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Growth response of downy birch (*Betula pubescens*) to moisture treatment at a cut-over peat bog in the Šumava Mts., Czech Republic

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The factors affecting the adaptation of downy birch (*Betula pubescens*) to different environmental conditions were studied in 2002–2003 by measurement of the production characteristics of saplings, which were experimentally planted in contrasting habitats at a cut-away peatland in the Šumava Mts., Czech Republic. These habitats varied in groundwater table depth. Together with this factor, we tested for the effect of shading, using shade cloth, on sapling growth. We conducted a greenhouse manipulative experiment to investigate the growth response of the downy birch saplings to varying groundwater table depths and soil types. We examined whether spatial distribution of naturally established birch stems changes along pronounced moisture gradient represented by transects placed at three distances from draining ditches. In the field, birch plants exhibited higher growth increments as well as higher leaf production under high groundwater table depth. This result is the opposite of the manipulated greenhouse experiment, which showed higher biomass increments for saplings under the low groundwater table depth. This was probably because downy birch, in principle, indicates terrestrification of peat bogs and high water table depth in greenhouse inhibited its growth. In field, birch saplings were probably stressed by drought. Positive shading effect on sapling growth was proven by leaf production measurements. The two term local variance method (TTLQV) revealed two contrasting dispersion patterns, for the birch population at drier and wetter sites of the post-mined peatbog. The aggregation was clear mainly at the drier site with lower abundance of birch plants within each sampled square. Higher abundance of individuals were found in squares of the wetter site, whereas the pattern was random there.

Key words: *Betula pubescens*, cut-over peatland, ecology, increment, facilitation, spatial pattern, water table depth

Introduction

During mechanical peat harvesting the original bog vegetation is completely destroyed. Thereafter, plants colonizing harvested peat surface must survive stress because the ecological conditions are extreme. The peat is dry, black and powder-like. During a sunny summer day, surface temperatures may be very high (Pfadenhauer & Klötzli 1996) and the water level fluctuates greatly (Lanta *et al.* 2004) and often abruptly. These conditions result in the killing-off of the colonized plants.

Exploitation of bogs for horticultural peat production results in complete removal of the original vegetation, which is replaced by a new plant cover consisting of species often with a reduced probability of survival in undisturbed bogs (Stewart & Lance 1991). The downy birch (*Betula pubescens*) is one such "pioneer" tree species in disturbed bogs, where it often forms stands near draining channels with favorable moisture conditions (Schouwenaars 1995). The birch and some herbs such as *Eriophorum vaginatum*, *E. angustifolium* and *Carex rostrata* are good colonizers and rapidly spread over unvegetated peat areas (Poschlod 1990). The birch, together with several grass species (for example *Molinia caerulea*), has been repeatedly observed as a rapidly invading species of cut-away bogs. This process often results in an expansion of these species and decline of mire and fen species. Recent studies in disturbed peat bogs provided evidence that water table fluctuation is also an important factor for the invasion of these species (Schouwenaars 1995, Price 1997, Robert *et al.* 1999). By contrast, the true mire species (e.g. *Sphagnum* sp.) grew on sites where the water level fluctuations are small and the peat layer is thick and has a low nutritional value (Wind-Mulder *et al.* 1996).

The distribution of individuals of the downy birch is unlikely restricted by water accessibility (Stewart & Lance 1991), with seedling and sapling growth being the most critical stages. Generally, the downy birch is intolerant of shade as juveniles and is replaced by slow-growing later-successional species (Silwertown & Doust 1993). Although shade-intolerant, at the early stages of post-mined succession, the shade effect of adult trees may help saplings to grow and survive adverse conditions. Furthermore, as saplings are more likely to survive at wetter than drier sites (Dierssen 1992), their growth rate is expected to be positively correlated with spatial distribution of adults, as their canopies may improve the moisture conditions.

The aim of this study was to evaluate the effects of different levels of water table depth and shading on the growth of downy birch saplings at a cut-away peatland in the Šumava Mts. (Czech Republic). This was achieved through measurement of production characteristics of downy birch saplings, experimentally planted in contrasting habitats with different water table depths. Shading was used to assess microclimatic conditions on birch saplings growth. We were particularly interested in changes in spatial distribution of naturally established birch stems along a pronounced moisture gradient represented by transects placed at three distances from draining ditches.

The second aim of this study was to evaluate the effect of different water table depths and two soil types differing in fertility (peat and sand) on the growth of downy birch saplings in a pot experiment under greenhouse conditions.

Methods

Study species

Downy birch is a polycormic, pioneer tree species, growing on moist and peat-rich soils. It is the dominant tree at our study site and occupies mainly four stands: (i) is scattered as saplings in the middle of *Eriophorum angustifolium* rings that probably made environmental characteristics more favorable for establishment of other plant species (Lanta *et al.* 2004), (ii) at the draining channels, (iii) at shaded dry and (iv) moist lower parts of the cut-off peatland. Canopy expansion takes place via the production of long shoots, which also produce axillary buds (Maillette 1982). Despite *B. pubescens*, *B. pendula* is scattered there. *Betula pubescens* was distinguished by the presence of sparsely or densely hairy leaves and densely hairy branches (Rothmaler 1976).

Study site

The field study was carried out in 2002–2003 on a cut-away peatland, Soumarský most peat bog (Šumava Mountains), Czech Republic, 48°54´N, 13°49´E, 650 m a.s.l. The mean annual precipitation is 810 mm and the mean annual temperature is 5.5 °C. The average effective growing season is 160 days (Lenora meteorological station, 4 km north-west of Soumarský most). Peat soil nutrient levels are low (total nitrogen 3.5–6.0 g kg^{-1} dry soil weight, total phosphorus 300–500 mg kg^{-1} dry soil weight). Peat harvesting at this location ended in 2001, however, the locality was gradually abandoned during the 1990s. The residual peat layer thickness is 1 m on average. The area of the field was 8 ha and it was divided by ditches into 10–70-m wide strips. Nowadays, the drainage system is still partly functioning. The area was originally covered by *Pino rotundatae–Sphagnetum* community (*Oxyccoco–Sphagnetea* class). At present, the spontaneous revegetation occurs mainly along the draining channels, with dominant trees and saplings of *Betula pubescens* and *Pinus sylvestris*, and *Carex canescens* with *C. rostrata*, *Eriophorum vaginatum* and *E. angustifolium* and *Molinia caerulea* dominating the understorey layer.

Greenhouse experiment

The experiment was run in an unheated greenhouse at the Faculty of Biological Sciences, České Budějovice. For the experiment, 11–36 cm saplings of *Betula pubescens* with peat soil were collected on 29 March 2003 at the Soumarský most peat bog. On 1 April, 84 individuals were weighted fresh and immediately planted into 84 pots (19 cm in diameter). The experiment was arranged into seven blocks. The following experimental treatments were imposed: (i) nutrient-level pots were filled with sand or peat collected at the Soumarský most bog, and (ii) 50% of the water-level (WL) pots were placed in 2-cm deep dishes and watered into these dishes with a sufficient amount of water to satisfy the plants' needs, and the remaining 50% were placed in 7-cm deep dishes and watered so as to maintain a constant water level in the dishes. The effect of different soil types was assessed because the downy birch grows in heterogenous environments and it is known that this species has a large ecological amplitude from peatlands to sites of nutrient poor sandy soils (Rothmaler 1976). A 1 × 2 × 2 (species × nutrient level × WL) randomized block design was adopted with three replicates in each of the seven blocks. The growth (height increment) of each birch plant was nondestructively measured six times during the experiment until 15 June, at which time the plants were harvested. Then the soil was washed from the roots, leaves were clipped, dried for 6 hours at 105 °C and weighed to the nearest 0.01 g. To calculate a "sapling increment" — the biomass of each plant at the end of the experiment minus biomass at the onset of the experiment — whole individuals including stem, branches and roots (but without leaves) were weighed fresh.

Field experiment

Within the whole mined area of Soumarský most bog we selected four drier sites with –34.3 cm of average water table depth (WTD) of five measurements during vegetation season, and wetter parts (with average WTD of –11.7 cm). The wet part was always located under the dry part in small 0.5–1-m deep depressions, roughly 10 × 10 m in diameter. One week before the start of the experiment on October 2002, 160 saplings (15–30 cm tall) were carefully sampled in the vicinity of the study site; the individuals were washed, weighed fresh (leaves were shed at this time) and stored for three days in a greenhouse. After this, twenty birch saplings were planted at regular distances of 15 cm in each dry and wet part within a block. Always 10 saplings were arranged into shaded and unshaded *Betula* groups.

The number of birch plants surviving the winter season was recorded and all dead individuals were replaced in March 2003. On 22 April, the experimental treatment shading was imposed to simulate two microclimatic conditions on sapling growth. A woody skeleton was installed approximately 30 cm above each *Betula* group at the drier and wetter sites. Then a well-ventilating shade cloth (with 1.5 × 1.5 cm mesh) was fixed to the skeleton. 2 × 2 (WTD × shading) randomized

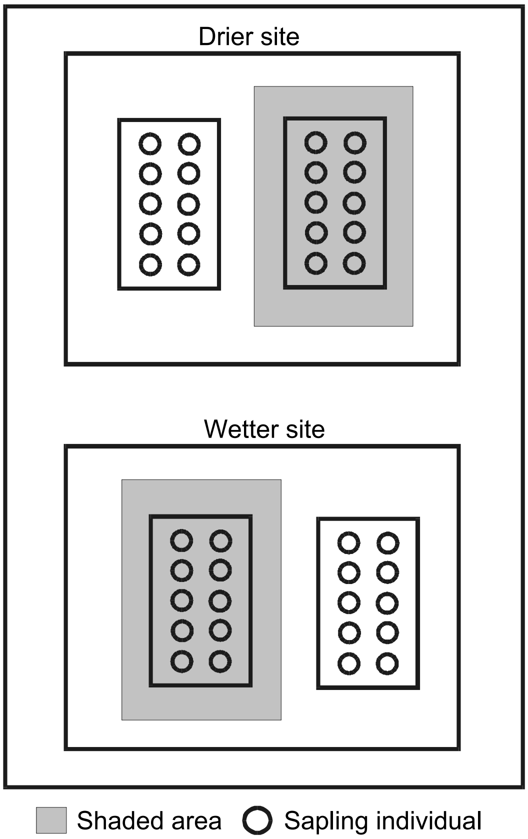

Fig. 1. A block of the field experiment with two levels of treatment: soil moisture and shading.

blocks were set up with ten replicates in each of the four blocks (Fig. 1). Plants were harvested on 12 September 2003, about four weeks before leaf shedding. After clipping the leaves, the plants were carefully rinsed to get rid of soil in the root system and then weighed fresh immediately in the field. Leaves were dried in the laboratory at 105 °C for six hours and weighed.

Spatial pattern of *Betula pubescens*

Within the area of the Soumarský most peat-bog two sites, the wetter one (average WTD of 3 measurements during vegetation season was –0.63 cm) and the drier one (with average WTD of –29 cm), were selected. Six longitudinal transects, each 50 m long, were established (D0, D5, D15 and W0, W5, W15 at the drier and wetter site, respectively) at 0 m (D0, W0), 5 m (D5, W5) and 15 m (D15, W15) distances from the draining channels on July 2003. The number of all birch seedlings and saplings was counted in each of the 167 30 × 30 cm quadrates along each transect. Saplings were defined as plants when their stems reached 1 m. At both field experiments, WTD was measured relative to the soil surface in perforated 1.5 m long, polyvinylchloride pipes (6 cm in diameter) inserted permanently in the peat.

Data analysis

Linear scale data measured in the field and greenhouse (leaf biomass, stem-root increment, sapling height) were analyzed using ANOVA (for a block design), including repeated measures when needed, and ANCOVA (with the stem weight at the start of the experiments used as a covariate).

Plant growth during the greenhouse and field experiments were analyzed for saplings using the methods of classical growth analysis (Hunt 1982) based on the increase of total plant biomass (B) between time t_1 at the start of the experiment and time t_2 at the end of the experiment:

$$\mathrm{RGR} = \frac{\ln(B_2) - \ln(B_1)}{t_2 - t_1} \qquad (1)$$

where RGR is mean relative growth rate in % d^{-1}. Differences in RGR were subsequently evaluated by testing the treatment interaction effect in ANOVA (for a block design).

Analysis of spatial data

Hill's (1973) two-term local quadrat variance method (TTLQV) was applied for analyzing the transect data. The method has been proposed for studying the spatial pattern of a single species in one dimension along which there is no environmental gradient (Dale 1999). The kind of data under consideration is density collected in a string of contiguous quadrats. The TTLQV analyzes data by examining how the mean square (MS) depends on the size of blocks of quadrats, which are grouped together in the analysis. For the analysis it is supposed that the data form a single transect consisting of $n + m$ basic units, where n is integer power of 2. The transect is represented by a sequence of birch quantities in particular sampling units x_i:

$$x_1, x_2, \ldots, x_n, x_{n+1}, \ldots, x_{n+m} \qquad (2)$$

The MS is defined as an average of overlapping terms, for example, for block size 1:

$$\mathrm{MS}(1) = \frac{1}{m+n+1} \times \left[\frac{\left(x_1 - x_2\right)^2}{2} + \frac{\left(x_2 - x_3\right)^2}{2} + \ldots + \frac{\left(x_{n+m-1} - x_{n+m}\right)^2}{2} \right] \qquad (3)$$

The mean square is defined analogously for any block; for example, at block size 3, the MS is defined as the average of overlapping terms:

$$\frac{\left(x_1 + x_2 + x_3 - x_4 - x_5 - x_6\right)^2}{6}, \qquad (4)$$
$$\frac{\left(x_2 + x_3 + x_4 - x_5 - x_6 - x_7\right)^2}{6}, \ldots, \text{etc.}$$

This pattern analysis is conveniently presented as graphs of mean square against block size, in which peaks indicate the scales of pattern present. A pattern analysis was always stopped at a block size of 56 to avoid decreasing reliability with the decreasing number of averaged terms (Dale 1999). This method is considered a purely descriptive one. *Betula pubescens* was most abundant towards the left end of the transects and was absent in < 43% and < 41%, on average, at the drier and wetter site, respectively.

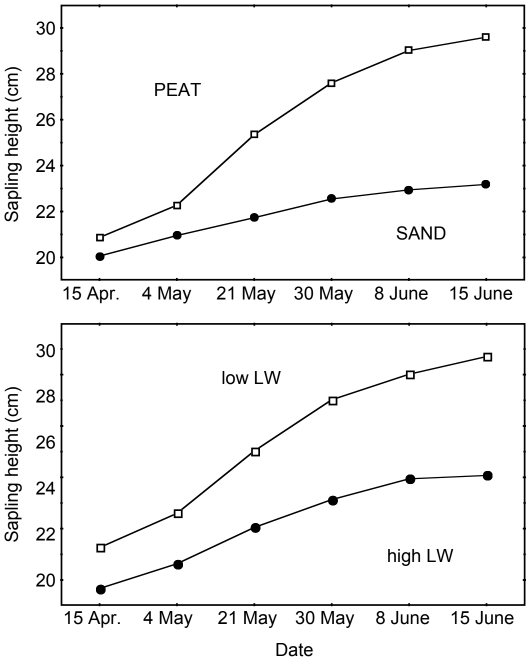

Fig. 2. Mean heights of *Betula pubescens* saplings repeatedly measured during greenhouse experiment. Statistical analyses are given in Table 1.

Results

Greenhouse experiment

On average, birch plants growing in peat soil were 1.3× taller at the harvest than when growing in sand (Table 1 and Fig. 2). High increment values differed under WL treatment, when values of low WL were 1.2× higher than values for high

Table 1. ANOVA for effects of depth of water (i.e., WL, low and high water table levels) and substrate (peat and sand) on growth dynamics, leaf biomass and sapling increment of downy birch grown under standard greenhouse conditions. Significance levels: n.s. = not significant; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; – = not enough data for statistical analysis.

Source	d.f. (effect)	Growth dynamics *F*	Leaf biomass *F*	Increment *F*
Substrate	1	29.40 **	9.28 *	0.01 n.s.
WL	1	4.63 n.s.	13.55 *	6.89 *
RepFactor	5	183.55 ***	–	–
Block	6	0.77 n.s.	0.39 n.s.	0.63 n.s.
Substrate × RepFactor	5	19.17 ***	–	–
WL × RepFactor	5	5.87 ***	–	–
Substrate × WL	1	0.00 n.s.	6.52 *	1.21 n.s.

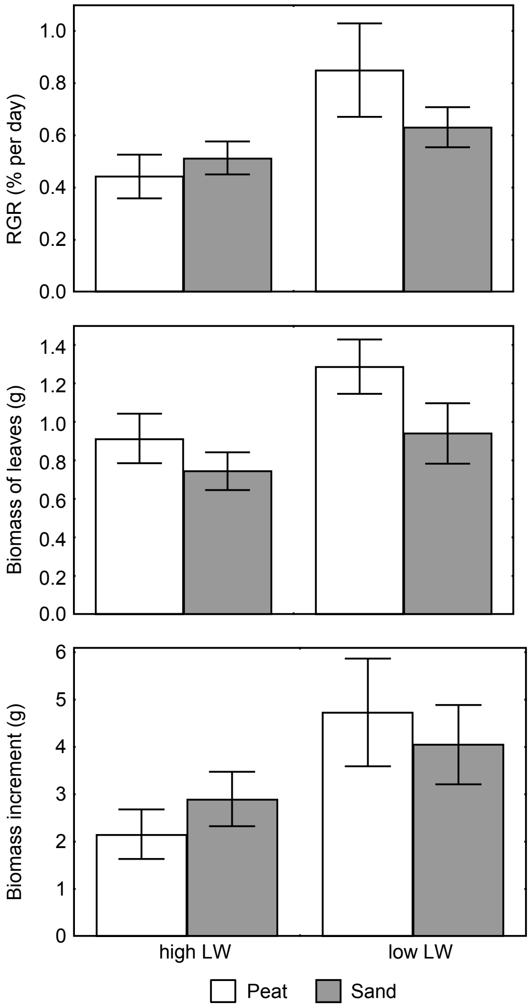

Fig. 3. Means (columns) and standard errors (whiskers) for relative growth rate, leaf biomass and sapling increment of *Betula pubescens* saplings grown under greenhouse conditions. Statistical analyses are given in Table 1.

WL. The WL × time interaction indicates that plants held under low WL attained higher growth rates than plants under high WL during the experiment. Peat soil under the low WL resulted in a significant increase in biomass increment values (Table 1 and Fig. 3). Sapling increment characteristics differed significantly between WL conditions, but did not differ relative to soil type. Leaf biomass differed significantly relative to soil × WL condition interaction (Table 1). Higher productivity of leaves was measured in plants growing on the peat soil depending on WL treatment level (Fig. 3).

The mean RGR was lower, but not significantly (Fig. 3; $F_{1,6} = 4.38$, $P = 0.08$), under the high WL treatment when compared with that under the low WL conditions. Under the soil treatment, there were no differences in RGR values ($F_{1,6} = 0.34$, $P = 0.57$). The soil × WL interaction was not significant ($F_{1,6} = 1.18$, $P = 0.31$). Thus, plants developed similarly and independently of the treatments during the growth period lasting for 61 days.

Field experiment

In March the number of survived plants varied between 3 and 10 (within a treatment combination). However, a contingency tables analysis showed no significant difference in plant survival between the drier and the wetter site ($\chi^2 = 0.48$, d.f. = 3, $P = 0.92$). Plant survival was not analyzed at the harvest time because of the very high survival rate of individuals (7–9 plants within a treatment combination), resulting in 124 survived plants (from the 160 planted) in total.

The significant effect of moisture indicates that birch had a higher increment at the wetter than drier site (mean averages over the treatments were 2.44 *vs.* 1.18 g, respectively; Fig. 4 and Table 2). In the shading experiment, the increment was greater in shaded plants than in the unshaded ones (2.28 *vs.* 1.33 g, respectively). There was no evidence of interaction between shading and water table depth.

The leaf biomass (Table 2) was significantly higher for the wetter than for the drier site (mean averages over the treatments were 0.47 and 0.18 g, respectively, *see* Fig. 4). There were significant differences in the leaf biomass between the shaded and unshaded plots (0.44 *vs.* 0.21 g, respectively). However, no significant effect of the moisture × shading interaction was detected.

The mean RGR was higher for the high WTD plots than for the low WTD plots, although this result was not significant (Fig. 4; $F_{1,3} = 8$, $P = 0.06$). Significant differences were detected in the RGR for the shading treatment, with higher values for shaded plots (Fig. 4; $F_{1,3} = 13.64$, $P = 0.03$). The moisture × shading interaction for RGR values was not significant ($F_{1,3} = 0.65$, $P =$

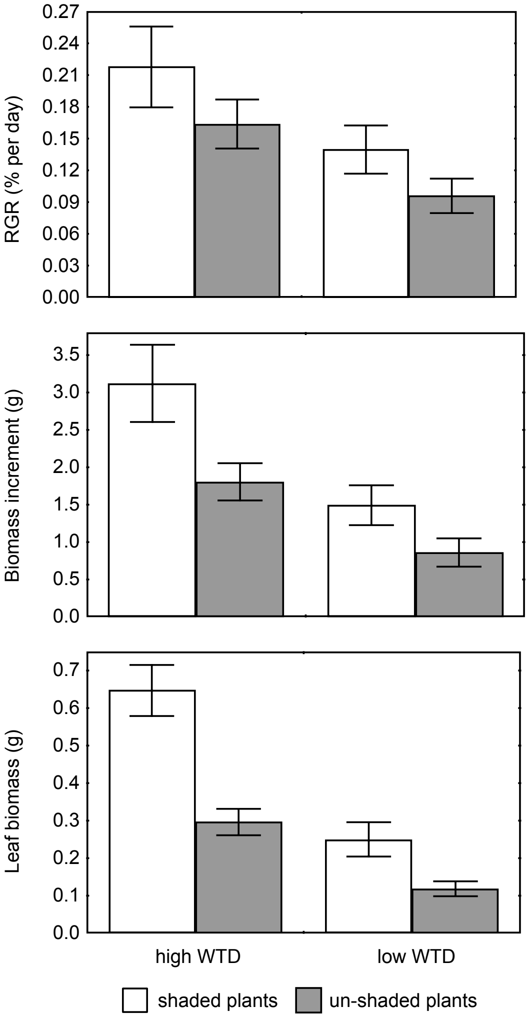

Fig. 4. Means (columns) and standard errors (whiskers) for relative growth rate, plant increment and leaf biomass of *Betula pubescens* saplings planted in field conditions. Statistical analyses are given in Table 2.

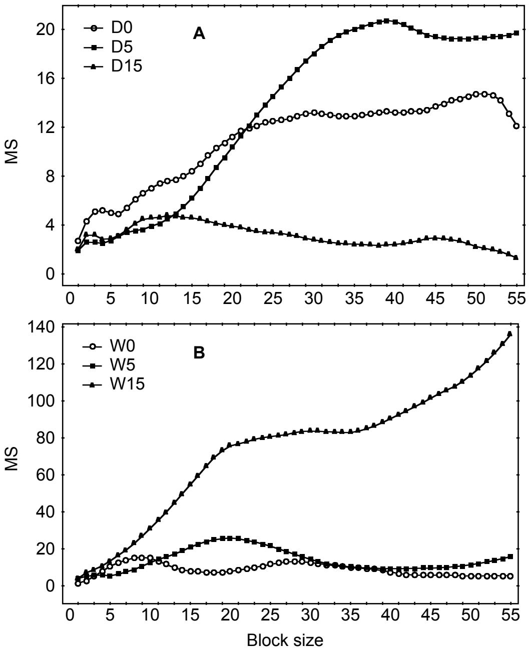

Fig. 5. Pattern analysis of two populations of *Betula pubescens*. (**A**) Drier and (**B**) wetter site of mined peat-bog. Results of analysis of transects within respective populations are shown.

0.48), indicating similar growth under both treatments during the study period of 289 days.

Pattern analysis

The TTLQV revealed differences in the spatial pattern between populations of the birch growing at wetter and drier sites. However, because of the large number of quadrates, the TTLQV curves were rather smooth.

There are distinct peaks at distances of 0.9–1.2 m in the D0, D5, D15 of drier population and at the 2.1 m distance in the W0 of wetter population (Fig. 5). The peaks correspond with the patches composed of stems originating from seedlings of established young birch trees. At the drier site, less distinct peaks at higher block size of 40 (12 m; D5) and 50 (15 m; D0) correspond to gaps between *B. pubescens* aggregations. The curve of D15 shows that birch formed relatively homogenous growth there without clear aggregations (random pattern). At the wetter site, a

Table 2. ANOVA for effects of shading (shaded and un-shaded subplots) and depth of water (i.e., WTD, high and low water table levels) on leaf biomass and sapling increment of downy birch planted in field conditions. Significance levels: n.s. = not significant; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Source	d.f. (effect)	Leaf biomass *F*	Increment *F*
Shading	1	10.64 *	6.19 n.s.
WTD	1	20.32 *	25.28 *
Block	6	1.88 n.s.	0.39 n.s.
Shading × WTD	1	3.43 n.s.	1.45 n.s.

pronounced peak was detected at the block size of about 20 units (6 m; W5). Spatial aggregation was not apparent in higher block size units at both transects of W0 and W15. The increase in MS values at the W15 detected environmental heterogeneity at higher scale (Dale 1999).

Discussion

The effects of large water table level fluctuations on natural revegetation of peat bogs after abandonment of mining activities have been repeatedly reported (Price *et al*. 1998, Stoneman & Brooks 1998, Robert *et al*. 1999, Goodyear & Sliva 2000, Girard *et al*. 2002, Vasander *et al*. 2003). These findings show that the changes in the water table level have profound effects on functioning of disturbed peatland ecosystems including further vegetation development. In this study we quantified effects of different WTD on the growth characteristics and leaf production of individual tree saplings under field conditions. Additionally, we investigated similar effects under standardized greenhouse conditions, and then we interpreted both experiments. Thus, our study could partly fill a gap between investigations of the effects of water table fluctuation on ecosystem level (*see* references above) and several experimental studies interested in plant growth of selected species under natural environmental conditions (Weih & Karlsson 1999, 2002, Hagen *et al*. 2003). We are aware of the limitation of our field experiment, mainly its short duration, covering only one winter and the subsequent growing season. However, we evaluated the growth responses of the downy birch to two levels of water table depth in the greenhouse and field experiments and also showed how realistic the pot experiment is in comparison with the field experiments (Diamond 1986).

Greenhouse and field experiments

The greenhouse experiment showed different growth responses of tested birch saplings to two soil treatments. At first sight, the results seem to be a little complicated to resolve the questions: (i) why the growth dynamics of birch saplings differed under soil treatment but not under the WL, and (ii) why the leaf biomass differed under the WL, not under the soil treatment and why the interaction term was significant. A possible explanation could be that the plants are able to allocate assimilates more rapidly under the low WL. Furthermore, water did not fluctuate randomly (in the high WL conditions) during the experiment as is characteristic for the conditions of cut-away peatlands where the water table fluctuates much (Joosten 1992, Schowenaars 1993, Price 1997). In our experiment the WL was stable, which suggests that the root system in the high WL conditions could be affected by some microbial and anoxic processes (anaerobic stress). However, the description of root systems was not investigated in this study. There is the possibility that plant growth could be abrupt by lower soil respiration at high WL (Kim & Verma 1992).

The peat soil containing more nutrients and water is more favourable for birch growth. This probably resulted in the increasing growth dynamics and leaf biomass of the downy birch growing on peat (Table 1), although the response on soil substrate was not strikingly clear in RGR. Similar values of RGR for plants planted on sand and peat could be a result of adaptations to past environments and could predispose plants to delay their growth responses to current environmental conditions (Kramer & Kozlowski 1979).

The growth of the downy birch was influenced by different WTD in the field. As we expected, the downy birch grew better under wetter conditions (high WTD), particularly when shaded. Under wetter conditions, the downy birch exhibited higher growth increments as well as higher leaf production, which is the opposite result of manipulated greenhouse experiment (higher increment values were under low water table level). As we proposed earlier, it might be explained by fluctuated water table level in natural field conditions. The downy birch does not tolerate flood (because of anaerobic conditions in soil) and it indicates terrestrification of peat bogs (e.g. Lanta *et al*. 1994, Salonen 1994). Thus, the high WL in greenhouse inhibited the growth. In contrast, the water level decreases during growth season in the field, peat dries out and birch saplings become stressed by drought and overheating. Therefore, in wetter sites the effect of drought was milder, and the measured growth was higher than in drier sites.

We are aware that the results of our study could be partly influenced by some environmental factors, such as differences in the start time (field experiment was started in October, greenhouse experiment in March) and the duration of experiments. In the field, environmental conditions could be partly influenced by the winter season, which could play a role in differences in soil temperatures or soil desiccation (Price *et al*. 1998). It is the reason why a cut-away peat surface is dark and overheated for a long time (Girard *et al*. 2002). This highly variable environment could not be reproduced in the greenhouse experiment.

Higher values of the leaf biomass and RGR for shaded saplings might be a cause of the effect of higher allocation to assimilation apparatus as was suggested by Henriksson (2001). Differences in leaf biomass could be explained by the existence of the facilitative mechanism, if we regard the shading treatment as simulating protection by adult plants on the sapling growth. However, we are aware that the "real" effect of facilitation (defined in Callaway & Walker 1997) could be proven only by a longer experiment and by studying the survival of saplings. The facilitation of adult trees is an important effect for survival and successful establishment of saplings in adverse environmental conditions (Egerton *et al*. 2000, Haase 2001). Our observations from the studied locality showed that the downy birch occupies wetter sites especially at the draining channels. There was already a relatively vigorous spontaneous revegetation presumably because of the higher water supply and protective shading of birch trees.

Environment and pattern

Although the downy birch occurs in a wide range of habitats at the study locality, moisture is the most important environmental factor influencing its spatial pattern. The aggregation was clear at the drier site (transects D5 and D0) probably because of the competition from other species growing nearby. The patches of aggregated saplings bordered sites of lower canopy of other plant species. These patches were characterized by lower competition effect or full absence of *Molinia caerulea* and *Eriophorum angustifolium*, both dominant plants at the drier sites. Both of those species are capable of fast vegetative spread, which helps them to modify the immediate environment and to become a major component in the plant community. Consecutively, they could produce marked spatial heterogeneity through their light competition on other species (Greigh-Smith 1979) and impose the aggregate pattern of the downy birch. Conversely, at the wetter site the pattern was random probably because of the absence of strong competitors. On this site there occurred only sparsely distributed vegetation of mosses (*Polytrichum* sp. and *Dicranella heteromalla*) and sedges (e.g. *Carex canescens* and *C. rostrata*).

In addition to competition, disturbances such as frost heaving and crust formation can influence the size of birch aggregation due to variable intensity of erosion at the bare peat surface. Drier sites are more prone to environmental extremes, where the highly fluctuating WTD and the drought are harmful to birch survival and might lead to an increase of heterogeneity in the birch population. This was the reason why we recorded fewer individuals in transects sampled at the drier site.

Expansion of *B. pubescens*

The conclusion of the study is that the tested variables (water table level, shading, soil substrate) influenced the measured growth characteristics of the downy birch in different ways. Furthermore, spatial pattern of the downy birch can be influenced by different water table level and competition from neighbouring species. The fact that draining ditches are now rapidly colonized by a dense population of birch supports the idea that the downy birch will probably expand in the near future over the mined peat surface at the locality. For that reason, we can expect that it leads to the development of a mixed forest with *B. pubescens* and *Pinus sylvestris* as dominant trees rather than to peat formation and accumulation.

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