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Radial growth and ring formation process in clonal plant *Eriophorum angustifolium* on post-mined peatland in the Šumava Mts., Czech Republic

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Eriophorum angustifolium (Cyperaceae) is a pioneer clonal sedge colonizing bare peat surface of harvested peatlands in central Europe. It forms circular patches of densely aggregated ramets, followed by central die-back and ring formation as circles develop. This study experimentally tested the importance of inter-ramet competition, interference with litter, soil nutrient depletion, and architectural constraints for radial clonal spread and ring formation process. Effects of fertilization, litter addition and competition of neighbor ramets on growth and survival of tillers transplanted into four distinct zones within individual circle were detected only in the first zone (green band) with high ramet density. This suggested that both above-ground competition for light and below-ground competition for soil nutrients can play an important role in population dynamics of *E. angustifolium*. A field study of clonal growth has shown that rhizomes orient preferentially towards the periphery. As the old ramets within the interior of the tussock died due to senescence and inter-ramet competition, disproportionately more ramets are recruited on the periphery, which reduce axillary bud availability within the interior of the tussocks. We also explored the soil nutrient content (NH_4-N, NO_3-N and PO_4-P). High values of NO_3-N outside the circles and low values inside patches might partly explain why *Eriophorum* rhizomes are oriented into open space. High accumulation of phosphorus (PO_4-P) in the centre of the patches was attributed to the leaching of phosphorus from decaying *Eriophorum* plants. We suggest that processes of nutrient foraging and utilization are responsible for development of circular patches of *E. angustifolium* in the harsh environment of cut-away peatland.

Key words: clonal plant, *Eriophorum angustifolium*, experiments, mined peatland, nitrogen, phosphorus

Introduction

The occurrence of ring patches in clonal herbaceous plants has been documented in a number of studies, but causes and mechanisms of ring formation remain still poorly understood. The species forming the ring starts with a circular monospecific stand of densely aggregated ramets (i.e. Ingram 1958, Adachi *et al.* 1996, Wikberg & Mucina 2002). However, as a circle develops, shoot density usually decreases in the middle part, and ring (the green band with high ramet density) is formed around the centre (the zone with low ramet density in the middle of ring and high accumulation of litter). This phenomenon is referred to as "central die-back" (Adachi *et al.* 1996, Wan & Sosebee 2000).

Shoot mortality inside tussock can be caused by a number of factors. A common interpretation involves a gradual senescence and disintegration beginning from the oldest part of the clone. Growth of the oldest part of the clone can also be limited because of physiological constraints such transition to reproduction. Another explanation involves intense competition among neighboring ramets for light and soil nutrients in denser patches inside the clone. Competition can cause individual growth decline and shoot death before any age-related decrease. The free space inside the clone can be also a natural consequence of developmental morphology (Phillips 1953, Gatsuk *et al.* 1980, Danin & Orshan 1995). As the old ramets within the interior of the tussock die due to senescence and inter-ramet competition, dead shoots prevent initiation of new ramets to the inside. Disproportionately more ramets are recruited on the periphery, which eventually reduce axillary bud availability within the interior of the tussocks (Butler & Briske 1988, Olson & Richards 1988).

The last three decades have seen major advances in description and modeling of clonal growth in tussock perennial plants (Callaghan *et al.* 1990, Cain *et al.* 1995), yet there is a lack of studies that would experimentally test several potential factors responsible for formation of ring plant patches. In order to improve our current understanding of ring formation in clonal plants, we chose as a model system the naturally-occurring stands of *Eriophorum angustifolium* on a post-mined peatland in central Europe. *Eriophorum angustifolium* is a pioneer species colonizing bare peat surface in early stages of post-mined succession. It forms distinct rings of densely aggregated ramets on bare surfaces left after peat mining. *Eriophorum angustifolium* develops new ramets intravaginally within each shoot. The older shoot increments are re-oriented downwards to form a creeping stem covered with dead leaves. The ramet population expands radially and after some time a wide circle is formed. As in other radial spreading phalanx plants such as *Carex humilis* (Wikberg & Mucina 2002, Wikberg & Svensson 2003), the oldest (central) part of the system gradually dies, previously connected ramets become separated, and ring patch becomes open to recolonization by other plant species.

A single genetic individual of *E. angustifolium* can consist of several potentially independent units (ramets) (Sarukhán & Halper 1973) connected to each other by rhizomes (Dostál 1989). *Eriophorum* patch develops outwards by sympodial branching of these rhizome systems. Thus, in *Eriophorum* as in other clonal plants, the below-ground parts are important connections that serve as paths for transport of water, nutrients and assimilates. However, within the ring zone competition for below-ground resources among densely aggregated independent rhizome systems can be intense reinforcing new ramets to recruit preferentially on the periphery of the ring. Since *E. angustifolium* forms a dense canopy, above-ground competition for light is expected to be also important, further contributing to ring formation. Within the interior of the tussock competition for light and soil nutrients is likely to be less important, but initiation of new ramets to the inside can be hindered by dead shoots. In particular, the zone of fresh litter that accumulates from one- to two-year-old dead ramets represents one of the main barriers, which can be viewed as a filter a new ramet must pass through. This zone is characteristic for the presence of standing dead biomass and for the absence of green living ramets.

Many generalizations about the observed patterns of ring formation in clonal plants are based on observational data (e.g. Adachi *et al.* 1996, Wikberg & Svensson 2003). Experiments manip-

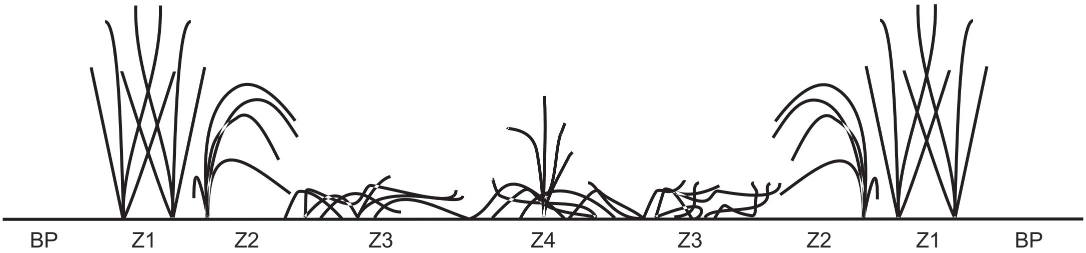

Fig. 1. Cross section through a *Eriophorum angustifolium* circle showing the four zones where the experiments with planted targets were conducted. Z1 = zone of green ramets; Z2 = zone of "young" litter; Z3 = zone of "old" litter; Z4 = central zone with very decomposed litter, where other plant species recruit, BP = surrounding bare peat. For clarity the ramets are drawn very sparsely.

ulating above- and below-ground competition as a factor causing ring formation are rather scarce. Although experiments are needed in order to test mechanistic hypotheses (Gibson 2002), experimental manipulations usually have side-effects and some manipulations are not feasible. Consequently, experimental evidence has to be combined with observational results. In the present study, we tested two possible hypotheses of ring formation in *E. angustifolium*. The first hypothesis is based on competition from the living ramets and interference with litter that prevent the recruitment of a new ramet within the interior of the tussocks. The second hypothesis is based on architectural constraints of clonal growth of *E. angustifolium*, i.e. reduction of axillary bud availability within the interior of the tussocks (Butler & Briske 1988, Olson & Richards 1988). To test for the effects of above- and below-ground competition on the ring formation, we conducted factorial experiments with planting tillers in different treatments within the individual zones of *Eriophorum* ring, and observing the tiller performance (i.e. growth and survival). Stress level below-ground was reduced by fertilization, above-ground competition for light was reduced by removal of living biomass around target tillers, and interference with dead shoots was reduced by litter removal. Whether clonal growth and axillary bud availability differ between plants located on the opposite side of the ring zone was analyzed *in situ* by measuring several parameters of clonal growth (spatial distribution of rhizomes and tillers). This short-term experiment was combined with observation of patch size dynamics over the period of three years.

Methods

Study area

The field study was carried out on an abandoned post-mined peatland Soumarský most in Šumava Mountains, Czech Republic, 48°58´N, 13°49´E, 650 m a.s.l. The locality is a continental raised bog (*sensu* Neuhäusl 1972) dominated by *Pino rotundatae–Sphagnetum* community, *Oxycocco–Sphagnetea* class. Mean annual precipitation is 810 mm and mean annual temperature 5.5 °C. The average effective growing season is 160 days (the Lenora meteorological station, 4 km northwest of Soumarský most). Peat harvesting at Soumarský most ceased in 2001; however, the locality was step by step abandoned during 1990s. The residual peat layer thickness is about 1 m. The post-mined fields have about 8 ha divided into 10–70 m wide strips by draining ditches. Nowadays, the drainage system is still partly functioning.

Zonation of *Eriophorum* circles

At our study site, *E. angustifolium* forms circular patches with a mean ring diameter of 4.43 ± 0.26 (mean ± SE) m, with some patches as wide as 12 m (Lanta *et al.* 2004). For the purpose of this study, we selected 8 circles. These were divided into four zones, from marginal green ring to the central part (Fig. 1):

Z1. The green band with high ramet density.
Z2. Zone of "young" litter, accumulated from

decaying ramets one year ago. This zone is characteristic for presence of standing dead material and for absence of green living ramets.

Z3. Zone of "old" litter, characteristic for presence of laying litter with absence of green living ramets.

Z4. Central zone with highly decomposed litter; here other plant species and green living ramets of *Eriophorum* tend to newly recruit (Lanta *et al*. 2004).

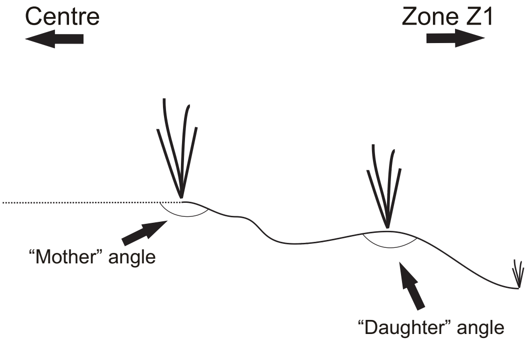

Fig. 2. Schematic picture of the "Mother" and "Daughter" angles.

Description of growth pattern of *E. angustifolium*

Changes in clonal growth were recorded within the green zone Z1 in the circular patches, where the manipulative experiment described below was not provided. We carefully removed peat soil around 37 randomly selected and interconnected ramets. Mother and daughter ramets were distinguished and two types of angles measured (*see* Fig. 2). First one (here called "mother" angle) was the angle between (1) hypothetical line going from the "mother" plant to the centre of the *Eriophorum* patch and (2) the "mother" rhizome which connects "mother" and "daughter" ramets. The second one (here called "daughter" angle) was the angle between (1) the "mother" rhizome and (2) the "daughter" rhizome, which is a connection between "daughter" and further "youngest" ramets (that is a product of the "daughter" ramet). As additional information we measured the length of a "mother" rhizome. Further, we dug out 71 ramets connected by rhizomes to estimate the length of rhizomes in three positions within the *Eriophorum* patch: at the outside border of the green zone Z1, in the middle of Z1 and inside of the *Eriophorum* patch. In June 2004, we marked the outside border of the *Eriophorum* patch (i.e. zone between the patch and bare peat surface) using woody sticks, and after 3 years in autumn 2006, the shift of green zone Z1 into open space was recorded and growth rate calculated.

Transplanting of target plants

To assess the effect of competition from the living ramets and interference with litter, we planted target ramets of *Eriophorum* into 20 × 20 cm plots (one ramet in the centre of each plot) located in the four zones in May 2004. The plots were arranged in a line at approximately 50-cm distances. In each plot, different experimental treatments were made up depending on the type of the zone; Z1, Z4: combinations of fertilization (yes/no), litter addition (yes/no) and competition from neighbor ramets (yes/no); Z2, Z3: only combinations of fertilization and litter addition because of the absence of green living ramets. Fertilization was carried out by applying a 5-cm fertilizer stick per plot (slow-released plant fertilizer FLORIA, AGRO CS, Česká Skalice, 10%N–7%P–6%K–2%Mg). Litter addition was provided by putting decaying *Eriophorum* material collected in patches not used for the experiment. Competition treatment was provided by hand-weeding of all ramets (including rhizomes) in the plots.

Numbers of surviving plants were recorded at the end of September when the experiment was terminated. For each target plant that survived until the end of the experiment, the length of the longest leaf, number of new rhizomes, total length of rhizomes and number of leaves was recorded. Aboveground biomass and biomass of rhizomes was oven-dried at 80 °C for 24 hours and weighted.

To assess the *Eriophorum* potential to establish and survive on bare peat surface, we conducted additional factorial experiment outside the *Eriophorum* patch with planting target ramets into 20 × 20 cm plots where fertilization (yes/no), addition (yes/no) of young or old litter and competition from neighboring ramets (yes/no) were combined. All treatment combinations were blocked and replicated eight times (each block was located ca. 1 m from the experimental *Eriophorum* circle used in the previous experiment). Fertilization and litter addition were provided in the same way as described above. Competition was provided by planting additional 4 ramets around the target one. We recorded survival of target ramets in September when the experiment was terminated. The length of target individual, number of new rhizomes, total length of rhizomes, number of leaves, aboveground biomass and biomass of rhizomes were used as response variables.

Foraging and penetration of ramets

To assess if *Eriophorum* growth is affected by connection between rhizomes, and if *Eriophorum* orients its rhizomes into nutrient rich patches rather than into nutrient poor patches, we conducted two factorial experiments (carried out from May to September 2004), the first one on the bare peat surface nearby Z1 and the second one in competitive environment within the first "green" Z1.

First experiment was carried out to asses foraging of *Eriophorum* ramets to the space around the circles by applying four levels of nutrients (0, 0.5, 1 and 2 fertilizer sticks) and three levels of litter addition (without addition, "young" litter added and "old" litter added). All possible treatment combinations were arranged into 15 blocks. Treatments were performed in 20 × 20 cm plots (the regular distance among plots was at least 30 cm), located nearby the circles on the bare peat surface. At the end of the season all ramets reaching the plots were harvested and total biomass (aboveground + rhizomes) measured. In the second experiment, biomass production of ramets and possible penetration of ramets through their rhizomes was assessed. The experiment was conducted in 20 × 20 cm plots within Z1. Treatments included fertilization (0, 0.5, 1 and 2 fertilizer sticks) and cutting connections between rhizomes, which was carried out around an experimental plot up to the depth of 30 cm. All possible treatment combinations were realized in 16 blocks. At the end of the 2004 vegetation season, aboveground biomass production was estimated by harvesting all ramets in treated plots.

Abiotic environment

We measured three soil parameters: total ammonium NH_4-N, nitrate NO_3-N and phosphorus PO_4-N in the four zones (Z1–Z4) and the reference zone on the bare peat surface (BP) nearby each circle. Soil samples were taken from 0–5 cm depth and the samples from one zone per circle were then pooled (9 replicates per zone). The soil fraction > 0.5 cm was removed from soil samples and the remaining fine soil was used to determine organic matter. All the parameters were estimated using the FIA technique, Foss-Tecator.

Data analyses

When analyzing the performance of planted tillers, we used the length of a ramet and the number of leaves as covariates to account for the possible variability caused by unequal size of ramets at the beginning of the experiments. In the "cutting experiment" the number of ramets present in the plots was used as a covariate. To evaluate the performance of planted tillers, separate ANCOVA analyses were performed for individual zones, because different treatment combinations were applied in different zones of the *Eriophorum* patch.

Binomial data on survival of target plants within an *Eriophorum* circle were evaluated for all zones together by using ANCOVA model with logit link function. The same analysis applied for binomial survival data from the experiment with planting tillers outside the *Eriophorum* circle. The effect of ramet foraging and soil data were evaluated with ANOVA. The differences in the length of rhizomes sampled from different positions within the *Eriophorum* patch were also analyzed with ANOVA. All calculations were performed with Statistica, ver. 5.5.

Results

Growth pattern of *E. angustifolium*

The average “mother” and “daughter” angles were 187.43° ± 10.31° (mean ± SE) and 174.32° ± 11.30°, respectively. This low variation in angles shows that disproportionately more ramets are recruited towards the periphery, which reduce axillary bud availability within the interior of the tussocks. The mean length of rhizomes connecting “mother” and “daughter” ramets was 12.68 ± 1.19 cm. The effect of different rhizome position (at the outside border of Z1, in the middle of Z1 and inside the patch) on rhizome lengths was found significant (ANOVA: $F_{2,169} = 4.60$, $P < 0.05$) with longer rhizomes at the outside border between the *Eriophorum* patch and the open bare peat (Fig. 3). The mean radial increment for the period of three years was 118.04 ± 7.48 cm. This means that all woody sticks that in 2004 marked the outside border of the Z1 green belt were in 2006 within Z3 of “old” litter.

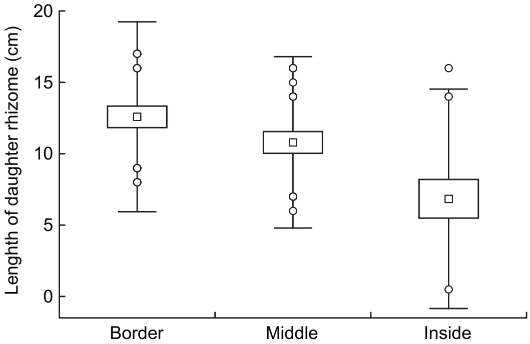

Fig. 3. Distribution of rhizome length (cm) within Z1 (Border: outside border of *Eriophorum* patch = location between *Eriophorum* patch and bare peat; Middle: the middle part of Z1; Inside: inside part of Z1 = direction to the centre of the *Eriophorum* patch). Means, SE of mean (boxes), SD (whiskers) and outliers (circles) are shown.

Performance of target plants within the *Eriophorum* patch

Analyses of Z1 showed that number of leaves of planted ramets was negatively affected by competition (ANCOVA: $F_{1,30} = 4.27$, $P < 0.05$; Fig. 4a), but positively by fertilization (ANCOVA: $F_{1,30} = 7.70$, $P < 0.01$; Fig. 3). This indicates that fewer leaves were developed when target plants were grown together with competitive neighbor ramets, and that more leaves were found in fertilized plots. Further, we found that the number of rhizomes was negatively affected by competition (i.e. fewer rhizomes produced in competitive environment) within Z1 (ANCOVA: $F_{1,30} = 3.92$, $P < 0.05$; Fig. 4b). Other characteristics were not significantly affected by used treatments. In the remaining zones (Z2–Z4) no significant effect of applied treatments was found.

Experimental treatments had a highly significant effect on the survival probability of the target plants. Survival was rather high (73%) and

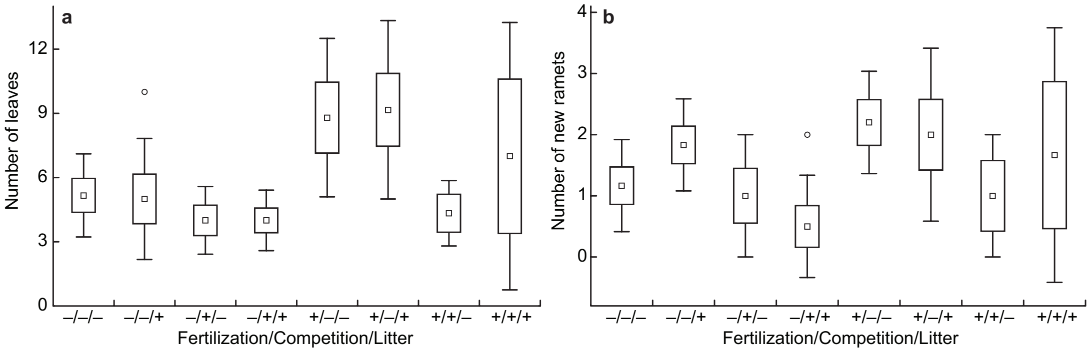

Fig. 4. — **a**: Number of leaves of planted individuals under three treatments. Only the values for Z1 are shown because significant effects of fertilization and competition were found there. Means, SE of mean (boxes), SD (whiskers) and outliers are shown. — **b**: Number of rhizomes of planted individuals under three treatments. Only the values for Z1 are shown because significant effects of fertilization and competition were found there. Means, SE of mean (boxes), SD (whiskers) and outliers are shown.

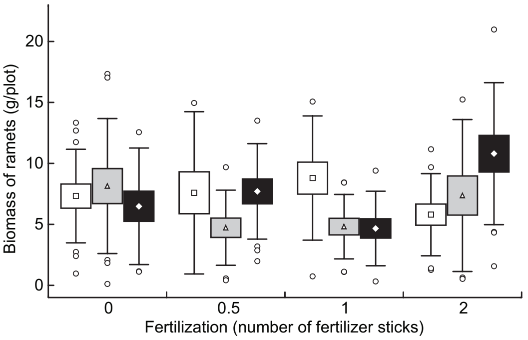

Fig. 5. Foraging (measured as biomass of ramets) for four fertilization levels and three levels of litter (empty boxes: without litter, gray boxes: "young" litter, black boxes: "old" litter). Means, SE of mean (boxes), SD (whiskers) and outliers are shown.

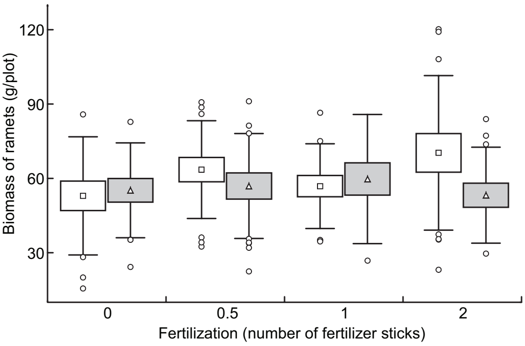

Fig. 6. Penetration of ramets (measured as biomass) at four fertilization levels and two levels of cutting (empty boxes: cutting of rhizome connections not applied, gray boxes: cutting). Means, SE of mean (boxes), SD (whiskers) and outliers are shown.

was negatively affected by competition (Wald's $F = 8.80$, $P < 0.01$) and surprisingly by fertilization (Wald's $F = 52.27$, $P < 0.001$); the effect of litter addition was not significant (Wald's $F = 2.91$, n.s.).

Performance of target plants outside the *Eriophorum* patch

This experiment showed that the number of leaves (ANCOVA: $F_{1,70} = 4.72$, $P < 0.05$) and the number of new ramets (ANCOVA: $F_{1,70} = 4.10$, $P < 0.05$) of planted ramets were positively affected only by fertilization. The litter addition and competition had no significant effect. Other measured characteristics (length and biomass of ramets, total length and biomass of rhizomes) were not significantly affected by the treatments. Survival of target plants was 62% and was negatively affected by both addition of "young" litter (Wald's $F = 6.93$, $P < 0.01$) and by fertilization (Wald's $F = 4.21$, $P < 0.05$). The effects of both addition of "old" litter and competition were not significant (Wald's $F = 0.49$ and 0.92, respectively).

Foraging and penetration of ramets

Neither the effect of litter addition (ANOVA: $F_{2,168} = 1.17$, n.s.) nor the effect of fertilization (ANOVA: $F_{3,168} = 1.37$, n.s.) had a significant effect on biomass production in experimental plots, however, the interaction term was significant (ANOVA: $F_{6,168} = 3.16$, $P < 0.01$). The significant interaction shows that in the nutrient-poor plots differences in biomass production were not as large between plots with different type of litter as compared with nutrient rich plots, where more biomass was produced in old and highly decomposed litter, which corresponds with our expectation (Fig. 5). In the experiment assessing ability of rhizome to penetrate within the first "green" zone (Z1), neither the effect of fertilization (ANCOVA: $F_{3,119} = 1.45$, n.s.) nor the cutting (ANCOVA: $F_{1,119} = 1.69$, n.s.) had a significant effect on biomass production (Fig. 6).

Abiotic environment

The total soil ammonium nitrogen (NH_4-N) content was higher in Z2 of old litter, but due to the high variation in the data, there were no statistically significant differences among the zones (ANOVA: $F_{4,40} = 1.44$, n.s.; Fig. 7). However, the total nitrate nitrogen (NO_3-N) content differed significantly among the zones (ANOVA: $F_{4,40} = 8.31$, $P < 0.001$), with higher values on the bare peat surface (Fig. 7). Total soil phosphorus (PO_4-P) content differed among the zones (ANOVA: $F_{\mathbf{00,00}} = 2.74$, $P < 0.05$), with higher values in the central parts of the *Eriophorum* circle (Fig. 7). Thus, phosphorus content seems to go in opposite way than nitrate content.

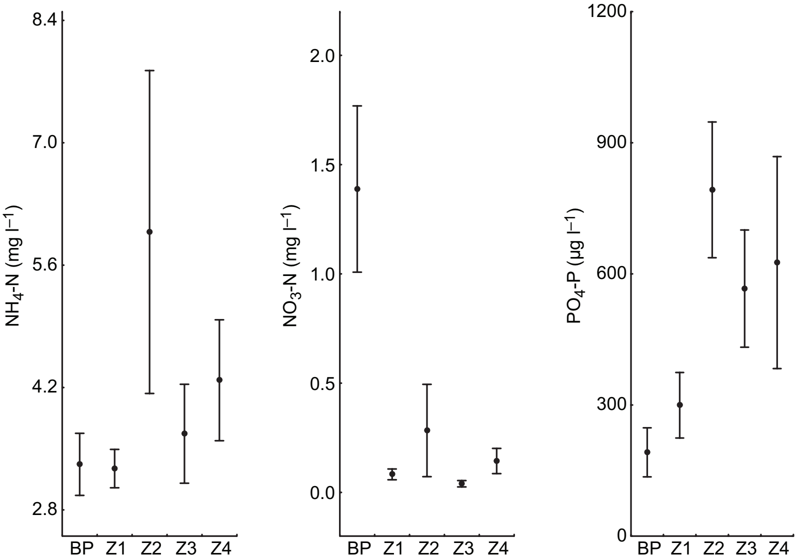

Fig. 7. Means ± SE of three soil parameters in the four zones (Z1–Z4) and on bare peat (BP).

Discussion

Eriophorum angustifolium is capable of specific radial clonal growth that leads to concentric circles of different sizes at our study site. In order to test several potential mechanisms of ring formation in *E. angustifolium,* we conducted several manipulative experiments. Their results suggest that both competition from the living ramets and architectural constraints of clonal growth of *E. angustifolium*, i.e. reduction of axillary bud availability within the interior of the tussocks (Butler & Briske 1988, Olson & Richards 1988) contribute to the ring formation process. The manipulative transplant experiments showed that within the green band of high ramet density, the number of leaves of planted ramets, the number of their rhizomes and ramet survival were negatively affected by competition. Moreover, production of new leaves was positively affected by fertilizer addition. This suggests that both above-ground competition for light and below-ground competition for soil nutrients play an important role in population dynamics of *E. angustifolium* and possibly in ring the formation process. The field study of clonal growth showed that rhizomes orient preferentially towards the periphery and, hence, disproportionately more ramets are recruited at the edge of the *E. angustifolium* patch. Therefore, as the old ramets within the interior of the tussock die due to senescence and inter-ramet competition, disproportionately more ramets are recruited on the periphery, which reduce axillary bud availability within the interior of the tussocks (Butler & Briske 1988, Olson & Richards 1988). The production of new ramets, their density and orientation is regulated by the existing ramets and characteristic features of plant architecture of *E. angustifolium* (Phillips 1953).

Eriophorum angustifolium on post-mined peatland forms circular patches that can be divided into several specific zones according to the amount of living and dead ramets and the litter decomposition rate. This pattern contrasts with *E. angustifolium* growing in natural peat-bogs not affected by peat harvesting activities, where populations do not show such ring formation pattern and consist of more or less restricted ramets connected by rhizomes of varying lengths. This classifies *E. angustifolium* as having a guerilla type of growth, for which extravaginal tillers and fast lateral spread about 10–25 cm per year are typical (Tolvanen *et al.* 2001). The growth of plants at our site was affected by emerging of a new open space on the bare peat surface. This unique environment with absence of competition from other plants enabled radial growth of *E. angustifolium* as one of the first colonizers (Lanta *et al.* 2004).

Radial growth in *E. angustifolium* has evolved in the first phases of vegetation succession on bare peat surface. In addition to *E. angustifo-*

lium, the ability to establish on bare peat surface immediately after abandonment of mining activities has been found in *E. vaginatum* (Tuittila *et al*. 2000). However, in *E. vaginatum* the rate of spread is much slower and it is not accompanied by die-back of central part. Growth pattern similar to that of *E. angustifolium* is known for some *Carex* species. The typical example is *C. humilis* (Wikberg & Mucina 2002) that grows on chalk grasslands known to have limitation in soil acidity (Wild 1993). Radial growth and ring formation have also been described in *Reynoutria japonica* in early phase of primary succession in harsh environment of volcanic desert on Mt. Fuji (Adachi *et al*. 1996) and *Stipagrostis ciliata* clumps in the Negev desert, Israel (Danin & Orshan 1995). These examples show that the fast vegetative spread of *E. angustifolium* at our site can be attributed to the relative homogenous but adverse environment remaining after abandonment and absence of competitive relationships between plant species at early phases of vegetational succession.

Our field observations suggest that for *E. angustifolium* vegetative regeneration and clonal spread are more important than regeneration from seeds. In fact, we did not find any seedling recruitment in the circle nor on the surrounding bare peat surface during the fieldwork. Contrary to this, generative reproduction probably played a very important role in the time immediately after the cessation of peat mining. *Eriophorum angustifolium* possess hairy seeds that are easily dispersed by wind. It is expected that plants will invest more into vegetative spread after initial recruitment from seeds (de Kroon & van Groenendael 1997).

The most critical phase for vascular plants colonizing post-mined peatlands is the early regeneration phase of seedling establishment and recruitment (Lavoie *et al*. 2003). When plants become established, new factors arise during the process of vegetation development to affect individual plant performance. Such factors include modification or lack of soil nutrients, increasing intensity of competition, and accumulation of litter (Grime 2001). Our first experiment manipulated these three factors within the *Eriophorum* circle and showed negative effects of competition and fertilization (the more fertilizer added the stronger the competition) on transplant survival. However, other characteristics measured (e.g. plant biomass and size) were not affected. These characteristics did not change under given treatments probably because of the specific lifespan and dispersal pattern of *E. angustifolium* and also because of the short duration of the experiment. *Eriophorum angustifolium* creates several ramets per year (Tolvanen *et al*. 2001), each ramet being a semi-rosette composed of leaves. The ramets that may occasionally flower. Formation of low number of leaves, which is connected with production of low biomass, could be responsible for the non-significant biomass response to our treatments. We expected that *Eriophorum* will have greater rhizome biomass in fertilized plots and that it will proliferate intensively into nutrient-rich plots as described for another clonal plants by Fransen *et al*. (1998). However, the effects of applied treatments were not significant. Our experiment conducted on bare peat, however, showed that the plants' survival was lower when the young litter was added suggesting that accumulation of litter (necromass) is an important factor (Chapman *et al*. 1975) affecting patch dynamics presumably by producing allelopathic substances, or by accumulation of pathogens (Falińska 1995).

The experiment with cutting rhizome connections showed that the biomass was the same under cut and uncut treatments. This finding may indicate that other non-biotic factors (for example the water table depth, a key factor in undisturbed peatlands) might influence effective clonal spread into open, competition-free bare-peat space. It was already hypothesized by Callaway *et al*. (2002) that non-biotic factors, such as temperature, wind and soil disturbance, limit plant growth in harsh environmental conditions more than biotic factors. In conditions of mined peatlands such a factor is water regime, because the water storage capacity during growing season is unstable and evaporation from the black peat surface is high (Price *et al*. 2003). The fundamental problem is an inadequate supply of water and rapid water loss. The water loss could be one of possible explanation of clonal radial growth. However, the water regime was not investigated in this study. In *Eriophorum* patches, competition for soil water among neighboring ramets may have caused a faster depletion of soil water within the interior of the *Eriophorum* patch. Lower soil water content would in turn intensify competition among ramets, causing mortality in some of them (e.g. Butler & Briske 1988).

Central die-back of *Eriophorum* circles is probably not simple consequence of tillering pattern (that is often associated with plant age). The factors such as resource depletion could be also important in regulating ramet dynamics within the interior of *Eriophorum* circles. Nutrients such as phosphorus, nitrogen and potassium are considered very limiting in fens and peat-bogs (Wheeler & Proctor 2000, Wind-Mulder *et al.* 1996). We found a high concentration of phosphorus (PO_4-P) and a low concentration of nitrogen (NO_3-N) in soils sampled from the central parts of the patches, and conversely, we found low concentration of phosphorus and high concentration of nitrogen nearby the patches on the bare peat surface. This is in accordance with our previous study (Lanta *et al.* 2004) regarding phosphorus accumulation in circles as a probable reason of its leaching from decaying plants. The high accumulation of limited phosphorus in the middle parts of the circles is one the important factors that enable the establishment of other species within the circles (Lanta *et al.* 2004). However, we must say that it did not explain the specific clonal growth of *E. angustifolium*. Nitrogen data might shed some light on this problem. High values in the neighborhood of the patches and low values in the centre suggests that *Eriophorum* can orient after some time its rhizomes into open space relatively rich in nitrogen. This can at least partly explain the expansion of the green belt towards the open space. Actually, *Eriophorum* depletes nitrogen accessible around the patch and tends to move into further space with higher levels of nutrients, where nitrogen has not been depleted yet. This was showed by the nitrogen form NO_3-N. Analysis of NH_4-N data showed no differences within zones (we found higher values only in Z2 (Fig. 5).

Comparison of utilization of both form of nitrogen indicates that *E. angustifolium* can take up more NO_3-N, and that it may do so preferentially in conditions of an abandoned mined peatland (Goodman 1963). Figure 7 also shows that average values of NH_4-N (3–6 mg l^{-1}) were higher than those of NO_3-N (0–1.5 mg l^{-1}). It is probably because the latter form is a product of oxidization of ammonium (NH_4-N) to nitrate (NO_3-N) through nitrification by *Nitrosomonas* and *Nitrobacter* in the upper aerobic layer of the peat (Charman 2002). A high NH_4-N content is associated with small particle sizes in the surface layer which is likely to be less aerated (Russell 1973). We could expect that external input of nitrogen in our studied system is mainly associated with precipitation containing nitrogen-reach airborne pollutants (Aerts *et al.* 1992, Økland *et al.* 2001). *Eriophorum angustifolium* as well as *E. vaginatum* is apparently well suited to colonize the bare peat surface because it tolerates acidic and nutrient-poor conditions (Chapin *et al.* 1979). It means that *E. angustifolium* is able to favor sites with ammonium in excess over nitrate, while the opposite is true for most other species (Salonen 1994).

We conclude that we have not yet found the ultimate explanation for formation of circle patches of *E. angustifolium*. We found that ramets creates shorter rhizomes in the interior of the green belt and longer rhizomes at the outside border and that competition could affect the plant survival similarly as litter accumulation. Depletion of soil nutrients can provide partial explanation for specific radial growth. However, if the circle formation is an optimal strategy to realize both extension and monopolization of the habitat, we need long-term study of the system on individual level, i.e. to work with marked plants.

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