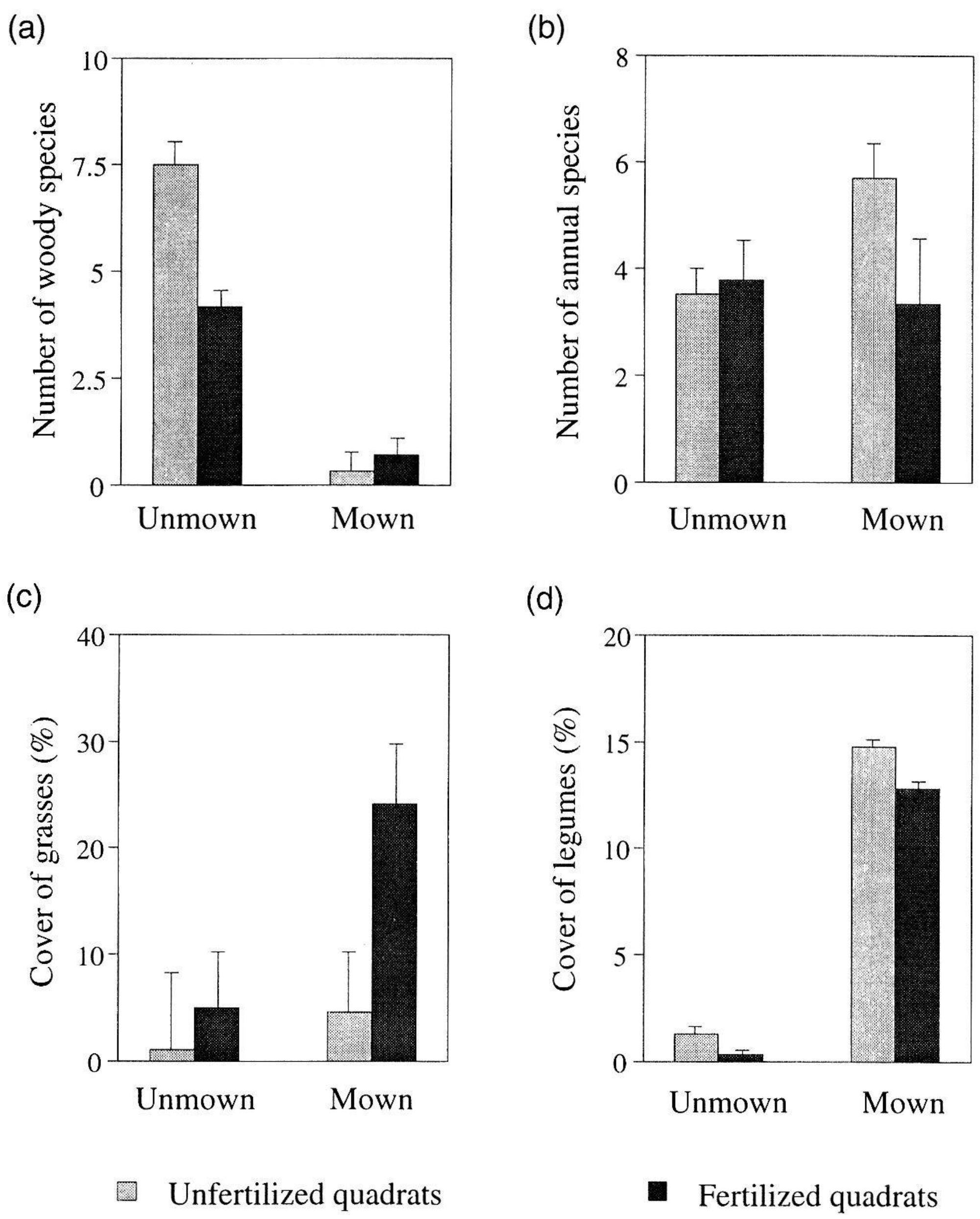

Fig. 2. *The effect of mowing and fertilization on different functional groups in an old-field succession: (a) number of woody species per quadrat, (b) number of annual species per quadrat, (c) cover of grasses, and (d) cover of legumes. Vertical bars denote one standard error.*

The other invasive species, the short-lived *Erigeron annuus,* was not influenced significantly by either mowing or fertilization.

A CA-ordination of the vegetation in the study quadrats indicated strong gradients in the vegetation, with eigenvalues for the first and second axis of 0.31 and 0.25, respectively. The first ordination axis, which indicated the main gradient in the vegetation, clearly separated unmown and mown quadrats (Fig. 4a). The eigenvalues of a CCA, in which the two treatments were used

Table 2. Results of analyses of variance of the effects of mowing and fertilization on different functional groups in an old field. (a) The number of woody and annual species per study quadrat, (b) the cover of grasses and legumes. (*), $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$

(a)		Number of woody species		Number of annual species	
Source of variation	df	SS	F	SS	F
Mowing	1	65.3	14.25**	2.1	0.54
Plot	4	18.3	22.00**	15.3	6.57*
Fertilization	1	2.5	12.00*	8.1	13.89*
Mowing x fertilization	1	6.7	32.00**	1.1	1.83
Plot x fertilization	4	0.8		2.3	

(b)		Cover of grasses		Cover of legumes	
Source of variation	df	SS	F	SS	F
Mowing	1	300.0	4.06	513.5	8.98*
Plot	4	295.3	2.30	228.8	0.38
Fertilization	1	404.5	12.59*	6.9	0.46
Mowing x fertilization	1	177.5	5.52(*)	0.4	<0.01
Plot x fertilization	4	30.6	1.31	599.9	

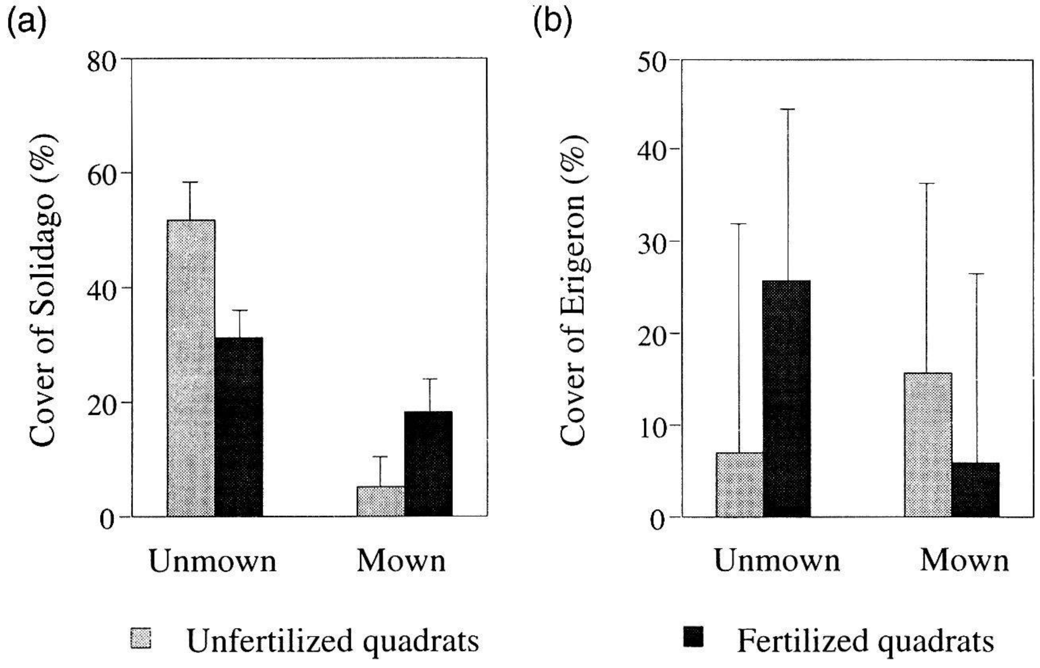

Fig. 3. Effects of mowing and fertilization on the two invasive plant species (a) Solidago altissima, and (b) Erigeron annuus. Vertical bars denote one standard error.

as environmental variables, were not much lower (0.23 and 0.18) than that of the CA, indicating that a large proportion of the variation in the composition of the vegetation could be accounted for by the two treatments. The effect of the treatments on the composition of the vegetation was significant *(P <* 0.03; Monte Carlo test of sum of eigenval-

***Table 3.** Results of analyses of variance of the effects of mowing and fertilization on the two invasive neophytes Solidago altissima and Erigeron annuus. (*), P < 0.1*

		Cover of *Solidago*		Cover of *Erigeron*	
Source of variation	df	SS	F	SS	F
Mowing	1	1633.3	4.64(*)	369.0	1.09
Plot	4	1407.3	3.31	1361.0	0.94
Fertilization	1	28.9	0.27	4.0	0.01
Mowing x fertilization	1	370.0	3.48	272.0	0.75
Plot x fertilization	4	425.1		1451.0	

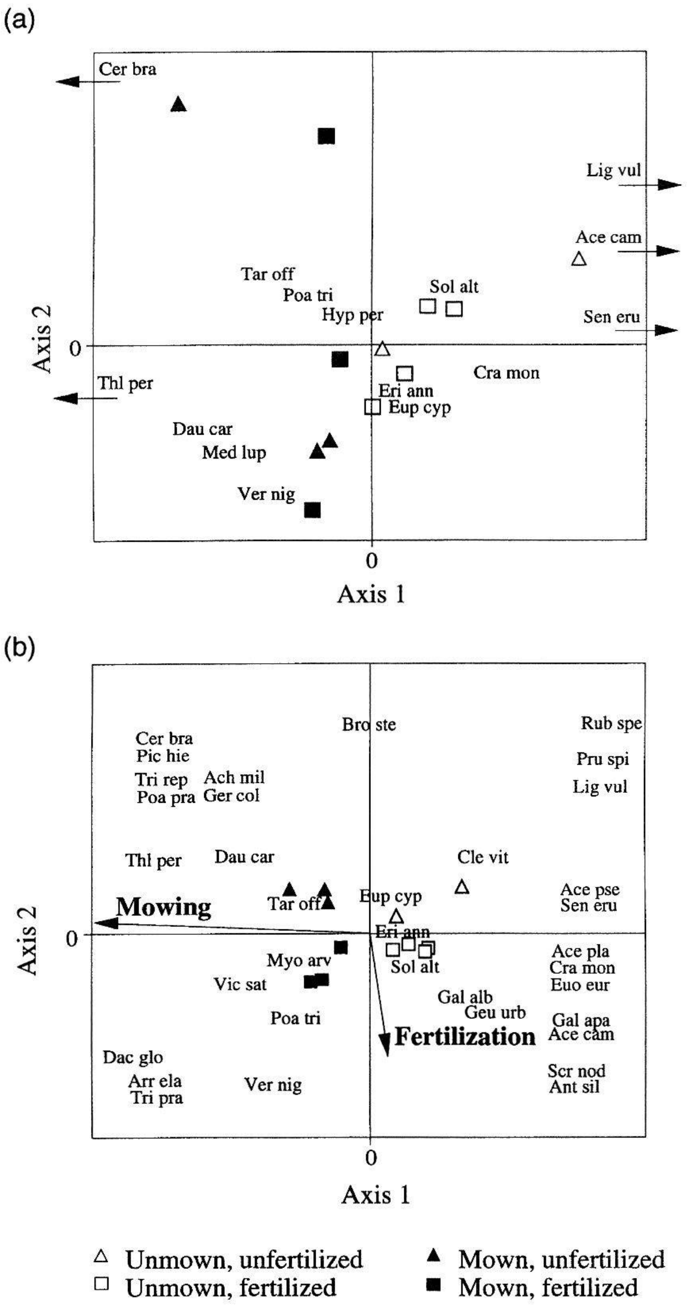

***Fig. 4.** Effect of mowing and fertilization on the vegetation of an old field. (a) Ordination diagram based on a correspondence analysis. The main (first) ordination axis separates mown and unmown quadrats. (b) Ordination diagram based on a canonical correspondence analysis with the two factors mowing and fertilization. Only species that occurred in more than one quadrat with a cover of more than 1% are presented; the species names have been abbreviated (see Table 1 for complete species names). Small arrows near species names indicate that their position is outside the presented part of the ordination diagram.*

Table 4. *Results of analyses of variance of the effects of mowing and fertilization on the diversity and dominance structure of the vegetation in an old-field. (*),* P < *0.10; *,* P < *0.05*

		Shannon Index (H')		Species number		Evenness	
Source of variation	df	SS	F	SS	F	SS	F
Mowing	1	0.164	2.27	70.08	6.95(*)	0.0531	10.10*
Plot	4	0.29	0.93	40.33	6.37*	0.0210	0.5
Fertilization	1	0.056	0.72	22.5	14.21*	0.0008	0.08
Mowing x fertilization	1	0.004	0.05	1.67	1.05	0.0004	0.04
Plot x fertilization	4	0.312		6.33		0.0420	

ues). The first axis of the CCA-ordination was highly correlated with the factor mowing ($r = -0.92$, Fig. 4b) and the second with the factor fertilization ($r = -0.92$). As indicated by its longer arrow, mowing had a stronger influence on the vegetation than fertilization.

Positively influenced by the mowing treatment, i.e. situated left in the diagram (Fig. 4b), were mainly species indicating conditions of high light, e.g. *Picris hieracioides, Achillea millefolium* and *Arrhenatherum elatius,* whereas woody species were negatively affected by mowing. Positively influenced by the fertilization treatment, i.e. situated at the bottom of the diagram, were species indicating high nutrient conditions (e.g. *Anthriscus sylvestris, Galium aparine, Verbascum nigrum).* Correspondingly, relevés of mown and fertilized quadrats are situated in the lower left of the diagram and those of unmown and unfertilized quadrats in the upper right quarter.

There were no effects of the treatments on the diversity of the community as measured by the Shannon index (H'). However, this was the consequence of opposite treatment effects on the two components of the Shannon index, i.e. on total number of species (S) and on evenness (H'/log S). The treatments influenced both the number of species and the dominance structure of the community. Mowing reduced the number of species in a 4-m^2 quadrat by 23% and fertilization by 12% (Fig. 5). In contrast, the evenness of the community was increased by mowing, but not influenced by fertilization. Thus, mowing reduced the differences in performance among species.

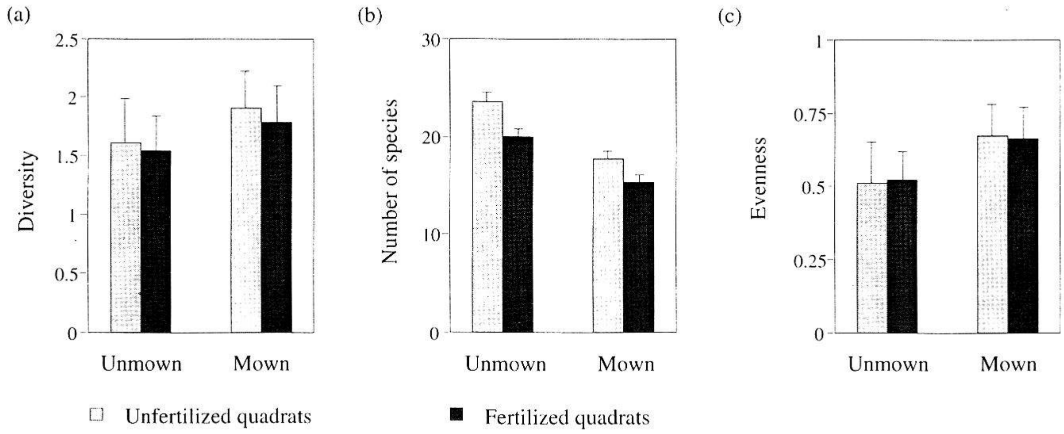

Fig. 5. *Effects of mowing and fertilization on the diversity and dominance structure of the vegetation of an abandoned field. (a) Diversity (Shannon index), (b) number of species, (c) evenness. Vertical bars denote one standard error.*

Discussion

COMMUNITY DEVELOPMENT

Annuals and short-lived perennials dominate in the first years after a field has been abandoned, then for a longer period herbaceous perennials are dominant before woody plants take over (e.g. Whittaker 1975; Bornkamm 1985; Schmidt 1993). The present study was carried out after nine years of succession. The vegetation was dominated by the clonal perennial *Solidago altissima,* although already a considerable number of woody species were present. However, annuals and short-lived perennials (especially *Erigeron annuus)* were still a very important component of the vegetation. This is in sharp contrast to observations on community composition in other European studies of old-field succession. After nine years of succession hardly any annuals were present in an old-field community on loam (Schmidt 1993) and in another study annuals had more or less disappeared on both loam and sand (Bornkamm & Hennig 1982). In the present study, succession appears to have proceeded much slower than at other sites, probably because of the extreme conditions due to the thin layer of soil over coarse gravel. As ecophysiological measurements have shown (Egli 1994), severe droughts occur frequently at the site, which keeps the vegetation rather open.

TREATMENT EFFECTS ON DIFFERENT GROUPS OF PLANTS

Multivariate analyses indicated that species composition was affected significantly by the treatments and that the overall effects of mowing on community composition were stronger than those of fertilization. Since mowing had been applied for five years, whereas there was only one complete growth period after fertilization, this was not surprising. Annual mowing favoured plants with meristems near the soil surface, especially grasses, but also rosette species and legumes. As expected, most woody plants were excluded by mowing. However, some groups of plants were influenced more strongly by fertilization than mowing. The number of annual species decreased, and conversely, the cover of grasses increased with fertilization. This increase of grasses was especially strong in mown quadrats. In other studies (Carson & Barrett 1988; Wilson & Tilman 1991) annuals increased in abundance after fertilization.

It has been suggested that nutrient enrichment accelerates old-field succession by the exclusion of smaller species through increased competition for light (Tilman 1987; see also Schmidt 1988) and thus favours woody species. However, in the present study the number of woody species was reduced by fertilization, as has been observed by Bornkamm & Hennig (1982). The reduction of woody species in our study was probably the consequence of increased competition for water between the seedlings of woody species and grasses, and not the result of increased shading by other components of the vegetation. Even in fertilized quadrats total plant cover was below 100 %.

THE ROLE OF INVASIVE SPECIES

With a cover of more than 50 % *Solidago* was by far the dominant species in unmown and unfertilized plots, in which succession had proceeded undisturbed for nine years. This "*Solidago*-stage" is a common feature of old-field successions both in North America and Europe. For instance, *Solidago* was dominant from year 9 to 17 in a long-term study of an old-field succession in Northern Germany (Schmidt 1993).

Mowing significantly reduced the cover of *Solidago* and fertilization tended to reduce the cover of *Solidago* in unmown quadrats. As detailed demographic studies have shown, the decrease of *Solidago* in mown quadrats is the consequence of both a lower survival of clones and a reduced production of shoots by each clone (Meyer & Schmid 1992). In contrast, mowing had no effect on *Erigeron annuus,* the second invasive neophyte at the study site. *Solidago* is a late flowering perennial with a high above-ground biomass at the time of mowing in late summer, whereas at that time the monocarpic *Erigeron* had already dispersed most of its achenes (Wille 1994).

The observed negative reaction of *Solidago* to fertilization in unmown quadrats is in contrast to observations from several other experimental studies from both North America and Europe, which have found increased dominance of *Solidago* after nutrient addition (Mellinger & McNaughton 1975; Bakelaar & Odum 1978; Bornkamm & Hennig 1982; Carson & Pickett 1990). However, a similar reduced dominance of *Solidago* in reaction to fertilization has been reported from an old-field community that was also strongly affected by seasonal droughts (Bollinger *et al.* 1991). This suggests that the negative effects of fertilization on *Solidago* may have been caused by increased competition for water (cf. Egli 1994).

SPECIES RICHNESS AND DIVERSITY

In the experiment, addition of fertilizer resulted in a significant reduction of species richness already after one year. This was mainly a consequence of a decrease in the number of annual plants and of woody species. Other studies have also found that experimental additions of nutrients to old-field communities lead to a reduction in the number of species, irrespective of the state of succession (Mellinger & McNaughton 1975; Bakelaar & Odum 1978; Bornkamm & Hennig 1982; Bollinger *et al.* 1991; Wilson & Tilman 1991; Song 1994). In contrast, Schmidt (1985) found no effect of nutrient addition on species richness in an old-field community in northern Germany in the first 15 years of a long-term experiment, but the soil was more nutrient-rich and the amount of fertilizer added (less than 34 kg N ha^{-1} $year^{-1}$) very low. In some studies, nutrient enrichment has resulted in increased number of species, but these effects were transient and followed by a decrease in species richness in the long term (Carson & Barrett 1988; Tilman 1993).

The observed reduction in species richness by nutrient addition is also consistent with the results of experiments in other types of vegetation, for example wet heathlands (Aerts & Berendse 1988) and grasslands (e.g. Silvertown 1980; Tilman 1982; Milberg 1992), and with general patterns of species diversity in herbaceous vegetation in relation to productivity (Al-Mufti *et al.* 1977).

Mowing also reduced the total number of species. This result is in contrast to observations from both other old-field communities (Schmidt 1993) and grasslands (e.g. Milberg 1992). However, the observed reduction in species richness was the result of the extinction of nearly all woody plants in mown quadrats. This suggests that the effects of mowing on species richness in old-field communities may depend on the importance of woody plants, i.e. on successional stage. Moreover, because mowing reduced dominance in the community (increased evenness), species diversity was not affected. This confirms that different components of species diversity may react differently to nutrient enrichment and disturbances in old-field communities (Mellinger & McNaughton 1975; Bollinger *et al.* 1991).

CONSERVATION ASPECTS

It is often expected that old fields will develop into grasslands of conservation value, especially as abandoned fields are often situated on marginal land (e. g. on shallow soils or slopes), that may potentially support species-rich grassland communities. Old fields on suitable soils can develop within a few decades into species-rich dry grasslands, if dry meadows are directly adjacent and provide a source of seeds (Willems & Bobbink 1990). However, in the studied old field, 9 years after the field was abandoned and after 5 years of mowing very few typical species of dry meadows were found. The presence of several indicator species for nutrient-poor conditions (N-indicator values less or equal 3, Ellenberg *et al.* 1992), suggest that the physical conditions were favourable for the establishment of species of dry meadows. However, the absence of species from a site is often not the result of physical conditions, but of biotic interactions and the inability of seeds to reach a site (Schmid & Matthies 1994; Matthies *et al.* 1995). In the present case, successful colonization by dry grassland species may have been prevented by competition from *Solidago*. Moreover, the distance to the next dry meadow (c. 50 m) that could have been a source of seeds did probably exceed the dispersal capabilities of most species (see e. g. Schenkeveld & Verkaar 1983).

Schmidt (1985) reported that in old-field successions mowing twice a year will lead to the development of a grassland vegetation, but that mowing once a year is insufficient to break the dominance of *Solidago*. However, in the present study five years of annual mowing were sufficient to strongly reduce the cover of *Solidago* and significantly increase that of grasses. An additional mowing in late spring could, however, also reduce *Erigeron* and favour the development of a dry meadow at the study site. Colonization of the old field by grassland species could be increased by bringing in hay containing seeds from existing meadows in the nature reserve (cf. Hillier 1990; Wells 1990).

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