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Effects of sowing and management on vegetation succession during grassland habitat restoration

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Abstract

The impact of sowing a seed mixture to recreate a semi-natural community in combination with six cutting and/or grazing treatments on the vegetation that developed on former agricultural land was examined over 6 years. Introducing seeds significantly increased the number and cover of sown species persisting. Summer grazing by cattle maintained the number, but not cover, of sown species. Few sown species persisted when grazed by sheep, although those that did maintained high cover. Sorenson's qualitative similarity index (based solely on species presence or absence data) revealed that pairs of sown and non-sown plots within a management treatment did not appear to converge during succession. However, using Sorenson's quantitative similarity measure (based on both species occurrence and abundance) pairs of plots became increasingly similar after the first year. The sown plots became less similar to each other using the qualitative similarity measure, but this was less marked using the quantitative measure. In contrast, the non-sown plots became less similar to each other with the quantitative measure, but no changes were observed with the qualitative measure. The vegetation in the sown plots became more like that in the non-sown plots as sown species failed to persist. In contrast, the non-sown plots became more like the sown plots as the sown grasses *Agrostis capillaris* and *Festuca rubra* increased in abundance. The exception to this was the cattle-grazed sown plots, which retained more sown species, however, succession in this treatment also converged towards the non-sown plots because the non-sown species *Trifolium repens* and *Ranunculus repens* increased in abundance in this treatment. The addition of seeds of a desired grassland community appeared to have less effect in directing the trajectory of succession than did the vegetation management.

Keywords: Community change; Habitat restoration; Set-aside; Similarity index; Sowing; Succession

1. Introduction

Practical restoration ecology frequently involves trying to manage and direct vegetation succession (Luken, 1990). Much of the knowledge of the dynamics of secondary vegetation succession is based upon studies of abandoned agricultural land in the USA (Brenchley and Adam, 1915; Billings, 1938; Booth, 1941; Shure, 1973; Tilman, 1987; Huberty et al., 1998), but during the 1980s and 1990s, the widespread 'setting aside' of surplus agricultural land in northwest Europe provided ecologists with new opportunities to study and experimentally manipulate vegetation changes on former arable land (Fisher et al.,

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1992; Wilson, 1992; Corbet, 1995; Warren and Topping, 1999). Recent interest in actively manipulating or accelerating secondary succession to encourage the development of plant communities considered of greater conservation value has resulted in experiments designed to direct the trajectory of vegetation change (Luken, 1990; Marrs, 1993; Tilman, 1996; Huberty et al., 1998).

Although results from field-scale manipulations of succession have varied, several factors have been identified which affect the rate of colonization of abandoned agricultural land. The transition from vegetation dominated by annuals to that dominated by perennial species is affected by soil nutrient status. Elevated nutrient levels are found in ex-agricultural land in western Europe as a result of the wide-scale application of large amounts of inorganic fertilizers over the last 50 years (Marrs, 1993). Increased soil nitrogen has sometimes been found to retard the rate of succession (Carson and Barrett, 1988; McLendon and Redente, 1991) while in other cases it has had no effect on species composition (Bakelaar and Odum, 1978; Huberty et al., 1998). Under conditions of high soil fertility, Frazer and Grime (1999) found that the presence of generalist invertebrate herbivores increased the rate of secondary succession, whereas Diaz (2000) reported that grazing of set-aside by rabbits tended to limit colonization by palatable perennial grasses.

Depauperate seed banks and limited seed dispersal from remnant habitats are known to reduce the rate of natural grassland restoration (Bakker and Berendse, 1999). In attempting to alleviate this and accelerate secondary successions to produce vegetation types resembling semi-natural communities, many studies have introduced propagules of desired species in combination with a variety of subsequent management prescriptions (Brown and Gibson, 1994; Gibson et al., 1987; Pywell et al., 1996). Unfortunately, because of technical difficulties in managing animals in small experimental plots, the majority of these studies have by necessity investigated the effects on secondary vegetation succession by defoliation by cutting rather than by grazing. However, the National Vegetation Classification (NVC) suggests that the majority of British semi-natural grassland communities are associated with grazing, rather than cutting alone (Rodwell, 1992). Furthermore, many such studies do not contain non-sown plots for all vegetation managements. It is therefore impossible to know how effective the addition of seeds has been in accelerating and/or diverting subsequent succession.

This study examines the effects of introducing a seed mixture designed to recreate a semi-natural grassland community on early successional dynamics of ex-arable land under different cutting and grazing treatments. After 6 years of results are reported from an ongoing experiment which examined the effects of sowing and vegetation management treatments on the plant communities that developed. This paper addresses the question: does sowing successfully divert succession, or do sown and non-sown plots within a management treatment converge towards the same vegetation type?

2. Methods

2.1. Study site

Experimental plots were established in 1993 at a site on the outskirts of Aberdeen on Craibstone estate (National Grid reference NJ869099). The field, which had previously been in an arable-ley rotation, lies 140 m above sea level, and has a mean annual rainfall of 825 mm (MORECS Climatology data, Craibstone station, 61-year mean). The soil is an imperfectly drained non-calcareous gley of pH 5.9. Analysis of top soil samples (0–20 cm) in 1993 showed that extractable (in ammonium acetate/acetic acid) P and K were 21.6 and 100 mg/l, respectively, and total N was 3760 mg/l. The site was ploughed from grass in April 1993, and divided into 24 (20 m $\times$ 40 m) fenced plots. Half of the plots were sown during May 1993 at a rate of 20 kg/ha with a seed mixture of UK provenance (Table 1). Although this rate is lower than recommended by some seed merchants, Stevenson et al. (1995) have shown that semi-natural grassland communities can be established with rates as low as 1 kg/ha. The seed mixture approximates to an MG5 *Cynosurus–Centaurea* grazed-hay meadow community (Rodwell, 1992) excluding those species that do not naturally occur in Scotland. It has recently been recognized that MG5 is a more cosmopolitan community than previous accounts suggest (Rodwell et al., 2000). It is considered to have been widespread in northeast Scotland, indeed fragments of it still occur in the boundary of the study site, suggesting that with the exception of the his-

Table 1
Seed mixture sown at 20 kg/ha

Forbs	Composition (wt.%)	Quadrats area (m^2)	Grasses	Composition (wt.%)	Quadrats area (m^2)
Achillea millefolium	1.20	144	*Agrostis capillaris*	4.87	1460
Centaurea nigra	2.25	18	*Anthoxanthum odoratum*	2.06	41
Galium verum	1.20	45	*Cynosurus cristatus*	30.00	900
Hypochaeris radicata	1.20	25	*Festuca rubra*	48.06	960
Leontodon autumnalis	1.90	37			
Lotus corniculatus	1.20	12			
Plantago lanceolata	1.80	10			
Prunella vulgaris	2.25	45			
Ranunculus acris	1.20	9			
Succisa pratensis	0.80	6			
Total	15.00	351		85.00	3361

tory of cultivation and fertilization the soil type was compatible with supporting the 'target' community. Following establishment, six different vegetation management treatments were applied, starting in April 1994, i.e.: summer grazing by sheep (April–October) or cattle (May–October), cutting in June with subsequent grazing by sheep or cattle, and cutting in early August with cuttings either left or removed. These treatments were also applied in non-sown plots and all treatments were replicated twice, one in each of two adjacent randomized blocks. Details of the full experimental design are given in Christal et al. (1997). Stocking rates and the duration of grazing were varied on the basis of mean sward height: cattle were given access when the mean vegetation height reached 15 cm and were removed at 5 cm, sheep were given access at 10 cm and removed at 3 cm. At no point did the stocking rates exceed one livestock unit per hectare. The cutting height was 6 cm.

2.2. Vegetation recording

The vegetation was recorded annually in June, before the early cut treatment was applied. Cover abundance estimates were made for all species (sown and non-sown) in each of 10 randomly placed 0.25 m^2 quadrats per plot. In addition, the presence or absence of species was recorded in 20 randomly placed 1 m^2 quadrats per plot. This classification into sown and non-sown species is a simplification, as low levels of some of the 'sown' species are likely to have established from the seed bank in the non-sown plots. However, this could not be distinguished from the establishment of 'sown' species in the non-sown plots following seed rain from the sown plots. Fuller details of the vegetation succession based on defining species by life histories is presented in Warren and Topping (1999).

2.3. Indices of abundance and similarity

Throughout this paper the mean number of species per 1 m^2 quadrat is referred to as species number, while cover abundance estimates are means based on the 0.25 m^2 quadrats. Both were calculated separately for the sown and the non-sown species on a yearly basis for each treatment combination.

Similarity of vegetation development between sown and non-sown plots within management treatments, and also between treatments within sown and non-sown plots, was compared using both Sorenson's qualitative measure C_S and Sorenson's quantitative measure C_N (Magurran, 1988). C_S is based solely on species presence or absence data, whereas C_N incorporates both species occurrence and abundance. Sorenson's qualitative similarity measure was calculated as $C_S = 2j/(a + b)$, where j is the number of species common to both sites, a the number of species in site A and b is the number of species in site B (Magurran, 1988). Sorenson's quantitative similarity measure was calculated as $C_N = 2jN/(aN + bN)$, where aN is the total vegetation cover at site A, bN the total vegetation cover at site B and jN is the sum of the lower of the two cover estimates for species

Table 2
Unsown species recorded in all plots in 1994

Species	Unsown plots[a] (%)	Sown plots[a] (%)
Poa annua	69.5–84.8	25.0–45.0
Polygonum aviculare	0.3–0.8	0.1–0.6
Polygonum persicaria	0.1–0.5	0.1–0.4
Ranunculus repens	0.8–5.5	0.3–2.7
Stellaria media	1.8–3.7	0.2–0.7
Trifolium repens	0.2–3.0	0.2–1.3

[a] Range of cover values observed.

which occur in both sites (Magurran, 1988). For each year's data both quantitative and qualitative similarity indices between each pair of sown and non-sown plots within each vegetation management treatments were calculated. Similarity indices were also calculated between each sown plot and the mean of all the sown plots, and between each non-sown plot and the mean of the non-sown plots. To determine whether different communities were becoming more or less similar, regression analysis was used to establish whether the two similarity measures were changing over time. The first year's data were not included in these regressions because the plots were atypically alike in 1994, with all treatments containing similar populations of arable weeds (Table 2).

3. Results

3.1. Species number and cover abundance

One year into the experiment, there was good establishment of the sown species, which had a combined mean cover of 95.15% in the sown plots, all the sown species except *Succisa pratensis* were recorded in all the sown plots. Additionally six non-sown species were recorded in all treatment plots (Table 2). After 6 years after establishment, the sown plots still contained more than twice as many sown species as did the non-sown plots ($4.88\pm0.42\,m^2$ versus $1.77\pm0.23\,m^2$). The sown plots were also found to have a greater cover of sown species than did the non-sown plots ($96.87 \pm 5.66\%$ versus $43.15 \pm 6.05\%$). Two-way analysis of variance of species number and cover abundance data recorded in 1999 revealed not only a significant effect of sowing but also a significant effect of vegetation management and a significant interaction (Table 3). Plots grazed by cattle were found to contain more than twice as many sown species as did plots grazed by sheep ($4.75 \pm 0.87\,m^2$ versus $2.20 \pm 0.42\,m^2$), but the sheep-grazed plots had a greater cover of sown species than cattle-grazed plots ($90.75\pm6.09\%$ versus $45.90\pm 5.77\%$). Similarly, plots cut in August, from which cuttings were removed, contained more sown species but had lower cover of sown species than those plots where cuttings were left ($3.35\pm0.76\,m^2$ versus $2.30\pm 0.48\,m^2$ and $62.80 \pm 4.04\%$ versus $76.25 \pm 3.57\%$, respectively).

To investigate changes in species number and cover abundance for sown and non-sown species within each treatment these were plotted against time, with the results for the sheep grazed treatment being presented in Figs. 1 and 2. As the experiment progressed, fewer species (both sown and non-sown) were recorded in all treatment plots (Fig. 1). The exception to this was the observed increase in the number of sown species within non-sown plots, except those summer-grazed

Table 3
Results of two-way analysis of variance on effects of sowing and subsequent management on the persistence and cover of sown species after 6 years

Variable	Source of variation	d.f.	Sum of squares	*F*	*P*
Species number	Sown/unsown	1	291.4	387.1	<0.001
	Management	5	97.5	25.9	<0.001
	Interaction	5	124.1	32.9	<0.001
	Error	108	81.3		
Cover abundance	Sown/unsown	1	86564	280.8	<0.001
	Management	5	31085	20.2	<0.001
	Interaction	5	20385	13.3	<0.001
	Error	108	33289		

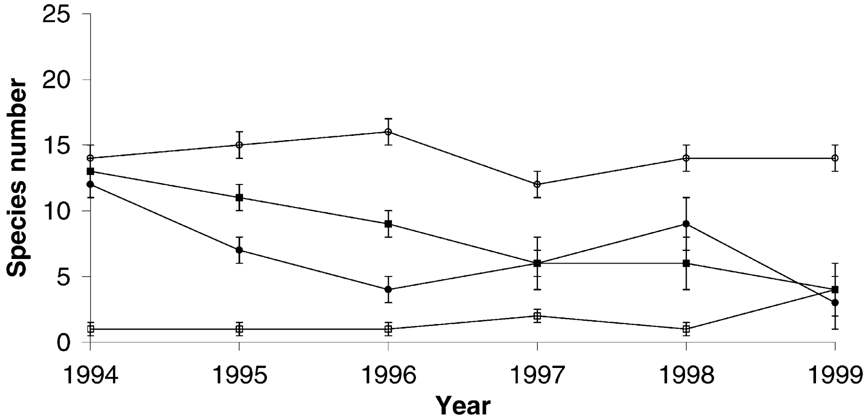


Fig. 1. Mean number of sown and non-sown species recorded per $1\,m^2$ (±S.E.) in the plots grazed by sheep. Squares represent sown species, circles represent non-sown species. Sown plots are represented as solid shapes, and non-sown plots as hollow shapes.

by cattle. There was a marked decline in the number of non-sown species in the sown plots following the first year, with the mean cover of non-sown species falling from 38.7 to 2.8%. This corresponds with the loss of non-sown annual species and the dominance of sown species in the second year. Changes in cover abundance of species were less marked than were changes in species number, except in 1999 (Fig. 2). In all non-sown treatment plots, the cover of non-sown species declined as the experiment progressed and this was associated with an increase in cover of sown species.

3.2. Community similarity

The similarity in species composition between pairs of sown and non-sown plots within treatments was compared using both qualitative and quantitative indices (Fig. 3) to determine whether sowing prevented convergence in vegetation composition over time. No significant change was observed in Sorensen's qualitative measure of similarity between 1995 and 1999 for any of the pairs of plots ($0.918 > P > 0.191$). Sorensen's quantitative measure of similarity decreased markedly between 1994 and 1995 for all

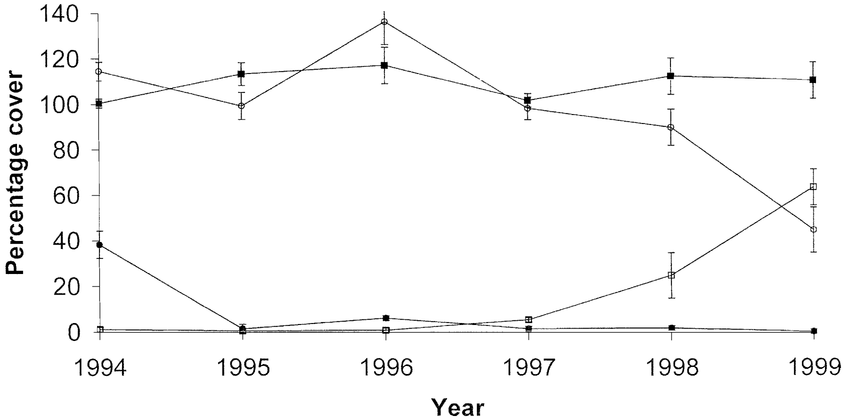


Fig. 2. Temporal patterns of change in mean cover abundance (±S.E.) based on 10 $0.25\,m^2$ quadrats, in the plots grazed by sheep. Squares represent sown species, circles represent non-sown species. Sown plots are represented as solid shapes, and non-sown plots as hollow shapes.

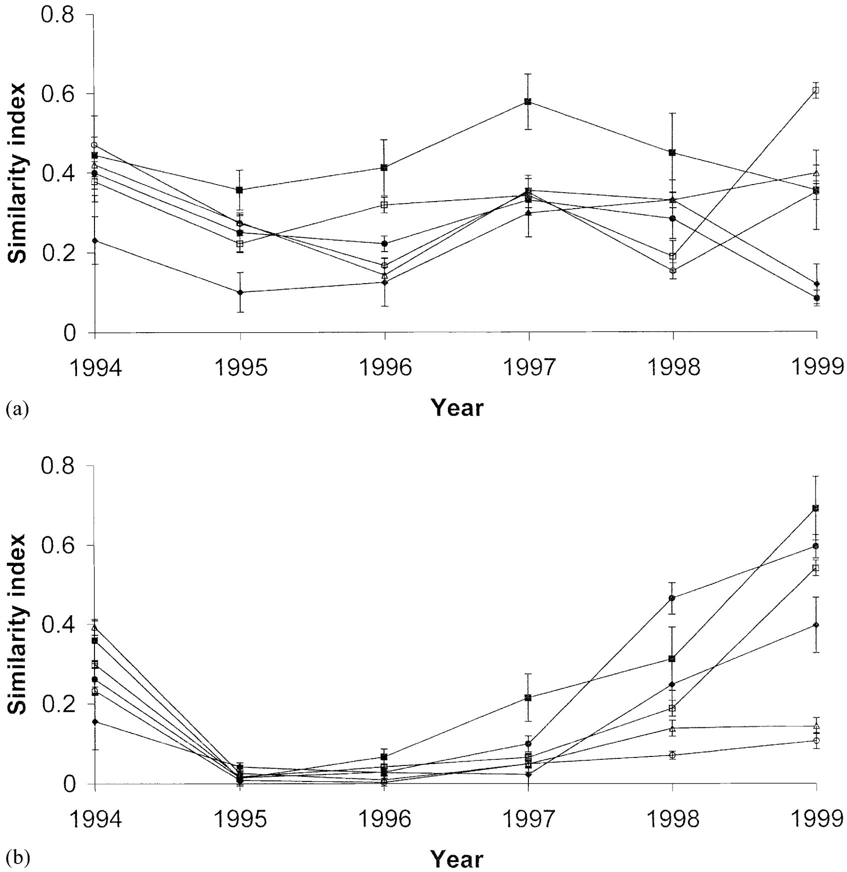
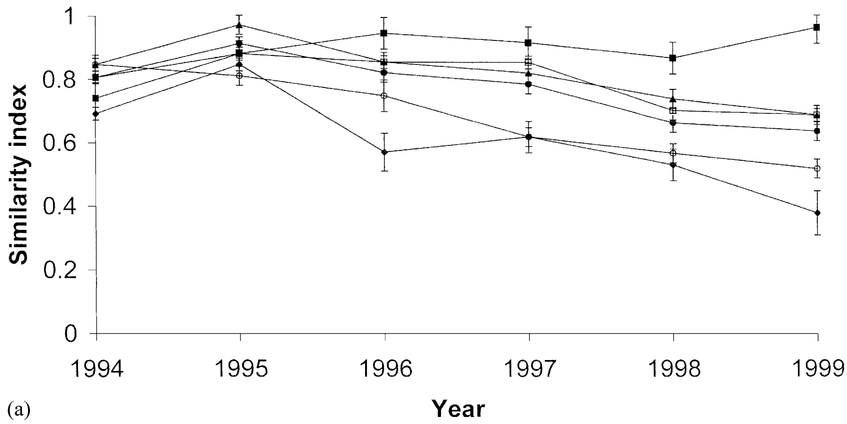


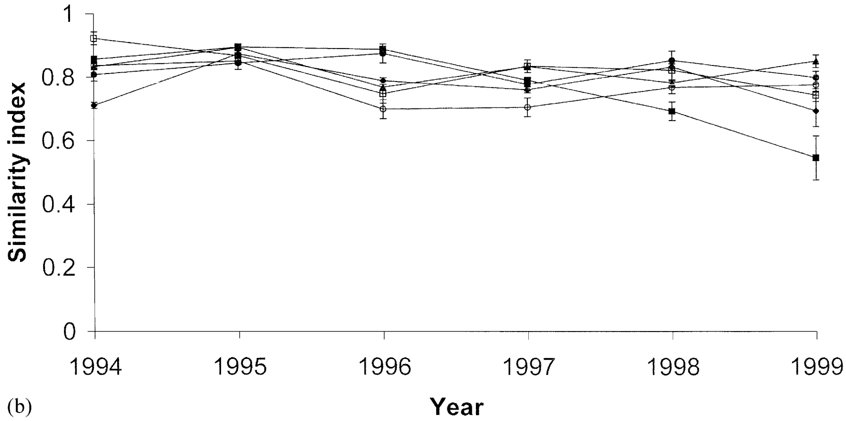
Fig. 3. Similarity in species composition between sown and non-sown plots as estimated by (a) Sorenson's C_S qualitative index and (b) Sorenson's C_N quantitative index. Comparisons made within the following treatments: sheep grazed (◆), cattle grazed (■), cut and grazed by sheep (□), cut and grazed by cattle (△), cut late with cuttings left (○), cut late with cuttings removed (●).

plots, as pairs of plots became less similar when the annual species that had initially occurred in all plots declined. This was most marked in *Poa annua*, which declined to a mean cover of 0.9% in the sown plots, but maintained a mean cover of 49.9% in the non-sown plots. Subsequently, Sorensen's quantitative similarity measure increased significantly between 1995 and 1999 for all pairs of plots, with the slope of all regression equations being positive and $0.05 > P > 0.009$. This indicates that the vegetation in sown and non-sown plots converged in terms of abundance of species, rather than in the number of species they contained.

The similarity in species composition between the different vegetation treatments in sown and non-sown plots (Figs. 4 and 5) was compared to determine whether the different cutting and grazing regimes caused a divergence in species composition over time. The vegetation that developed in the different sown plots became less similar from the second year of the experiment. The qualitative measure of similarity declined significantly between 1995 and 1999 with all regression equations having a significant negative slope, with $0.05 > P > 0.002$ for all treatments except the cattle-grazed where $P = 0.532$. However, during the same period the quantitative similarity measure only changed significantly between the cattle-grazed treatment and the mean of the sown plot, where $P = 0.009$ and the slope was negative. This is reflected in the fact that by 1999



(a)



(b)

Fig. 4. Similarity in species composition between each sown plot and the mean of the sown plots as estimated by (a) Sorenson's C_S qualitative index and (b) Sorenson's C_N quantitative index. Comparisons made between the mean and the following treatments: sheep grazed (◆), cattle grazed (■), cut and grazed by sheep (□), cut and grazed by cattle (△), cut late with cuttings left (○), cut late with cuttings removed (●).

the sown plots summer-grazed by sheep, contained <1% forbs, the vegetation comprising 94% cover of *Agrostis capillaris* with the other sown grasses combined contributing a further 10%. In contrast, the cattle-grazed treatment still contained 13 of the original 14 sown species. No change in similarity was observed between the vegetation that developed in different non-sown plots when the qualitative measure of similarity was used with $0.986 > P > 0.382$. However, the non-sown plots became significantly less similar over time when the quantitative measure was used, with the slope of all regression equations being negative and $0.042 > P > 0.001$. This indicates that as the experiment progressed, divergence in community composition occurred between the sown plots in the species they contained, but not in the cover of the dominant species that persisted. In contrast, the vegetation in the non-sown plots became less similar in terms of cover abundance of the species present, but the plots did not change in terms of the species present. By the sixth year (1999) in the unsown treatment summer-grazed by sheep, the sown grasses *A. capillaris* and *Festuca rubra* dominated the vegetation with 77.0 and 13.2% cover, respectively, in contrast in the unsown late-cut treatment the total cover of sown species remained as low as 30.5%.

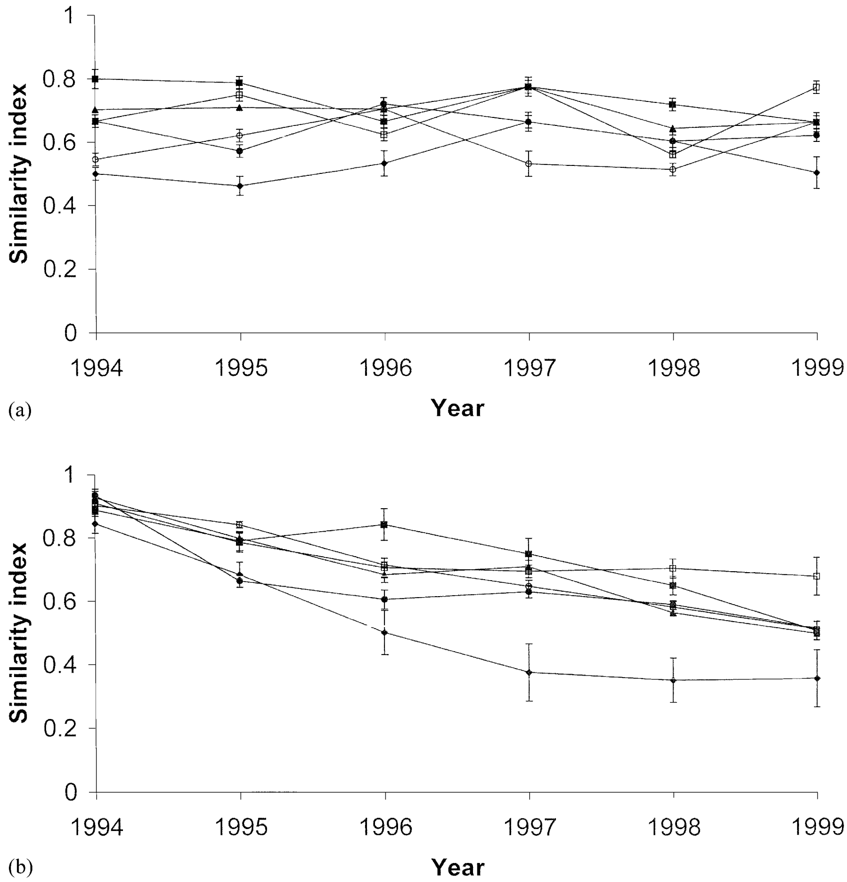


Fig. 5. Similarity in species composition between each non-sown plot and the mean of the non-sown plots as estimated by (a) Sorenson's C_S qualitative index and (b) Sorenson's C_N quantitative index. Comparisons made between the mean and the following treatments: sheep grazed (◆), cattle grazed (■), cut and grazed by sheep (□), cut and grazed by cattle (△), cut late with cuttings left (○), cut late with cuttings removed (●).

4. Discussion

Ecological succession was investigated under different vegetation managements from two different starting points. This allowed for the interactions between the initial assemblage of plant species and subsequent cutting and grazing treatments to be examined. The sowing of seed into some plots resulted in the rapid establishment of vegetation that was markedly dissimilar from that which developed in the non-sown plots. After 6 years, the sown plots continued to contain significantly more sown species and had a greater total cover of these species than the neighboring non-sown plots.

As with most old-field successions, all treatments initially contained a high proportion of annual species (Table 2). This is reflected in the high degree of similarity found between all plots in the first year. In the sown plots, the species, which replaced the annuals, were the sown species themselves. In the non-sown treatments, the species that dominated in the second year appeared to be related to the management, thus, the biennials *Cirsium vulgare* and *Senecio jacobaea* which were generally tall and unpalatable species, thrived under grazed-only treatments but did less well when prevented from flowering by cutting (Warren and Topping, 1999). In contrast, the low-growing perennial forbs *Ranunculus repens* and *Trifolium repens* became more abundant when the vegetation was cut, but not under conditions of extreme defoliation associated with sheep grazing.

Different grassland communities have been shown to develop under different management regimes (Van der Marrel, 1988; Warren and Topping, 1999). Over a relatively short period of time the vegetation that developed within the sown and non-sown plots of each management treatment became increasingly similar. Thus, although the process was not complete after 6 years, each management treatment appeared to be developing its own plant community irrespective of initial starting position. In the longer-term, the introduction of seeds appears unlikely to be effective at deflecting succession. The mechanism of this community-level change appeared to differ between the sown and non-sown plots among management treatments, reflected in the significant interaction between these two. In sown plots that were cut, there was a decline in both the number of sown and non-sown species present, which is consistent with competition from the sown grasses excluding the lower-growing species. The loss of sown forbs from the short swards grazed by sheep may be a result of selective grazing (Ausden and Treweek, 1995). In all cases the exclusion of sown forbs occurred with little corresponding change in the cover of the sown grasses. Thus, over time the different sown plots became less similar to each other as assessed by the qualitative measure of similarity based entirely on species occurrence. However, since the majority of the sown vegetation consisted of the sown grasses, the treatments did not become increasingly different over time when the quantitative measure based on occurrence and abundance was used (Fig. 4). In the non-sown plots, the sown grasses increased in abundance at the apparent expense of non-sown forbs. Over time the non-sown plots became increasingly dissimilar as measured with the quantitative measure of similarity, because they differed in the rate of spread of the sown grasses. However, they did not change in terms of the qualitative measure because the species lists recorded within the plots remained similar (Fig. 5).

Of the sown plots, only the cattle-grazed treatment experienced no decline in the number of sown species persisting. In this case, community change occurred as a result of an increase in cover of two non-sown species, *T. repens* and *R. repens*. Warren (2000) reported that *T. repens* increases in both frequency and abundance in short swards produced by cattle grazing during grassland habitat creation.

The vegetation that developed in the sheep-grazed plots was species-poor, it had <1% cover of forbs by the sixth year and was dominated by the sown grasses. It has been suggested (Christal et al., 1997) that the failure of *T. repens* and *R. repens* to spread in the plots grazed by sheep was due to selective grazing. Because the mechanisms of vegetation change appeared to vary among treatments, it appears that species loss was due to management effects rather than being due to non-local ill-adapted genotypes failing to thrive.

Vegetation change in the sown plots not grazed by cattle appeared to result from competitive exclusion of species by the sown grasses, or by selective grazing. The community within each treatment appeared to be converging towards their non-sown counterparts, with the same sown grasses increasing in abundance in all cases. Community convergence in these plots is consistent with the Connell and Slatyer (1977) tolerance model of succession. The significant interactions observed between management treatment and sowing (Table 3) is a reflection of the different mechanism of succession observed within the cattle-grazed plots. The cattle-grazed treatment alone appeared to favor the spread of *T. repens*, which, through its nitrogen fixing ability, has been shown to encourage the spread of grasses at the expense of sown forbs (Warren, 2000). This process is therefore more consistent with the Connell and Slatyer (1977) facilitation model of succession.

The observed rapid spread of sown grasses through the non-sown plots is likely to have been accelerated by their proximity to the sown plots, which provided a seed source. It is not easy to envisage how this effect could be avoided. However, since *A. capillaris* and *F. rubra* are both widespread and abundant in northeast Scotland it seems unlikely that removing this supply of seeds would have prevented their spread.

It has been argued (Inouye and Tilman, 1995) that long-term studies are required to detect the effects of manipulating successional communities. The results presented here suggest that some factors affecting the rate and direction of community change can bring about rapid responses in the developing vegetation. This experiment suggests that unless vegetation management is consistent with the development of the 'target' community, then the addition of seeds is likely to have little long-term effect in directing the trajectory of succession towards the desired community.

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