

# Demography of *Carex rostrata* in a boreal mesotrophic fen: shoot dynamics and biomass development

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A demographic study of *Carex rostrata* Stokes was carried out in a boreal mesotrophic fen between spring 1993 and spring 1995. Mean minimum shoot densities measured in spring were 270–366 shoots m<sup>2</sup> during the study, and mean maximum shoot densities between 440–466 shoots m<sup>2</sup>. New shoots emerged throughout the growing seasons, but highest rates of mortality were measured in late autumn–winter. Mean maximum shoot biomass was 166–195 g dw m<sup>2</sup> and mean shoot production 163–186 g dw m<sup>2</sup> yr<sup>-1</sup>. The annual turnover rate of shoots was 0.50–0.53 yr<sup>-1</sup>, resulting in an average shoot lifespan of 1.9 years. The turnover of shoots did not correlate with the density of shoots. The possible mechanisms controlling the shoot density are discussed with reference to climate change and accumulation of carbon in fen ecosystems.

Key words: biomass, *Carex rostrata*, density, production, shoots, turnover

## INTRODUCTION

Fen vegetation dominated by monospecific stands of *Carex* species are widespread in northern latitudes (Bernard *et al.* 1988). Minerotrophic fens are also important sinks of carbon: according to Tolonen and Turunen (1996), the long-term average rate of carbon accumulation in boreal minerotrophic fens is 15.1 g C m<sup>-2</sup> yr<sup>-1</sup>. The shoots produce litter at the surface of the acrotelm peat, where the rate of decomposition is high. In fen ecosystems, however, a majority (in some cases more than 90%) of living biomass of vascular plants is located belowground (Sjörs 1991, Saarinen 1996). The roots may reach a depth of 2 me-

ters, providing a direct input of organic matter to the slowly decomposing catotelm peat. The high contribution of fine roots both to the total biomass and to the total production (more than 70% for both) indicates that roots are a major component of the carbon and nutrient cycles in fen ecosystems (Saarinen 1996), as well as in most terrestrial ecosystems (Hendricks *et al.* 1993).

In *Carex rostrata* Stokes, which is one of the dominating sedge species in northern fens, new shoots emerge either from the axillary buds of older shoots (sometimes called “daughter” and “mother” shoots, respectively) or from the apical part of the rhizome. When a new shoot initiates from the basal meristem of an older shoot, the

new shoot grows first, and new roots appear at the base of the shoot only later on (Hultgren 1989a). In some sedge species, roots grow both from rhizomes and from the basal parts of shoots, while in other species (including *C. rostrata*) roots arise mainly from or close to the bases of shoots (Bernard & Fiala 1986, Hultgren 1989a). Hence, factors controlling the demography of sedges, especially the density of shoots and the initiation of new shoots, clearly affect both the above- and belowground productivity of fens, as well as the accumulation of peat.

Seasonal changes in the density and biomass of shoots in natural communities dominated by *Carex rostrata* are well documented in e.g., Gorham and Somers (1973), Bernard and Hankinson (1979), Hultgren (1988, 1989a), Konings *et al.* 1992, and Francez (1993). Nutrient dynamics and the effects of nutrients and other environmental factors on the growth characteristics has also been studied intensively (e.g., Bernard & Hankinson 1979, Konings *et al.* 1989, 1992, Aerts *et al.* 1992, Aerts & de Caluwe 1994). Little attention, however, has been paid to the control of the rate of turnover and the density of shoots, which may considerably affect accumulation of carbon in fens. Solander (1983) noticed that fertilization increased shoot density of *C. rostrata* in a subarctic lake. Also in a previous greenhouse experiment (Saarinen 1998), shoot density increased with increasing N supply, but the size of individual shoots was not affected. According to Aerts and de Caluwe (1994), increased supply of nitrogen significantly decreased the shoot lifespan of *C. rostrata*, whereas mean leaf lifespan was not affected.

In a review on shoot competition in clonal plants, de Kroon (1993) concluded that in some species shoot mortality seems to be density-dependent, while in others this correlation seems to lack. The lack of density-dependent mortality may be partly attributed to an effective density-dependent control of shoot production. Whether there is a connection between shoot density and turnover in sedge fens is not known. The aim of this work was to measure shoot dynamics and biomass production in a boreal mesotrophic fen, where the below-ground biomass and the turnover of fine roots was measured previously (Saarinen 1996). Special attention was also paid to the possible connection between density and turnover of shoots within the stand.

## MATERIAL AND METHODS

Shoot demography of *Carex rostrata* was followed for two years in a boreal mesotrophic fen located in Suurisuo mire complex, Janakkala, southern Finland (60°59'N, 24°40'E). The site is dominated by *C. rostrata* and *Potentilla palustris* (L.) Scop. together with *Sphagnum fallax* (Klinggr.) Klinggr. and *S. teres* (Schimp.) Ångstr. in the ground layer. A more detailed description of the site is in Saarinen (1996).

Ten sample plots sized 25 × 25 cm were established in the beginning of the growing season on 18 May 1993. The plots were placed along a transect with 1 m distances. All the overwintered shoots were tagged individually with a plastic stripe. The length of each shoot was also measured. During the growing season 1993, the lengths of all shoots were measured and new shoots were tagged on 15 June, 13 July, 4 August and 2 September, resulting in five shoot cohorts. The measurements were repeated on 18 May, 14 June, 21 July, 15 August, 3 September and 11 October 1994 (six shoot cohorts), as well as on 18 May 1995. A total of 442 shoots were tagged and measured during the study period. As only three flowering shoots were found, they are not treated separately here.

The length measurements were converted to biomass values using a regression between length and dry mass (*see* Saarinen 1998). Twenty randomly chosen shoots were harvested in the vicinity of the sample plots at each date. Attached dead leaves or parts of leaves were removed, the shoots were dried (+70°C, 48 hours) and weighed. Because the shoots collected at various times had a similar relationship between the length and the dry mass, the same power model equation (Fig. 1) was applied to convert length to dry mass:

$$w = 0.00123l^{1.56} \quad (1)$$

where  $w$  and  $l$  are the mass and the length of a shoot, respectively. No attempt was made to measure seasonal changes in the amount of litter in the current study.

The annual turnover rate of shoots was calculated for each sample plot according to dead shoots formed (*see e.g.*, Verhoeven *et al.* 1988) as:

$$TC = LS/TS \quad (2)$$

where TC = annual turnover coefficient (yr<sup>-1</sup>); TS = total number of living shoots observed in the beginning of a growing season in May; LS = number of TS shoots alive in May a year later. Thus, turnover coefficients were calculated for two successive periods from May 1993 to May 1994 and from May 1994 to May 1995. The equation used is also analogous to the equation in a <sup>14</sup>C method applied for measuring the turnover rate of fine roots in the same fen (*see* Saarinen 1996).

Annual production of shoots (g dw m<sup>-2</sup> yr<sup>-1</sup>) was calculated using two different methods. First estimate was calculated by subtracting the minimum biomass (measured in May) from the maximum biomass (measured in August). The second estimate of production was calculated by summing all the positive changes in the dry mass of individual

shoots.

Statistical analyses were made using the SPSS for Windows 6.1.3 programme. Curve estimation operation was used to fit a power model in the relationship between the dry mass and the length of the shoots.

## RESULTS

Seasonal variation in shoot density was relatively low. In the beginning of May 1993, the density of overwintered shoots was  $270 \pm 24$  shoots  $m^{-2}$  (mean  $\pm$  SE; Fig. 2). Shoot density reached a maximum value of  $440 \pm 51$  shoots  $m^{-2}$  in early September. In May 1994 and 1995, shoot densities were slightly higher ( $366 \pm 58$  shoots  $m^{-2}$  and  $336 \pm 45$  shoots  $m^{-2}$ , respectively). Compared with 1993, the maximum shoot density was also higher ( $466 \pm 61$  shoots  $m^{-2}$ ) in 1994.

New shoots emerged throughout the growing seasons (Fig. 2). During both growing seasons, however, natality was highest in the beginning of the season (May–early June). Mortality was highest between late autumn and early spring. Low mortality was observed among the overwintered shoots during the growing season, and practically all the current-year shoots survived the first summer (Fig. 2). The annual turnover rate of shoots calculated according to dead shoots formed (*see* Eq. 2) was  $0.53 \pm 0.06$   $yr^{-1}$  and  $0.50 \pm 0.05$   $yr^{-1}$  between May 1993–May 1994 and May 1994–May 1995, respectively, resulting in an average shoot lifespan of 1.9 years. The annual turnover coefficients of individual sample plots did not correlate with the shoot densities (data not shown).

The dry mass of overwintered shoots (calculated using the length-biomass regression) reached a maximum of  $468 \pm 10$  mg dw and  $513 \pm 9$  mg dw in early August 1993 and 1994, respectively (Fig. 3). Compared with overwintered shoots, the maximum dry mass of the current-year shoots remained clearly lower. Between early August and early September, overwintered shoots already senesced when current-year shoots still continued growing, indicating an overlap in these processes.

The biomass of overwintered shoots was  $24 \pm 3$  g dw  $m^{-2}$ ,  $27 \pm 5$  g dw  $m^{-2}$ , and  $23 \pm 3$  g dw  $m^{-2}$  in May 1993, 1994 and 1995, respectively (Fig. 4). A maximum biomass of  $166 \pm 21$  g dw  $m^{-2}$  and  $195 \pm 29$  g dw  $m^{-2}$  was reached in August 1993

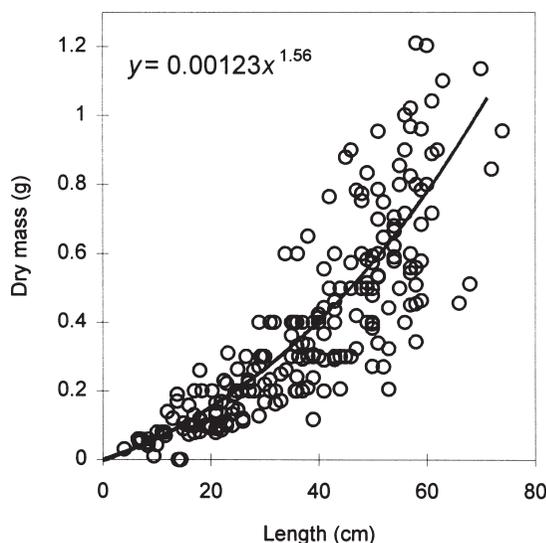


Fig. 1. Relationship between length (cm) and biomass (g) of shoots of *Carex rostrata* Stokes in a boreal mesotrophic fen. Twenty randomly chosen shoots were collected on twelve dates between May 1993 and May 1995. Because there were no differences between the dates, the same power model equation was fitted to the combined data of all dates.

and 1994, respectively. Overwintered shoots accounted for more than 70% of the maximum biomass in both years ( $72\% \pm 3\%$  in 1993 and  $76\% \pm 5\%$  in 1994, Fig. 4). Shoot production calculated by subtracting the minimum biomass measured in May from the maximum biomass in August resulted in an estimate of  $142 \pm 19$  g dw  $m^{-2}$   $yr^{-1}$  in 1993, and  $169 \pm 25$  g dw  $m^{-2}$   $yr^{-1}$  in 1994. Higher values were obtained by summing all the positive changes in dry mass of individual shoots:  $163 \pm 25$  g dw  $m^{-2}$   $yr^{-1}$  in 1993 and  $186 \pm 27$  g dw  $m^{-2}$   $yr^{-1}$  in 1994.

## DISCUSSION

Late summer shoot densities of *Carex rostrata* measured in the current study are within the upper range reported for northern fens reviewed by Hultgren (1989a) and Bernard *et al.* (1988). Only Mörnjö (1969) measured higher densities, up to 630 shoots  $m^{-2}$ . Between-year variation of shoot densities was relatively low in the current study. This is typical for mires with a relatively constant water level; wider variation may be caused by fluc-

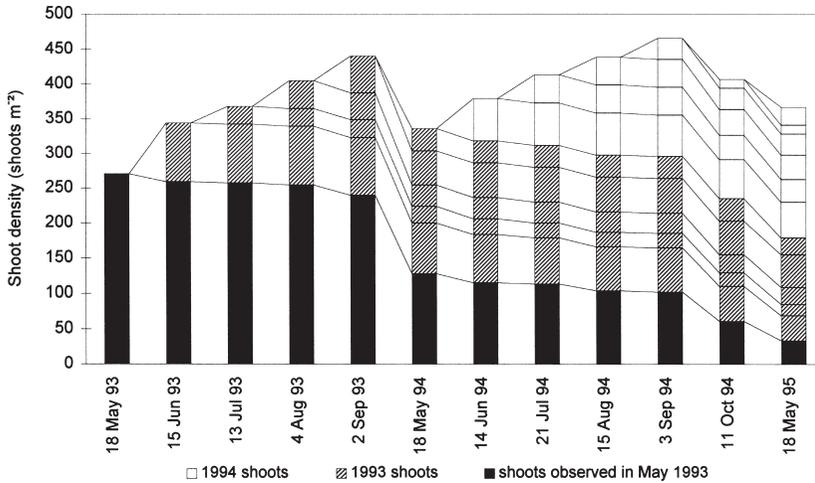


Fig. 2. Shoot density (shoots m<sup>-2</sup>) of *Carex rostrata* Stokes in a boreal mesotrophic fen. Life spans of all shoots were followed on ten sample plots sized 25 × 25 cm for two years. Data presented are mean values of all the plots. The uppermost segment in each bar represents the new shoots formed since the previous sampling date.

tuating water level e.g. due to regulation in reservoirs (Hultgren 1988, 1989a). According to Hultgren (1988), the density of the winter population is about half of that during the summer. In the current study, the winter population was slightly higher, up to 60%–70% of the shoots surviving the winter.

Emergence of new shoots is usually rather evenly distributed throughout the growing season, highest rates usually occurring in early summer (Bernard 1976, Bernard & Hankinson 1979, Hultgren 1988). This was also the case in the current study. Inconsistent observations, however, have been made on the timing of shoot mortality. Bernard (1976) and Bernard and Hankinson (1979) measured high rates of mortality throughout the growing season, especially among overwintered shoots. My results support Hultgren's (1988) observation of increased mortality during autumn and winter. The variation in timing may be affected by hard climatic conditions in northern latitudes: the study site of Bernard and Bernard and Hankinson was located further south (42°N) than the sites of Hultgren and the current study (both at 60°N). In addition to the timing of mortality, the lifespan of shoots also seems to be dependent on latitude. Bernard (1976) measured a maximum lifespan of 2 years at 42°N, Verhoeven *et al.* 2 years at 52°N, Hultgren (1988) 3 years at 60°N and Solander (1983) up to 6 years at 68°N. The maximum lifespan was not measured in the current study, but 12% of the shoots tagged in May 1993 still survived in May 1995, suggesting

that the maximum lifespan is probably close the value of Hultgren. The average lifespan of 1.9 years in the current study is in accordance with the estimate of 1.5–2 years measured by Gorham and Somers (1973). At least in the current study site, the turnover coefficient of shoots (0.50–0.53 yr<sup>-1</sup>) was almost equal to that of the fine roots (0.59 yr<sup>-1</sup>; Saarinen 1996), indicating that the fine roots persist for almost the same length of time as does the shoot.

The proportion of shoot biomass remaining green also seems to increase with increasing latitude. The dry mass of individual overwintered shoots in May was approximately 20% of the maximum dry mass obtained by mid-August. Comparable proportions of overwintering biomass can be calculated from the data of other authors: 11% at 42°N (Bernard & Hankinson 1979), 24% at 51°N (Gorham & Somers 1973) and 44% at 60°N (Solander 1983). The maximum dry mass of the current-year shoot cohorts remained clearly lower than that of the overwintered shoots — an observation made earlier by e.g., Bernard and Hankinson (1979). Slow growth of new shoots has also been observed by measuring the length growth (Bernard 1976, Hultgren 1989b).

According to Bernard *et al.* (1988), the above-ground standing crops in *Carex* dominated wetlands are approximately 500–1050 g m<sup>-2</sup>. The biomasses reported here remain below this range. Low above-ground biomasses are typical for northern or high elevation sites or sites with a dense moss layer (Mörnsjö 1969, Bernard *et al.* 1988). Even

Fig. 3. Mean dry mass (mg shoot<sup>-1</sup>) of shoot cohorts of *Carex rostrata* Stokes in a boreal mesotrophic fen. Length growth of all shoots was followed on ten sample plots sized 25 × 25 cm for two years. Biomasses were calculated based on a length-biomass regression. Data presented are mean values of all the plots.

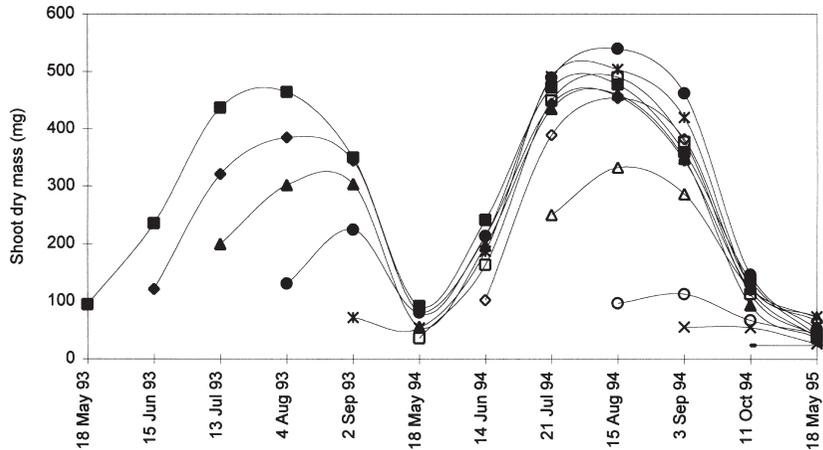
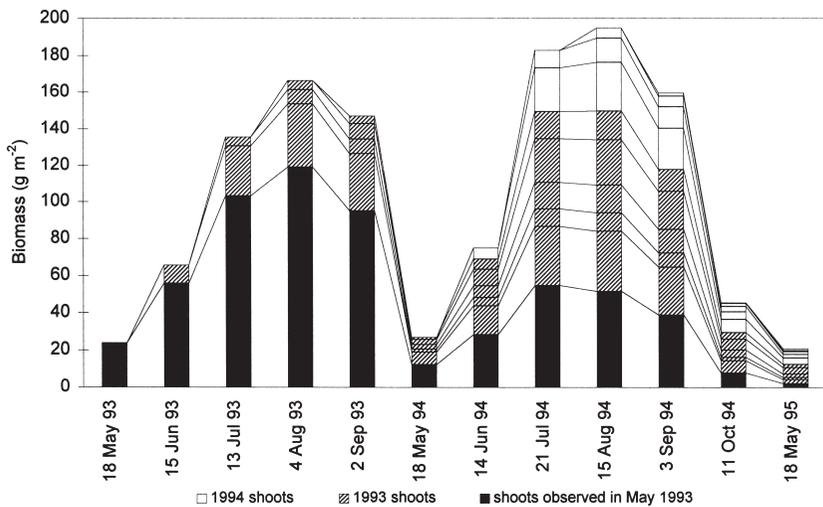


Fig. 4. Shoot biomass (g dw m<sup>-2</sup>) of *Carex rostrata* Stokes in a boreal mesotrophic fen. Length growth of all shoots was followed on ten sample plots sized 25 × 25 cm for two years. Biomasses were calculated based on a length-biomass regression. Data presented are mean values of all the plots. The uppermost segment in each bar represents the new shoots formed since the previous sampling date.



if the shoot biomass was low, a considerably high below-ground biomass of 2 100 g m<sup>-2</sup> has been measured in this site, fine roots contributing 78% to the total biomass (Saarinen 1996).

Due to the simultaneous growth and senescence of shoots, production calculated by subtracting the minimum biomass measured in spring from the maximum late-summer biomass results in an underestimation. Approximately 10%–15% higher production was obtained by summing all the positive changes in the dry masses of individual shoots. As simultaneous growth and senescence of leaves within the same shoot may also occur, even this method results in an underestimate. According to Solander (1983), however, the loss of biomass during the growing season is only about 2% of the maximum biomass.

According to de Kroon (1993), the mortality of shoots is density-dependent in some species, while in other species, including *Carex rostrata* in the current study, no correlation has been found. De Kroon (1993) also suggested that e.g., effective control of meristem activity may explain the lack of correlation: if shoots are not produced in excess, self thinning does not occur. In a previous greenhouse experiment (Saarinen & Haansuu, unpublished results), shoots with a low ratio of non-structural carbohydrates (TNC) to free amino acids (FAA), representing biochemically available fractions of carbon and nitrogen, respectively, started developing new shoots from axillary buds. The same phenomenon was observed also in field measurements: TNC/FAA ratios were lower in a mesotrophic site with a high density of shoots than

in an oligotrophic site with a low density of shoots (Saarinen & Haansuu, unpublished results). Thus, shoots having a availability of nitrogenous compounds originating from the roots in relation to carbohydrates originating from the shoot start growing a daughter shoot. The internal carbon/nitrogen balance of shoots seems to be a possible factor controlling meristem activity in stands of *C. rostrata*.

In the future, the predicted warming of climate may increase the turnover of shoots, especially in northern latitudes. As an increased supply of nitrogen decreases the lifespan of shoots (Aerts & de Caluwe 1994), increased atmospheric deposition of nitrogen may further enhance the turnover of shoots. Little, however, is known about the interacting effects of climate change, nitrogen deposition and increasing atmospheric concentration of CO<sub>2</sub> on the demography of sedges. Turnover of shoots and roots were closely related in the current study site, suggesting that the changes observed in shoots may also occur in the below-ground organs. Because over 90% of biomass may be located belowground (Sjörs 1991, Saarinen 1996), roots are clearly a major component of the carbon cycle in fen ecosystems. Roots may also reach a depth of 2 meters, providing a direct input of carbon to slowly decomposing cat-telm peat (Saarinen 1996). Therefore, any changes in the shoot demography of sedges may also have an influence on both above- and below-ground productivity and on the input of carbon — especially through the turnover of fine roots — in fen ecosystems.

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