

Soil carbon addition affects plant growth in a species-specific way

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Summary

1. Restoration of ex-arable land to species-rich habitats has become common practice in Europe as a result of Agri-Environment Regulations. The results, however, are highly variable and often disappointing. Competition from weedy species as a result of high soil inorganic nitrogen levels can negatively affect the establishment and growth of desirable grassland plant species. One method that has been put forward to alter competitive interactions among plant species on restoration sites is the addition of carbon (C) to the soil. To make C addition a tool for successful restoration of species rich grassland, it should affect plant growth in a species-specific way.

2. We present results of a greenhouse study to assess the species-specific responses of 29 plant species to a range of C volumes added to the soil. Specifically, we tested whether functional group affiliation (legumes, other forbs and grasses), life form (annual and perennial) or nitrophilic status could explain parts of the variation in the response of the selected plant species to C addition.

3. Amending soil with increasing levels of C resulted in a log-linear reduction in biomass accumulation of all plant species tested, but the responses varied significantly between the plant species. Functional group and life form explained a significant amount of variation observed among the plant species tested. The response of legumes to C addition was less pronounced than that of other forbs and grasses. Grasses showed a decrease in shoot : root ratio in response to C addition, while the shoot : root ratio of legumes and forbs remained constant. A greater shoot biomass reduction in response to C addition was found for annual species than for perennial species.

4. No correlation was found between the slope of the regression of log biomass vs. the amount of C added and the Ellenberg N-values, indicating that there is no simple relationship between the nitrophilic status of a plant species and its response to C addition.

5. *Synthesis and applications.* The results suggest that adding C to soil is a promising tool in grassland restoration. C addition disproportionately reduced above-ground biomass accumulation by annual plant species and grasses, which often dominate early succession on ex-arable land. This may facilitate the establishment and growth of late-seral species and thus the restoration of species-rich grassland on ex-arable land.

Key-words: arable reversion, carbon addition, competition for nitrogen, functional group, grassland restoration, life form, plant biomass, shoot : root ratio

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Introduction

Restoration of ex-arable land to species-rich habitats has become common practice in Europe through Agri-Environment Regulations that favour the envir-

onment through extensification of farming, including the conversion of arable land into extensive grassland (Anonymous 1998). Although widely practised, the outcome of such management schemes is highly variable and remains difficult to predict (Buckingham *et al.* 1999; Kleijn & Sutherland 2003). This has been attributed to a number of factors, including high soil nutrient availability (McLendon & Redente 1992; Marrs 1993), lack of seed propagules (Bekker *et al.* 1997),

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herbivory (Kleijn 2003), pathogens (Kirkpatrick & Bazzaz 1979) and a lack of trophic linkages (Van der Heijden 2004). In restoration projects on fertile soils, a rapid establishment of annual and fast-growing perennial plants often characterizes the initial phase of vegetation development, while late-seral plant species, even when initially sown, remain sparse (McLendon & Redente 1992; Hansson & Fogelfors 1998; Baer *et al.* 2004). Rapidly growing, early seral plant species may continue to dominate as long as the nutrient availability remains high, and thus impede the restoration and maintenance of species-rich plant communities (Marrs 1993; Kindscher & Tieszen 1998).

One method that has been put forward to alter competitive interactions among plant species is the addition of carbon (C) to the soil (Morgan 1994; Blumenthal, Jordan & Russelle 2003). Based on the assumptions that plant growth is primarily limited by inorganic nitrogen (N; Tilman 1985) and that plants can only use that part which exceeds the microbial demand (Blumenthal, Jordan & Russelle 2003; but see Schimel & Bennett 2004), it has been hypothesized that C addition induces the resident soil bacteria and fungi to immobilize plant-available soil nutrients (Schmidt, Michelsen & Jonasson 1997; Blumenthal, Jordan & Russelle 2003). Several studies have found that C addition can indeed decrease inorganic N concentration in the soil (Schmidt, Michelsen & Jonasson 1997; Török *et al.* 2000), and reduce above-ground vegetation biomass (Michelsen *et al.* 1999; Alpert & Maron 2000; Blumenthal, Jordan & Russelle 2003).

To make C addition a tool for successful restoration and augmentation of diversity, it should affect plant growth in a species-specific way. A shift in vegetation composition after C addition has been reported from a number of field studies (McLendon & Redente 1992; Michelsen *et al.* 1999; Alpert & Maron 2000; Blumenthal, Jordan & Russelle 2003; Corbin & d'Antonio 2004; Perry, Galatowitsch & Rosen 2004). However, none of the published studies we are aware of was designed to distinguish between direct C effects on plant growth and other factors that could influence the growth of plants, such as competition for light. Under conditions of high nutrient availability, early seral species, with their characteristically high potential growth rates, are favoured over late-seral species, which tend to have slower growth rates (Bazzaz 1979). On the other hand, slow-growing plant species share traits that optimize their pattern of nutrient allocation, thereby increasing their competitive ability at nutrient levels too low to support the high-production requirements of fast-growing plant species (Tilman 1985). Theoretically, C addition to the soil should therefore adversely affect the growth of faster growing species disproportionately, thereby benefiting slower growing species (Paschke, McLendon & Redente 2000). Yet, species-specific responses to C addition may also vary among functional plant groups. Legumes, which live in symbiosis with free N-fixing bacteria located in the

root nodules, are likely to respond less to inorganic N shortage in the soil than other forbs and grasses. Species-specific responses to different amounts of C addition may also depend on the life form of the species. Annual species tend to have higher relative growth rates and allocate most of their biomass in shoot and reproductive tissue, in order to flower and set seed in a short period of time, while perennial species generally have lower relative growth rates and allocate more biomass to their roots, in order to be able to acquire mineral nutrients (Tilman 1985; Van der Werf *et al.* 1998). A reduction in the growth rate and cover of annual species during the initial restoration phase may leave open gaps in the vegetation over an extended period, thereby facilitating the recruitment of desirable perennial plant species present in the soil seed bank or introduced by sowing (Hansson & Fogelfors 1998).

We report the results of a greenhouse study that aimed to quantify the species-specific relationship between C concentration and plant biomass. As C addition is expected primarily to reduce inorganic N availability relative to the amount of C added (Blumenthal, Jordan & Russelle 2003; Corbin & d'Antonio 2004), plants are expected to reduce growth and change their allocation pattern as if they are growing on a nutrient gradient (Thornley 1972; Tilman 1985; Marschner, Kirkby & Cakmak 1996). We used a C gradient over a range that covered the rates used in most of the published studies and tested the effect of C addition on biomass production of 29 plant species with different sets of life-history traits. Specifically, we asked whether the factors (i) functional group affiliation (legumes, other forbs and grasses), (ii) life form (annual and perennial) and (iii) nitrophilic status (Ellenberg N-value; Ellenberg 1974) at least partly explain the variation in the response of the selected plant species to C addition.

Methods

Plant species were chosen to represent a range from nitrophilic 'classic weeds' to typical species of nutrient-poor late-seral grassland vegetation. The list of plant species, with their affiliation to three functional groups (grasses, legumes and other forbs), life form and an indicator value of N availability in the natural habitat in which the species reaches its highest abundance (Ellenberg N-value; Ellenberg 1974), is given in Table 1. Species with high Ellenberg N-values occur primarily on N-rich soils, and species with lower Ellenberg N-values on soils with low N availability. If the Ellenberg N-values of the selected plant species are correlated with their response to increasing levels of C addition, then this indicator system might offer a simple tool to predict species and plant community responses to C addition.

Soil was taken from a 2-year-old fallow arable field in the Swiss Jura. At the beginning of the experiment, the soil contained 14.1 ± 5.0 p.p.m. nitrate and 8.3 ± 1.2 p.p.m. ammonium (means \pm SE; $n = 3$). The soil was sieved through a 5-mm mesh and used to fill

Table 1. Species used in the experiment, life forms, functional groups and Ellenberg N-values (Ellenberg 1974). High Ellenberg N-values indicate high N content in the natural habitat where the species is most abundant; 'X' indicates that the species' abundance does not correlate with the N content of the natural habitat. Summaries of the linear regressions of total biomass for each species as affected by increasing C volumes (alpha, beta and P-values)

Species	Life form	Functional group	Ellenberg N-value	Regression		
				alpha	beta	P
<i>Stellaria media</i> L.	Annual	Forb	8	2.8227	-0.0024	0.000
<i>Veronica persica</i> Poiret	Annual	Forb	7	2.6711	-0.0019	0.000
<i>Echinochloa crusgalli</i> P.B.	Annual	Grass	8	1.8579	-0.0015	0.003
<i>Poa annua</i> L.	Annual	Grass	8	2.201	-0.0019	0.000
<i>Medicago lupulina</i> L.	Annual	Legume	X	2.6529	-0.0009	0.000
<i>Achillea millefolium</i> L.	Perennial	Forb	5	2.5068	-0.0024	0.000
<i>Centaurea jacea</i> L. s.l.	Perennial	Forb	X	2.633	-0.0009	0.000
<i>Galium mollugo</i> L.	Perennial	Forb	X	2.6201	-0.0017	0.000
<i>Leontodon hispidus</i> L. s.l.	Perennial	Forb	3	2.6778	-0.0015	0.000
<i>Leucanthemum vulgare</i> Lam.	Perennial	Forb	3	2.2763	-0.0017	0.002
<i>Plantago lanceolata</i> L.	Perennial	Forb	X	2.8938	-0.0018	0.000
<i>Rumex acetosa</i> L.	Perennial	Forb	5	2.5803	-0.002	0.000
<i>Rumex obtusifolius</i> L.	Perennial	Forb	9	2.9774	-0.0013	0.000
<i>Salvia pratensis</i> L.	Perennial	Forb	4	2.2785	-0.001	0.000
<i>Sanguisorba minor</i> Scop. s.l.	Perennial	Forb	2	2.5372	-0.0014	0.000
<i>Taraxacum officinalis</i> Weber <i>sensu lato</i>	Perennial	Forb	7	2.6073	-0.0024	0.000
<i>Thymus serpyllum</i> L.	Perennial	Forb	1	1.3636	-0.0019	0.000
<i>Veronica officinalis</i> L.	Perennial	Forb	4	1.3041	-0.0016	0.008
<i>Arrhenatherum eliatum</i> Presl.	Perennial	Grass	7	2.6337	-0.0013	0.000
<i>Briza media</i> L.	Perennial	Grass	2	1.9998	-0.0015	0.000
<i>Bromus erectus</i> Hudson	Perennial	Grass	3	2.3084	-0.0012	0.002
<i>Dactylis glomerata</i> L.	Perennial	Grass	6	2.5325	-0.002	0.000
<i>Festuca arundinacea</i> Schreber s.l.	Perennial	Grass	4	2.9348	-0.0015	0.000
<i>Holcus lanatus</i> L.	Perennial	Grass	4	2.2934	-0.0026	0.000
<i>Lolium multiflorum</i> Lam.	Perennial	Grass	X	2.8467	-0.0011	0.000
<i>Anthyllis vulneraria</i> L. s.l.	Perennial	Legume	3	2.4725	-0.0007	0.000
<i>Lotus corniculatus</i> L.	Perennial	Legume	3	2.1582	-0.0005	0.032
<i>Trifolium montanum</i> L.	Perennial	Legume	2	1.1904	-0.0006	0.003
<i>Trifolium repens</i> L.	Perennial	Legume	7	1.6695	-0.0007	0.001

pots (diameter 10 cm; c. 40 cL). Pots were arranged in a completely randomized order on a bench in an unheated greenhouse. Surface-sterilized seeds of 29 species were germinated in Petri dishes on moist filter paper in a climate chamber (20 °C, 8/16 h dark/light). A seedling at the cotyledon stage was planted in each pot. Four levels of C were applied as sugar equal to 0, 250, 500 and 1000 g C m⁻². C was added in three equal increments (summing up to the levels indicated above) at 3-week intervals. The first addition was made immediately after planting the seedlings. The pots were watered immediately after addition of sugar in order to dissolve the sugar and to prevent damage to the plants as a result of osmosis. There were four replicates per species and treatment combination, resulting in a total of 464 pots. During the experiment, plants were watered as needed. Two months after the start of the experiment, roots of several species started accumulating at the side and bottom of the pots. Therefore, all plants were harvested after 62 days, the soil carefully washed off the roots, and the plants dried at 60 °C for 36 h. Above-ground, below-ground and total biomass were determined, and the shoot : root ratio calculated.

The effect of C addition on species of different functional groups and life forms was analysed using ANOVAS

with C treatment, functional group and life form as fixed factors and species as a random factor, nested in functional group and nested in life form. Species and species-C interactions were tested against the residuals, the other factors and interactions against the species-C interaction. Above-ground, below-ground and total biomass were log-transformed, and the shoot : root ratio was arcsin-transformed in order to meet the assumptions of ANOVA. Mean total biomass of the different functional groups in the control treatment was compared with a pairwise *t*-test. Data of each species were used in linear regression analyses, to describe the changes of above-ground, below-ground and total plant biomass along the gradient of C volumes applied. The results of linear regressions were significant for all species (Table 1). *R*² values of all except two species were > 0.5. Visual examination of the data and regression lines for the two species with relatively low *R*² values revealed large variation in the data within C levels, but the means of the C levels were close to the linear model. We therefore decided to use linear regression to use the linear model for all species tested. The responses of different functional groups were tested using pairwise *t*-tests with regression slopes (Table 2) as the response variable. *P*-values were corrected for

Table 2. The effect of C treatments, functional group affiliation and life form of species on above-ground, below-ground and total biomass and shoot : root ratio of plants. Shown are degrees of freedom (denominator, numerator), *F*-ratios and *P*-values

Factor	d.f.	Above-ground biomass		Below-ground biomass		Total biomass		Shoot : root ratio	
		<i>F</i> -ratio	<i>P</i>	<i>F</i> -ratio	<i>P</i>	<i>F</i> -ratio	<i>P</i>	<i>F</i> -ratio	<i>P</i>
Carbon	3,75	155.310	< 0.000	150.140	< 0.000	168.910	< 0.000	9.978	< 0.000
Functional group	2,75	0.620	0.532	0.510	0.594	0.820	0.435	6.486	0.002
Life form	1,75	0.002	1.000	7.890	0.003	1.050	0.229	43.453	< 0.000
Carbon × functional group	6,75	4.980	< 0.000	6.050	< 0.000	5.700	< 0.000	4.140	0.002
Carbon × life form	3,75	2.200	0.116	0.430	0.706	1.660	0.220	9.442	< 0.000
Species	25,330	35.982	< 0.000	45.221	< 0.000	41.508	< 0.000	12.163	< 0.000
Carbon × species	75,330	3.040	< 0.000	3.019	< 0.000	2.995	< 0.000	2.091	< 0.000

multiple comparisons using the Bonferroni method. To test the prediction that the biomass accumulation of fast-growing, nitrophilic species was more reduced under increased levels of C addition than that of slow-growing, less nitrophilic species, the regression parameters alpha (intercept) and beta (slope) of all species were plotted against the corresponding species' Ellenberg N-values (Ellenberg 1974) and logarithmic equations fitted to the data set. Species with Ellenberg N-value 'X' were omitted from the analysis, as Ellenberg assigned this value to plant species that are indifferent to high or low N availability.

Statistical analyses were performed using R, version 1.8.1 for Windows (<http://www.r-project.org>).

Results

CARBON

C addition resulted in a significant decrease in total biomass accumulation for all species tested (Table 1). The total biomass of 23 of the 29 plant species was more than 50% lower when 250 g C were applied, compared with the control (Table 1; a beta value of -0.0009 indicates a biomass reduction of 50% when 250 g C was applied). However, there was substantial variation in the species-specific responses to increasing levels of added C (Tables 1 and 2).

FUNCTIONAL GROUP

C affected the above-ground, below-ground and total biomass and shoot : root ratio of functional groups differently, as indicated by the significant C–functional group interaction terms (Table 2). Overall, the total biomass of legumes was significantly less affected by C addition than it was for other forbs and grasses (legumes vs. forbs $P < 0.001$, legumes vs. grasses $P = 0.002$). In the control treatment, the total biomass of legumes was significantly lower than that of the other groups (legumes vs. forbs $P < 0.001$, legumes vs. grasses $P < 0.001$). The total biomass of plants did not differ among functional groups in the 250- and 500-g C treatments (both $P > 0.2$), while in the 1000-g C treatment

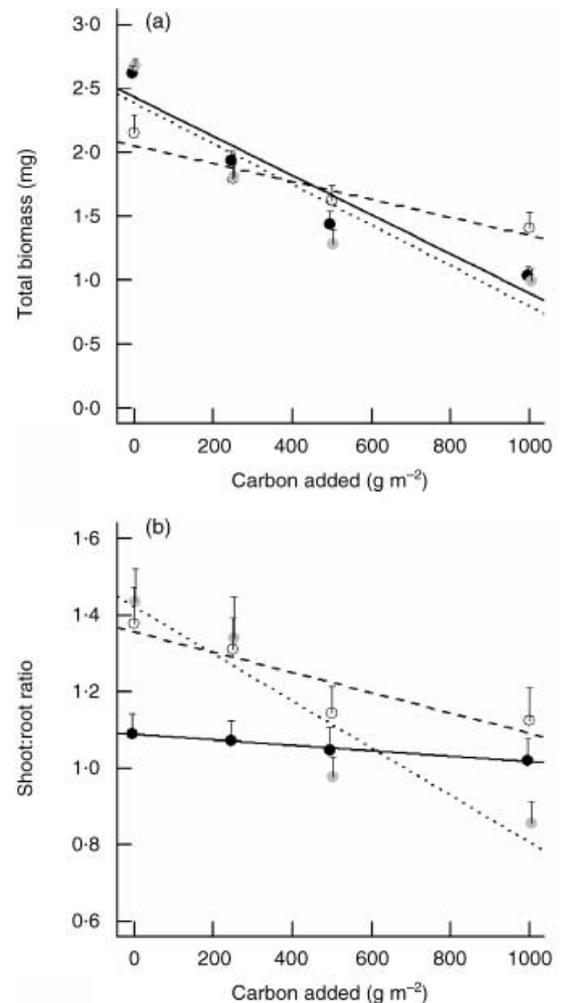


Fig. 1. The effect of C treatments on species of different functional groups. Total biomass (log-transformed) (a) and shoot : root ratios (arcsin-transformed) (b) on a gradient of C volumes. Open circles and dashed line, solid black circles and solid line, and solid grey circles and dotted line indicate means and regression lines of legumes, other forbs and grasses, respectively, in the different treatments. Error bars indicate standard errors.

the total biomass of the legumes was higher than that of the other groups (legumes vs. forbs $P = 0.036$, legumes vs. grasses $P = 0.026$; Fig. 1). The shoot : root ratio of legumes and grasses was significantly higher

than that for forbs in the control (Fig. 1; legumes vs. forbs $P = 0.041$, grasses vs. forbs $P = 0.001$). In contrast, the shoot : root ratio of grasses was significantly lower than that of legumes when 1000 g C were added (grasses vs. legumes $P = 0.043$).

LIFE FORM

Total biomass of species of both life forms was similarly affected by the C addition. However, the shoot : root ratio of annual and perennial plant species responded differently to C addition (Table 2; significant life form–C interaction): while the shoot : root ratio of annuals was higher than that of perennial species in the control and 250-g C treatments (both $P < 0.001$), it did not differ at higher C levels (Fig. 2; both $P > 0.3$).

ELLENBERG N-VALUES

In the control treatment, total biomass was positively correlated with the species' Ellenberg N-values (Fig. 3; logarithmic curve $y = 1.7076 + 0.4039 \times \log[x]$; $n = 23$, $R^2 = 0.21$, $P = 0.002$). No correlation was found between Ellenberg N-values and reduction in above-ground, below-ground or total biomass accumulation, suggesting that the species-specific response to C addition among the species tested did not depend on their nitrophilic status (Fig. 3; data for shoots and roots not shown). Also, no relationship was found between intercept and slope of the regression lines.

Discussion

In our study, amending soil with increasing levels of C led to a log-linear reduction in biomass accumulation by all plant species tested. A considerable amount of the interspecific variation in reduced biomass accumulation at increasing levels of C addition was explained in terms of functional group affiliation and life form (Table 2). Legumes were only moderately affected by C addition, which was probably because of their symbiotic association with free N-fixing bacteria in the root nodules, making the growth of legumes relatively independent of the available inorganic N in the soil. No difference was found between other forbs and grasses with regard to biomass accumulation at increasing levels of C addition. However, the shoot : root ratio of grasses was significantly reduced by C addition, whereas the shoot : root ratios of legumes and other forbs were not. The reduction of the shoot : root ratio of grasses following C addition, as shown in Schmidt, Michelsen & Jonasson (1997) and in the present study, may lead to reduced above-ground competition for light. On nutrient-rich soil, where competition for light is important (Tilman 1988), a reduction in shoot : root ratio of grasses after C addition is therefore likely to improve the relative competitive ability not only of legumes but also of other forbs, despite the fact that biomass accumulation of non-leguminous forbs and grasses was similarly

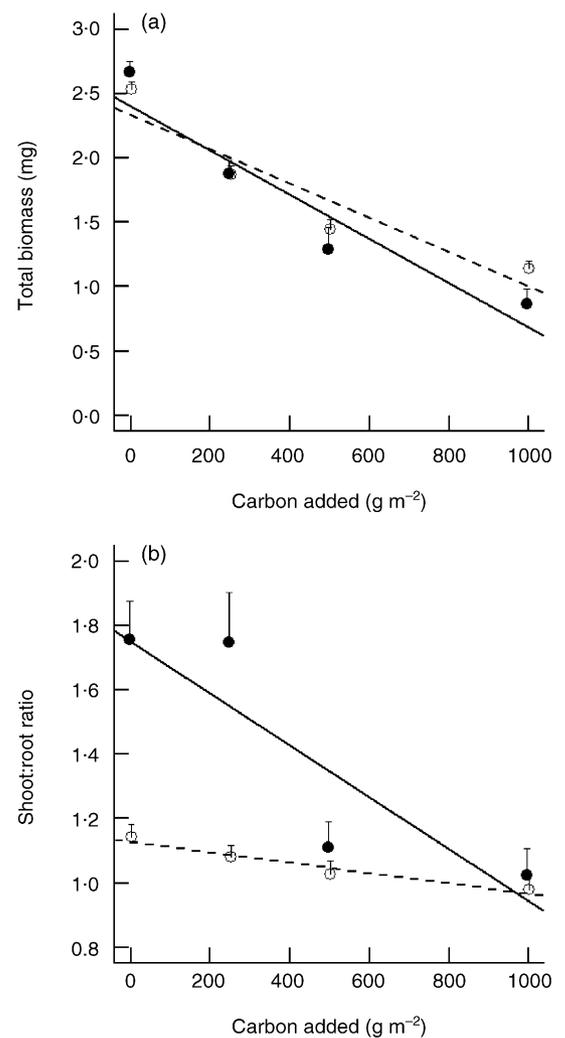


Fig. 2. The effect of C treatments on species with different life forms. Total biomass (log-transformed) (a) and shoot : root ratios (arcsin-transformed) (b) on a gradient of C volumes. Solid circles and line and open circles and dashed line indicate means and regression lines of perennial and annual species, respectively, in the different treatments. Error bars indicate standard errors.

affected in the absence of competition. The results of a field study aiming to assess the effect of C addition on vegetation development on ex-arable land are in agreement with these predictions. After 2 years of C addition, cover of grasses was significantly reduced and cover of legumes increased, compared with control plots, while the cover of other forbs remained unaffected (R. Eschen, unpublished results).

The shoot : root ratios of annual species were more affected by the C treatment than those of perennial species. This is probably an effect of N limitation of the plants (Marschner, Kirkby & Cakmak 1996). The reduced allocation to above-ground biomass negatively affected the reproductive output of several annual species. *Stellaria media* L., *Echinochloa crusgalli* P.B. and *Poa annua* L. flowered after 3–6 weeks in the control treatment and some of those set seeds before the end of the present experiment, whereas none flowered

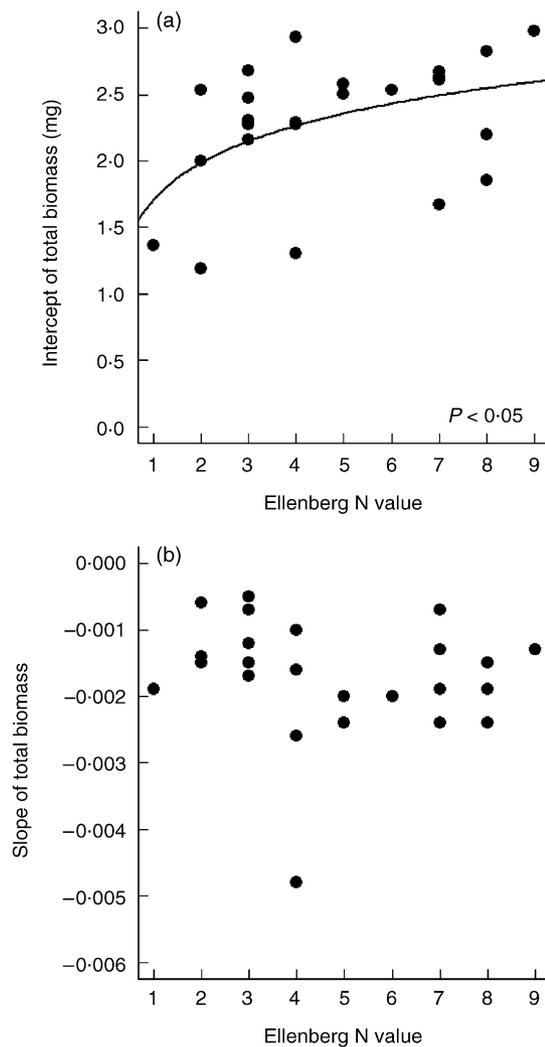


Fig. 3. (a) Intercept and (b) slope of total biomass vs. Ellenberg N-value. Total biomass is log-transformed. The line in (a) represents the relationship between total biomass in the control treatment (no C addition) and Ellenberg N-value. For details see text.

in any of the C addition treatments. Hence, C addition may significantly reduce the build-up of a soil seed bank of early seral species on ex-arable fields.

The level of biomass reduction of individual species following C addition did not correlate with Ellenberg N-values of the species. The results therefore do not support the hypothesis that nitrophilic species are generally more sensitive to C addition than species characteristic of nutrient-poor, late-seral grassland communities (Paschke, McLendon & Redente 2000; Blumenthal, Jordan & Russelle 2003; Corbin & d'Antonio 2004). For example, the perennial forb *Rumex obtusifolius* L. is a problem weed on nutrient-rich, disturbed grassland, yet its growth was only moderately reduced by C addition in our experiment. It should be noted, however, that we found only relatively small differences in biomass (a surrogate for optimal growth rate) among the tested plant species in the control treatments (no C addition), suggesting that the

initial level of N availability may not have been high enough for the fast-growing species to attain their maximal growth rate. The relatively low variation in biomass in the control treatment may have masked a significant relationship between the species' Ellenberg N-values and their responses to C addition. However, in the control treatment biomass was correlated with the Ellenberg N-value, supporting the proposed correlation between a species' relative growth rate and the N availability in its preferred habitat (Ellenberg 1974). We conclude that the differences between species' responses to C addition are best explained by functional group affiliation and life form.

Our results, that addition of C affects plant growth in a species-specific way, are largely in agreement with previous studies assessing effects of C addition on vegetation composition. C addition in a heath affected the shrub *Vaccinium uliginosum* L. less than the perennial grass *Festuca ovina* L. (Michelsen *et al.* 1999). On a C-enriched ex-arable field, perennial species tended to increase in cover, while annual forb cover decreased (McLendon & Redente 1992). Moreover, a number of studies have found that C addition significantly decreased biomass or cover of non-native weeds, while native plant species were less affected (Corbin & d'Antonio 2004; Perry, Galatowitsch & Rosen 2004) or even increased in biomass (Blumenthal, Jordan & Russelle 2003; Perry, Galatowitsch & Rosen 2004). An increase in biomass of plant species after C addition, as found by McLendon & Redente (1992) and Blumenthal, Jordan & Russelle (2003), appears to contradict the results of our study, in which the growth of all plant species investigated decreased with increasing C addition. However, both studies were conducted in a competitive environment that did not allow the direct effect of C addition to be separated from changes in other environmental parameters, such as increase in light availability. In a diverse plant community, a significant overall reduction in above-ground biomass production, as observed in Blumenthal, Jordan & Russelle (2003) and in this study, could therefore lead not only to a relative but also to an absolute increase of those species or species groups that are less affected by C addition, such as perennial species and legumes. This process, however, is driven by light availability as the limiting resource, and will change when soil nutrients become limited.

The range of application rates for C addition to soils as reported in the literature is very wide, from a few grams to more than a kilogram per square metre (Morgan 1994; Schmidt, Michelsen & Jonasson 1997; Hopkins 1998; Averett, Klips & Curtis 2002; but see Blumenthal, Jordan & Russelle 2003). Based on the findings that a sufficiently large decrease in N appears to have been met only at high levels of C addition, and that the increase in biomass of desirable species in a diverse vegetation showed no signs of levelling out at higher C addition rates (Blumenthal, Jordan & Russelle 2003), Blumenthal, Jordan & Russelle (2003)

suggested that further increases in C addition would lead to an even more desirable shift in vegetation composition. However, in Blumenthal, Jordan & Russelle's (2003) experiment total above-ground biomass at the highest level of C addition was some 50% of that in the control plots. Amendment of the soil with large amounts of C may therefore limit growth of all species and lead to the persistence of bare patches in the vegetation. Therefore, a trade-off exists between the magnitude of overall biomass reduction and change in vegetation composition. To establish a closed vegetation that remains stable even after C addition is stopped, it seems desirable to find a level of C addition that significantly reduces the growth of weedy species while harming the growth of desirable species as little as possible. This question, however, needs to be addressed in a field study (R. Eschen, unpublished results).

Although we carried out the experiment with individually potted plants, we believe that these results are a relevant contribution to current knowledge about the applicability of C addition in grassland restoration programmes. First, using individual growing seedlings enabled us to quantify the relationship between plant growth and increasing amounts of soil C addition without confounding factors such as competition or differences in initial storage reserves in below-ground organs. Secondly, a low-competitive environment is characteristic of the initial period of restoration on recently abandoned arable land. Finally, the results obtained in this greenhouse study are in agreement with initial results from an ongoing field experiment, in which the functional groups largely responded to C addition as predicted by this study and perennial forb species that were sown initially became better established (R. Eschen, unpublished results).

Our results suggest that adding C to soil can indeed be a useful tool in grassland restoration programmes to facilitate early establishment of late-seral species. We hypothesize that the shift in competitive abilities of plants among the different functional groups and life forms may result in increased establishment of species that are little affected by C addition, such as legumes. Through reduced above-ground growth of annual plant species and grasses, succession can be accelerated as a result of improved abiotic and biotic conditions for establishment and growth of late-seral species, and the risk of sown target species being lost from the seed bank can be reduced. Further work should assess the relationship between target site properties and optimal level of C addition to find a balance between the facilitation of establishment and growth of late-seral grassland species on the one hand, and maximizing vegetation cover to reduce habitat instability on the other.

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