Zeitschrift: Bulletin of the Geobotanical Institute ETH
Herausgeber: Geobotanisches Institut, ETH Zürich, Stiftung Rübel
Band: 66 (2000)

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DOI: https://doi.org/10.5169/seals-377830

Why remove the topsoil for fen restoration? – Influence of water table, nutrients and competitors on the establishment of four selected plant species

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Summary

1 Around Lake Nussbaumen in northern Switzerland, 50 ha of former agricultural area will be restored to semi-natural wet grasslands similar to those before drainage in 1943. This involves re-establishment of the characteristic plant species. In previous experiments, the establishment of target species by seeding or planting was more effective when the topsoil was removed. For practical reasons, removal of the topsoil can hardly be applied on a large scale, the question being whether this measure could not be replaced by one with less environmental implications.

2 The three main factors influenced by topsoil removal are relative water table (distance from soil surface), nutrient conditions and competing plant species from the soil seed bank. If a single factor could be identified as inhibiting – directly or indirectly – the establishment of the target species, it might be possible to manipulate only this one factor and thus avoid topsoil stripping.

3 In a cross-factorial field experiment we tested these three factors, i.e. relative water table, nutrients and competitors, for their effects on the growth of four wetland species (*Carex flava, Filipendula ulmaria, Ranunculus flammula, Selinum carvifolia*) after planting on peat soil. Both the mean above-ground biomass after one growing season and the coefficient of variation in biomass (as a measure of asymmetric competition) were considered.

4 The mean biomass of the planted species was severely reduced by competitors, but enhanced by nutrient addition. The effect of competitors tended to be stronger when nutrients were added, probably because of additional shading. However, this *nutrients x competition* interaction was only marginally significant ($P = 0.07$). A lower relative water table tended to enhance the mean biomass of target species when no nutrients and no competitors had been added (the effect of water table was only examined under these conditions and only marginally significant).

5 The coefficient of variation was higher with a lower relative water table, indicating more asymmetric competition, and thus a higher importance of above- than below-ground competition under drier conditions. No other factor had a significant influence on the coefficient of variation.

6 When the topsoil cannot be removed, depletion of the soil seed bank to reduce competitors seems to be the most effective method for the restoration of fen grasslands, at least in the short term. However, long-term studies with more levels of the factors are needed to substantiate this recommendation for wetland restoration.

Keywords: competition, fen restoration, nutrients, seedling establishment, topsoil removal, water table

Bulletin of the Geobotanical Institute ETH (2000), **66**, 25–35

Introduction

For about two centuries, wetlands in central Europe have been drained and numerous wetland species have become endangered (Grünig 1997). In order to preserve these plant species, many projects for wetland restoration were initiated in the last three decades, albeit with varying success. Excessive nutrients remaining from times of agricultural use and insufficient re-wetting seem to be the major reasons for failures of such restoration projects (Pfadenhauer & Klötzli 1996).

In a current restoration project focused on fen meadows around the three lakes Nussbaumersee, Hüttwilersee and Hasensee in the Canton Thurgau in northern Switzerland, about 50 ha of drained area are being restored to semi-natural grasslands similar to those before drainage in 1943 (Akeret 1997). Projects at the Geobotanical Institute ETH are currently developing methods to achieve this restoration in a cost- and labour-effective way. In a previous experiment, we transferred hay from fen litter meadows (Molinietum) containing autochthonous seeds, and turf blocks from the same situation (Barchetsee, Canton Thurgau), to our experimental plots, and we also developed and applied seed mixtures of wetland species. All experiments were carried out with and without the removal of the topsoil. The results were unequivocal: removal of the topsoil enabled the species from fen meadows to become well established, whereas when the topsoil remained, only few species could establish in the first year and even these disappeared almost completely in the second and third year (D. Ramseier & A. Gabriel, unpubl. data). This result is consistent with other experiments where removal of the topsoil led to better establishment of target species, e.g. Nagler (1999) near Bremen, or Patzelt & Pfadenhauer (1998) for the Donaumoos, north of Munich.

If applied on a larger scale, the removal of 30 cm of topsoil would produce 3000 m^3 of soil (i.e. 400–600 truck loads) per hectare which have to be transported away. This measure is not acceptable for the majority of the public because of its environmental implications. Therefore, we can only remove the topsoil in certain parts of the area and have to find alternative methods for the remaining sites.

By removing the topsoil, we simultaneously manipulate three different factors: the soil nutrient pool, the soil seed bank, and the relative water table, i.e. mean distance of the groundwater table from soil surface. Should one of these factors turn out to be the most important, we might be able to avoid removal of the topsoil by manipulating only the relevant factor. Therefore, we considered the following contrasting hypotheses:

(1) *Competitors emerging from the soil seed bank are the main cause for the failure of the target species to establish.* In this case, one could deplete the soil seed bank by harrowing the fields several times in two-week intervals to let the seeds germinate and then subsequently destroy the emerging seedlings (Ammon *et al.* 1985).

(2) *Abundant nutrients are the main factor limiting the establishment of the target species, probably through indirect effects.* Thus, one

had to focus on the reduction of the availability of the limiting nutrients.

(3) *The main reason for the failure of the target species to establish is the low relative water table.* In this case, either the groundwater table must be raised, or the soil surface must be lowered. At our study site one would have to lower the soil surface by removing the topsoil since raising the groundwater table is not possible because of the adjacent farmland.

The second hypothesis requires some additional explanation. It is very unlikely that nutrients have a negative effect by themselves, but they may benefit competitors and thus have indirect effects (e.g. Keddy *et al.* 1997; Schwinning & Weiner 1998). Therefore we were looking for a *nutrient x competitor* interaction in terms of an analysis of variance. A mechanistic explanation of this could be that the added nutrients lead to a shift from the more or less symmetric competition for nutrients to asymmetric competition for light (Connolly & Wayne 1996; Weiner *et al.* 1997; Schippers *et al.* 1999). "Asymmetric competition" means here that taller plants are able to obtain a disproportionate share of the light, and this leads to an increasingly uneven distribution of the biomass (Thomas & Weiner 1989; the term "asymmetric competition" has been used in a different sense by other authors, e.g. Keddy & Shipley 1989). In this case, the coefficient of variation of the biomass within a species is likely to increase over time, so that it might, with some care, be taken as a measure for asymmetry of competition. This is relevant in our context since many target species in the restoration of wet grasslands are inherently small-sized. Asymmetric competition is expected to lead to their exclusion in the presence of taller competitors. Therefore, in our experiment we studied both the main effects of the three factors and the *nutrient x competition* interaction, and we considered both the mean above-ground biomass of the target species and the coefficient of variation in this biomass after one growing season.

Material and methods

EXPERIMENTAL DESIGN

As part of the restoration project at Lake Nussbaumen, we set up an experiment in spring 1999 to test the above hypotheses. An incomplete factorial design was used with two levels of nutrients, two levels of competitors, i.e. of soil seed bank, and two levels of relative water table, i.e. of soil surface. The factor "high relative water table" was only applied to low nutrient levels and low density of competitors. This is because high relative water table can only be achieved by removing the topsoil at our study site, so that it is necessarily associated with the removal of seeds and nutrients. Thus, the situation of high relative water table and high nutrient loads and/or high seed density should not occur in a situation similar to ours, at least shortly after the removal of the topsoil, and when the soil is removed to a deeper level than when formerly ploughed.

We needed to control the factors of nutrients and density of competitors both in the plots with topsoil removal and in those without removal. Since it is not possible to deplete nutrients and seeds from the topsoil in a short time, we used soil from the sub-surface, which is deficient in nutrients and seeds, in all plots, and added nutrients and competitors as needed. For the plots with low relative water table (W-), we removed 25 cm of the topsoil and refilled the pit with soil from 25–50 cm depth from a second plot that was not used for the experiment (Fig. 1). For the plots with high relative water table (W+), we removed

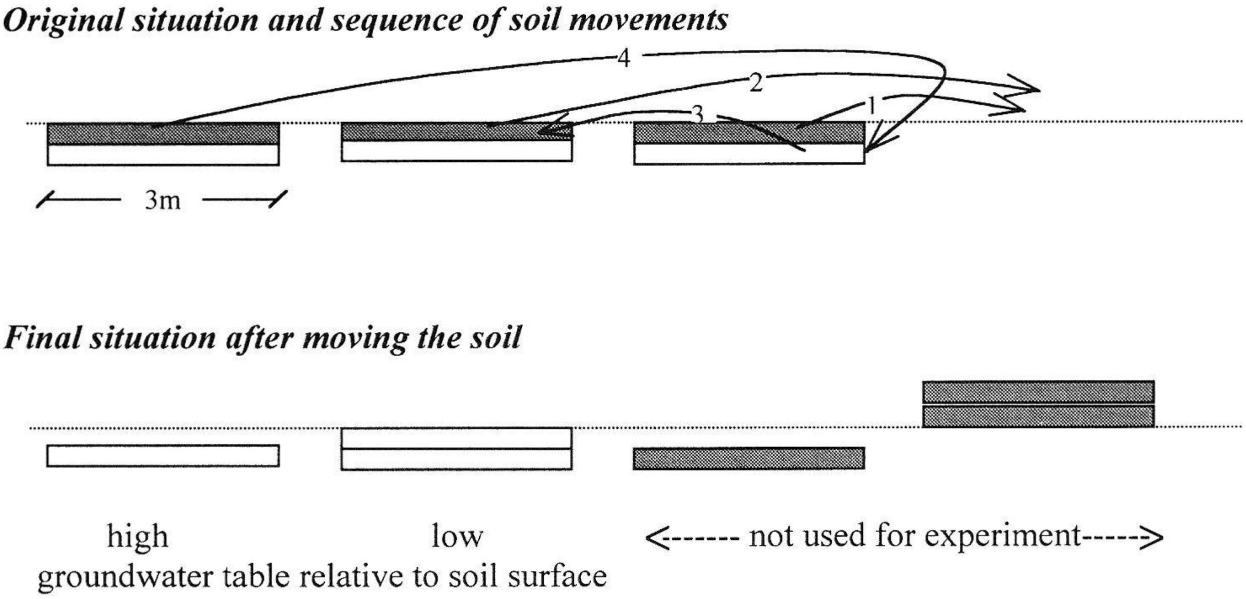

Fig. 1. Soil movements for one of the four blocks. Shaded boxes indicate topsoil rich in nutrients and seeds, unshaded boxes were poor in nutrients and seeds. Only the soil poor in nutrients and seeds has been used for the experiment, with nutrients and competitors added as needed.

25 cm of the topsoil and treated the underlying soil layer (25–50 cm depth) with a spade in order to get the same soil texture as in the plots with low relative water table. Four squares, each 3 x 3 m^2, were prepared for each relative water level. Overall, 45 m^3 of soil were translocated. This work was carried out in March 1998, one year before transplanting the target species and competitors. Thus, the soil was able to recover at least partly from the disturbance and to build up an almost natural structure.

Each of the four 3 x 3 m^2 squares with low relative water table (W-) contained four 1 x 1 m^2 subplots with the treatments no nutrients/ no competitors (N-C-), nutrients/no competitors (N+C-), no nutrients/competitors (N-C+), and both added (N+C+), being assigned to the position within the squares at random. As explained above, the squares with topsoil removed (W+) had only the treatment N-C-. For the nutrient treatment (N+), nutrients were added as NH_4NO_3, K_2HPO_4, and $MgSO_4 * 7H_2O$ according to a total of 60 kg N, 45 kg P_2O_5, 77 kg K_2O, and 8 kg Mg ha^{-1}. Half of the nutrients were added at the time of transplanting and the rest in three portions in intervals of two weeks. The nutrients were dissolved in deionised water, and the same amount of water was given to those subplots not receiving nutrients to compensate for watering effects.

On 3 April 1999, four individuals of each of the four target species were planted in a hexagonal arrangement with a distance of 16 cm between each target individual (Fig. 2). In the subplots with competitors, each interspace had one competitor planted. To reduce border effects, an additional row of competitors was planted around those subplots.

PLANT MATERIAL

We chose four target species with different size, growth form and habitat requirements (cf. Hess *et al.* 1967–1972; Landolt 1977). These were: (1) *Carex flava* L. (Cyperaceae), up to 70 cm tall, occurring in calcareous and acidic fens on nutrient poor sites; (2) *Filipendula ulmaria*

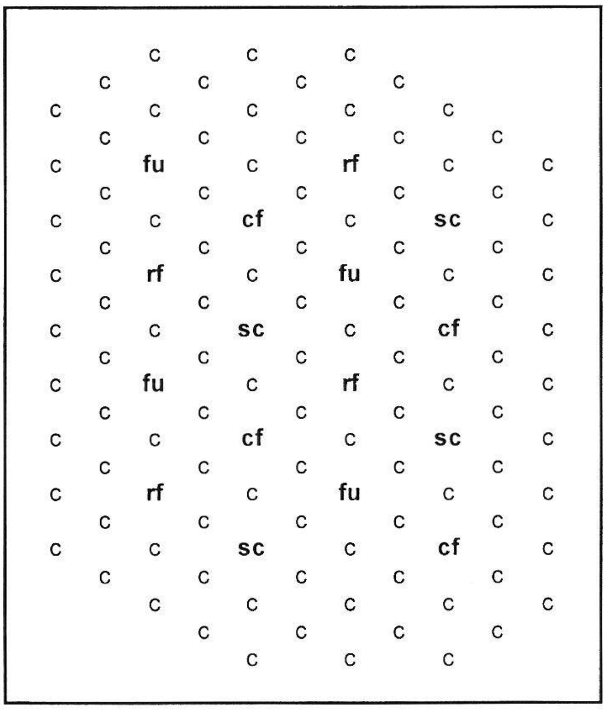

Fig. 2. Design of a subplot. Each individual of a target species was surrounded by two individuals of the other three target species. In the case of competitors added (C+), in each interspace of the target species one individual of the four competitor species Ranunculus repens, Poa pratensis, Lolium multiflorum *and* Rorippa silvestris *was planted (c in the picture). Those have been assigned at random. The distance between two individuals of the target species was 16 cm; the whole area planted per plot was 70 x 88 cm^2, (**cf**,* Carex flava; ***fu**,* Filipendula ulmaria; ***rf**,* Ranunculus flammula; ***sc**,* Selinum carvifolia*).*

(L.) Maxim. (Rosaceae), up to 2 m tall, occurring on calcareous and acidic soils at rather nutrient-rich sites; (3) *Ranunculus flammula* L. (Ranunculaceae), up to 70 cm tall, occurring on temporary flooded, humose soils, often as a pioneer species at nutrient-poor sites; and (4) *Selinum carvifolia* L. (Apiaceae), up to 1 m tall, occurring in nutrient-poor wet meadows with fluctuating humidity.

As competitors, we used herbaceous species from the study site which had strongly competed with sown and transplanted target species in a previous experiment (D. Ramseier & A. Gabriel, unpubl. data): (1) *Ranunculus repens* L. (Ranunculaceae), up to 50 cm tall, creeping on nutrient-rich, rather damp soils, sometimes noxious weed; (2) *Poa pratensis* L. (Poaceae), up to 1 m tall, on nutrient-rich grasslands; (3) *Lolium multiflorum* L. (Poaceae), up to 1 m tall, mainly on nutrient-rich, rather damp soils; and (4) *Rorippa silvestris* (L.) Besser (Brassicaceae), up to 60 cm tall, on nutrient-rich sites with high groundwater table, mainly in ditches and river banks.

The competitors were dug out from grasslands close to the experimental site and split into ramets before planting. The target species were grown from seed to a size of about 10 cm in the unheated greenhouse of the Geobotanical Institute ETH in Zürich. The seed source of the target species were wet meadows in the vicinity not further than 6 km.

HARVEST

Harvesting took place on 16 June 1999, 74 days after transplanting. All individuals of the target species were cut near the soil surface and dried to constant weight at 70 °C before weighing.

DATA ANALYSIS

Means and coefficients of variation of the above-ground biomass of the four individuals per species per subplot were calculated and used as data units in subsequent statistical analyses. Two analyses of variance were carried out: one to compare the four treatments with low relative water table among each other and a second to investigate the effect of relative water table by comparing the treatment W- N- C- with W+ N- C-. All analyses of variance were performed as a split-plot design with *block, nutrients, competition* and *nutrients x competition* as the main plot factors, species and all the according interactions as

Table 1. Analysis of variance of the effects of nutrients and competition on the above-ground biomass of four wetland species competing with each other, 74 days after planting. The analysis is based on a split-plot design

	df	Mean square	*F*-value	*P*
Error: Block x nutrients x competition				
Block	3	0.050	0.08	0.96
Nutrients	1	9.06	15.5	0.003
Competition	1	21.9	37.5	0.000
Nutrients x competition	1	2.46	4.20	0.070
Residuals	9	0.586		
Error: Within				
Species	3	5.49	29.2	0.000
Competition x species	3	1.42	7.57	0.000
Nutrients x species	3	0.607	3.23	0.033
Competition x nutrients x species	3	0.033	0.18	0.91
Residuals	36	0.188		

Table 2. Analysis of variance of the effect of the relative water table on the above-ground biomass of four wetland species competing with each other, 74 days after planting. The analysis is based on a split-plot design

	df	Mean square	*F*-value	*P*
Error: Block x water				
Block	3	0.087	0.10	0.95
Water	1	7.75	8.72	0.059
Residuals	3	0.889		
Error: Within				
Species	3	3.27	12.5	0.000
Water x species	3	0.503	1.93	0.160
Residuals	18	0.260		

the subplot factors. The residuals were reasonably normally distributed; a log transformation led to a worse distribution of the residuals. Thus, no data transformation was applied. S-PLUS 2000 professional for windows (Math Soft Inc. 1999) was used for statistical analyses.

Results

INFLUENCE OF THE THREE FACTORS ON MEAN BIOMASS OF TARGET SPECIES

Competition had a strong negative effect on the mean above-ground biomass of the target species ($P < 0.001$, Table 1, Fig. 3), while the effect of added nutrients was clearly positive ($P < 0.01$; Table 1, Fig. 3). There was a tendency of a *nutrients x competitor* interaction in the sense that the effects of additional competitors were more severe when nutrients were added, but it was only marginally significant ($P = 0.07$). The *species x competition* interaction was significant ($P < 0.001$); *Carex flava* was the species reacting most, and *Selinum carvifolia* reacted least strongly to competition. There was also a *species x nutrients* interaction ($P < 0.05$), where *Filipendula ulmaria* had the strongest reaction to additional nutri-

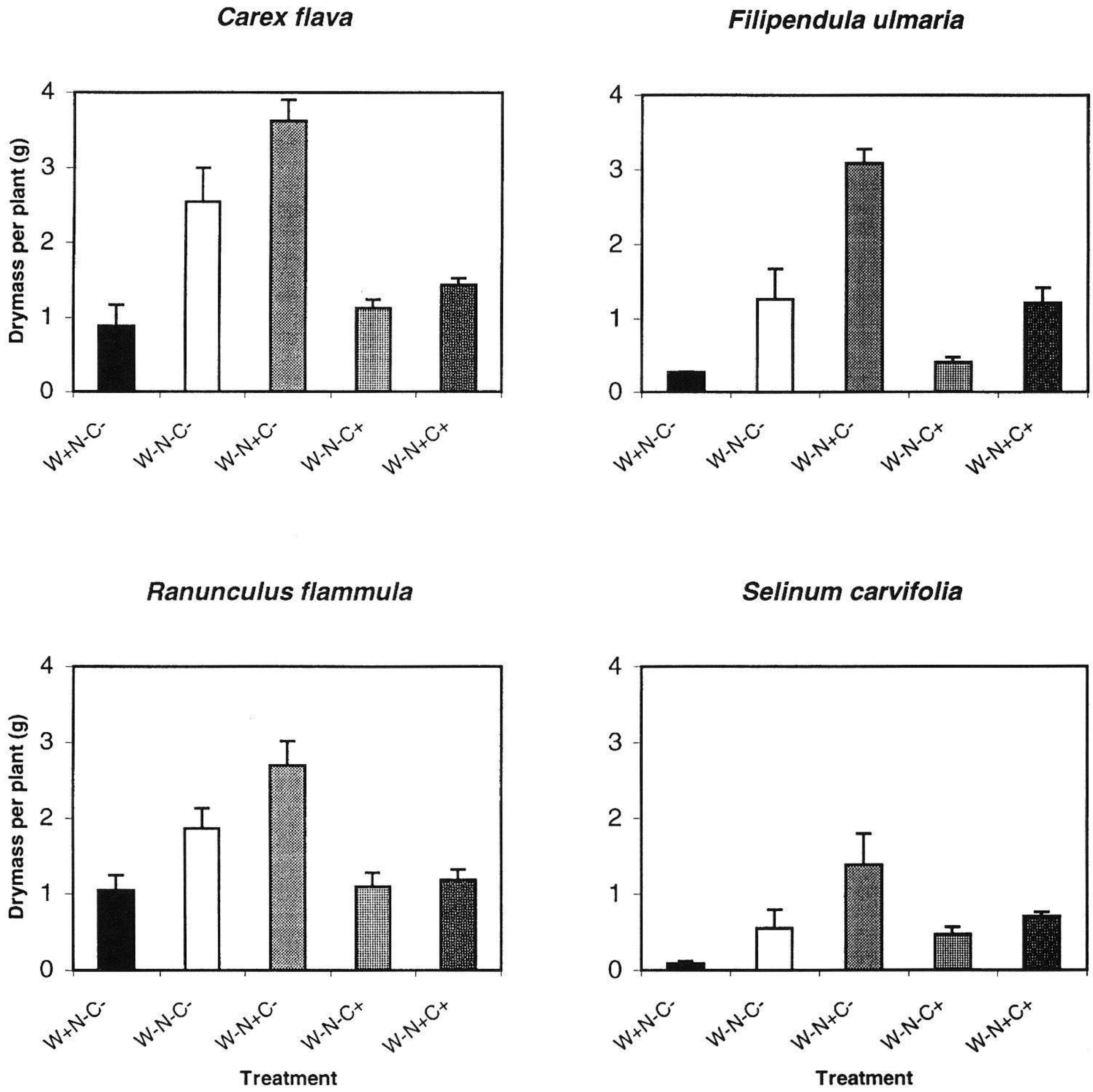

Fig. 3. Response of the four study species to five combinations of treatments (N+, nutrients added; N–, no nutrients added; W+, high relative water table (topsoil removed); W-, low relative water table; C+, competitors added; C-, no competitors added). Error bars indicate 1SE calculated from the means per plot per species.

ents. No interaction *competitors x nutrients x species* could be detected.

The effect of the relative water table on the mean above-ground biomass of the target species was only marginally significant (P = 0.06, Table 2), even though all species had higher biomass with a lower relative water table; in three out of four species the biomass was about three times higher with the low than with the high relative water table (Fig. 3). Obviously, high error variation led to the low significance of the results. *Ranunculus flammula* was the species least constrained by a relatively high water table. Out of the four species, it is the one occurring naturally in the wettest locations (Landolt 1977). However, the *species x water* interaction was not significant (Table 2).

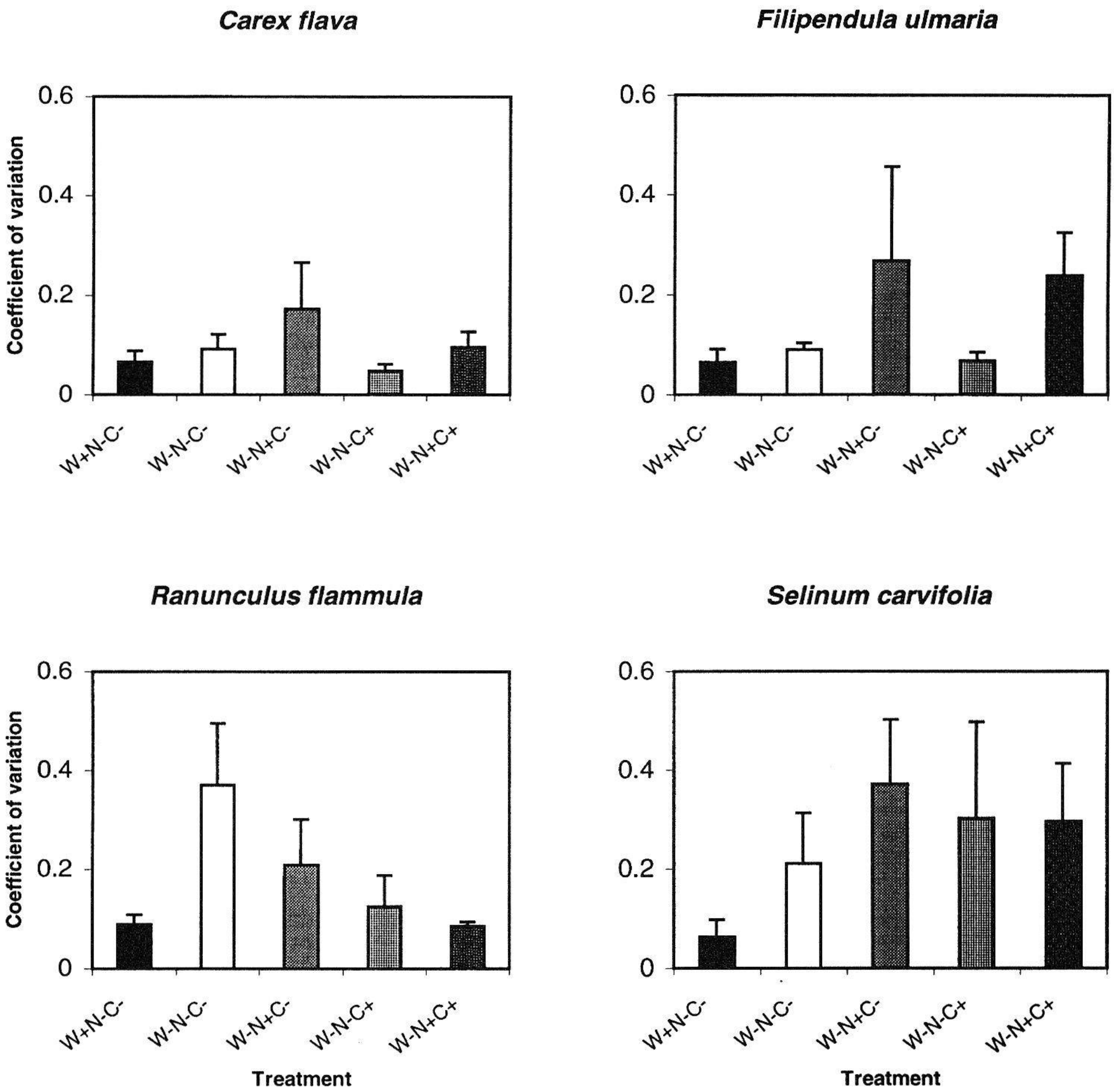

Fig. 4. Coefficient of variation of the drymass per plot of the four species depending on the five combinations of treatments (N+, nutrients added; N–, no nutrients added; W+, high relative water table (topsoil removed); W-, low relative water table; C+, competitors added; C-, no competitors added). Error bars indicate 1SE.

INFLUENCE OF THE THREE FACTORS ON THE COEFFICIENT OF VARIATION OF PLANT BIOMASS

In comparing the effects of nutrients and competitors, no factor had a significant influence on the coefficient of variation (Fig. 4, table with results of analysis of variance not presented), nor could a significant interaction be detected. Thus, there was no proof of enhanced asymmetric competition due to these factors.

In contrast, a high relative water table clearly led to a reduced coefficient of variation ($P < 0.001$, Fig. 4), with no detectable interaction effects. An interesting observation (even though statistically not significant) was that *Ranunculus flammula* was the only species with a reduced coefficient of variation due to nutrient addition. This finding might be explained by the plant's growth form: it is a creeping species which can avoid light competition to a certain extent by growing into gaps.

Discussion

INFLUENCE OF THE THREE FACTORS ON MEAN BIOMASS OF TARGET SPECIES

The first hypothesis of this study could be confirmed, i.e. *Competition is the main factor limiting the establishment of the target species* in our experimental set-up. The second hypothesis (*Abundant nutrients are the main factor limiting the growth of the target species*) had to be rejected. The nutrients did have a significant effect on the target species but this was enhancing rather than limiting their growth. However, as mentioned in the Introduction, we should have expected a reduction of the target species performance with additional nutrients only through the indirect effect of enhanced performance of competitors. This would become apparent as a *nutrient x competitors* interaction. Our data suggested the presence of such an interaction but it was not statistically significant ($P = 0.07$), probably due to the relatively low replication in our experiment. Our results are consistent with the findings of Pauli (1998) for *Primula farinosa,* a subordinate species of fen communities. In her experiments, both fertilization and removal of neighbours increased the number of rosettes per *Primula* plant. The effect of neighbour removal on the number of rosettes per plant was greater in fertilized compared to non-fertilized plots.

The third hypothesis (*The main reason for the failure of the target species to establish is the low relative water table*) could also not be confirmed. The effect of relative water table was only marginally significant, and most importantly, a higher relative water table reduced, rather than enhanced, the growth of target species. Similar results were obtained by Bollens (2000) in a pot experiment where wetland species, grown without competition, produced less biomass at higher water table. However, analogous to reduced nutrients, a high relative water table might have an indirect positive effect on the target species by limiting the performance of competitors. Since only few competitors emerged from the soil seed bank in the subplots without added competitors, this indirect positive effect was probably not strong enough in our experiment to compensate for the direct growth inhibition caused by a high water table. A *water x competitors* interaction is likely to occur, but our experiment was not designed to test for such an interaction because this was not practically relevant at our field site (cf. Methods).

INFLUENCE OF THE THREE FACTORS ON COEFFICIENT OF VARIATION OF BIOMASS

The fact that there was no significant nutrient effect on the coefficient of variation of biomass is consistent with the rejected second hypothesis (*Abundant nutrients are the main factor limiting the growth of the target species*). The effect of nutrients would have been through enhanced light competition, which should have led to a higher coefficient of variation.

The lower coefficient of variation under high relative water table is consistent with the observation that the biomass was reduced when the water table was higher, leading to reduced light competition.

RELEVANCE FOR FEN MEADOW RESTORATION PROJECTS

Based on these results, the depletion of the soil seed bank should have the highest priority if removal of the topsoil is not possible. If the topsoil can be removed or another method of re-wetting can be applied, this would be the safer way of re-establishing fen meadow species (Pfadenhauer & Grootjans 1999), since the effect of remaining competitors would be reduced by the higher water table and potentially by lower nutrient availability.

However, one has to be aware that we only considered the relatively small "time window" between germination and reproduction. However, this early phase of establishment is very important (Stockey & Hunt 1994) since later, when the grassland sward is more compact, it will be difficult for most plant species to establish. Of course, in the long run, the importance of the factors tested might change. Short term and long-term treatment effects can be quite different, at least at the individual species level (Güsewell *et al.* 1998). It is likely that management will have a pronounced effect as well. One also has to consider that we were working in a simplified system with only four target and four competitor species and only two levels of nutrients and water table, respectively.

Thus, our findings should not be taken as generalized recommendations for the practice of wetland restoration projects. However, they are a step towards a better understanding of processes during restoration of fen meadows, especially the establishment phase of some target species. In the long run and with more experiments, we are confident that our understanding of the system will lead to more specific recommendations based on a thorough understanding of the mechanisms of plant establishment and competition, thereby contributing to a better understanding of wetland ecosystems in general. Certainly, restoration experiments are great opportunities to study ecosystems as one can manipulate the study systems to a wide degree.

Acknowledgements

I would like to thank Rahel Adin, Tamara Barthelmes, Iris Klaus and Andrea Ott for the careful fieldwork they have done, and the group from Werkhof Frauenfeld for the laborious job of moving the soil. Many thanks to Sabine Güsewell and Johannes Kollmann for valuable comments on the manuscript and to Andreas Gigon for support.

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Submitted 14 March 2000
revised version accepted 17 June 2000