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Effects of soil P status on growth and P and N uptake of *Carex* species from fens differing in P-availability

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SUMMARY

We studied the effects of different soil P status (P-deficient, P-poor and P-rich fen soils) on growth, root allocation and P and N-uptake of *Carex* species from fens differing in P-availability. We carried out a 3-month pot experiment where the three species were grown in each soil. *Carex acutiformis*, a species from eutrophic fens, showed the highest production under all soil conditions and changes in biomass allocation to belowground parts, but not in specific root length (SRL) or root length/leaf area ratio (RLLA) in response to changes in the P-soil status. *Carex lasiocarpa* Ehrh., a species from P-limited areas, showed intermediate biomass production and low inherent root weight ratio (RWR). *Carex diandra* Schrank., a species from areas where the growth of the vegetation is limited by nitrogen, showed low biomass production in all three fen soils studied, and no changes in its high specific root length (SRL) or root weight ratio (RWR) with soil phosphorus status. All three *Carex* species showed the best growth under P-poor conditions and a very reduced growth on the P-limited soil. Phosphorus uptake by *Carex* species was affected by P-soil status being lowest under P-deficient conditions for all three *Carex* species. P-soil status also affected N-uptake which was lower under P-deficient conditions than in the other two soils.

It can be concluded that the success of both small *Carex* species in nutrient poor sites cannot be explained by higher relative growth rate, biomass production or nutrient uptake than the species from eutrophic areas. Other factors (water and soil chemistry other than N and P richness, presence of a bryophyte layer, establishment of seedlings, clonal reproduction, competition ability) must play a role in determining the distinct distribution pattern of these species.

Key-words: biomass production, nutrient uptake, P-limitation, relative growth rate.

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INTRODUCTION

Fens are wetland ecosystems in which the recycling of nutrients is not complete, and plant growth may become more strongly limited by the availability of nitrogen and/or phosphorus, than in terrestrial systems (Verhoeven *et al.* 1990). The availability of nutrients in these fen systems is mainly determined by their special hydrological characteristics. Fens receive nutrients from surface water and/or groundwater as well as rainfall. The balance between nutrient inputs and outputs can strongly influence the availability of nutrients to the vegetation (Koerselman & Verhoeven 1992). Further, the water chemistry (macro-ionic concentration, e.g. calcium, sulphate, etc.) and pH of these different water flows is also a very important factor determining the nutrient availability to the plants (Sjörs 1950; Moore & Belamy 1974). Finally, the management of some fen areas can also interfere with the nutrient dynamics of the fen by the addition or extraction of nutrients to or from the system.

Fen vegetation is dominated by graminoids (Verhoeven *et al.* 1990) and several works have shown that the botanical composition and production in fen systems differed in relation with the plant nutrient availability (Vermeer 1986; Wassen *et al.* 1990; Koerselman & Verhoeven 1992). *Carex diandra* Schrank. is a species from low-productive fens which have a low rate of mineralization and a seepage of groundwater rich in iron, calcium and bicarbonate (Verhoeven *et al.* 1983, 1988). This leads to chemical precipitation of phosphate in non-available compounds mainly related to Fe and Ca (Richardson & Marshall 1986; Boyer & Wheeler 1989; Nichols 1983; Wassen *et al.* 1990). The result of low mineralization and chemical precipitation is a relatively low availability of N and P for the vegetation (Verhoeven *et al.* 1983). However, in these low-productive fens, characterized by the *Scorpidio-Caricetum diandrae*, the growth of the vegetation is limited only by nitrogen, as several fertilization experiments have shown (Vermeer 1986; Verhoeven & Schmitz 1991). *Carex lasiocarpa* Ehrh. is a characteristic species in mesotrophic fens characterized by the *Sphagno-Caricetum lasiocarpae*, where the growth of the vegetation is limited by phosphorus (Verhoeven & Schmitz 1991). The limitation by phosphorus in these fens was related to late secondary succession stages which usually had implied prolonged periods of harvesting for hay which had removed much phosphorus from the system (Koerselman *et al.* 1990; Verhoeven & Schmitz 1991). *Carex acutiformis* Ehrh. occurs as a dominant species in highly productive eutrophic fens (*Magnocaricion*) (Verhoeven *et al.* 1988).

In their natural habitats, fen *Carex* species show differences in biomass production (Verhoeven *et al.* 1983). These differences may be related both to the nutrient availability in the soil and to the interspecific differences in response to nutrient availability. For example, it has generally been found that when a nutrient is limiting, *Carex* plants increase their root biomass (Konings *et al.* 1988; Veerkamp *et al.* 1980; Aerts *et al.* 1992) in order to increase the capacity for taking up nutrients. It is also described that plants show a higher efficiency in the use of the limiting nutrients (Loneragan & Asher 1967). Besides, physiological adaptations to the low availability of P in the medium have been described such as, for instance, the active mobilization of soil organic-P by plants or soil microorganisms (Richardson & Marshall 1986; Adams & Pate 1992; Polglase *et al.* 1992) or the mobilization of P from soil inorganic P-pools by means of the excretion of organic acids or H^+ in the rhizosphere and uptake of P (Dinkelaker *et al.* 1989; Hoffland 1990). The performance of the three *Carex* species mentioned has up to now not been related to the soil phosphorus availability nor the presence of the different organic or inorganic phosphorus pools in the peat soil, although phosphorus dynamics is an important factor which does control the plant growth in some of these fens (Verhoeven & Schmitz 1991).

This paper deals with the growth of three characteristic fen *Carex* species when grown in three fen peat soils which differ in their nutrient limitations for the vegetation (Verhoeven & Schmitz 1991). Our hypothesis was that species from low productive P or N limited fens would show better growth under P-deficient or P-poor soil conditions than the species from non nutrient limited sites. We tested this by growing *Carex diandra*, *Carex lasiocarpa* and *Carex acutiformis* on the soils where these species typically grow which differ in their P availability for the plants, i.e. fen soil with moderate P-limitation (P-poor), fen soil with strong P-limitation (P-deficient) and P-rich fen soil (P-rich). It was expected that the first two species would show better growth and P-uptake on the low nutrient soils, and that *C. acutiformis* would show the highest production and P-uptake on the nutrient-rich soil. It was also expected that all three species would increase biomass allocation to the belowground parts in the P-deficient conditions.

MATERIAL AND METHODS

Soil and plant material

The soils used for the experiment were collected in the field in April 1993. All of them came from a floating fen area (Vechtplassen area), 10–15 km north of Utrecht (NL). A detailed description of these sites is given in Verhoeven & Schmitz (1991). We selected three soils from three different and characteristic fens, according to the vegetational and hydrological criteria of classification (Verhoeven *et al.* 1988). The first soil was taken from a highly productive alder forest in Westbroek polder and it will be further referred to as 'P-poor soil'. The second soil was collected also in Westbroek polder, in a low productive fen in which it is known that the plant growth is limited by nitrogen (Verhoeven & Schmitz 1991). This soil will be referred to as 'P-rich'. Finally, the third soil was taken in a low productive fen in Het Hol polder, where the plant growth is limited by phosphorus (Verhoeven & Schmitz 1991). It will be referred to as 'P-deficient'. Living roots were carefully removed from the soils. The indications P-rich, P-poor and P-deficient were based on the chemical analyses made on the soils that are described later on in this section.

Plants were grown from green and rooted cuttings collected from the field. Clumps were dug out from the field and individual young shoots were detached from them and placed on the soils. We have selected three *Carex* species which were each dominant in the vegetation in a particular fen: *Carex acutiformis* Ehrh. (highly productive, eutrophic fens), *Carex lasiocarpa* Ehrh. (low-productive, mesotrophic, P-limited fens) and *Carex diandra* Schrank. (low productive, mesotrophic N-limited fens). To ensure that the initial biomass was similar for all species, shoots were clipped to a height of 40 mm.

Experimental design

Shoots of *C. acutiformis*, *C. lasiocarpa* and *C. diandra* were grown in the three soils collected in the field. We carried out an experiment in a full factorial design with 20 pots per soil and species. The pots were filled with 1500 cm^3 of peat soil. One shoot of *Carex* spp. was planted in every pot. Pots were placed in containers which were filled up with nutrient solution (with all nutrients except for phosphorus) till the level of the soil on the pots. The nutrient solution contained 0·6 mM $Ca(NO_3)_2$, 0·8 mM KNO_3, 0·27 mM $MgSO_4$, 2 μM $MnSO_4$, 0·8 mM $ZnSO_4$, 0·15 μM $CuSO_4$, 20 μM B_3BO_3, 0·25 mM $NaMoO_4$ and 40 μM Fe-EDTA. The containers which were situated outdoors in a plastic tunnel in a random way, were refilled every 2 days with demineralized water, for maintaining good conditions of moisture in the soil, similar to the field conditions. The experiment took 3 months (April–June 1993).

Harvest procedure and growth parameters

The plants were harvested at the end of the experiment. The plants were divided in shoots, roots and rhizomes. Leaf areas were measured with a Li-cor leaf area meter (Model LI-3000, Lambda Instruments, USA) and the total root length with a Comair root length scanner (Comair, Australia). Dry weights of each plant part were determined after drying for 48 h at 70°C.

Root weight ratio (RWR), specific root length (SRL), root length/leaf area ratio (RLLA) and relative growth rate (RGR) were calculated according to Hunt (1978).

Phosphorus and nitrogen uptake were estimated from the total amount of nutrients in the plants at the end of the experiment, assuming that plants of each species had equal amounts of nutrients at the beginning of the experiment.

Chemical analyses in soil and plant material

Five replicate samples of fresh soil material were used for the sequential extraction of phosphorus (Golterman & Booman 1988; de Groot & Golterman 1990). The extraction method obtains sequentially different phosphorus soil fractions by means of different extractants. Distilled water for orthophosphate (a), solution of Ca-NTA (0·02 M) and dithionite (0·045 M) for Fe (OOH) $\approx$ P (b) and EDTA-Na (0·05 M) for $CaCO_3 \approx$ P (c). The rest of the sample was considered organic phosphorus and its amount was determined by a digestion with H_2SO_4 and salicylic acid and a mixture of sodium sulphate, copper sulphate and selenium. (a) (b) and (c) solutions were also digested with K_2SO_3 and H_2SO_4 for knowing the organic phosphorus associated with Fe and Ca (Fe $\approx$ OrgP and Ca $\approx$ OrgP, de Groot & Fabre 1992). Afterwards, the P content of all the diluted digestion samples were determined colorimetrically with a Skalar SA-40 continuous flow analyser. The sum of all those fractions was considered as total phosphorus.

The results of the sequential extraction and total phosphorus contents in the fen soils are presented in Table 1. The P-rich soil had the highest content of total-P and $CaCO_3 \approx$ P ($P<0{\cdot}05$) and there was no difference between the P-deficient and P-poor soils for these P pools. The rich soil had also the highest content of ortho-P and organic-P, whereas the P-deficient soil had the lowest ortho-P content ($P<0{\cdot}05$). Phosphorus bonds related to iron (Fe(OOH) $\approx$ P and Fe $\approx$ Org-P) did not show differences between soils.

All plants parts were finely ground and 200 mg were digested in the same way as the soil samples. The diluted digests were measured colorimetrically for phosphorus and nitrogen.

Statistical analyses

The data were statistically analysed by analysis of variance using the STATGRAPHICS computer program (Statgraphics 1991). Multiple comparisons among pairs of mean

Table 1. Inorganic phosphorus fractions (μg/g) and organic and total phosphorus content (mg/g) in peat soils (mean ± SE; $n=5$). Different letters in rows indicate significant differences between peat soil ($P<0·05$).

	P-deficient	P-poor	P-rich
Total-P	0·46 ± 0·06 b	0·59 ± 0·05 b	0·84 ± 0·03 a
Ortho-P	2·2 ± 0·3 c	6·6 ± 0·3 b	8·6 ± 0·5 a
Fe(OOH) ≈ P	3·0 ± 0·4 a	3·3 ± 0·8 a	5·9 ± 0·6 a
Fe ≈ Org-P	24·0 ± 3·3 a	64·9 ± 9·0 a	61·4 ± 2·8 a
$CaCO_3$ ≈ P	4·8 ± 1·2 b	4·5 ± 0·7 b	12·3 ± 1·9 a
Ca ≈ Org-P	36·8 ± 11·8 a	49·9 ± 14·9 a	71·5 ± 11·7 a
Organic-P	0·39 ± 0·05 b	0·46 ± 0·04 ab	0·68 ± 0·05 a

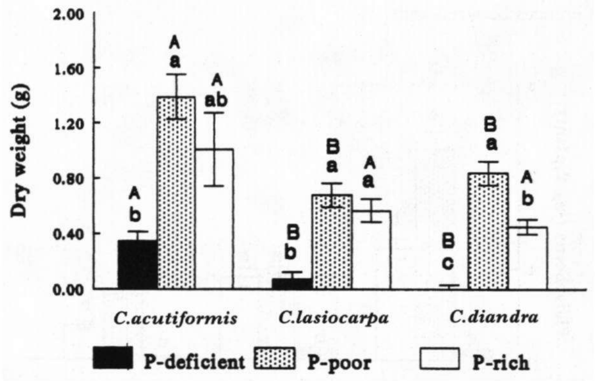

Fig. 1. Total dry biomass production of *Carex* species grown in three peat soils (mean ± SE; $n=20$). Soil types or species marked with the same letter are not different ($P<0·05$). Upper case for differences between species and lower case for differences between soils.

values were made using Tukey's studentized range test, and if the differences were significant the species rank order for the various parameters was determined. In the case of unequal variances the data were transformed logarithmically or reciprocally.

RESULTS

Biomass production and RGR

Figure 1 shows the results for total biomass production of the three *Carex* species on different peat soils. Comparison of the growth response of the three species for each soil showed that, on P-rich soil, no differences between species occurred. However, in P-poor and P-deficient soils, *C. acutiformis* had a significantly higher biomass than *C. lasiocarpa* and *C. diandra* ($P<0·01$). If we compare the results within the species we can see that all the species showed a reduction of biomass production under P-deficient conditions. Only *C. diandra* increased its production from P-rich to P-poor soil. It is remarkable that *C. diandra* did not grow at all under P-deficient conditions.

C. lasiocarpa and *C. diandra* showed a significantly lower RGR in the P-deficient soil (Fig. 2) but no differences between P-rich and P-poor soils ($P<0·01$). *C. acutiformis* showed no significant differences in RGR when grown on the different soils. The

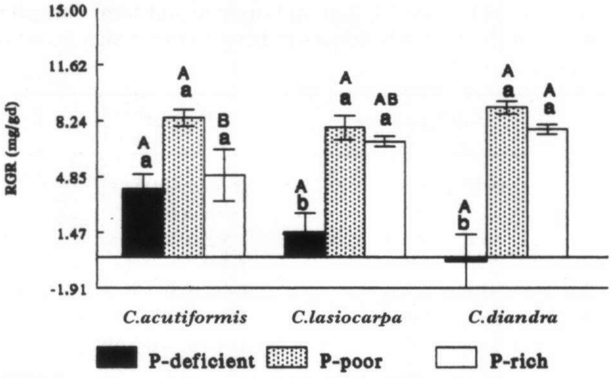

Fig. 2. Relative growth rate (RGR) of *Carex* species grown in three peat soils (mean ± SE; n=20). Soil types or species marked with the same letter are not different (P<0·01). Upper case for differences between species and lower case for differences between soils.

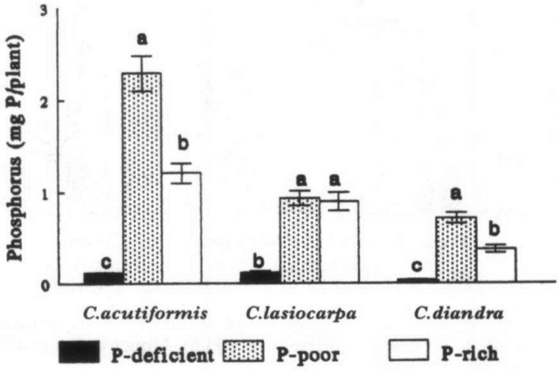

Fig. 3. P uptake of three *Carex* species grown on three peat soils (mean ± SE; n=20). Soil types marked with the same letter are not different (P<0·01).

comparisons between the species indicated that there are no differences between them when they were grown on P-deficient or P-poor soils. In P-rich soil *C. diandra* showed higher RGR than *C. acutiformis* (P<0·01).

Phosphorus and nitrogen uptake

The P-uptake by *C. acutiformis* and *C. diandra* was highest in P-poor soil, intermediate in P-rich and lowest under P-deficient conditions (P<0·01; Fig. 3). For *C. lasiocarpa* there were no significant differences in P-uptake in the P-poor or P-rich soils but both were higher than the P-uptake in P-deficient soils.

C. acutiformis showed no differences in N-uptake (Fig. 4) between the P-deficient and P-rich soils and a significantly higher N-uptake in the P-poor soil (P<0·01). *C. lasiocarpa* had significantly higher N-uptake in the P-rich than in the P-deficient soil. *C. diandra* showed differences among the three soils showing lower uptake under P-deficient conditions (P<0·01) and higher uptake in P-poor soil.

P concentration in the plant for all three *Carex* species was lowest in P-deficient soil (P<0·01; Fig. 5). *C. lasiocarpa* showed higher values than the other two species in P-rich and P-poor soils and higher than *C. acutiformis* in P-deficient soil (P<0·01).

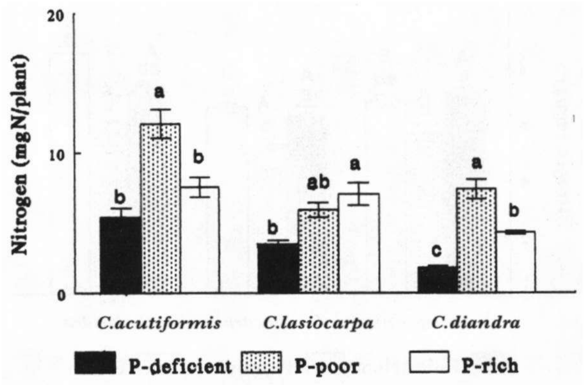

Fig. 4. N uptake of three *Carex* species grown on three peat soils (mean ± SE; $n=20$). Soil types marked with the same letter are not different ($P<0{\cdot}01$).

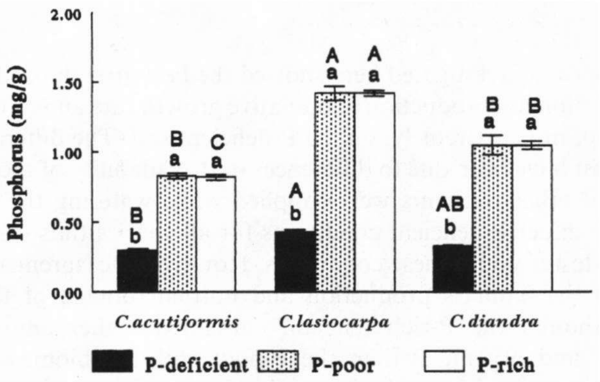

Fig. 5. P concentration of three *Carex* species grown on three peat soils (mean ± SE; $n=20$). Soil types or species marked with the same letter are not different ($P<0{\cdot}01$). Upper case for differences between species and lower case for differences between soils.

There were no significant differences in N concentration in the plant between species in P-poor and P-deficient soils ($P<0{\cdot}01$; Fig. 6). In P-rich soil *C. diandra* showed higher values than the other two species.

Root allocation and root morphology

In all the three soils considered, the biomass allocation to the roots (root weight ratio:RWR) showed the highest values for *C. diandra* followed in this order by *C. acutiformis* and *C. lasiocarpa* (significant differences $P<0{\cdot}01$; Table 2). RWR for *C. acutiformis* is lowest under P-poor conditions and highest in the P-deficient soil. *C. lasiocarpa* and *C. diandra* did not show differences for RWR between soils.

Specific root length (SRL) of *Carex lasiocarpa* was lower under P-deficient than under P-poor or P-rich conditions, whereas the other two species did not show such differences (Table 2). *Carex acutiformis* showed the lowest SRL values except for the P-rich soil. The ratio between root length and leaf area (RLLA) of *Carex acutiformis* and *C. diandra* was higher under P-deficient than under P-poor or P-rich conditions. RLLA was generally lowest for *Carex acutiformis* and highest for *C. diandra.*

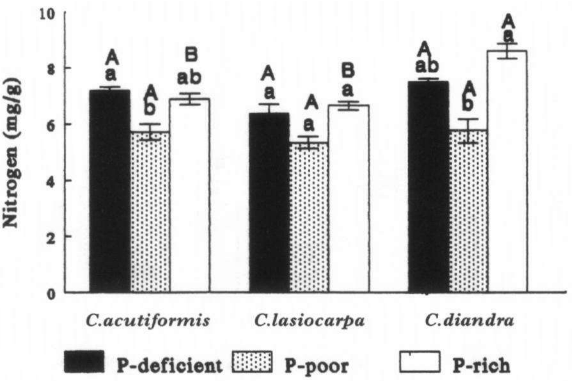

Fig. 6. N concentration of three *Carex* species grown on three peat soils (mean ± SE; $n=20$). Soil types or species marked with the same letter are not different ($P<0{\cdot}01$). Upper case for differences between species and lower case for differences between soils.

DISCUSSION

All three *Carex* species investigated here showed the best growth on the P-poor soil, as it is shown by the biomass production and relative growth rate and a reduced growth on the P-rich soil and, more extremely, on the P-deficient soil. The differential response to the three soils must have been due to differences in P availability of the different P-pools in the soils, as all other nutrients were supplied while watering the pots. The lowest biomass response under P-deficient conditions for all species thus seems logical, as all the P-pools were lower under these conditions. However, measurements of the various soil P pools and the biomass production and nutrient uptake of the *Carex* species showed that, although the P-rich fen soil contained higher amounts of ortho-P, calcium-bound P and organic P than the P-poor soil, the biomass production and P-uptake of the three species was higher under P-poor than under P-rich conditions. These results suggest that other factors more than the P status of the soil influenced the performance of these species when grown under these conditions. For example, differences in the quality of the organic matter between the soils that were evident from the much higher degree of humification of the peat in the P-poor soil. Besides, it is also possible that part of the organic P pool in the P-poor soil was accessible for the plants, in contrast to the organic P pool in the P-rich soil.

Carex acutiformis showed the highest biomass in all three soils investigated. This is a highly productive species which characteristically occurs in nutrient-rich fen sites (Verhoeven *et al.* 1983; 1988) and also has shown high biomass accumulation in outdoor and greenhouse nutrient enrichment experiments (Konings *et al.* 1988; Aerts *et al.* 1992; Konings *et al.* 1992). It is remarkable and unexpected that this species grew better on the P-deficient soil than *Carex lasiocarpa*, a potentially high-productive species (Aerts *et al.* 1992) which only occurs in our study area as a low-productive species in strongly P-limited soils (Verhoeven & Schmitz 1991). It was expected that this species would have morphological or physiological adaptations to make available and efficiently take up phosphates from soils low in P, and would therefore be at a relative advantage over the other two species under such conditions. It is possible that both small-sedge species, i.e. *C. lasiocarpa* and *C. diandra*, had difficult starting conditions in the experiment because they were more susceptible to environmental changes when they were collected, transported or manipulated during the initial phases of the experiment than

Table 2. Growth parameters related to the roots for three *Carex* species grown in different peat soils ($n=20$). Data are mean with SE in parentheses ($n=20$). Significant differences between soil types are represented by lower case, between species are in uppercase ($P<0{\cdot}01$). Root weight ratio (RWR), specific root length (SRL), root length/leaf area ratio (RLLA)

	C. acutiformis			*C. lasiocarpa*			*C. diandra*		
Parameter	P-deficient	P-poor	P-rich	P-deficient	P-poor	P-rich	P-deficient	P-poor	P-rich
RWR ($g\ g^{-1}$)	0·36 a B (0·01)	0·30 b B (0·01)	0·34 ab B (0·01)	0·22 a C (0·01)	0·24 a C (0·01)	0·26 a C (0·01)	0·48 a A (0·02)	0·49 a A (0·01)	0·46 a A (0·02)
SRL ($m\ g^{-1}$)	103·42 a B (12·77)	132·96 a C (9·46)	104·66 a A (2·80)	136·75 b AB (8·00)	230·28 a A (7·05)	192·70 a A (11·02)	167·66 a A (10·18)	191·97 a B (9·28)	221·77 a A (56·12)
RLLA ($km\ m^{-2}$)	15·32 a B (1·40)	9·68 b B (1·02)	10·44 ab B (0·60)	38·71 a BB (9·30)	28·36 a B (2·18)	36·79 a AB (9·30)	679·80 a A (187·68)	62·95 b A (9·80)	69·79 b A (11·58)

C. acutiformis. However, the small-sedge species did grow well in the P-poor soil and would, if especially adapted to live in nutrient limited conditions, have shown at least a similar growth response. Instead, their growth was strongly reduced, especially on the P-deficient soil. Although we have tried to make the initial size and weight of the plants uniform, it would be possible that a different initial weight could have slightly affected the measured RGR and biomass production.

Carex acutiformis was also the only one of the three species investigated which showed a higher RWR under P-deficient conditions. Both *Carex diandra* and *C. lasiocarpa* did not adapt to the P shortage by investing more biomass into the roots, as it is expected when a resource is limiting (Bradshaw *et al.* 1964; Loneragan & Asher 1967; Brouwer 1983; Aerts *et al.* 1992). This is consistent with Grime's generalization that species characteristic of favourable habitats show greater plasticity in allocation patterns than do species from stressful environments (Grime 1979). Chapin (1980) has suggested that the evolution of plants adapted to poor environments could be towards the genetic fixation of biomass allocation patterns for maximizing the resources absorption and reducing the requirements of the plants and this would apply for *C. diandra* and *C. lasiocarpa*. However, *C. diandra* showed higher RWR under all conditions than *C. lasiocarpa*. These results have been also quoted by Aerts *et al.* (1992). Furthermore, Powell (1974) suggested that plant responses to low P availability could involve an increase in root length or surface rather than in root biomass. However, *Carex acutiformis* and *C. diandra* did not show a higher SRL in the P-deficient treatment, and *C. lasiocarpa* even showed a lower SRL in this treatment. This does not agree with other reports on a higher SRL at lower nutrient supply (Robinson & Rorison 1983; Fitter 1985). On other hand, the generally higher SRL for *Carex diandra* and *C. lasiocarpa* than for *C. acutiformis* is in agreement with their field occurrence in nutrient-poor and nutrient-rich habitats, respectively. SRL values are similar to those from the literature (Konings *et al.* 1988). *C. diandra* showed higher RLLA than the other two species under all conditions which has often been cited as relevant for its nutrient uptake because it also facilitates greater transpiration connected with greater photosynthesis (Konings *et al.* 1988).

All the three *Carex* species responded to higher ortho-P, $CaCO_3 \approx P$ and organic-P contents in the soil with higher P-uptake, as it has been quoted by Atwell *et al.* (1980). In general the P-uptake followed the same pattern as the biomass production, with the same significant differences between soils for the three species. Species from poor habitats generally have higher tissue concentrations (lower efficiency) of a limiting nutrient than do species from more fertile areas (Chapin 1980). At high availabilities, interspecific differences in tissue concentration are particulary pronounced and are due to luxury consumption of species from poor areas (Clarkson 1967). These two ideas are in agreement with our results. Species from poor areas, and specially *C. lasiocarpa* for P-limited areas, showed higher P concentrations than the species from rich areas (*C. acutiformis*). N uptake in the three *Carex* species is also clearly affected by the P status of the soil, as Shaver & Melillo (1984) have suggested for other species, and this mainly affected the species from poor areas. The mechanisms involved in this effect are related to the reduction of the potential of the roots for absorbing non-limiting nutrients when another nutrient is in short supply (Chapin 1991).

Summarizing, all three species showed a rather similar response to the three treatments, and among them the species characteristic for eutrophic conditions performed best in the P-rich as well as the P-poor treatments. The results of the experiment do not fit in the general expectation: better growth of *C. diandra* and *C. lasiocarpa* under low P levels, compared with the eutrophic species. Thus, it can be concluded that the success of both small *Carex* species in nutrient limited sites cannot be explained by specific adaptations to the nutrient poverty of the soil reflected in a higher biomas production, P-uptake, root biomass allocation, etc., although constant RWR and/or high SRL and high P concentration have been shown by the species from low productive areas. Some studies have suggested that the success of plant species in environments with low availability of P, is based on their ability for mobilizing a considerable amount of non-exchangeable P (Tyler 1994) and this could apply to the *Carex* species. Furthermore, other factors both from the habitat (water and soil chemistry other than N and P richness, presence of a bryophyte layer, seed germination, seedling establishment) and from the species (different retranslocation patterns, clonal reproduction, nutrient losses, performance over a longer time) that were not considered in our initial hypothesis, must play an important role in determining the distinct distribution patterns of these species. A more comprehensive study which would consider all these other factors is needed to understand the ecological mechanisms which rule the success of the *Carex* species in the fen area.

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