Ann. Bot. Fennici 41: 189–199 ISSN 0003-3847
Helsinki 23 June 2004

Eriophorum vaginatum plays a major role in nutrient immobilisation in boreal peatlands

Niko Silvan, Eeva-Stiina Tuittila, Harri Vasander & Jukka Laine

Peatland Ecology Group, Department of Forest Ecology, University of Helsinki, P.O. Box 27, FIN-00014 University of Helsinki, Finland

Received 22 May 2003, revised version received 26 Nov. 2003, accepted 2 Jan. 2004

Silvan, N., Tuittila, E.-S., Vasander, H. & Laine, J. 2004: *Eriophorum vaginatum* plays a major role in nutrient immobilisation in boreal peatlands. — *Ann. Bot. Fennici* 41: 189–199.

The temporal growth pattern, above- and below-ground biomass allocation of *Eriophorum vaginatum* (cottongrass) and its nutrient immobilisation dynamics were studied in a greenhouse experiment. The temporal growth pattern was also studied in a field experiment with three N and P addition levels in a restored peatland buffer in central Finland. The greatest seasonal increase in accumulated N and P occurred in roots and stems and leaf sheaths concurrently with the highest leaf elongation and new daughter tiller production. The amounts of N and P immobilised in cottongrass tissues were 73 g N m^{-2} (91% of the added N) and 13 g P m^{-2} (77% of the added P). A remarkable liberation of P into outflow water was observed at the end of the growing period. The annually increasing mass of dead organs of cottongrass, typically highly resistant to decomposition, forms a potential long-term sink for nutrients.

Key words: biomass allocation, cottongrass, nitrogen, nutrient dynamics, phosphorus

Introduction

Eriophorum vaginatum (cottongrass) is a plant species typically flourishing in disturbed peatland ecosystems. It can rapidly become dominant after restoration of cut-away peatlands (Tuittila *et al.* 2000) and peatlands drained for forestry (Heikkilä & Lindholm 1997, Komulainen *et al.* 1998, 1999), and following fire (Wein & Bliss 1973, Keatinge 1975). In sites drained for forestry it has a peak in abundance following drainage succession (Laiho 1996), as well as clear-cuts (Kuusipalo & Vuorinen 1981) and fertilisations (Päivänen 1970).

Buds of cottongrass are formed in the leaf axils and develop rapidly into new tillers (Kummerow *et al.* 1988). This particular growth pattern, in combination with slow decomposition of the stems and leaf sheaths, results in the formation of characteristic tussocks (Polozova 1970, Wein 1973, Fetcher & Shaver 1982). Cottongrass has annual roots, which show signs of suberization only at the very end of the growing season (Kummerow *et al.* 1988). These roots tend to grow vertically downward showing only occasional ramification (Kummerow *et al.* 1988).

Cottongrass has many properties that facilitate its high nutrient immobilisation capacity, such as effective biomass production and a nutrient storage system mainly based on stems and leaf sheaths (Shaver *et al.* 1986), the sequential pattern of leaf production (leaf cohorts) through the growing season (Jonasson & Chapin 1985) and the long lifespan of individual tussocks (Mark *et al.* 1985). The well recognizable residues of dead organs (leaf sheaths and roots) can be found in the peat layers formed thousands of years ago (Mäkilä 1994).

Cottongrass has a highly developed tolerance to low resources and a high competitive ability in disturbed ecosystems (McGraw & Chapin 1989, Thormann & Bayley 1997). It is a typical opportunistic plant species, with high nutrient use efficiency under low-nutrient conditions (Thormann & Bayley 1997) and high nutrient uptake efficiency in luxuriant conditions (Shaver *et al.* 1986). The overwhelming importance of nutrients, especially N and P, in controlling the growth of cottongrass in Alaskan tussock tundra was demonstrated by Shaver *et al.* (1986).

In boreal peatlands, especially in disturbed peatland ecosystems, the same restricting environmental conditions, i.e. low temperature, nutrient limitation and high water table level also persist (Tuittila *et al.* 2000). Despite the many studies concerning the growth of cottongrass especially in Alaskan permafrost tundra, its growth dynamics and long-term nutrient immobilisation are still poorly known in the boreal peatland ecosystems, especially for below ground organs. Additionally, the use of cottongrass in water pollution control is an important aspect in Finland, where it is a common peatland plant (Hotanen 2000) and therefore readily available in the construction of wetland buffers.

This study was conducted to assess the temporal growth pattern and the nutrient retention dynamics of cottongrass, and to investigate the growth dynamics in different N and P levels. Since cottongrass has high nutrient use efficiency under low-nutrient conditions and high nutrient uptake efficiency in high-nutrient conditions, we postulated that cottongrass as a nutrient conserving plant allocates biomass and nutrients in the slowly decomposing storage organs (stems and leaf sheaths) proportionally more than in the rapidly decomposing organs (leaf blades).

Materials and methods

This study was divided into a greenhouse experiment and a field experiment. The temporal growth pattern, above- and below-ground biomass allocation of cottongrass and its nutrient immobilisation dynamics were investigated in the greenhouse experiment, and the temporal growth pattern also in the field experiment with three N and P addition levels in a constructed wetland buffer.

Growth dynamics study in the greenhouse

The greenhouse experiment was conducted to assess the seasonal growth and nutrient immobilisation dynamics of cottongrass in situation with controlled nutrient input. For the experiment, 50 vigorous tussocks of cottongrass were collected from the site of the field experiment in late November 1998. The tussocks were wintered in a cellar at +5 °C. In May 1999 the tussocks were separated into individual tillers and roots were removed, and on average 15 tillers of a uniform size were planted into 36 cylindrical tubes (12 cm diameter, 60 cm height) filled with quartz sand. The 36 tubes were divided randomly into three harvest groups, 12 tubes in each group. The first group was harvested in July, the second in August and the third in November 1999.

The tubes were inserted into the ground with only the uppermost 5 cm of the tube protruding above the surrounding ground level. Water table level was regulated by irrigation (on average two or three times a week) to 10 cm below the quartz sand surface level, equal to the average water table level of the field experiment.

A water-soluble multi-nutrient fertilizer was given with the irrigation water at a concentration of 0.1%, amounting to 81 g N m^{-2} and 17 g P m^{-2} during the growing season. Nutrient content (g kg^{-1}) of the multi-nutrient fertilizer used in the greenhouse experiment was 64 for NO_3^-, 50 for P, 260 for K and 27 for Mg. Irrigation and outflow water was sampled simultaneously with irrigation at two weeks intervals, and their total N and P concentrations were analysed using Tecator 5020 FIA and ICP ARL 3580 analysers.

At each harvest group, living and dead leaf blades, stems and leaf sheaths and roots were separated. The dry masses (at 60 °C) of each separate organ were measured, and the concentrations of N and P were analysed using Leco CNS 1000 and ICP ARL 3580 analysers. The mass values were related to the surface area of the tubes and expressed as g m^{-2}.

The exsertion, elongation and senescence of leaves from 12 tillers of the third harvest group were measured, and the genesis of new tillers was observed at two-week intervals, following the method that Shaver and Laundre (1997) used in Alaska. The tillers were marked by placing small wires attached to a coloured stick around them. On each measurement date, the length of the green part of each leaf, from oldest to youngest, was measured using the end of the leaf sheath as a baseline. The lengths of roots of these 12 tillers were measured individually in November during the harvest of the third group.

Because each leaf could be uniquely identified, and because repeated measurements could be made of each leaf from the same baseline, it was possible to follow individual leaf life histories.

Growth dynamics study in a restored peatland

The field experiment was conducted to assess the seasonal growth dynamics of individual tillers in three different N and P levels formed by artificial N and P addition through a feeder ditch in the upper end of the site (Silvan *et al.* 2002). Along the distance from the feeder ditch, a gradient in moisture and nutrients was formed (Table 1).

The experiment was carried out in a peatland in central Finland (61°48´N, 24°17´E) that had been drained for forestry in the 1950s and restored in 1995 by rewetting and clearcutting the forest stand (Komulainen *et al.* 1998, 1999). The original mire type before forest drainage was oligotrophic tall-sedge pine fen (for mire site type description *see* Laine & Vasander 1996) which is the most widespread mire type in Finland (Kalliola 1973).

One tiller from each of nine tussocks was selected for intensive observation of the leaf and tiller growth dynamics, and they were measured as in the greenhouse experiment. Nine tussocks situated in three groups along a decreasing gradient of altitude, moisture and N and P concentration in soil water were selected for the study. There was a height difference of 0.8 m in 70-m distance between the upper and lower experimental areas, and the N and P load in the central and lower areas was received through water transport through the upper experimental area. The soil was rather humified *Carex* peat and the peat depth more than two meters (Jauhiainen *et al.* 2003).

The leaf length and tiller number data in the field were analysed using ANOVA with repeated measurements using the SYSTAT software package (SYSTAT 1999) for determining the differences in total average leaf lengths and tiller numbers between the field experimental areas. The total average leaf length or tiller number of three mother tillers in each group was used as a dependent variable in the model. Nutrient level (experimental area, three levels: upper experimental area, lower experimental area and control area) was used as a grouping factor and sampling time (seasonal effect) as a within factor (together with their interaction) in the analysis.

Results

Growth dynamics

Following our results, the growth dynamics of cottongrass is determined by four processes: (1) the development of leaf cohorts, (2) leaf elongation, (3) new tiller production and (4) root elongation.

The leaves of the 3rd and 4th cohorts never reached the same lengths as the leaves of the 1st and 2nd cohorts (Fig. 1). Additionally, the length of the 3rd and 4th cohort leaves decreased along the decreasing N and P concentration and moisture gradient, and the 4th cohort was completely missing in the lower experimental area (Fig. 1).

Table 1. Concentrations (± SE) of NO_3^- and PO_4^{3-} (μg l^{-1}) in soil water and water table levels (cm below soil surface) in the three experimental areas in 1998–2000.

	Upper	Central	Lower
NO_3^-	7596.34 ± 3036.36	12.22 ± 2.36	6.96 ± 0.65
PO_4^+	764.40 ± 314.60	68.66 ± 55.32	20.83 ± 8.14
WT	7.46 ± 0.44	9.49 ± 0.58	22.93 ± 1.90

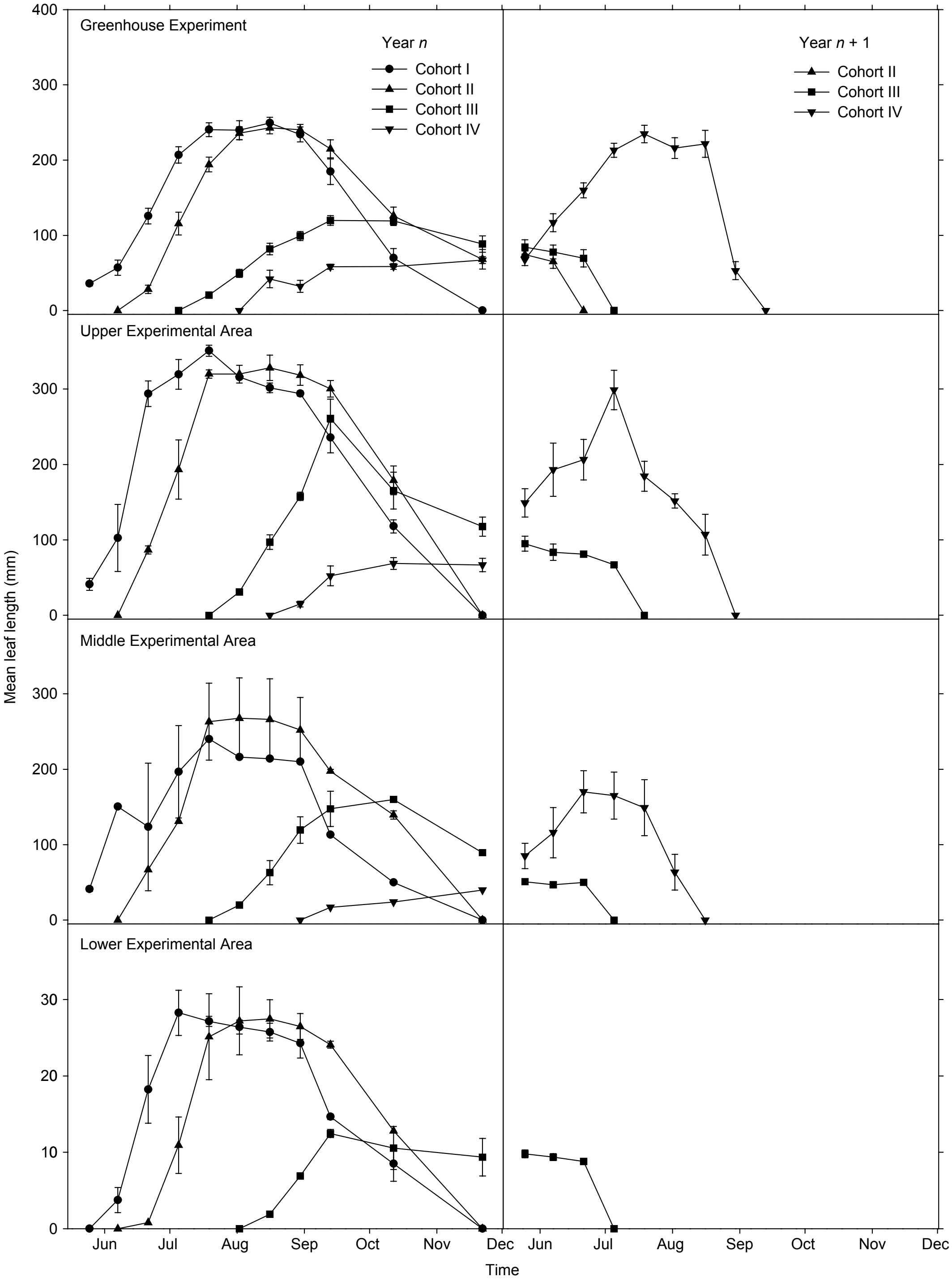

Fig. 1. Development of the mean length of individual leaf cohorts of cottongrass in different NP-treatment areas of the field experiment and in the greenhouse experiment measured in 1999. Year *n* represents the leaf cohorts emerged in 1999, the overwintered leaves from 1998 were used to mimick the development of overwintered leaf cohorts during the next growing season (*n* + 1). Upper experimental area = high added NO_3^- and PO_4^{3-} concentration in 1999, middle experimental area = lower added NO_3^- and PO_4^{3-}, lower experimental area = lowest added NO_3^- and PO_4^{3-}. Vertical bars are the S.E. of means.

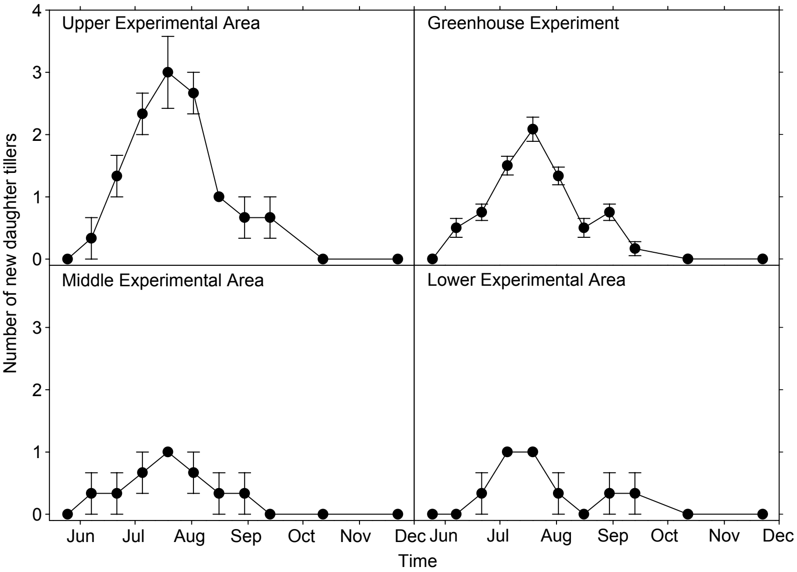

Fig. 2. Number of new daughter tillers per mother tiller protruded during measuring interval (2–4 weeks) in different NP-treatment areas and in the greenhouse experiment. Upper experimental area = high added NO_3^- and PO_4^{3-} concentration in 1999, middle experimental area = lower added NO_3^- and PO_4^{3-}, lower experimental area = lowest added NO_3^- and PO_4^{3-}. Vertical bars are the SE for means ($n = 3$).

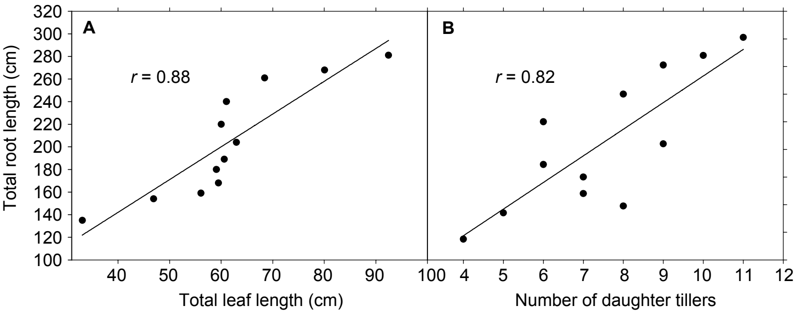

Fig. 3. Linear correlation of the total root length of (**A**) one tiller with its total leaf length and (**B**) the total root length of one tiller with the number of its daughter tillers in the greenhouse experiment.

This difference in the development of 3rd and 4th cohorts between experimental areas was reflected in the total leaf lengths and their seasonal development. The seasonal pattern in leaf elongation and senescence was rather similar in the greenhouse and in the upper experimental area with similar nutrient and moisture availability (Fig. 1).

Nutrient level (experimental area) affected significantly ($F = 9.53$, $P = 0.020$) the total average leaf lengths in the experimental areas in the field. The leaves in the upper experimental area were approximately 50 mm longer than those in the other areas (Fig. 1). Nutrient level affected also the seasonal pattern in leaf elongation and senescence which differed significantly ($F = 2.13$, $P = 0.016$) between the experimental areas.

In conditions with high availability of nutrients and moisture new tiller production increased rapidly from the beginning of the growing season and reached a peak in late July (Fig. 2). In poorer conditions tiller production was weak: during a two-week period a mother tiller hardly produced a single tiller (Fig. 2). The total number of tillers produced during a growing season decreased with the decreasing N and P concentration and moisture: 12 in the upper experimental area, 3.7 in the middle and 3.3 in the lower experimental area on average (Fig. 2). Repeated measures ANOVA showed a significant effect of nutrient level (experimental area) on new tiller production ($F = 41.667$, $P < 0.001$), and also on seasonal pattern in new tiller production ($F = 2.01$, $P = 0.046$). New tiller production followed a rather similar pattern in the greenhouse experiment and in the upper experimental area with similar nutrient and moisture availability (Fig. 2) and the level of new daughter tillers, 7.5, was also rather similar.

The average root length in the greenhouse experiment at the end of the growing period was

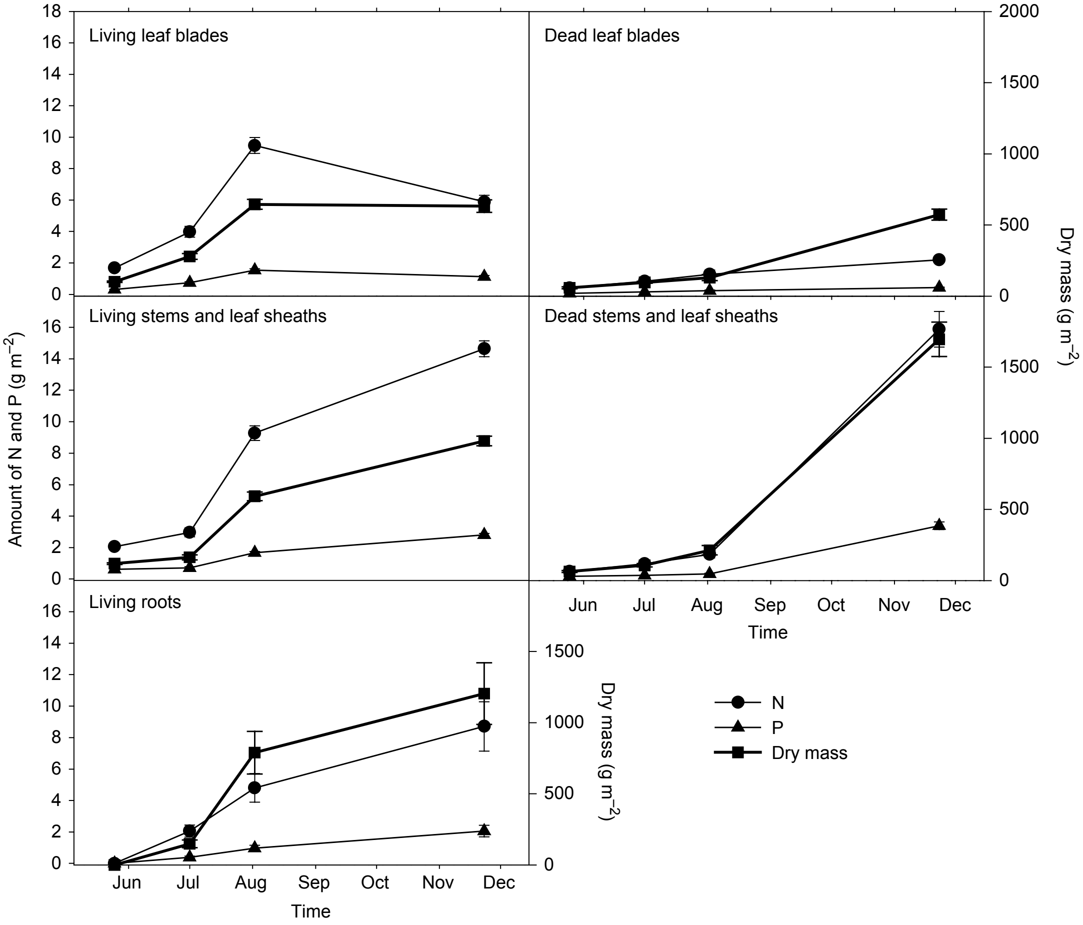

Fig. 4. Dry masses and N and P amounts in individual organs of cottongrass in the greenhouse experiment. The amounts are expressed relative to the area of the growing tube. Vertical bars are the S.E. of means.

39.0 ± 2.5 cm, the maximum root length being 80 cm. There was a positive correlation between the total root (sum of all the roots) and leaf lengths of individual tillers ($r = 0.88$, $P \leq 0.001$) (Fig. 3) as well as between the total root length and the number of daughter tillers ($r = 0.82$, $P \leq 0.001$) (Fig. 3).

Dynamics of biomass accumulation

In the greenhouse experiment, all organs increased in biomass throughout the growing period (May–November) (Fig. 4). In May the greatest dry mass proportion was in the living stems and leaf sheaths (Fig. 5). During the seven months period the biomass of the living leaf blades increased approximately sevenfold and living stems and leaf sheaths up to twelvefold. The biomass of roots increased from 0 to 1400 g m^{-2} (Fig. 4). In November up to 45% of the dry mass of the living organs (Fig. 4) and over 20% of the total dry mass (Fig. 5) was in the roots. In November the greatest dry mass proportion was in the dead stems and leaf sheaths (Fig. 5). The biomass of the living leaf blades peaked in August–September and started to decrease, while the mass of the roots and dead stems and leaf sheaths increased rapidly towards the end of the growing season (Figs. 4 and 5).

N and P dynamics

Except in living leaf blades, the amounts of N and P increased throughout the growing period

(May–November) (Fig. 4). In May the greatest N and P proportions, following the biomass, were in living stems and leaf sheaths (Fig. 5). A rather even increase in accumulated N and P occurred in roots and living stems and leaf sheaths over the season, while inleaf blades accumulated N and P decreased towards November after the peak (Fig. 4). In November the greatest N and P proportions, following the biomass accumulation dynamics, were in dead stems and leaf sheaths (Fig. 5).

Similarly, differences between the amounts of N and P in irrigation and outflow water indicated a clear accumulation of N and P into the cottongrass tissues during the growing period (Fig. 6). The immobilised amounts of N and P were 73 g N m^{-2} (91% of the added N) and 13 g P m^{-2} (77% of the added P) (Fig. 6). At the end of the growing period a clear liberation of P into the outflow water was observed (Fig. 6). The greatest difference in the input and output water N and P amounts was observed in July–August (Fig. 6). The greatest N and P uptake occurred in June–August (Fig. 6), concurrent with the highest leaf elongation and new daughter tiller production (Figs. 1 and 3).

Seasonal changes were very similar for both N and P concentrations (Fig. 7). While in all living tissues concentrations decreased from May to November (Fig. 7), this trend was clearest in leaf blades and roots (Fig. 7).

Discussion

Early growing season

At the start of the growing season the storage organs, namely stems and leaf sheaths, form a significant part of the overwintered biomass (Fig. 5), which contains high concentrations of mineral nutrients (Fig. 6) as well as carbohydrates (Shaver *et al.* 1986). This, together with partial overwintering of photosynthetic organs: leaf blades (Fig. 5), facilitates the rapid early growth of cottongrass (Fig. 1). The overwintering of green leaf blades is functionally similar to the habit of evergreen shrubs (Mark & Chapin 1989). This trait may enable evergreens to initiate seasonal activity earlier (Mark & Chapin

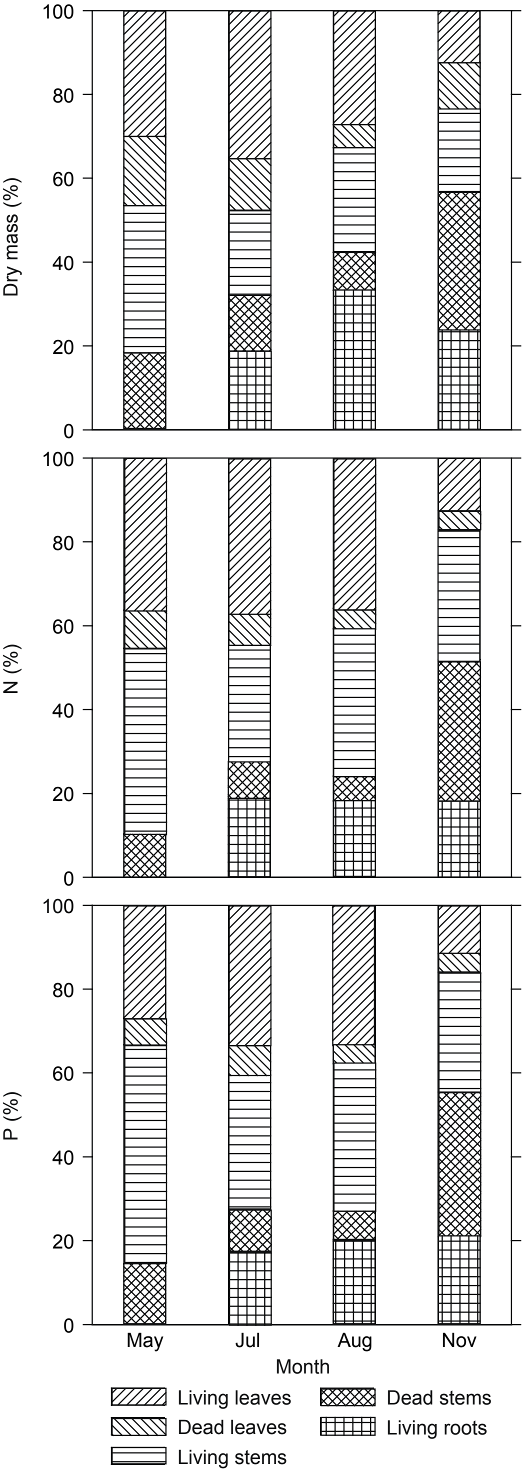

Fig. 5. Proportions of dry masses and N and P in individual organs of cottongrass in the greenhouse experiment.

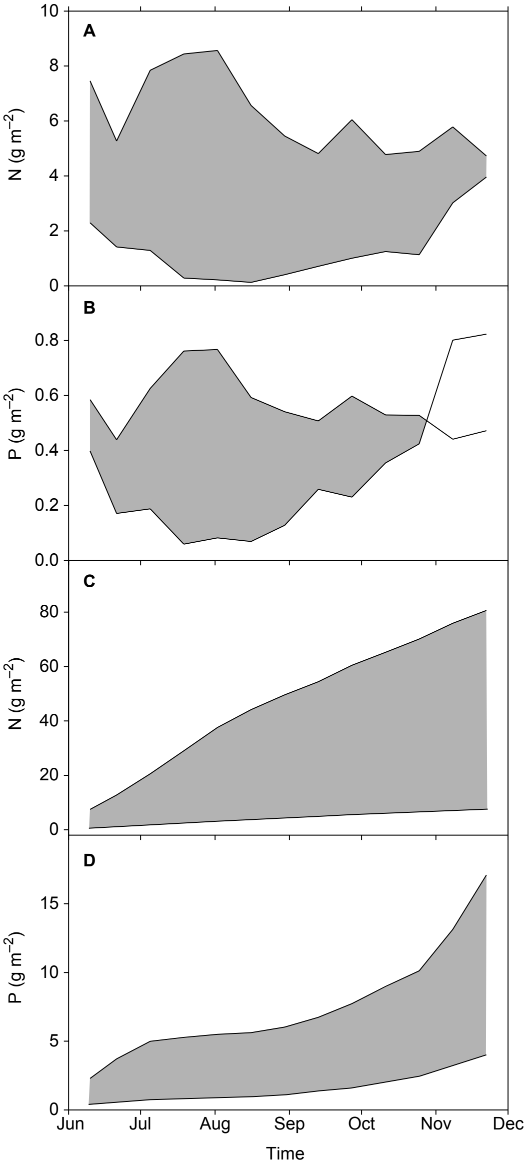

Fig. 6. Differences in N and P amounts in irrigation (upper line) and outflow water (lower line) in the greenhouse experiment. — **A**: retained proportion of N (shaded area); — **B**: retained proportion of P (shaded area); — **C**: retained proportion of cumulative N (shaded area); — **D**: retained proportion of cumulative P (shaded area). The N and P input was not constant over the growing period, because surplus N and P was given with additional irrigation water during dry periods to compensate for the increased transpiration.

1989, Bubier *et al.* 1998), photosynthesise over a longer period (Chabot & Hicks 1982), and reduce annual nutrient requirement for leaf production (Chapin 1980). The evergreen habit of cottongrass is consistent with the theory of evergreen species being the effective exploiters of infertile soils (Grime 1977, Mark & Chapin 1989).

The survival of several leaf blades and leaf stems, only to die early in the growing season suggests that these serve mainly as a source of carbohydrates and nutrients to support early spring growth. The high accumulation of biomass, as well as N and P in the overwintering storage organs supports this. The rapid early growth of cottongrass in the greenhouse experiment (Fig. 4), even though all roots were removed before the planting, reveals the insignificant role of root system in the early season.

Peak season

The high biomass of new photosynthetic tissues was mainly produced with recently uptaken nutrients. The maximum leaf elongation and new daughter tiller production occurred in June–August (Figs. 1 and 3), concurrently with the highest nutrient uptake (Fig. 6) and increased with nutrient availability.

The sequential pattern of leaf production (Fig. 1) can be seen as an adaptation to effective photosynthesis in infertile habitats (Jonasson & Chapin 1985). The large leaf area enables effective photosynthesis (Tuittila *et al.* 1999) and accumulation of photosynthates into roots and stem bases and sheaths, as shown in the clear relation between total root length and the amount of photosynthetic tissues (Fig. 3). Similarly Kummerow *et al.* (1988) reported a clear trend between the root and leaf areas of cottongrass in Alaska.

In spite of the moderately increased leaf lengths and the number of cohorts (Fig. 1) the high nutrient input was mainly allocated to the production of new daughter tillers (Fig. 2). This strategy in allocation was similarly observed in Alaskan tussock tundra (Shaver *et al.* 1986).

Late season

Towards the end of the growing season, additional nutrients were stored in the stems and leaf

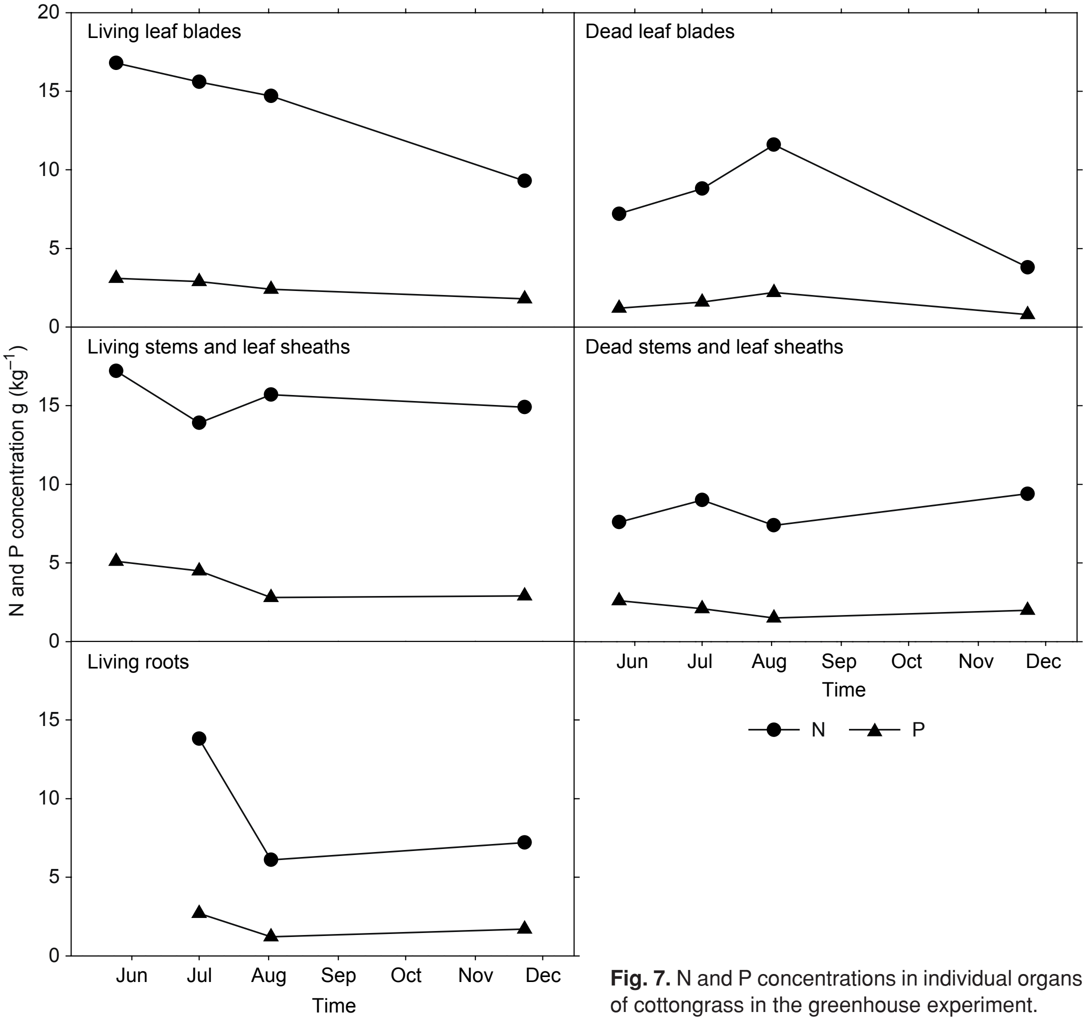

Fig. 7. N and P concentrations in individual organs of cottongrass in the greenhouse experiment.

sheaths to support the start of the next season's production (Fig. 4), similarly to Alaska (Shaver *et al.* 1986). Most cottongrass tissues die during winter (Wein 1973), except the storage organs and part of the leaves (Fig. 5), and at the beginning of the next growing season previous years' living root biomass will form the dead root mass (Wein 1973). In spite of effective storing of nutrients, a part will stay in dying biomass (Shaver & Chapin 1995). Macroscopically identifiable residues of roots and leaf sheaths found in large quantities in peats with ages of several thousands of years (Mäkilä 1994), imply a long-term retention for this part. The annually increasing mass of dead roots may form a major long-term sink for nutrients. The results supported the postulate that cottongrass allocates biomass and nutrients in the slowly decomposing storage organs (stems and leaf sheaths and roots) proportionally more than in the rapidly decomposing organs (leaf blades).

Conclusions

The growth and nutrient immobilisation dynamics of cottongrass can be simulated with the greenhouse experiments, as shown by the similarity in growth dynamics between the field and the greenhouse with similar nutrient and moisture conditions. This direct, budget-oriented approach has led to the conclusions that although cottongrass is capable of thriving in nutrient poor habitats it has an adaptation to efficient nutrient uptake and biomass accumulation in conditions with excessive nutrient supply. Although this study concentrated on short-term allocation patterns of biomass and uptake of nutrients of cottongrass, the slow decomposition of annually increasing mass of dead organs, especially of roots, forms a potential long-term sink for nutrients, and thus cottongrass may play an essential role in the long-term nutrient immobilisation of restored peatland buffers.

Acknowledgements

Financial support from The Finnish Ministry of Agriculture and Forestry is gratefully acknowledged. In addition we would like to thank Jouni Meronen for expert technical assistance and Anna Laine and Päivi Mäkiranta for the separation of cottongrass organs.

References

Bubier, J. L., Crill, P. M., Moore, T. R., Savage, K. & Varner, R. K. 1998: Seasonal patterns and controls on net ecosystem CO_2 exchange in a boreal peatland complex. — *Glob. Biogeochem. Cycles* 12: 703–714.

Chabot, B. F. & Hicks, D. J. 1982: The ecology of leaf life spans. — *Ann. Rev. Ecol. Syst.* 13: 229–259.

Chapin, F. S. 1980: The mineral nutrition of wild plants. — *Ann. Rev. Ecol. Syst.* 11: 233–260.

Fetcher, N. & Shaver, G. R. 1982: Growth and tillering patterns within tussocks of *Eriophorum vaginatum*. — *Holarctic Ecol.* 5: 180–186.

Grime, J. P. 1977: Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. — *Am. Nat.* 111: 1169–1194.

Heikkilä, H. & Lindholm, T. 1997: *Soiden ennallistamistutkimus vuosina 1987–1996* [*The mire restoration study from 1987 to 1996*]. — Survey Report, Finnish Forest & Park Service, Nature Protection. [In Finnish with English summary].

Hotanen, J.-P. 2000: *Eriophorum vaginatum*, Tupasvilla. — In: Reinikainen, A., Mäkipää, R., Vanha-Majamaa, I. & Hotanen, J.-P. (eds.), *Kasvit muuttuvassa metsäluonnossa*: 170–171. Tammi Oy, Helsinki.

Jauhiainen, S., Pitkänen, A. & Vasander, H. 2003: Chemostratigraphy and vegetation in two boreal mires during the Holocene. — *Holocene*. [In press].

Johnson, D. A. & Tieszen, L. L. 1976: Aboveground biomass allocation, leaf growth, and photosynthesis patterns in tundra plant forms in arctic Alaska. — *Oecologia* 24: 159–173.

Jonasson, S. & Chapin, F. S. 1985: Significance of sequential leaf development for nutrient balance of cotton sedge, *Eriophorum vaginatum* L. — *Oecologia* 67: 511–518.

Kalliola, R. 1973: *Suomen kasvimaantiede*. — WSOY, Porvoo.

Keatinge, T. H. 1975: Plant community dynamics in wet heathland. — *J. Ecol.* 63: 163–172.

Komulainen, V.-M., Nykänen, H., Martikainen, P. J. & Laine, J. 1998: Short term effect of restoration on vegetation succession and methane emissions from peatlands drained for forestry in southern Finland. — *Can. J. For. Res.* 28: 402–411.

Komulainen, V.-M., Tuittila, E.-S., Vasander, H. & Laine, J. 1999: Restoration of drained peatlands in southern Finland: initial effects on vegetation change and CO_2 balance. — *J. Appl. Ecol.* 36: 634–648.

Kummerow, J., Mills, J. N., Ellis, B. A. & Kummerow, A. 1988: Growth dynamics of cotton-grass (*Eriophorum vaginatum*). — *Can. J. Bot.* 66: 253–256.

Kuusipalo, J. & Vuorinen, J. 1981: Pintakasvillisuuden sukkessio vanhalla ojitusalueella Itä-Suomessa [Vegetation succession on an old, drained peatland area in Eastern Finland]. — *Suo* 32: 61–66. [In Finnish with English summary].

Laiho, R. 1996: Changes in understorey biomass and species composition after water level drawdown on pine mires in southern Finland. — *Suo* 47: 59–69.

Laine, J. & Vasander, H. 1996: Ecology and vegetation gradients of peatlands. — In: Vasander, H. (ed.), *Peatlands in Finland*: 10–19. Finnish Peatland Soc., Helsinki.

Mark, A. F. & Chapin, F. S. 1989: Seasonal control over allocation to reproduction in a tussock-forming and rhizomatous species of *Eriophorum* in central Alaska. — *Oecologia* 78: 27–34.

Mark, A. F., Fetcher, N., Shaver, G. R. & Chapin, F. S. 1985: Estimated ages of mature tussocks of *Eriophorum vaginatum* along a latitudinal gradient in Central Alaska, USA. — *Arctic Alp. Res.* 17: 1–5.

McGraw, J. B. & Chapin, F. S. 1989: Competitive ability and adaptation to fertile and infertile soils in two *Eriophorum* species. — *Ecology* 70: 736–749.

Mäkilä, M. 1994: Suon energiasisällön laskeminen turpeen ominaisuuksien avulla [Calculation of the energy content of mires on the basis of peat properties]. — *Rep. Investig.* 121: 1–73. Geol. Survey Finland, Espoo. [In Finnish with English summary].

Polozova, T. G. [Полозова, Т. Г.] 1970: [Biological features of *Eriophorum vaginatum* L. as a hummock-forming plant (according to the observations in the tundras of the western part of Taimyr peninsula)]. — *Bot. Zh.* 55: 431–442. [In Russian].

Päivänen, J. 1970: Hajalannoituksen vaikutus lyhytkortisen nevan pintakasvillisuuden kenttäkerrokseen [On the influence of broadcast fertilization on the field layer of the vegetation of open low-sedge bog]. — *Suo* 21: 18–24. [In Finnish with English summary].

Shaver, G. R. & Chapin, F. S. 1995: Long term responses to factorial, NPK fertilizer treatment by Alaskan wet band moist tundra sedge species. — *Ecography* 18: 259–275.

Shaver, G. R., Chapin, F. & Gartner, B. L. 1986: Factors limiting seasonal growth and peak biomass accumulation in *Eriophorum vaginatum* in Alaskan tussock tundra. — *J. Ecol.* 74: 257–278.

Shaver, G. R. & Laundre, J. 1997: Exsertion, elongation and senescence of leaves of *Eriophorum vaginatum* and *Carex bigelowii* in Northern Alaska. — *Global Change Biol*. 3: 146–157.

Silvan, N., Regina, K., Kitunen, V., Vasander, H. & Laine, J. 2002: Gaseous nitrogen loss from a restored peatland buffer zone. — *Soil Biol*. *Biochem*. 34: 721–728.

SYSTAT 1999: *Systat 9.0 for Windows: Statistics*. — SPSS Inc., Chicago, U.S.A.

Thormann, M. N. & Bayley, S. E. 1997: Aboveground plant production and nutrient content of the vegetation in six peatlands in Alberta, Canada. — *Plant Ecol*. 131: 1–16.

Tuittila, E.-S., Komulainen,V.-M., Vasander, H. & Laine, J. 1999: Restored cut-away peatland as a sink for atmospheric CO_2. — *Oecologia* 120: 563–574.

Tuittila, E.-S., Vasander, H. & Laine, J. 2000: Impact of rewetting on vegetation of a cut-away peatland. — *Appl*. *Veg*. *Sci*. 3: 205–212.

Wein, R. W. 1973: Biological flora of the British Isles: *Eriophorum vaginatum* L. — *J*. *Ecol*. 61: 601–615.

Wein, R. W. & Bliss, L. C. 1973: Changes in arctic *Eriophorum* tussock communities following fire. — *Ecology* 54: 845–852.