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Ekologie borovice blatky (*Pinus rotundata* LINK) ve vztahu k regeneraci blatkových borů

Ecology of bog pine (*Pinus rotundata* LINK) in relation to regeneration of bog pine forests

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doktorská disertační práce
Ph.D. Thesis

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Anotace / Annotation:
Ecology of *Pinus rotundata,* and partly also of accompanying trees *Pinus sylvestris* and *Picea abies,* was studied. Experiments with seedlings and field observations were conducted to find the limitations in rejuvenation of studied species. Succession in bog pine forest after different types of disturbances and changes of the *Pinus rotundata* forests during the last fifty years were analyzed.

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Marek Bastl

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Úvod

Blatková rašeliniště

Středoevropská rašeliniště s dominancí mokřadních borovic jsou unikátním ekosystémem, přetrvávajícím kontinuálně na stejném místě a přibližně ve stejném rozsahu od časného holocénu (Jankovská 1980). V této trvalé a stabilní existenci jsou těžko srovnatelná s jinými ekosystémy příslušné geografické oblasti. Mohou být nahlíženy jako ekologické ostrovy (Spitzer 1994) se všemi důsledky s tím souvisejícími, jako je poměrně rychlá mikroevoluce, reliktnost taxonů i společenstev a citlivost k vnějšímu narušování. Extrazonální charakter, uvažujeme-li rozsáhlou zónu severských rašelinišť, dává středoevropským rašeliništím významný biogeografický kontext (Dierssen 1996, Mikola et Spitzer 1983, Soukupová 1996).

Ráz jednotlivým lokalitám dávají příslušné populace dominantních borovic, jejichž taxonomické postavení je složitější (podrobněji níže), nápadný je však přechod čistě stromových forem až v nízké, keřové formy se vzrůstající nadmořskou výškou. Nejsem si vědom žádného podobného případu, kdy by byly tak úzce svázány životní forma a taxonomické postavení edifikátoru, vegetační gradient a gradienty faktorů prostředí, tak jak tomu je v případě šumavských a přilehlých rašelinišť. Jejich význam zvyšuje skutečnost, že hlavní taxon zúčastněných borovic *Pinus rotundata* má poměrně malý areál, nejmenší ze všech středoevropských dřevin tvořících dominanty lesních porostů (obr. 1 na straně 41).

Blatková rašeliniště jsou v současnosti ohrožena především často dlouhodobým vlivem odvodnění a atmosférickou depozicí živin. Jelikož je existence tohoto ekosystému přímo závislá na prosperitě populací borovice *P. rotundata*, pokusil jsem se v předkládané práci přispět k poznání její ekologie, které je nezbytné pro účinnou ochranu zbývajících lokalit, na nichž se poměrně často můžeme setkávat s jejím významným vymíráním a ústupem (Rektoris et al. 1997, Sengbusch et Bogenrieder 2001, Boratyńska et. al. 2003, Freléchoux et al. 2004).

Poznámky k taxonomii mokřadních borovic

Borovice na středoevropských rašeliništích, nepočítaje *Pinus sylvestris*, byly nejprve řazeny k *Pinus mugo*. Taxonomické názory na hodnocení celého agregátu *P. mugo* jsou však velmi rozporuplné. Nejasnosti pramení zejména z různě širokého chápání taxonů různými autory, z tradovaných omylů minulosti a ze značné variability a ne zcela ostrého ohraničení jednotlivých taxonů, které jsou v určitých částech areálu spojeny poměrně rozsáhlými hybridogenními populacemi.

Vyčerpávající přehled různých taxonomických pojetí jednotlivých autorů podávají Hamerník et Musil (2007).

Raději ponechávám stranou, že do již tak složité taxonomické problematiky vnáší další nejistotu Businský et Kirschner (2006) zjištěním, že neotyp *P. rotundata* (Austria, Tirol, Mt. Zwieselberg above lake Plansee), který stanovil Christensen (1987), není intermediární mezi *P. uncinata* a *P. mugo*, ale je na pomezí *P.uncinata* a *P. uliginosa* (neotyp Poland, Kłodzko Region, Wielkie Torfowisko Batorowskie (Christensen 1987)), s bližším vztahem k *P. uncinata* a nelze jej proto použít jako pojmenování borovice blatky. Na úrovni druhu by se borovice blatka měla jmenovat *P. hartenbergiensis* (Businský et Kirschner 2006). Na úrovni poddruhu *P. uncinata* subsp. *uliginosa* (Businský et Kirschner 2006).

Pro ulehčení orientace v následujícím textu uvádím seznam platných jmen středoevropských borovic z širokého okruhu *P. mugo* a jejich nejčastěji používaných synonym, jak je uvádí Businský (1998, 1999) doplněný o další synonyma, s kterými jsem se nejčastěji při studiu literatury setkal, která uvádím v hranatých závorkách:

***Pinus mugo* TURRA (1764)**
syn. *Pinus mughus* SCOPOLI (1772)
syn. *Pinus pumilio* HAENKE (1791)
[syn. *Pinus montana* MILLER (1768)]

***Pinus uncinata* RAMOND ex DE CANDOLLE. (1805)**
syn. *Pinus uncinata* MILLER ex MIRBEL. (1806)
syn. *Pinus mugo* var. *rostrata* (ANTOINE 1840) HOOPES (1941)
[syn. *Pinus mugo* subsp. *uncinata* (RAMOND) DOMIN (1935)]

***Pinus rotundata* LINK. (1827)**
syn. *Pinus uliginosa* NEUMANN ex WIMMER (1837)
[syn. *Pinus mugo* subsp. *rotundata* (LINK) JANCHEN et NEUMAYER (1941)]
[syn. *Pinus uncinata* subsp. *rotundata* (LINK) JANCHEN et NEUMAYER (1941)]
[syn. *Pinus uncinata* subsp. *uliginosa* (NEUMANN) BUSINSKY comb. nova]

Pro úplnost je ještě třeba zmínit jména relativně často se vyskytujících hybridů mokřadních borovic:

***Pinus* × *pseudopumilo* (WILLK.) BECK (1890)**
Pinus mugo × *Pinus rotundata*

***Pinus* × *digenea* BECK (1888)**
Pinus sylvestris × *Pinus rotundata*

Rozšíření jednotlivých taxonů, tak jak jsou chápány v této práci, ukazuje obr. 1 na straně 41.

Vlastní *P. rotundata* LINK. je druh s diskutabilním taxonomickým postavením. Z toho pramení mnoho problémů při vyhledávání a studiu literárních podkladů, jelikož se daný druh v literatuře vyskytuje pod více různými jmény. Hlavním problémem je však skutečnost, že i stejná užívaná jména v literatuře mohou v důsledku rozdílného chápání u různých autorů označovat rozdílné taxony. Proto považuji za vhodné, zmínit v úvodu alespoň základní názorové proudy týkající se této problematiky, se kterými se můžeme setkat:

a) *Pinus rotundata* – samostatný taxon na různé taxonomické úrovni v rámci polymorfní skupiny taxonů agregátu *P. mugo*.
b) *Pinus rotundata* – introgresívní hybrid mezi *P. mugo* a *P. uncinata*.
c) *Pinus rotundata* – hybrid mezi *P. sylvestris* a *P. mugo* (vyvrácený omyl).

V následujícím doplňujícím textu (psaný petitem), který rozvádí výše zmíněné názorové proudy, uvádím názvy druhů přesně podle jednotlivých článků. Přestože si netroufám názvy přímo překládat do taxonomického pojetí použitého v této práci, uvádím pro snazší orientaci ve složené závorce, o jaký druh by se mohlo dle mého názoru jednat.

Výše zmíněné názorové proudy najdeme např. v těchto pracích:

ad a) Prus-Glowacki et al. (1998) studovali taxonomickou pozici *P. uliginosa {P. rotundata}*. Doba divergence od společného předka je podle nich u *P. uliginosa {P. rotundata}* z lokality Wielke Torfowisko Batorowskie podle genetické vzdálenosti (Nei) dvakrát větší než pro *P. uncinata {P. rotundata}*. Můžeme vyloučit, že by *P. uliginosa {P. rotundata}* z této lokality byla okrajovou populací *P. uncinata*.

Siedlewska et Prus-Glowacki (1995) studovali genetickou strukturu *P. uliginosa {P. rotundata}* z Wielkie Torfowisko Batorowskie na základě variability isoenzymů a porovnávali se strukturou *P. mugo* z Tater a *P. sylvestris* z údolí Klodzka a Czersku. Koeficienty genetické podobnosti (Nei, Hedrick) ukázaly odlišný charakter od *P. sylvestris* a jen volný vztah s *P. mugo*. Také genetická diferenciace populací ukázala specifitu *P. uliginosa {P. rotundata}*.

Když Boratyńska et al. (2003) provedli porovnání více znaků na stejných lokalitách jako Staszkiewicz et Tyszkiewicz (1972), dospěli k názoru, že místní populace *P. uliginosa {P. rotundata}* má daleko větší podobnost s *P. mugo*, než s *P. sylvestris*.

Lewandowski et al. (2000) při výzkumu genetické diferenciace mezi blízce příbuznými druhy borovic, které zahrnovaly *P. sylvestris*, *P. mugo*, *P. uncinata* a *P. uliginosa {P. rotundata}*, zjistili, že genetická vzdálenost (Nei) mezi *P. sylvestris* a *P. mugo* je dvojnásobná proti *P. uliginosa {P. rotundata}* a *P. uncinata*. *P. uliginosa {P. rotundata}* a *P. uncinata* považují spíše za poddruhy, k nimž dodávají, že jsou pravděpodobně vzniklé dávnou hybridizací mezi *P. sylvestris* a *P. mugo*.

ad b) Holubičková (1980) považuje borovici blatku, kterou nazývá *P. uncinata* subsp. *uliginosa {P. rotundata}*, za taxon, který je (stejně jako *P. mugo* subsp. *pseudopumilio*) produktem introgresívní hybridizace mezi *P. mugo* a *P. uncinata*.

ad c) Staszkiewicz et Tyszkiewicz (1969, 1972) uvádějí borovici blatku dokonce jako hybrida mezi *P. mugo* a *P. sylvestris*. V novějších pracích je však již jako název hybrida uvedena *P.* × *rhaetica* BRÜGG. (Staszkiewicz 1996) a uvedena původní záměna křížence na lokalitě Dolina Białego v Tatrách s *P. montana* subsp. *uncinata {P. rotundata*, pravděpodobně použito nesprávné synonymum pro *P uncinata}*.

Do již tak dosti nepřehledné situace navíc v nedávné době přispěli Minghetti et Nardi (1999) zjištěním, že lectotyp *P. mugo* ze Seguier Herbarium náleží introgresívní populaci mezi východní *P. mugo* subsp. *mugo* a západní *P. mugo* subsp. *uncinata*. Jméno *P. mugo* subsp. *mugo* by tedy mělo reprezentovat *P. mugo* subsp. *rotundata*. Zmínění autoři, však sami uznávají, že tato změna by vyvolala takový zmatek, že lepší bude zachovat jméno *P. mugo* s typem, který bude odpovídat současnému užití.

Podobně problematické taxonomické postavení má i *P. uncinata*.

Neet-Sarqueda (1994) provedl elektroforézní allozymovou diferenciaci na 11 lokusech na populacích *P. sylvestris* a *P. mugo* agg. a 3 populacích s morfologií mezi *P. sylvestris* a *P. uncinata*. Při klastrové analýze vznikly 2 skupiny: *P. sylvestris* (zahrnující intermediární typy) a *P. uncinata*. Nebyl nalezen žádný důkaz pro existenci zóny introgresivních hybridů mezi *P. sylvestris* a *P. uncinata*. Intermediární populace jsou směsí jedinců *P. sylvestris* a *P. uncinata*.

Naproti tomu Lauranson-Broyer et Lebreton (1993) ukázali při studiu flavonoidů u *P. sylvestris* a *P. uncinata* existenci přirozených hybridů. Hybridy se většinou velmi přibližovaly jednomu z rodičovských druhů a bylo velmi málo intermediárních jedinců.

Lauranson et Lebreton (1991) analyzovali 120 jedinců *P. uncinata* na obsah flavonoidů v jehlicích. Procento quercetinu rozlišilo pět studovaných populací. Každá z nich byla dle sledovaných obsahových látek jedinečná.

Jelikož se *P. rotundata* vyskytuje na mnoha relativně izolovaných lokalitách, lze předpokládat významnější genetické odlišnosti jednotlivých populací i v jejím případě.

Boratynska et Bobowicz (2001) studovali odlišnosti v 11 charakteristikách jehlic mezi *P. mugo*, *P. uncinata* a *P. sylvestris*. Zjistili bližší vztah *P. uncinata* k *P. mugo*. *P. uncinata* se od *P. sylvestris* liší počtem siličných kanálků a v tloušťce buněk pokožky a vzdáleností mezi cévními svazky.

Camarero et Gutierrez (2002) popisují v centrálních Pyrenejích na lokalitě Ordessa s dominancí *P. uncinata* přechod od mnohokmenných „krummholz" forem k větším stromovitým se snižující se nadmořskou výškou. Což opět odporuje základnímu popisu druhu *P. uncianta* jako monokormního stromu. V článku Wiemken et Boller (2006) je dokonce dokumentováno fotografií *P. mugo* var. *uncinata* v „krummholz" formě a dle autorů stejný druh tvoří i okolní porosty s výškou až 15 m, což zřetelně poukazuje na monokormní jedince.

Popis hlavního studovaného druhu - borovice blatky

Ve své práci jsem se držel pojetí druhu tak, jak jej uvádí Skalický (1988) a Businský (1998, 1999). Druhy *P. mugo* s. str. a *P. uncinata* vykazují takové morfologické a chorologické charakteristiky, že je lze považovat za vývojově starší, než pravděpodobně později vyštěpený – ale přesto dobře vyhraněný a ustálený (zřejmě během pleistocénu) druh *P. rotundata*, představující typický „drobný druh" v pojetí taxonomických kategorií přijatých v díle Květena ČSR (Businský 1998, Businský 1999).

Při determinaci druhu jsem používal především tyto znaky uváděné Skalickým (1988): *P. rotundata* – borovice blatka (borovice bažinná) je strom, s jediným, přímým, až 20 m vysokým kmenem. Borka je šedočerná, rozpraskaná, v horní části kmene a na větvích šedohnědá, šupinatá, ale neodlupující se v pergamenovitých útržcích. Jehlice tuhé, po 2 na brachyblastech, jen mírně stočené podél osy, rovné až mírně srpovitě zahnuté, oboustranně sytě zelené, neojíněné. Šišky vejcovité, zygomorfní na zakřivené krátké stopce, odstálé, na bázi excentricky zešikmené až nepravidelně zaokrouhlené; štítky semenných šupin mírně vyklenuté, na osluněné straně šišky s nízce jehlanovitými mírně zakloněnými výrůstky.

Znaky o barvě borky jsou použitelné pouze u stromů nedotčených sběrem šišek pomocí stupaček či jiným způsobem, který odírá kůru. Oloupáním svrchních vrstev borky dochází k barevnému posunu směrem k hnědé barvě i u fenotypově čistých borovic blatek (osobní pozorování).

Znak o počtu 7 děloh u klíčních rostlin, který uvádí Skalický (1988), je zřejmě chybný. V pokusech se tento počet děloh u *P. rotundata* vůbec nevyskytl. Většinou se pohyboval v rozsahu 4-6. U *P. sylvestris* byly počty děloh většinou v rozsahu 5-7, což je podobný údaj, jako počet děloh 4-8, který pro daný druh uvádí Skalický (1988).

Dalším znakem, užívaným při determinaci *P. rotundata*, byl úhel odklonu koneletů (jednoletých šištic u rodu *Pinus*) od osy větve, jak jej uvádí Businský (1998). Zatímco u *P. sylvestris* jsou konelety vždy nápadně zpět ohnuté na dlouhých stopkách, u *P. rotundata* jsou vždy vzpřímené na krátkých stopkách (Businský 1998).

Z nastíněné taxonomické problematiky je zřejmé, že pojetí druhu se u jednotlivých autorů značně liší, což komplikuje porovnávání výsledků v diskuzi. Veškeré pokusy prezentované v předkládané práci se konaly na populacích *P. rotundata* pocházejících z České republiky (která je centrem areálu daného druhu) a jejich výsledky lze tedy s jistotou aplikovat pouze na našem území. Případné širší zobecnění výsledků by vyžadovalo provést pokusy s potomstvem pocházejícím z celého areálu studovaného druhu.

V provedených pokusech bylo potomstvo vniklé ze semen fenotypově čistých jedinců jednotlivých druhů považováno opět za „čistý" druh. To bylo možné jednak díky výběru lokalit s nízkou mírou výskytu hybridních jedinců a taktéž po ověření, že potomstvo jednotlivých stromů je vzhledově relativně jednotné a v znacích na sekundárních jehlicích podobné matečnému jedinci. Izolace samičích šištic a následné umělé opylování nebylo při rozsahu pokusů technicky zvládnutelné.

Rozšíření

Skalický (1988) udává celkové rozšíření *P. rotundata* v České republice (západní a jižní Čechy, Žďárské vrchy (Velké Dářko), Hrubý Jeseník (Rejvíz)), Polsku (slezká část - což bych rád upřesnil na Góry Bystrzyckie (Torfowisko pod Zieleńcem), Góry Stołowe (Wielkie Torfowisko Batorowskie) a Bory Dolnośląskie (Torfowisko pod Węglińcem)), Německu (Sasko, Schwarzwald, v Bavorsku v předhoří Alp, v Smrčinách, v Nábské kotlině, Hornofalckém lese a v nižších polohách Šumavy), Rakousku (Vitorazsko, předhoří Alp a snad i v alpské oblasti).

Velmi důležité je zmínit i rozšíření druhu *P. uncinata* v podání stejného autora. *P. uncinata* je rozšířena v Pyrenejích, Francouzském středohoří, Ligurských Apeninách, z. Alpách, Švýcarské Juře a Vogézách (Skalický 1988).

Přibližnou mapku rozšíření druhů agregátu *P. mugo* ukazuje obr. 1 na straně 41.

Fytocenologie

(Dle Chytrý et al. 2001, upraveno.)

Své optimum nachází borovice blatka ve společenstvu *Pino rotundatae–Sphagnetum* (KÄSTNER et FLÖSSNER 1933) NEUHÄUSL 1969 (svaz *Sphagnion medii* KÄSTNER et FLÖSSNER 1933). Na převážně srážkovou vodou sycených rašeliništích s hloubkou rašeliny přes 2m. Hladina podzemní vody zde obvykle neklesá více než 30cm pod povrch terénu a často zde probíhá cyklická, mozaikovitá sukcese. Výška blatek zde dosahuje nejčastěji 8-10m (při ovlivnění odvodněním až 18m). Rozeznávají se tři varianty asociace *Pino rotundatae–Sphagnetum* v závislosti na výšce hladiny podzemní vody (od nejvyšší k nejnižší) s dominujícím *Eriophorum vaginatum, Ledum palustre* nebo *Vaccinium myrtillus.*

Dále blatku nalézáme ve společenstvu *Vaccinio uliginosii–Pinetum sylvestris* KLEIST 1929 (svaz *Dicrano–Pinion* (LIBBERT 1933) MATUSZKIEWICZ 1962), které představuje závěrečné sukcesní stádium na vrchovištních rašeliništích nižších poloh a původně se vyskytovalo zřejmě jen na okrajích vrchovišť a přechodových rašelinišť. Stromové patro může dosahovat výšky až 25m. Hladina podzemní vody se nachází většinou hlouběji než 30cm pod povrchem. Blatka je zde přimíšena především na kontaktu se společenstvem *Pino rotundatae–Sphagnetum.*

Ještě je třeba zmínit společenstva ze svazu *Sphagnion medii* KÄSTNER et FLÖSSNER 1933 (např. *Eriophoro vaginati–Sphagnetum recurvi* HUECK 1925) s nimiž blatkové bory často tvoří mozaiku směrem k centru rašelinišť a s nimiž vývojově souvisí.

Směrem k okrajům rašelinišť zase můžeme nalézt společenstva svazu *Piceion excelsae* PAWLOWSKI et al. 1928 (např. *Sphagno–Piceetum* (TÜXEN 1937) HARTMANN 1953), které na blatkové bory často navazují.

Směrem do vyšších nadmořských výšek jsou porosty blatky na rašeliništích často nahrazovány společenstvy ze svazu *Oxycocco–Empetrion hermafroditii* NORDHAGEN ex HADAČ et VÁŇA (např. *Pino mugo–Sphagnetum* KÄSTNER et FLÖSSNER 1933). Místo čistého druhu *P. mugo* se zde (zvláště v nižších polohách) spíše setkáváme s jeho kříženci s *P. rotundata* nazývanými *P.* × *pseudopumilio*. Na některých lokalitách, kde dominuje *P.* × *pseudopumilio*, můžeme nalézt v okrajových částech rašelinišť i stromové jedince borovice blatky (např. Kladské rašeliny, Mrtvý luh, Multerberg).

Rozmnožování

P. rotundata se množí zřejmě výhradně semeny. Hypotetická možnost vegetativního rozmnožování zakořeněním spodních větví nebo i větví vyšších částí koruny stromů ohnutých k zemi především v důsledku váhy sněhu, či zakořenění větví u stromů, které přišly v mládí o vzrostný vrchol, a proto rostou ve formě „krummholz“, není v literatuře zmiňována. Osobně jsem kořenění větví na lokalitách taktéž nepozoroval. I větve dlouhodobě překryté porosty rašeliníku, nejevily známky kořenění. To se neobjevilo ani na kmínku u semenáčků snažících se dlouhodobě uniknout přirůstajícímu koberci rašeliníku. Přestože se současnými znalostmi není možné vegetativní rozmnožování úplně vyloučit, jistě hraje, pokud vůbec, v populaci *P. rotundata* zanedbatelnou roli.

Během sběru semen, který probíhal v sezónách (1997-2004), jsem zjistil několik zajímavých skutečností. V rámci populace borovice blatky se významnější plodnost soustřeďuje pouze na některé jedince. V populaci se vyskytuje mnoho jedinců, kteří vůbec neplodí. Buďto vůbec netvoří šišky, nebo se šišky nedokážou plně vyvinout a neobsahují vyvinutá, klíčení schopná semena. Během sezón sběru nebyly u blatek pozorovány výrazné semenné roky. V roce 2002 se pouze vyskytla výrazně snížená plodnost především na lokalitě Kyselov, která však zřejmě souvisela s částečným zatopením lokality během povodní. Dalším zajímavým jevem bylo, že plodnost označených stromů (tj. těch co byly plodné v prvé sezóně sběru) byla v průběhu mnoha sezón sběru relativně velmi pravidelná a vyrovnaná (v podstatě každoroční). Jelikož se tyto stromy navenek nijak významně nelišily od dalších v porostu (které však byly v průběhu sledování plodné jen minimálně či vůbec), mohla by zjištěná situace naznačovat, že významnější tvorba plodných samičích šištic je v blatkových porostech soustředěna pouze na relativně úzký okruh jedinců. Sbíraná semena měla velmi dobrou klíčivost a semenáčky byly celkem vitální. Samozřejmě není ověřena jejich konkurenční úspěšnost ve srovnání s potomky méně plodných stromů, což by měl ověřit připravovaný pokus. V dále prezentovaných pokusech nebylo možné méně plodné jedince zahrnout v důsledku velkých nároků na množství semenáčků od jednoho jedince daných rozsahem jednotlivých experimentů.

Ekologie

Ekologicky by se měla *P. rotundata* od *P. uncinata* velice výrazně lišit. *P. rotundata* tvoří porosty na přechodových rašeliništích a vzácně na obvodu vrchovišť (Skalický 1988, Sengbusch 2004). *P. uncinata* je druh subalpínského stupně na nerašelinných biotopech

(Skalický 1988). Skalický (1988) udává z Švýcarské Jury pouze *P. uncinata*, to je však v rozporu s některými terénními pracemi (např. Freléchoux et al. 2000a, 2000b, 2003, 2004), kteří ze stejného pohoří popisují populace, které nazývají *P. uncinata* var. *rotundata* na rašeliništích. Pro tento spor mne napadají např. tato vysvětlení: buďto může *P. uncinata* růst též na rašeliništích a Freléchoux et al. udávají špatný název druhu, nebo je areál *P. rotundata* širší a překrývá se s areálem *P. uncinata*. Pokud se areály těchto druhů skutečně překrývají, pak bude jistě zajímavá genetická struktura jejich populací v místě jejich setkání. Striktní vymezení druhu podle stanoviště nemusí vždy fungovat, zvláště v případě extrémních stanovišť jakými jistě jsou jak rašeliniště, tak subalpínský stupeň. *P. mugo* nalezneme jak nad hranicí lesa, tak na vrchovištích i v supramontánním stupni (Skalický 1988). V obou případech druh přežívá vytlačen na extrémní stanoviště, kde ostatní dřeviny velmi obtížně vegetují. Proto nelze vyloučit podobné chování i u blízce příbuzného druhu *P. uncinata*.

I v případě regenerace najdeme u *P. rotundata* a *P. uncinata* některé paralely.

Pinus uncinata na přirozeném stanovišti Ordessa v centrálních Pyrenejích regenerovala v „krummholzi“ tvořeném vlastním druhem (Camarero et Gutierrez 2002), kde můžeme předpokládat facilitační mechanismus. Na přirozeném stanovišti Tesso, v stejném pohoří regenerovala v místech snížené pokryvnosti *Rhododendron ferrugineum* (Camarero et Gutierrez 2002), tj. v místech snížené kompetice (minimálně o světlo).

Světlo hraje v regeneraci blatkových borů velmi důležitou roli. Borovice blatka je relativně světlomilná dřevina. Maximální výška borovice blatky, udávaná Skalickým (1988), je 20 m. U borovice lesní 40 m a u smrku ztepilého až 60 m. Z toho vyplývá, že pokud druhy konkurující blatce naleznou vhodné podmínky k růstu, postupem času ji přerostou a zastíní. Konkrétní výška *P. rotundata* na jednotlivých lokalitách je pravděpodobně kontrolována nejen hladinou podzemní vody, ale i obsahem kyslíku ve vodě v půdních pórech (Sengbusch 2004). Výškový růst *P. abies* je zřejmě podpořen snížením hladiny podzemní vody (Sengbusch 2004). Zastínění nejen oslabuje růst dospělých stromů, ale také brání v uchycení a růstu semenáčků (Sengbusch 2004).

Druh *P. uncinata* je udáván jako druh odolávající suchu, a proto růstově relativně více závislý na teplotě než na srážkách (Rolland 2002). Rolland (2002) tak vyvozuje ze vzájemné podobnosti dendrochronologií na velké vzdálenosti, v případě tohoto druhu (>500 km). Srovnatelné hodnoty udává ještě u *Picea abies* (>477 km). Oproti tomu *Pinus cembra* (>254 km) a *Larix decidua* (>189 km) dosahují výrazně nižších hodnot. Jejich růst je totiž relativně více závislý na lokálních srážkových poměrech dané sezóny než na průměrné teplotě, která je oproti srážkám korelována na větší vzdálenosti. Odolnost k suchu u *P. rotundata* nepředpokládám, jelikož na rozdíl od *P. sylvestris* není schopna regenerovat na stanovištích s velkými výkyvy vlhkosti (osobní pozorování). Na lokalitách s narušeným vodním režimem dochází k umírání blatek ještě před dosažením fyziologického věkového limitu (Sengbusch 2004). Možnou příčinou se jeví acidifikace akrotelmu v okrajích narušených rašelinišť a snížená dostupnost vápníku v průběhu léta a podzimu (Sengbusch 2004).

Přírodní lesy mají velkou prostorovou a časovou heterogenitu (Rathgeber et Roche 2003). Hlavní úlohu v temperátním klimatu při tvorbě heterogenity mají malé disturbance korun, tj gap dynamics (Rathgeber et Roche 2003). U lesa *P. uncinata* v subalpínské zóně zjistili

Rathgeber et Roche (2003) průměrnou velikost disturbance mezi 0,036 ha a 0,073 ha a průměrnou dobu trvání změněných podmínek 6 let. Tak malé disturbance pravděpodobně způsobil pád jediného stromu, který částečně uvolnil konkurenční tlak na okolní stromy (Rathgeber et Roche 2003).

Blatkové bory regenerují v procesu cyklické sukcese (Rektoris et al. 1997). Důležitou roli v jejich regeneraci hrají jednotlivé vývraty a maloplošné polomy (Neuhäusl 1972) a žír specializovanými druhy lýkožroutů (Liška et al. 1989). Jankovská (1980) nalezla stopy po opakovaných narušeních ohněm na lokalitě Červené blato, ve formě uhlíkových vrstev v rašelinném profilu. Což poukazuje na fakt, že výrazné narušení ohněm, které nastalo v poslední době na rašeliništi Žofinka (Kučerová et al. 2008), nebylo v historii blatkových rašelinišť výjimkou. Na druhou stranu pozdní kvetení a absence šišek adaptovaných k požárům u *Pinus nigra*, *P. sylvestris* a *P. uncinata* (platí i pro *P. rotundata*) ukazuje, že jejich přirozené lesy se nevyvíjely za častých korunových požárů (Tapias et al. 2004).

Četné dlouhodobě prosperující výsadby *P. rotundata* v jižních Čechách na minerálním podkladu poukazují na nevyhraněné nároky na substrát a relativní toleranci starších jedinců k různým vláhovým poměrům v případě dostatku světla.

Ohrožení

Výrazný úbytek borovice blatky z různých lokalit v rámci jejího areálu v posledních desetiletích je dokumentován např. z Polska (Boratyńska et. al. 2003), České republiky (Rektoris et al. 1997), Německa (Sengbusch et Bogenrieder 2001, Sengbusch 2004). Rychlost degradace i relativně zachovalých lokalit je v některých případech alarmující (Kučerová et al. 2000). I když v současnosti většinou nehrozí přímá likvidace lokalit těžbou v důsledku jejich ochrany, stále aktuální (a navíc i řešitelný) je problém narušení vodního režimu. K narušení docházelo hlavně v minulosti přímo na lokalitě či v jejím okolí, ale může k němu docházet i v současnosti odvodňováním okolních nechráněných porostů. Vliv odvodnění je většinou dlouhodobý, čímž se kumulují jeho negativní dopady. Negativní roli hraje pravděpodobně i zvýšená atmosférická depozice živin.

Cíle

Hlavním cílem předkládané práce bylo zjistit, jaké podmínky potřebuje borovice blatka k úspěšné regeneraci s důrazem na stádium semenáčků. Sledovány byly zejména vlhkostní poměry a dále světelné podmínky a obsah živin v substrátu. Nároky borovice blatky byly srovnávány s nároky borovice lesní a smrku ztepilého, s kterými je v konkurenčním vztahu. Další zkoumanou oblastí byla schopnost společenstev blatkových borů vyrovnat se s různými typy narušení lokalit. V potaz byla brána jak přírodní narušení, tak narušení činností člověka. Pozornost byla věnována i změnám blatkových borů na gradientu nadmořské výšky.

Dílčí otázky a hypotézy jsou uvedeny v jednotlivých kapitolách.

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Early development of *Pinus rotundata*, *P. sylvestris* and *Picea abies* - growth responses to abiotic factors in controlled experiments and consequences for bog pine forest restoration

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Abstract

The aim of the study was to find the ecological requirements of tree seedlings involved in bog pine forest dynamics. Requirements of bog pine (*Pinus rotundata*), in comparison to the co-occurring tree species Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), were studied in relation to groundwater, light and nutrient conditions. The first one-year garden experiment (3 shading, 3 groundwater and 3 nutrient levels) showed the best growth (highest biomass) for *P. rotundata* in the no shading, low water, and high nutrient treatment, followed by *P. sylvestris* and *P. abies*. The second two-year garden experiment (7 water levels) showed the highest biomass for *P. rotundata*, followed by *P.* × *digenea* (*P. rotundata* × *P. sylvestris*), *P. sylvestris* and *P. abies*. The relative differences in studied species growth show a clear trend of decreasing towards lower water levels. The height growth of *P. rotundata* was the best at all levels of water. But differences between *P. rotundata* and *P. sylvestris* height growth decreased towards lower water levels when high and low water treatments were compared. The experiment showed that a high groundwater table level would probably favour seedlings of *P. rotundata* compared to *P. sylvestris* and *P. abies*. Therefore, a "no action" management plan for *P. rotundata*-dominated peat bogs appears not to be suitable for preserving this species in such habitats in which the water regime has been disturbed (mainly by drainage). Cautious rising of the groundwater table, after damming drainage ditches, may partly suppress *P. abies* establishment and support seedling recruitment of *P. rotundata*.

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opakuje předchozí větu

Keywords: Bog pine; Scots pine; Norway spruce; Water table; Nutrients; Eutrophication; Drainage, Peat bog; Seedlings

Introduction

Bog pine *Pinus rotundata* Link (syn.: *P. mugo* Turra ssp. *rotundata* (Link) Janchen et Neumayer, *P.* uliginosa Neumann, *P. uncinata* ssp. *rotundata* (Link) Janchen et Neumayer) is endemic to peat bogs in Central Europe. *P. rotundata* grows optimally in lower altitudes on relatively nutrient rich peat bogs. Unfortunately, these are the areas most disturbed by peat harvesting and drainage. There is a clear decline in *P. rotundata* during the last 30 years, in spite of recent protection of its natural stands. The decline usually starts with massive dieback of old trees (Sengbusch and Bogenrieder 2001, Rektoris et al. 1997, Freléchoux et al. 2004). After that *Picea abies*, *P. sylvestris* and Betula pubescens start to dominate in the tree layer and Frangula alnus in the shrub layer (Rektoris et al. 1997). Another type of decline is caused by slower successional changes with expansion of *P. abies* and sometimes *P. sylvestris* (Horn and Bastl 2000). Establishment of *P. rotundata* is usually very low in both cases. Hybridization between *P. rotundata* and *P. sylvestris* may also occur. Seedling establishment is crucial for establishment of the studied trees, because their ability to vegetatively reproduce is negligible. In addition, seedlings are usually the most sensitive stage in tree development (Kozlowski et al. 1991). This study was undertaken to find the ecological requirements of *P. rotundata* seedlings in comparison to the other co-occurring tree species and recommend changes in the management of protected areas to reinforce *P. rotundata* populations. It focused on ecological requirements of groundwater, light and nutrient conditions.

proč uvolení faktory!

Material and methods

Seeds of *P. rotundata*, *P. sylvestris*, and *P.* × *digenea* (*P. rotundata* × *P. sylvestris*; trees are habitually intermediate between the parent species) were collected from marked trees in natural peat bog localities in South Bohemia, Czech Republic. (description see in Table) Seeds from a single tree were used separately throughout the experiment to see also the intraspecific variability of each species response to experimental factors. Seeds of *P. abies* were not collected in the same way, because there was no seed year of this species during the experiments. Thus, two seed mixtures were used in this case. Site numbers, location and altitude of the sites are presented in **Table 1**.

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Table 1. Localities used for seed collection.

Site	Site number	Latitude	Longitude	Altitude
Borkovická blata	1	49 14' N	14 37' E	425m
Červené blato	2	48°52' N	14°52' E	470m
Žofinka	3	48°49' N	14°52' E	474m
Široké blato	4	48°54' N	14°59' E	495m
Vltavský luh	5	48 50' N	13 56' E	731m
Kyselov	6	48°41' N	14°03' E	735m
Mrtvý luh	7	48°52' N	13°52' E	740m
Březina	8	48°53' N	13°51' E	745m
Multerberg	9	48°36' N	14°08' E	790m
Nový Brunst	10	49 11' N	13 15' E	885m
Prášily	11	49 07' N	13 23' E	925m
Modrava	12	49 02' N	13 30' E	1010m

A one-year garden experiment was conducted investigating *P. rotundata*, *P. sylvestris* and *P. abies* seedling growth under different nutrient, light and groundwater table conditions (Experiment no. 1). Seeds of *P. sylvestris* and *P. rotundata* were from sites 1, 3, 4 and 6, while *P. abies* seeds originated from sites 11 and 12.

Seedlings were grown in pots (5 × 5 × 9cm) filled with peat originating in a natural stand of *P. rotundata*. Three cold-moist stratified seeds (30 days, 5°C in the dark) were sown in each pot. The experiment was established as a split-plot design, with the sets of pots (blocks) as the whole-plots, nutrients, light and water table as the whole plot factors, and split-plot factor species. The blocks are subjected to the same combination of external factors, and correspond to the whole-plot in the split-plot design. A factorial combination of the three environmental factors, in 3 levels each, was applied on the level of the block. There were three different nutrient levels: (i) "no nutrients" added, (ii) "low nutrients" (10% nutrient solution according to Ingestad and Kähr (1985)), and (iii) "high nutrients" (100% nutrient solution according to

Ingestad and Kähr (1985)). Nutrients were added once a week into blocks. There were three different light levels: (a) "no shading", (b) "low shade" (approximately 25% reduction of light), and (c) "high shade" (approximately 75% reduction of light). Light levels were [illegible] 2 controlled in blocks. There were three different levels of groundwater table: (a) "low water" (8cm below ground), (b) "medium water" (4cm below ground), and (c) "high water" (water table at ground level). Water tables were controlled in blocks twice a week. Pots were watered [illegible] only by natural precipitation (cca 650 mm a year) and by capillary rise. There were 10 pots in one block (4 pots with *Pinus rotundata*, 3 pots with *P. sylvestris* and 3 pots with *P. abies*). Two blocks were used in each combination of factors. In total, 540 pots (3 × 3 × 3 × 10 × 2) were used. Seedlings were randomly thinned to one per pot in the middle (for removing competition effect) and harvested at the end of the first growing season. Each seedling was separated into roots, shoot (part above hypocotyl) and stem (hypocotyl), and oven-dried at 80°C to constant dry weight (dw). The number of lateral branches was also recorded for each seedling.

The two-year experiment was conducted to investigate *P. rotundata*, *P. sylvestris*, *P.* × *digenea* and *P. abies* seedling growth under different groundwater table conditions, taking into account also overwintering (Experiment no. 2). Seeds of *P. sylvestris* originated from sites 1, 4, 5, 6, 7 and 9, seeds of *P. rotundata* from sites 1, 2, 3, 6 and 10, seeds of *P.* × *digenea* were from sites 8 and 10 and seeds of *P. abies* originated from sites 11 and 12. (Table 1)

In this case, the seedlings grew in pots (5 × 5 × 9cm) filled with peat originating in a natural stand of *P. rotundata* under full light and without added nutrients ~~("no shading", "no nutrients" treatment)~~. Three cold-moist stratified seeds (30 days, 5°C in the dark) were sown in each pot. The experiment was established as a split-plot design, with the sets of pots as the whole-plots, water table and environment as the whole plot factors, and split-plot factor species. The sets of pots (blocks) are subjected to the same combination of external factors, and correspond to the whole plot in the split-plot design. A factorial combination of the two environmental factors, in 7 and 2 levels respectively, was applied on the level of the block. There were seven different groundwater levels: low (water table 9cm (a) and 8.5cm (b) below ground level), medium (water table 6.5cm (c) and 4cm (d) below ground level), high (water table 2cm (e) below ground level and at (f) ground level) and flooded (water table 1cm (g) above ground level). Water tables were controlled in blocks twice a week. The whole experiment was divided into two parts: One set of seedlings was grown in garden conditions and the other set in the greenhouse (factor environment). Pots were watered by capillary rise, pots in the garden also by natural precipitation (cca 650 mm a year). There were 24 pots in one block (10 pots with *Pinus rotundata*, 9 pots with *P. sylvestris, 3 pots with P.* × *digenea* and 2 pots with *P. abies*). Based on the results of the first experiment, the number of *P. sylvestris* and *P. rotundata* seedlings was increased in comparison to *P. abies* to find also the differences between these two species with similar response to abiotic factors. *P.* × *digenea* was added to experiment to compare the reaction of hybrid and both parent species. Two blocks were used in each combination of factors. A total of 672 pots (7 × 2 × 24 × 2) were used.

proč tak složité?

proč?!

Seedlings were randomly thinned to one per pot (for removing competition effect) in the first growing season. Seedlings were harvested at the end of the second growing season. The height, number of lateral branches and number of buds were recorded for each seedling harvested. Each seedling was divided into roots, shoot (part above hypocotyl) and stem (hypocotyl), and oven-dried at 80°C to constant dry weight. The number of buds and the number of lateral branches were also recorded for each seedling.

Data were processed using split-plot analysis of variance (ANOVA) (Potvin 2001) and generalised linear models (GLM) (McCullagh and Nelder 1989) using the S-plus statistical software ver. 3.3 (Statistical Sciences 1995a, Statistical Sciences 1995b). Dry weights were log transformed and the number of buds and the number of lateral branches square-root transformed in split-plot ANOVA. Box and whiskers plots were used for the majority of graphical presentations.

Results

Experiment no. 1

The results of split-plot ANOVA are presented in **Table 2**. Differences in growth (total biomass, above ground biomass and the number of branches) among the studied species were highly significant. All of the studied factors (light, groundwater table and amount of nutrients) significantly affected the growth of the studied species. The effect of nutrients and water on root biomass was on the border of significance. The effects of interactions between particular factors and between particular factors and species on growth were also frequently significant (**Table 2**). The best growth of all species was found in the no shading treatment, followed by the low shade and high shade treatments. The addition of nutrients improved growth of all studied species, while all studied tree species grew best in the low water treatment.

marginally significant

and

Table 2. Results of F-tests – split-plot ANOVA (Experiment no.1). Abbreviation dw means dry weight.

Independent Variable	Dependent variable	p	
nutrients	total dw	<<0.001	***
nutrients	above ground dw	<<0.001	***
nutrients	root dw	0.058	NS
nutrients	branches	<0.001	***
light	total dw	<<0.001	***
light	above ground dw	<<0.001	***
light	root dw	<<0.001	***
light	branches	<<0.001	***
water	total dw	<<0.001	***
water	above ground dw	<<0.001	***
water	root dw	0.063	NS
water	branches	<<0.001	***
nutrients × light	total dw	<<0.001	***
nutrients × light	above ground dw	<<0.001	***
nutrients × light	root dw	0.015	*
nutrients × light	branches	<<0.001	***
nutrients × water	total dw	0.067	NS
nutrients × water	above ground dw	0.009	**
nutrients × water	root dw	0.448	NS
nutrients × water	branches	0.629	NS
light × water	total dw	<<0.001	***
light × water	above ground dw	<<0.001	***
light × water	root dw	0.143	NS
light × water	branches	<<0.001	***
nutrients × light × water	total dw	0.121	NS
nutrients × light × water	above ground dw	0.039	*
nutrients × light × water	root dw	0.451	NS
nutrients × light × water	branches	0.412	NS
species	total dw	<<0.001	***
species	above ground dw	<<0.001	***
species	root dw	<<0.001	***
species	branches	<<0.001	***
nutrients × species	total dw	<<0.001	***
nutrients × species	above ground dw	<<0.001	***
nutrients × species	root dw	<<0.001	***
nutrients × species	branches	0.017	*
light × species	total dw	<<0.001	***
light × species	above ground dw	<<0.001	***
light × species	root dw	<<0.001	***
light × species	branches	0.006	**
water × species	total dw	0.004	**
water × species	above ground dw	<<0.001	***
water × species	root dw	0.356	NS
water × species	branches	0.013	*
nutrients × light × species	total dw	<<0.001	***
nutrients × light × species	above ground dw	<<0.001	***
nutrients × light × species	root dw	<0.001	***
nutrients × light × species	branches	0.006	**
nutrients × water × species	total dw	0.293	NS
nutrients × water × species	above ground dw	0.260	NS
nutrients × water × species	root dw	0.410	NS
nutrients × water × species	branches	0.269	NS
light × water × species	total dw	0.019	*
light × water × species	above ground dw	0.001	**
light × water × species	root dw	0.521	NS
light × water × species	branches	0.047	*
nutrients × light × water × species	total dw	0.552	NS
nutrients × light × water × species	above ground dw	0.493	NS
nutrients × light × water × species	root dw	0.709	NS
nutrients × light × water × species	branches	0.602	NS

The experiment showed (**Fig. 1**) that growth and survival of *P. abies* were very poor (especially in the highest water table) in comparison to both *Pinus* species. The best growth was shown by *P. rotundata* in the no shading - low water - high nutrient treatment, followed by *P. sylvestris* and *P. abies* in the same treatment.

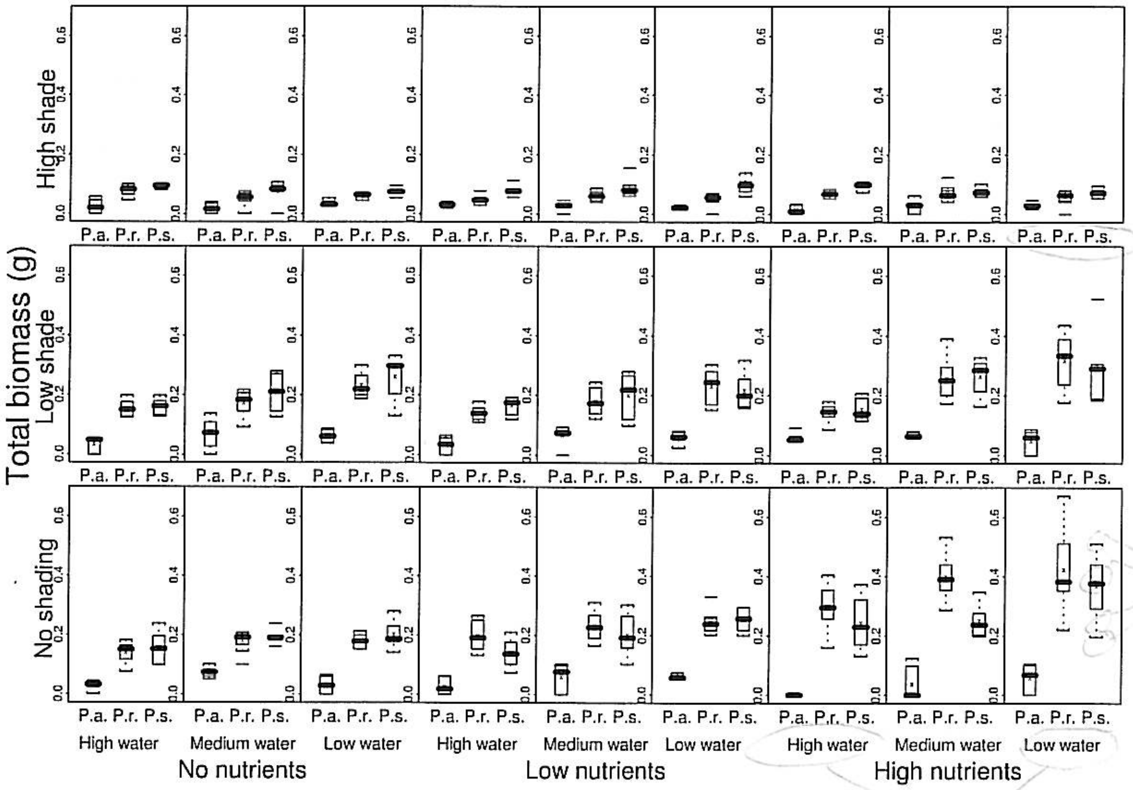

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Fig. 1. Total biomass of *Picea abies* (P.a.), *Pinus rotundata* (P.r.) and *Pinus sylvestris* (P.s.) seedlings under different combinations of light, nutrient and groundwater table levels (Experiment no. 1).

Pinus sylvestris had the highest biomass in the high shade treatment, followed by *P. rotundata* and *P. abies*. The greatest growth dynamics (the relative increase of dry weight between the middle and end of the first vegetation season) in shade was shown by *P. abies*, followed by *P. rotundata*. *P. sylvestris* had the lowest growth dynamics in most cases.

kde jsou výsledky [illegible]

Experiment no. 2

The results of split-plot ANOVA are presented in **Table 3**. Groundwater level significantly affected all growth characteristics of the studied species. The effect of factor environment (greenhouse × garden) was also significant with the exception for the number of buds and the number of lateral branches. Differences in growth (total biomass) among the studied species were also highly significant with the exception for the number of lateral branches. The effects of interactions between water and species and environment and species on growth were also significant with the exception of height and number of buds and only number of buds, respectively (**Table 3**). Total biomass was higher in the greenhouse than in the garden. A high water table suppressed growth, resulting in decreasing total biomass with higher water levels (**Fig. 2**). The same pattern was also shown by the other measured growth characteristics.

The highest biomass was found for *P. rotundata*, followed by *P.* × *digenea*, *P. sylvestris* and *P. abies* (**Fig. 2, Fig. 3**). The relative differences in the growth of the studied species showed a clear trend of decreasing towards lower water levels (**Fig. 4**). The height growth of *P. rotundata* was the best in all water levels (**Fig. 2**). However, differences between *P. rotundata* and *P. sylvestris* height growth decreased towards lower water levels, when high and low water treatments were compared (**Fig. 5**). A more detailed analysis of the low water treatment disclosed that the offspring of two *P. sylvestris* individuals showed better height growth than all offspring of *P. rotundata* individuals (**Fig. 6**).

→ likely higher!

Table 3. Results of F-tests – split-plot ANOVA (Experiment no.2). Abbreviation dw means dry weight.

Independent Variable	Dependent variable	p	
water	total dw	<<0.001	***
water	above ground dw	<<0.001	***
water	root dw	<<0.001	***
water	height	<<0.001	***
water	buds	<<0.001	***
water	branches	<<0.001	***
environment	total dw	0.007	**
environment	above ground dw	0.004	**
environment	root dw	0.008	**
environment	height	<<0.001	***
environment	buds	0.099	NS
environment	branches	0.711	NS
water × environment	total dw	0.862	NS
water × environment	above ground dw	0.600	NS
water × environment	root dw	0.723	NS
water × environment	height	0.865	NS
water × environment	buds	0.700	NS
water × environment	branches	0.952	NS
species	total dw	<<0.001	***
species	above ground dw	<<0.001	***
species	root dw	<<0.001	***
species	height	<<0.001	***
species	buds	0.012	*
species	branches	0.110	NS
water × species	total dw	0.002	**
water × species	above ground dw	0.011	*
water × species	root dw	<<0.001	***
water × species	height	0.166	NS
water × species	buds	0.093	NS
water × species	branches	<<0.001	***
environment × species	total dw	0.002	**
environment × species	above ground dw	<0.001	***
environment × species	root dw	0.002	**
environment × species	height	0.015	*
environment × species	buds	0.665	NS
environment × species	branches	<<0.001	***
water × environment × species	total dw	0.604	NS
water × environment × species	above ground dw	0.784	NS
water × environment × species	root dw	0.273	NS
water × environment × species	height	0.350	NS
water × environment × species	buds	0.333	NS
water × environment × species	branches	0.053	NS

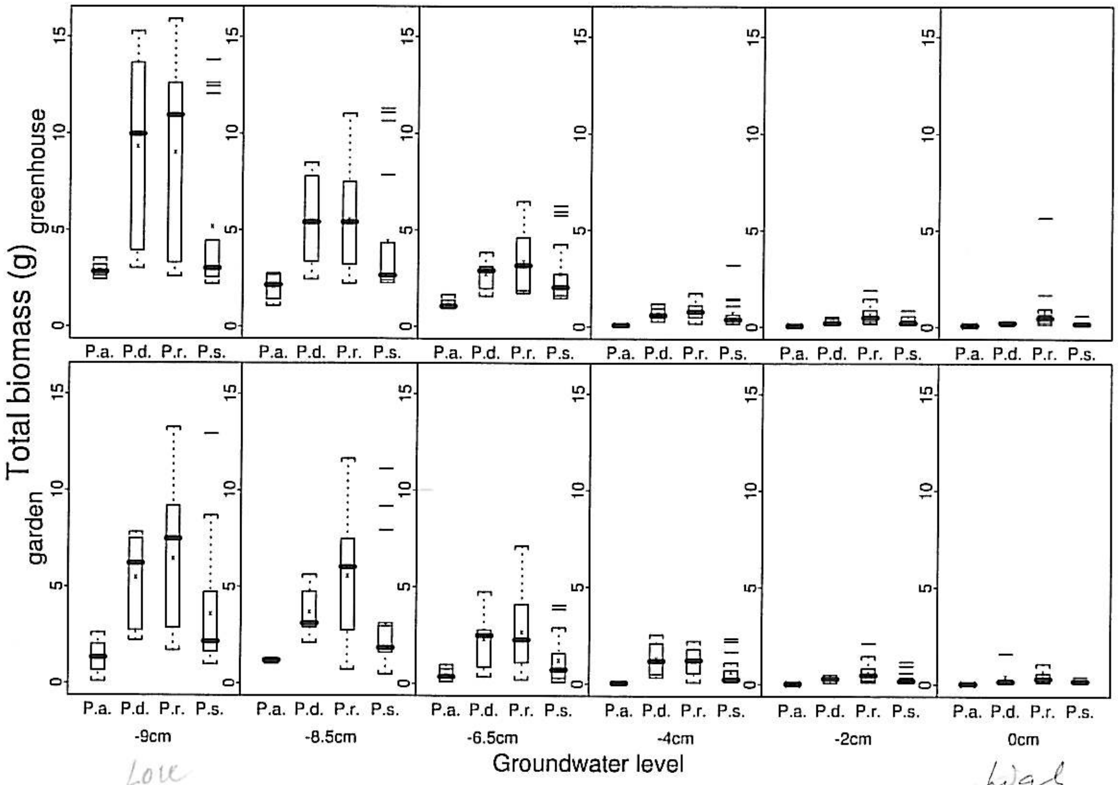

Fig. 2. Total biomass of *Picea abies* (P.a.), *Pinus* × *digenea* (P.d.), *Pinus rotundata* (P.r.) and *Pinus sylvestris* (P.s.) seedlings under different combinations of environment (greenhouse, garden) and groundwater table levels (Experiment no. 2).

Discussion

Experiments with different groundwater levels showed that, in high water conditions, *P. abies* growth was very poor, while *P. rotundata* showed relatively better growth. Thus, a high groundwater level plays a crucial role in the continuing existence of natural *P. rotundata* stands. This is in agreement with findings made by Rektoris et al. (1997), who stated that optimum hydrological conditions for *P. rotundata* community regeneration include a relatively high groundwater table with annual mean fluctuation between 20 and 30cm below the ground surface, with a possible summer decline to 50cm. Despite a higher decrease will favour also *P. rotundata* growth (Freléchoux et al. 2000a, Freléchoux et al. 2000b) in long term coexistence *P. sylvestris* will probably profit better (Rektoris et al. 1997). This was indicated by better height growth for two *P. sylvestris* individuals in the lowest water treatment although the mean total biomass of *P. sylvestris* was lower than for *P. rotundata.* It is probable that the tallest individuals will have a competitive advantage in a bog pine forest through the overshadowing of smaller trees. A continued decrease of water level will favour *P. abies.* The response of *P.* × *digenea* to groundwater was intermediate between both parent species. Too high of a water table suppresses growth of all studied tree species and creates long-term open treeless stands inside some peat bogs. The lowering of the groundwater table is caused mainly by direct drainage of a bog, draining of the surrounding area, as well as by the tree growth with associated increased transpiration (Heathwaite 1995). The effect of climate change is also probable. Increasing temperatures are connected with increased evapotranspiration which, together with possible decreased precipitation, leads to decreasing groundwater levels (Evans et al. 1999).

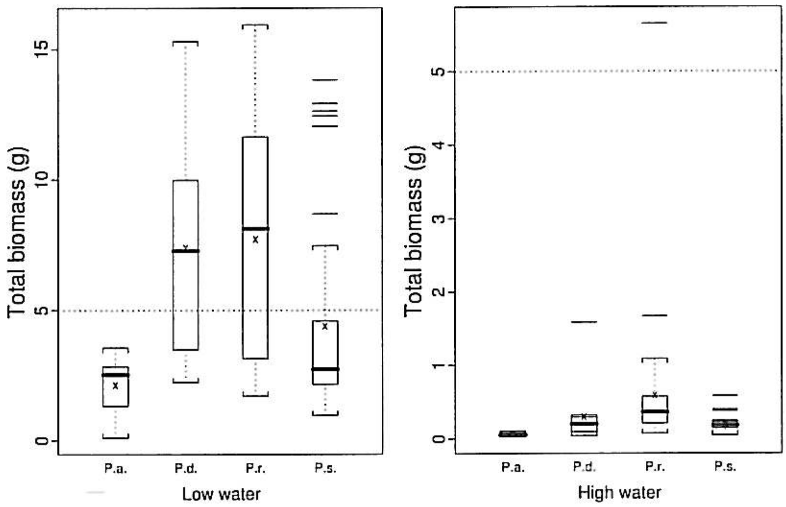

Fig. 3. Total biomass of *Picea abies* (P.a.), *Pinus* × *digenea* (P.d.), *Pinus rotundata* (P.r.) and *Pinus sylvestris* (P.s.) seedlings at low (-9cm) and high (0cm) groundwater table levels (Experiment no. 2).

P. sylvestris had the highest biomass in the high shade treatment, followed by *P. rotundata* and *P. abies*. This is in contrast with the generally accepted view of *P. abies* shade tolerance and *P. sylvestris* shade intolerance (de Chantal et al. 2003). However, *P. abies* had the greatest growth dynamics in shade, followed by *P. rotundata*, when the relative increase of dry weight between the middle and the end of the first growing season was analyzed. The low biomass of *P. abies* was probably caused by a too high water level in the experiment and partly by lower biomass of the *P. abies* seeds. *P. sylvestris* had the lowest growth dynamics in most cases. It is likely that longer experiments will suppress the effect of the initial differences in seed weight and resulting seedling biomass of particular species (especially in the high shade treatment). In the long term coexistence of these species, shade tolerant *P. abies* probably overgrows both pine species if the conditions, especially low ground water table, are favourable for *P. abies* growth. This is in agreement with Schmid et al. (1995), who stated that *P. sylvestris* and *P. rotundata* are unable to compete with shade tolerant *P. abies* over the long term in situations of lowering of groundwater

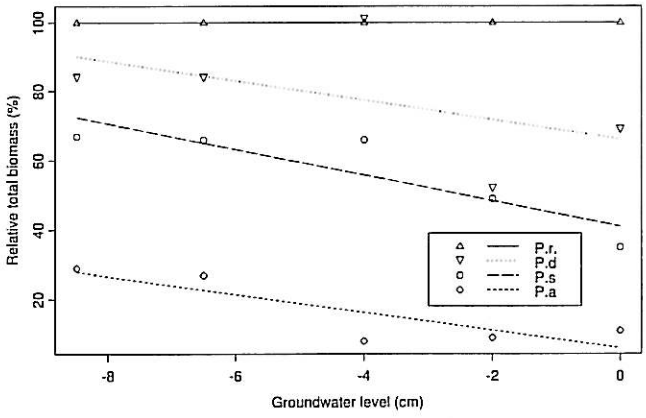

Fig. 4. Dependence of relative total biomass of *Picea abies* (P.a.), *Pinus* × *digenea* (P.d.), *Pinus rotundata* (P.r.) and *Pinus sylvestris* (P.s.) seedlings on groundwater table (Experiment no. 2). Biomass of *Pinus rotundata* in a particular groundwater level treatment = 100%.

table level, with the two former species gradually disappearing from affected peat bogs being overgrown by *P. abies*. Expansion of *P. abies* on peat bogs is also documented by Horn and Bastl (2000).

napřed diskutuj studované faktory!

Fire is another factor that could suppress fire intolerant *P. abies* and boost up relatively fire tolerant *P. sylvestris* (Pennanen 2002) and may be also *P. rotundata* are nowadays only rarely reported from Central European pine bogs (Holubičková 1960, Kučerová et al. 2008). But its role could be higher in the past (Jankovská 1980, Kuhry 1994). Seeing that *P. rotundata* has thinner rhytidome than *P. sylvestris* (personal observation) and decrease of *P. rotundata* in favour of *P. sylvestris* after fire found by Kučerová et al. (2008), the risk of possible fire injury to *P. rotundata* has to be studied before management application.

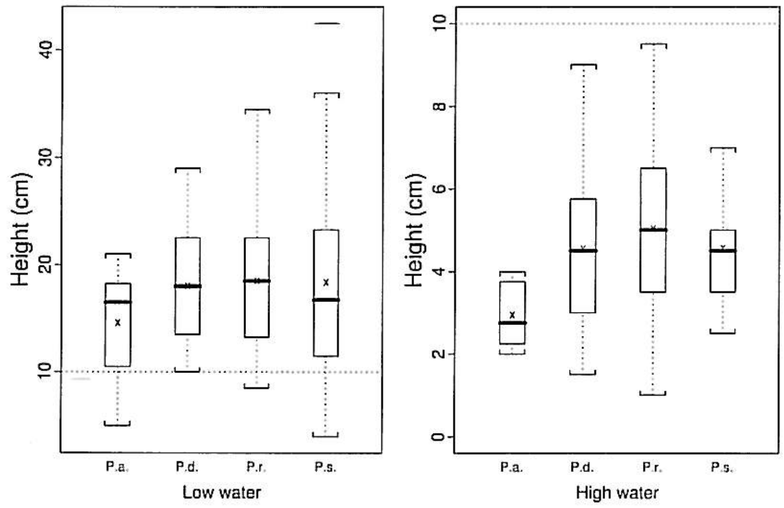

Fig. 5. Height of *Picea abies* (P.a.), *Pinus × digenea* (P.d.), *Pinus rotundata* (P.r.) and *Pinus sylvestris* (P.s.) seedlings at low (-9cm) and high (0cm) groundwater table levels (Experiment no. 2).

Added nutrients enhanced growth of all studied species, which was expected. Currently, there are two main causes of increased nutrient availability in peat bogs: drainage and atmospheric deposition. Both factors may move the balance towards denser tree cover on peat bogs, which is unfavourable for shade intolerant pine species. Schmid et al. (1995) found higher growth rates of *P. rotundata* in drained peat bogs. But they stated that *P. rotundata*, in contrast to *P. abies*, is obviously not able to profit from increased atmospheric deposition.

Another possible factor causing successive changes is increase of atmospheric CO_2 concentrations, which may also affect growth of the studied tree species. Hattenschwiler et al. (2002) found that artificially increased CO_2 concentrations resulted in higher net photosynthesis, lower stomatal conductance, and increased accumulation of nonstructural carbohydrates in *Pinus uncinata* and Larix decidua trees in the first year of treatment. Quite unexpectedly, shoot length increment increased significantly at elevated CO_2 levels (up to 23%) compared with controls in both species (Hattenschwiler et al. 2002). It is likely that elevated CO_2 concentrations will also affect *P. rotundata, P. sylvestris* and *P. abies* and other accompanying peat bog species, resulting in changes in peat bog ecosystems.

Human-induced disturbances, which lower the groundwater table, are probably the main factors leading to changes in peat bogs with bog pines (Freléchoux et al. 2000a, Freléchoux et al. 2000b). The ecotone between bog pine forest and *P. abies* stands is usually sharp in undisturbed bogs in the Jura Mountains, Switzerland, while there is no succession from pine forest to spruce forest (Freléchoux et al. 2003). Situation in disturbed peat bogs in the Jura Mountains is different. Following clear cut and drainage in a shallow and oligotrophic peat bog, *P. rotundata*, Betula pubescens, and *P. abies* established simultaneously. The birch disappeared rapidly, while the cohort of pine grew rapidly, and then declined because of competition from spruce (Freléchoux et al. 2003).

In addition, colonization of open parts of peat bogs by pines may result in the subsequent drying up of the peat, which will stress plant species of hollows and wet lawns (Freléchoux et al. 2004). *P. rotundata* dieback and its replacement by *P. abies* is probably caused also by the lowering of the groundwater table.

It is very interesting that the decline of *P. rotundata* is a problem in the Czech Republic, while the expansion of the same species is in some cases a problem in Switzerland. Both situations have in common the successive changes towards drier conditions in very similar successional seres. The only difference is whether to preserve the open peat bog or bog pine forest sere.

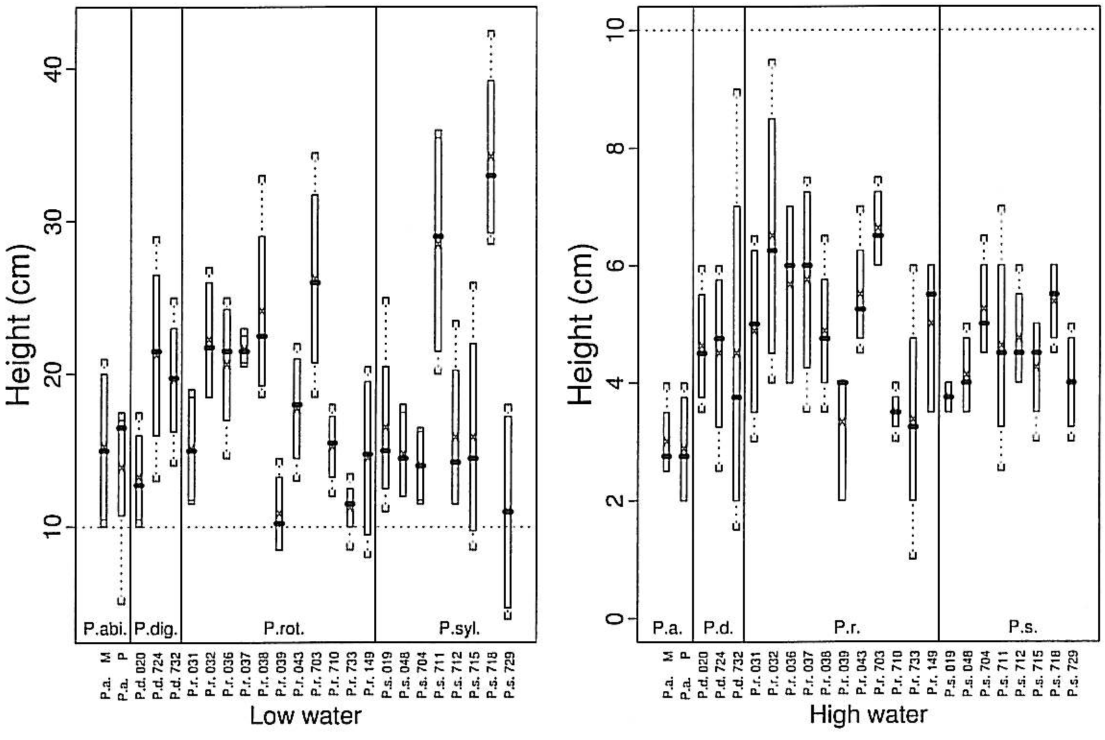

Fig. 6. Height of *Picea abies* (P.a.), *Pinus* × *digenea* (P.d.), *Pinus rotundata* (P.r.) and *Pinus sylvestris* (P.s.) seedlings at low (-9cm) and high (0cm) groundwater table levels. Species are separated into offspring of particular seed trees (indicated by letter or number after species abbreviation) to show the intraspecific variability in response (Experiment no. 2).

Based on this study, there are two possible solutions for suppressing or at least slowing down the negative changes in composition of seedling and sapling communities in *P. rotundata* dominated peat bogs:

a) In critical situations of imminent danger of collapse and disappearance of a *P. rotundata* local population, it is possible to suppress the competition from *P. abies* by selective cutting.

This would improve light conditions (Lilja et al. 2005) and partially increase the groundwater table due to reduced transpiration. On the other hand, artificial tree thinning of a stand can lead to increased windthrow susceptibility of remaining bog pine trees that are not adapted to wind (personal observation). Effect of another possible intervention, which is prescribed burning (Linder et al. 1998, Lilja et al. 2005) on *P. rotundata* populations is questionable and needs to be more studied in Central European pine bogs.

The effect of selective cutting is expected to be immediate, with the duration of positive effects being relatively shortlasting for seedlings (years) and longer for mature trees (decades).

b) In peat bogs with water regimes disturbed by drainage, it is probably the best solution to raise the groundwater table by damming the drainage ditches. Cautious raising of the groundwater table may suppress *P. abies* establishment, which is one of the main targets in the conservation of *P. rotundata* dominated peat bogs in Central Europe (Horn and Bastl 2000). Only slow raising is necessary, because of a danger of *P. rotundata* dieback due to a too high groundwater table. Freléchoux et al. (2004) found reduced growth of *P. rotundata* under wet conditions and stated that high water levels may have caused tree mortality in the centre of Les Veaux bog, Jura Mountains, Switzerland, during the last 10 years. None the less, it is better to raise the level too much than too little as the only risk to a peat bog is reverse succession to treeless patches.

The positive effect of this intervention accedes slower (years) than in solution a) and the duration of the effect is expected to be long-term (centuries).

This study was conducted over a relatively short time period (maximum 2 years) and in a controlled environment. That is why experiments in natural *P. rotundata* stands were recently established to verify the results of these garden experiments.

Conclusions

The study showed that a high groundwater table would probably favour seedlings of *P. rotundata* compared to *P. sylvestris* and *P. abies*. Therefore, a "no intervention" management plan for *P. rotundata*-dominated peat bogs appears not to be suitable for preserving this species in such habitats in which the water regime has been disturbed (mainly by drainage). Cautious rising of the groundwater table, after damming the drainage ditches, may partly suppress *P. abies* establishment and support seedling recruitment of *P. rotundata* due to lowered competition by *P. abies* and *P. sylvestris*.

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Vegetation changes following different disturbances in peat bogs with *Pinus rotundata* in the Třeboň Basin, Czech Republic

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Abstract

Various stages of plant succession were studied in peat bogs in the Třeboň Basin of the Czech Republic, after different disturbances. Two main types of disturbance occurred: (a) natural, represented by windthrow, with subsequent bark beetle attack and fire, and (b) human-made, such as peat digging and industrial peat harvesting. Species composition of successional stages after the above mentioned disturbances were compared to that of undisturbed plots. Regeneration of peat bog vegetation was faster after natural disturbances than after human-made ones. The lowest impact was caused by windthrow, followed by fire. Regeneration after peat digging was also possible, but it took much longer. Regeneration after industrial peat harvesting was possible only if the groundwater table level remained high.

Keywords: bark beetle, bog pine, cryptogams, fire, peat harvesting, regeneration, species composition, succession, vascular plants, windthrow

Nomenclature: Kučera & Váňa (2003) for bryophytes, Kubát et al. (2002) for vascular plants

Introduction

Peat bogs dominated by the bog pine *Pinus rotundata* Link. represent distinct relic habitats in the Central European landscape (Steiner 1992; Spitzer 1994; Dierssen & Dierssen 2001; Bastl et al. 2008). The bog pine itself is a remarkable taxon endemic to a part of central Europe (Jalas & Suominen 1973) with a rather limited distribution. Moreover, it is sensitive to hybridisation with *Pinus mugo* and partly *P. sylvestris*, with the later species especially under disturbed site conditions (Businský 1998; Bastl et al. 2008). Peat bogs dominated by tree-shaped *P. rotundata* typically occur at altitudes of up to ca. 800 m a.s.l.. Towards the higher altitude hybrids with *P. mugo* prevail.

bdy ?

The Třeboň Basin before it was disturbed in some localities by peat harvesting was one of the two areas with the highest concentration of peat bogs with non-hybridised *P. rotundata* (the other was the Black Forest in Germany, Dierssen & Dierssen 2001). Recent vegetation of undisturbed sites was described in the Třeboň Basin in detail by Neuhäusl (1972); the Holocene history was precisely described by Jankovská (1980).

Peat harvesting started on a large scale in the nineteenth century. However, at that time it was carried out in a traditional manner accompanied by only shallow drainage. In the second part of the twentieth century, large scale industrial peat harvesting was adopted, accompanied by deep drainage. Beside the peat harvesting, some peat bogs were occasionally disturbed by wind, being followed by bark beetle outbreaks (Kučerová et al. 2000) and recently also by fire. In contrast to the undisturbed peat bog vegetation, these disturbed sites were not systematically described. Knowledge of vegetation dynamics after disturbances could substantially contribute to potential restoration of the peat bog vegetation (Salonen 1987; Phadenhauer & Grootjans 1999; Schrautzer et al. 2007). We expected different effects of different disturbances on vegetation and subsequent courses of succession (Pickett & White 1985).

Considering the real situation of peat bogs in the studied area, we developed the following aims for our study: (a) To compare sites disturbed by different natural events, i.e., fire, wind, and a bark beetle outbreak, with undisturbed vegetation inside one locality; (b) To compare sites disturbed by the natural factors with those disturbed by humans due to peat harvesting; (c) To describe the succession following fire, which was exactly dated and observed for several years; (d) To describe the succession sere after industrial peat harvesting; and (e) To evaluate the results from the point of view of potential restoration of the natural peat bog vegetation.

Methods

Site description

The Třeboň Basin is located in the southern part of the Czech Republic, latitude 48° 49' N, longitude 14° 53' E, altitude 430 - 480 m a.s.l.. The studied peat bogs (7) are spread there in separated patches over app. 600 km^2 large area (**Fig. 1**). The mean annual temperature is about 7 °C, mean annual precipitation varies between 600 and 650 mm (Veseckẏ et al. 1958).

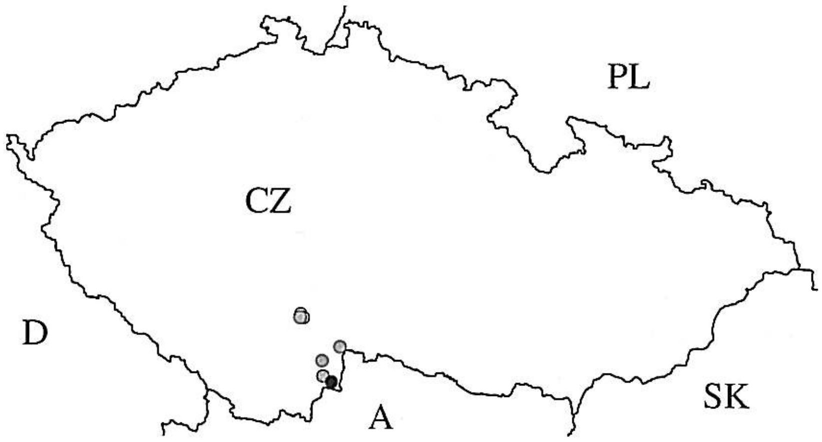

Fig. 1. – Location of the study sites in the Třeboň Basin in Czech Republic. Study site Žofinka is indicated by black symbol.

The research was focused especially on the area of the Žofinka National Nature Reserve (**Fig. 1**), where several different disturbed sites were identified. A large area of the old growth *P. rotundata* forest was damaged by wind in the first half of the Eighties, followed by a bark beetle outbreak. It must be mentioned that even this natural disturbance could be stimulated by human activities, because the area around the reserve itself was largely drained up until 1970, which probably destabilised the sensitive climax vegetation inside the reserve. Consequently, nearly all pines died due to the combined effect of the perturbations. In 1994, a fire, initiated probably by lightning, damaged an area of several hectares; a similar fire in August 2000 nearly completely destroyed further 1.5 ha of the remaining old growth. Thus, four different stages were available in the locality: two differently aged stages disturbed by fire, one disturbed by wind and the bark beetle, and an untouched section with old growth *P. rotundata*.

Man-made disturbances were represented by several other localities where peat was extracted both by the traditional (Kozohlůdky and Červené blato) and industrial way (Borkovice, Mažice, Příbraz and Branná). Type of disturbance, the age of the successional stages and the number of analysed relevés in particular localities were presented in **Table 1**.

Table 1. Localities and stages used for data collection.

Site	Latitude	Longitude	Disturbance	Successional age [years]	Respective numbers of vegetation samples
Příbraz	49°02' N	14°57' E	mining	2, 4, 10	2, 2, 4
Branná	48°57' N	14°48' E	mining	3, 6, 8	2, 2, 2
Mažice	49°13' N	14°37' E	mining	15, 20	5, 2
Borkovice	49°14' N	14°37' E	mining	25	9
Kozohlůdky	49°13' N	14°39' E	digging	50	15
Červené blato	48°52' N	14°52' E	digging	90	12
			undisturbed	200	2
Žofinka	48°49' N	14°53' E	fire	1, 2, 4, 7, 8	10, 10, 1, 10, 8
			wind	14, 18	5, 5
			undisturbed	200	9

Field sampling

Vegetation records were performed in 5 × 5 m plots, using the traditional method of phytosociological relevés based on visual estimation of cover of all species present. The adapted 7-degree Braun-Blanquet scale was used with dividing the degree 2 (van der Maarel 1979). Both vascular plants and cryptogams were recorded. 10 plots were permanently fixed in each of the two burned sites in representative (homogenous) parts and observed for two seasons. Thus, we obtained data for the 1st, 2nd, 7th and 8th year of succession in the burned sites (Jakšičová 2003). Five relevés of the same size were taken in the sites disturbed by wind and the bark beetle, and 5 in the untouched part of the Žofinka National Nature Reserve (Jakšičová 2003). Five relevés ($400m^2$) taken in sites disturbed by wind and one relevé ($400m^2$) made in the older burned site by A. Kučerová in 1998 (Kučerová et al. 2000), i.e. in the 4th year since the fire, were also included. We additionally used 4 relevés ($500m^2$) recorded in the locality in 1971 by S. Kučera, before the disturbances occurred (Kučerová et al. 2000).

For peat bogs damaged by peat harvesting we used vegetation records (68 in total) previously made by M. Bastl (Bastl 1994). The size of these samples was also 5 × 5 m. The age since the disturbance was estimated using official records from the mining companies, by interviewing local people and by ring analyses of trees present. In this case, only higher plants and mosses *Sphagnum* spec. div. were considered.

Data elaboration

The data were processed by ordination methods of Principal Component Analysis (PCA) based on the model of linear species response to the underlying environmental gradient or Detrended Correspondence Analysis (DCA) based on the model of unimodal species response to the underlying environmental gradient. PCA was used if the length of the longest gradient in trial DCA was less than 3 SD units (Lepš & Šmilauer 2003). DCA was used if the length of the longest gradient in trial DCA was more than 4 SD units (Lepš & Šmilauer 2003). No analysis has the longest gradient between 3 and 4 SD units. PCA was used for data from site disturbed by fire and windthrow and DCA for data from sites disturbed by peat extraction as well as for analysis of all studied sites together. All species occurring in tree (E_3) or shrub (E_2) layers, which strongly affected the results, were excluded from analysis of all studied sites together.

For data from burned plots, for which the quantitative explanatory variable (time since disturbance) was available, we used the constrained ordination method Redundancy Analysis (RDA) considering a linear response of species to an environmental gradient (Lepš & Šmilauer 2003). For data from the plots after industrial peat harvesting, for which the quantitative explanatory variables, i.e. time since disturbance, and groundwater table level, were available, we used the constrained ordination method Canonical Correspondence Analysis (CCA) considering a unimodal response of species to an environmental gradient (Lepš & Šmilauer 2003). Species of tree layer (E_3), which strongly affected the results, were excluded from both above mentioned constrained analyses to focus on changes in shrub (E_2), herb (E_1) and moss (E_0) layers.

The statistical significance of the environmental variables was tested by the Monte-Carlo permutation test (MCPT), including the split-plot design model to exclude the effect of subsequent sampling of the same plots. All analyses were performed using the program package CANOCO for Windows version 4.5 (ter Braak & Šmilauer 2002).

Results

The results of the ordination (PCA) of all relevés from different disturbed sites in the Žofinka NNR were shown in **Fig. 2.** The first ordination axis explained 30.7% and first two ordination axes explained 45.4% of the variability in vegetation data. The samples from the burned plots formed a clear sequence in the ordination diagram corresponding to their successional age. The older samples became close to those disturbed by wind and the bark beetle and the latter do not differ too much from the undisturbed plots.

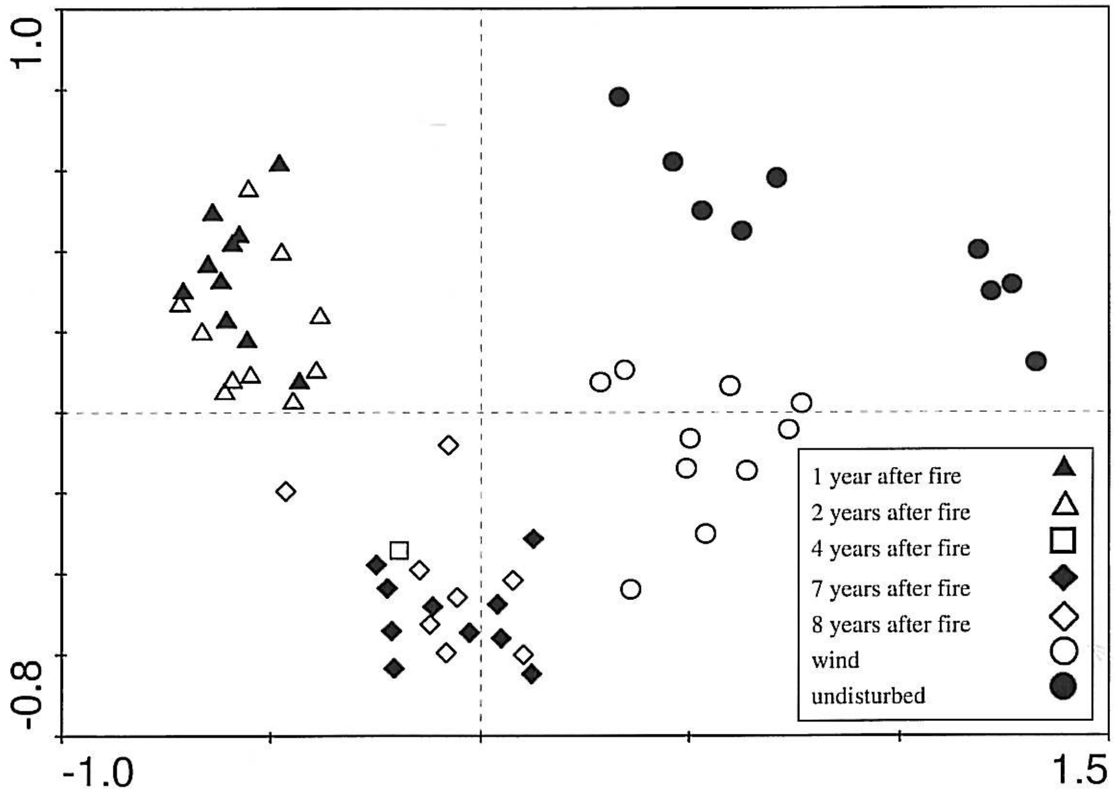

Fig. 2. – Unconstrained ordination (PCA) of samples from sites disturbed by different events and undisturbed one in the Žofinka National Nature Reserve.

The results of the ordination (DCA) of all relevés from sites disturbed by peat extraction were presented in **Fig. 3** with groundwater table as a passive variable**.** The first ordination axis explained 11.1% and first two ordination axes explained 18.4% of the variability in vegetation data. The samples from the plots affected by peat harvesting formed a clear sequence in the ordination diagram corresponding to their successional age, from industrially harvested plots (left side) to plots disturbed by peat digging (right side). Plots with higher groundwater tables were placed in the upper side and the plots with lower groundwater tables in the bottom. The oldest samples from industrially harvested sites (i.e., 25 and 20 years) were closer, in the case of relatively high groundwater table, to those from the sites traditionally harvested. The successional trend even in these, heavily disturbed sites, seems to run in the direction of restoring more natural vegetation.

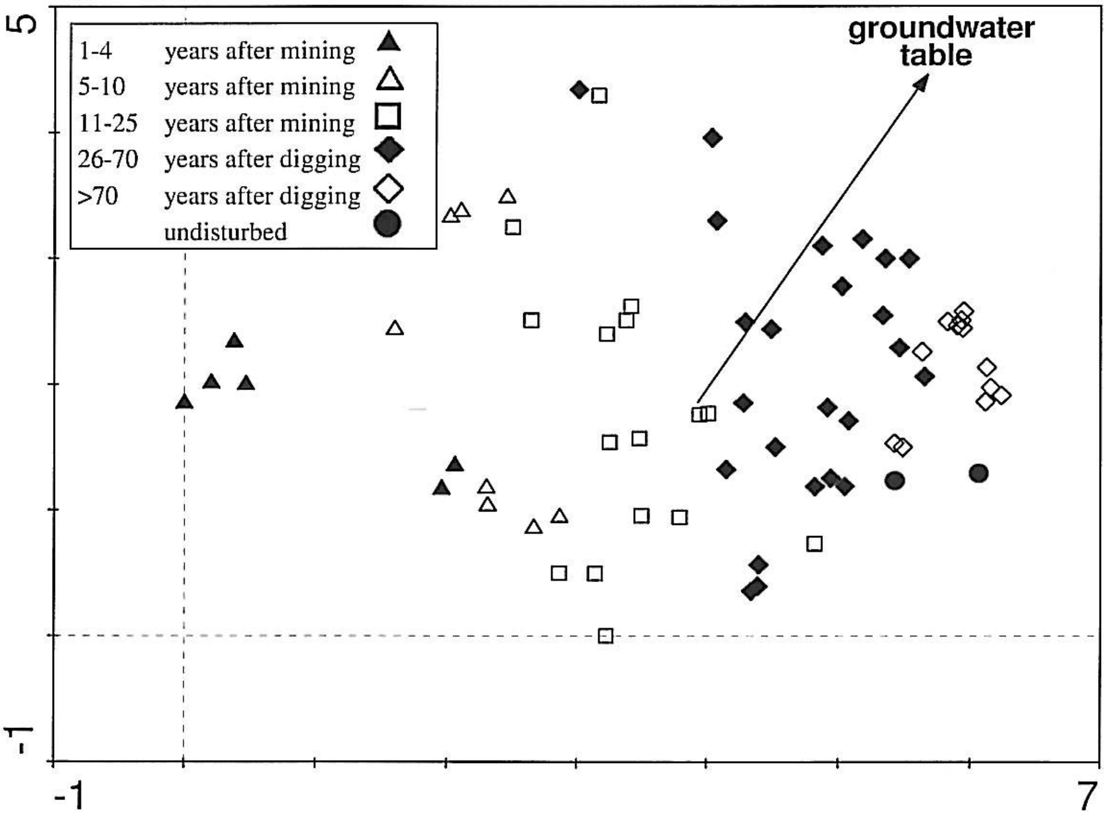

Fig. 3. – Unconstrained ordination (DCA) of samples from sites disturbed by peat extraction and undisturbed in the Branná, Borkovice, Červené blato, Kozohlůdky, Mažice and Příbraz peat bogs with groundwater table projected as the passive variable.

The DCA ordination of all relevés from all analysed plots and peat bogs was presented in **Fig. 4**, with plotted passive variables representing the type of disturbance. The first ordination axis explained 11.2% and first two ordination axes explained 18% of the variability in vegetation data. The centroid of samples from industrially harvested bogs appeared rather far from the centroid of undisturbed plots. All centroids of the sites disturbed by natural forces appeared very close to centroid of undisturbed vegetation. Species typical for particular types of disturbance were e.g. *Rumex acetosella*, *Calamagrostis epigejos*, *Agrostis canina*, *Juncus effusus* for mined sites, *Oxycoccus palustris*, *Carex nigra* for sites affected by digging, *Epilobium* sp., *Calluna vulgaris* for burned sites and *Ledum palustre*, *Vaccinium uliginosum* for sites affected by windthrow and undisturbed ones.

Detailed views into the particular successional seres for which we have sufficient data, i.e. the sere after burning and the sere after industrial peat harvesting, are presented in **Fig. 5** and **Fig. 6**.

In the case of the post-fire succession, species in the diagram of direct ordination (RDA) clearly demonstrate their relationships to the time since burning (**Fig. 5**). The first ordination axis explains 30.4% and first two ordination axes explains 41.2% of the variability in the vegetation data. The effect of the first canonical axis is highly significant (MCPT, 999 permutations, F=16.139, p=0.001). In the initial stages of succession, i.e. in the opposite directions to the vector of successional age, there are species such as *Conyza canadensis*, *Sonchus* spec. div., *Senecio* spec. div., *Taraxacum* spec. div., *Epilobium* spec. div., *Salix* spec. div. and *Populus tremula*, all the species typically colonizing only initial stages of succession. They are accompanied by cryptogams of similar strategy: *Funaria hygrometrica* (typical for burned sites), *Ceratodon purpureus*, *Pohlia nutans*, and *Marchantia polymorpha.*

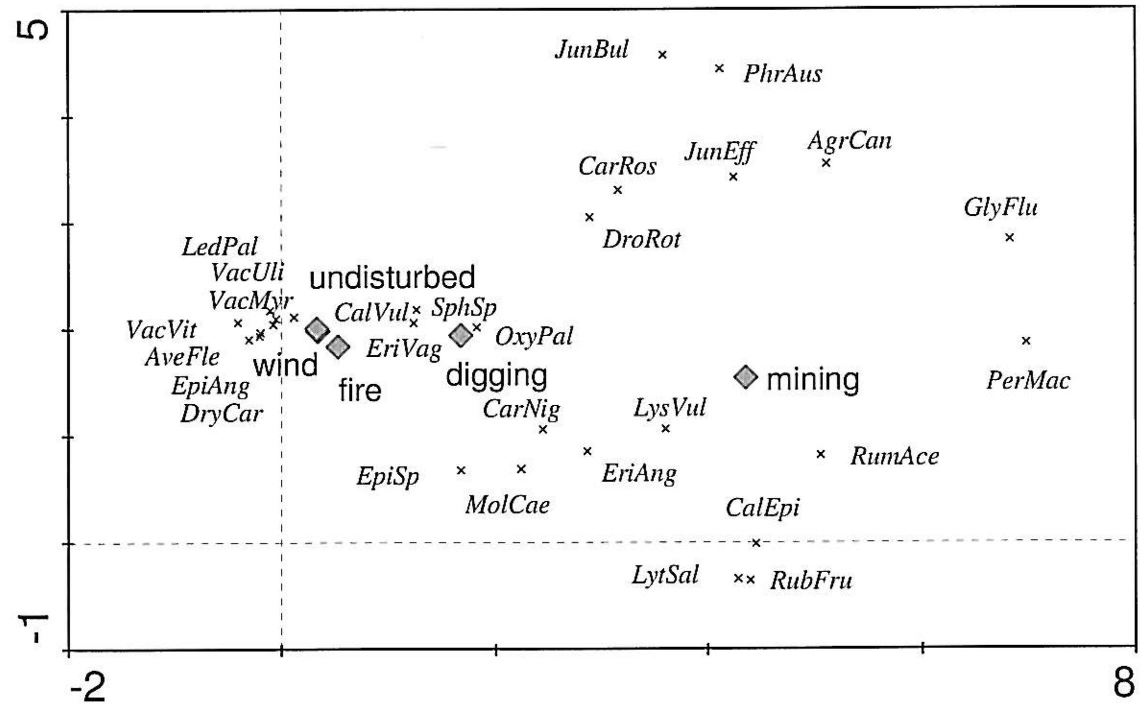

Fig. 4. – Unconstrained ordination (DCA) of samples from all studied peat bogs in the Třeboň Basin with projected centroids for types of disturbance which where used as passive variables. Scores of the samples on the axis 1 approximately reflect a relative measure of intensity of disturbance.
AgrCan (Agrostis canina) , (AveFle) Avenella flexuosa, CalEpi (Calamagrostis epigejos), CalVul (Calluna vulgaris), CarNig (Carex nigra), CarRos (Carex rostrata), DroRot (Drosera rotundifolia),), DryCar (Dryopteris carthusiana), EpiAng(Epilobium angustifolium), EpiSp (Epilobium sp.), EriAng (Eriophorum angustifolium), EriVag (Eriophorum vaginatum), GlyFlu (Glyceria fluitans), JunBul (Juncus bulbosus), JunEff (Juncus effusus), LedPal (Ledum palustre), LysVul (Lysimachia vulgaris), LytSal (Lythrum salicaria), MolCae (Molinia caerulea), OxyPal (Oxycoccus palustris), PerMac (Persicaria maculosa), PhrAus (Phragmites australis), RubFru (Rubus fruticosus agg.), RumAce (Rumex acetosella), SphSp (Sphagnum sp.div.), VacMyr (Vaccinium myrtillus),), VacUli (Vaccinium uliginosum), VacVit (Vaccinium vitis-idaea)

However, during eight years of observation the species substantially decreased in their occurrence or completely disappeared. Instead, species typical for peatland either regenerated from underground organs and then spread or newly established from seeds (*Ledum palustre, Calluna vulgaris, Vaccinium myrtillus*). New individuals of *Pinus* sp. div. (*P. rotundata, P. sylvestris* and the hybrid *P.* × *digenea*), *Picea abies* and *Betula* spec. div. (*B. pubescens* and *B. carpatica*) established from seeds. A group of typical peatland species, which regenerated immediately after the disturbance exhibited neither positive nor negative correlations with successional age (*Vaccinium uliginosum*, *Andromeda polifolia*, *Sphagnum magellanicum*). The following cryptogams, typical for the natural peat bog forests, expanded fast: *Sphagnum capillifolium*, *S. flexuosum* and *S. fallax*, or *Pleurozium schreberi* in drier sites. *Polytrichum commune* and *P. strictum* established largely immediately after burning. Since they were typical even for the natural forests they do not exhibit any trend during the observed period. The only species which seemed to be typical for all the burned plots disregarding age, was *Molinia caerulea*, which was also present but with a much lower dominance in the untouched vegetation. It continuously increased over time.

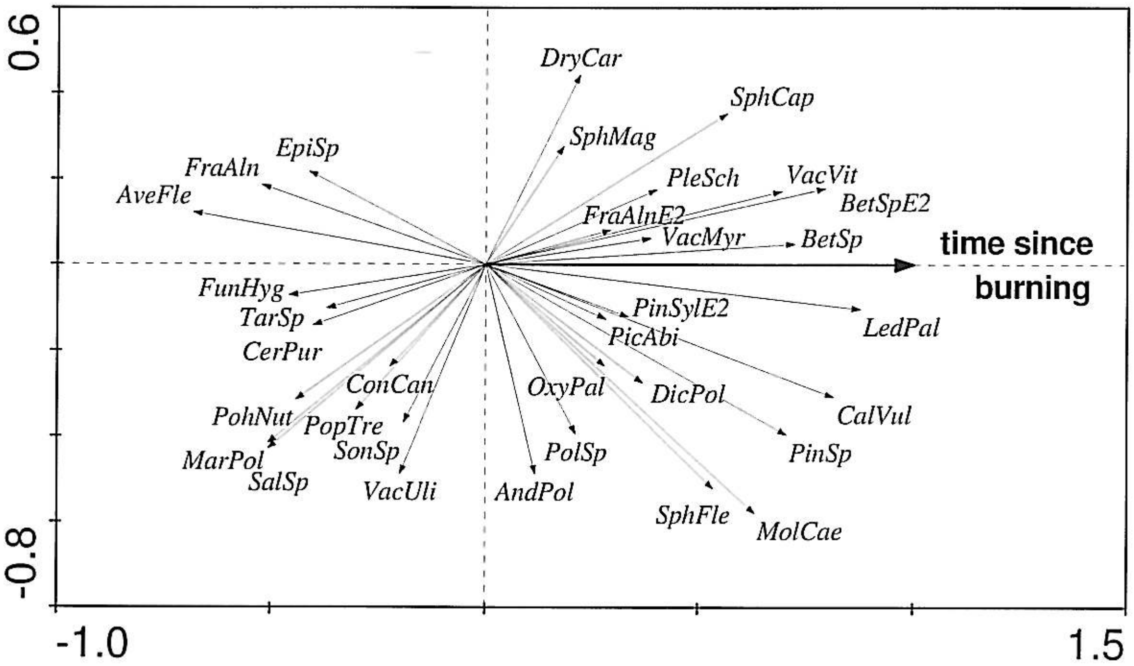

Fig. 5. Constrained ordination (RDA) of species from burned plots in the Žofinka National Nature Reserve. Time since burning (1 – 8 years) was used as the only measured explanatory variable.
AndPol (Andromeda polifolia), AveFle (Avenella flexuosa), BetSp (Betula sp.), BetSpE2 (Betula sp. E_2), CalVul (Calluna vulgaris), CerPur (Ceratodon purpureus), ConCan (Conyza canadensis), DicPol (Dicranum polysetum), DryCar (Dryopteris carthusiana), EpiSp (Epilobium sp.), FraAln (Frangula alnus), FraAlnE2 (Frangula alnus E_2), FunHyg (Funaria hygrometrica), LedPal (Ledum palustre), MarPol (Marchantia polymorpha), MolCae (Molinia caerulea), OxyPal (Oxycoccus palustris), PicAbi (Picea abies), PinSp (Pinus sp.), PinSylE2 (Pinus sylvestris E2), PleSch (Pleurozium schreberi), PohNut (Pohlia nutans), PolSp (Polytrichum sp.), PopTre (Populus tremula), SalSp (Salix sp.), SonSp (Sonchus sp.), SphCap (Sphagnum capillifolium), SphFle (Sphagnum flexuosum), SphMag (Sphagnum magelanicum), TarSp (Taraxacum sp.), VacMyr (Vaccinium myrtillus), VacUli (Vaccinium uliginosum), VacVit (Vaccinium vitis-idaea)

In the case of succession after industrial peat harvesting, the species in the diagram of direct ordination (CCA) clearly demonstrated their relationships to the time since the disturbance and to the groundwater table (**Fig. 6**). The first ordination axis explained 10.7% and the first two ordination axes explained 19.5% of the variability in the vegetation data. The effect of the first canonical axis and both canonical axes together was highly significant (MCPT, 999 permutations, F=3.225, p=0.001 and F=3.264, p=0.001 respectively). Species typical of a wet sere appeared in the upper part of the diagram, while those typical for a dry sere in the lower part. In the initial stages of succession, there were species (listed from high to low groundwater levels) such as *Carex canescens*, *Glyceria fluitans*, *Persicaria* spec. div.,

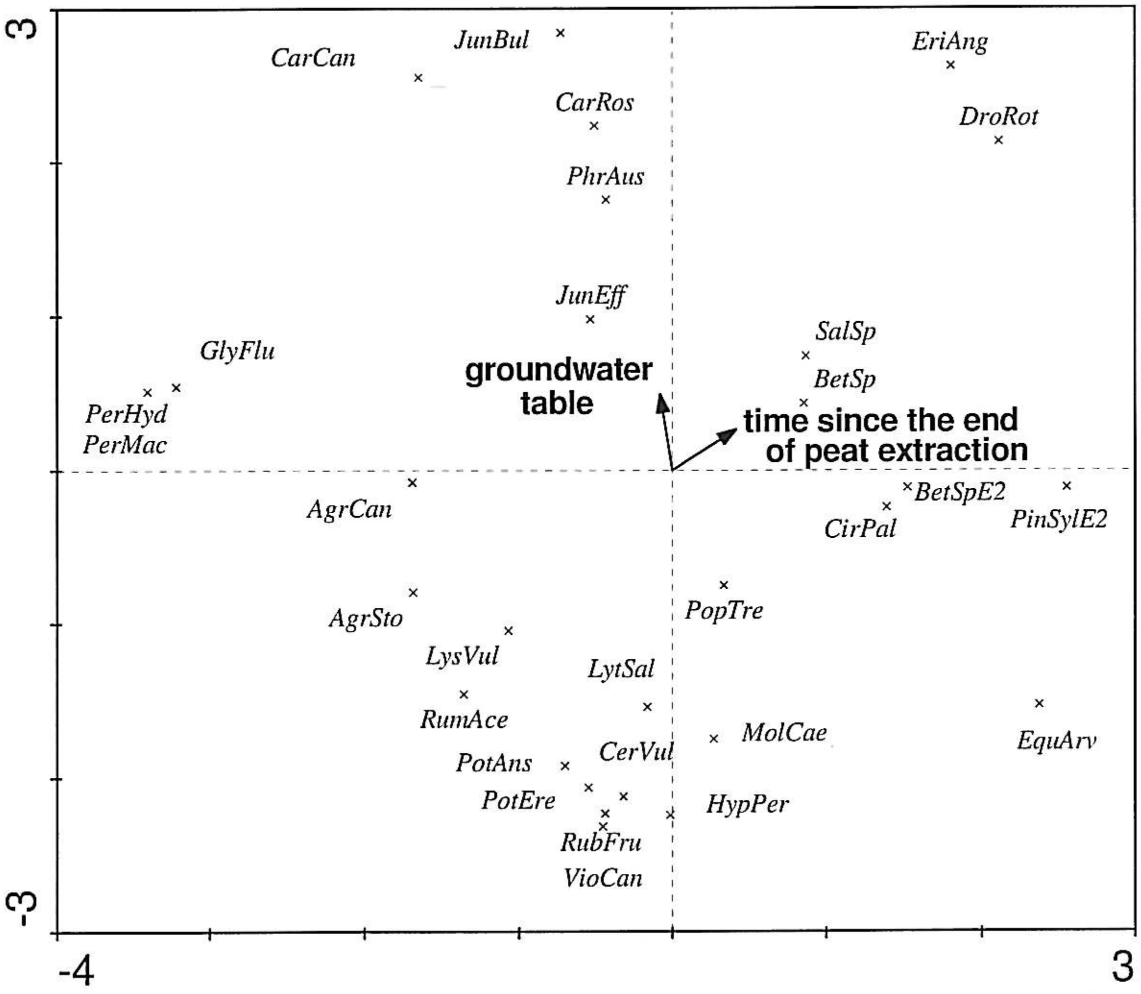

Fig. 6. Constrained ordination (CCA) of species from plots disturbed by industrial peat harvesting in Branná, Borkovice, Mažice and Přîbraz peat bogs. Time since the end of peat extraction (2 – 25 years) and groundwater table level (-10 – -110cm) were used as measured explanatory variables.
AgrCan (Agrostis canina), AgrSto (Agrostis stolonifera), BetSp (Betula sp.), BetSpE2 (Betula sp. E_2), CarCan (Carex canescens), CarRos (Carex rostrata), CerVul (Cerastium vulgatum), CirPal (Cisrsium palustre), DroRot (Drosera rotundifolia), EquArv (Equisetum arvense), EriAng (Eriophorum angustifolium), GlyFlu (Glyceria fluitans), HypPer (Hypericum perforatum), JunBul (Juncus bulbosus), JunEff (Juncus effusus), LysVul (Lysimachia vulgaris), LytSal (Lythrum salicaria), MolCae (Molinia caerulea), PerHyd (Persicaria hydropiper), PerMac (Persicaria maculosa), PhrAus (Phragmites australis), PinSyE2l (Pinus sylvestrisbE_2), PopTre (Populus tremula), PotAns (Potentilla anserina), PotEre (Potentilla erecta), RubFru (Rubus fruticosus agg.), RumAce (Rumex acetosella), SalSp (Salix sp.), VioCan (Viola canina)

Agrostis spec. div., *Rumex acetosella*, *Potentilla* spec. div., *Rubus fruticosus agg.*, *Viola canina*. In the middle successional stages about 10 to 15 years old, we found *Carex rostrata*, *Phragmites australis*, *Juncus effusus*, *Molinia caerulea*. First established fast growing trees started to dominate (*Salix* spec. div., *Betula* spec. div., *Populus tremula*). In the oldest recorded stages (25 years) we found *Eriophorum angustifolium* and *Drosera rotundifolia* in wet sere and *Pinus sylvestris* and *Equisetum arvense* in dry sere.

Discussion

The presented results clearly demonstrate that the impact of natural disturbances, i.e. fire, wind and herbivorous insect outbreaks, on peat bog vegetation is only temporary and not very severe in comparison to anthropogenic disturbances. Regeneration of the typical bog pine community is rather fast even after an apparently severe disturbance such as a nearly complete burning.

In the burned plots, the ruderal species, which typically colonize newly disturbed substrata (see Grime et al. 1988), were rather numerous; however, the species did not achieve high dominance and disappeared during the first several years. The low importance of the species was probably caused by the fact that the disturbed sites were comparably small and surrounded by natural and semi-natural vegetation. Thus the diaspores of easily dispersed ruderal species had a smaller chance to be transported to the sites (Strykstra at al. 2002).

Quite the opposite situation was observed in the case of large-scale burning of pine (*P. sylvestris*) plantations in the Záhoří lowland in western Slovakia, which was in more or less the same climatic region. There, ruderal species totally dominated during the first six years of succession for which it was studied (K. Prach, unpublished). A similarly high importance of ruderal species in initial and early stages of post-fire succession was reported also from other geographical areas. It must be emphasised that in the zone of temperate deciduous forests fires were always only rare events and confined to only very limited local spots. Thus species did not adapt to them as much as in the boreal zone (Archibold 1989). The fast spread of species from the *Ericaceae* and *Vacciniaceae* families, either based on vegetative regeneration (resprouting) from underground organs or from seeds has been reported from a burned heathland (Sedláková & Chytrý 1999). The trend observed in the case of vascular plants has been followed also by cryptogams. The set of species typical for initial post-fire succession has been followed quite fast by species typical for natural peat bog forests.

Succession after peat harvesting evidently depended substantially on the water table. In the case of the traditional peat extraction, the water table did not drop down too much and peat was often extracted just up to the water table (Dohnal et al. 1965). Thus, a regeneration of peat-forming process was possible (see also Dierssen & Dierssen 2001, Lindsay 1995, Sliva 1997, Salonen 1990). As evident from the oldest plots (ca. 90 years), the species composition was very similar to undisturbed plots with only different quantitative cover values. A weak point, which limited further generalization in the case of this sere, was the fact that no young successional stages existed after traditional peat extraction, because this kind of harvesting was not practiced in the area for more than 50 years. On the other hand, no really old stages were available after industrial harvesting, which was more recent.

The succession following industrial peat harvesting does not run towards a re-establishment of peatland vegetation unless the water table is artificially increased (Lindsay 1995, Rochefort & Campeau 1997, Sliva et al. 1997, Brooks & Stoneman 1997, etc.). Assisted restoration of water regime after the large-scale harvesting has started in the studied area recently. Based on initial data available from such an attempt in the nearby Šumava Mts., some regeneration is possible (P. Horn and M. Bastl, unpublished). If the water table remains low, the succession runs towards a pine-birch woodland, however without the participation of bog pine (*Pinus rotundata*) but common Scots pine (*P. sylvestris*) (Bastl 1994, Prach & Pyšek 2001, Konvalinková 2006).

Despite that, a general successional trend among the industrially harvested plots seems to follow the direction of re-establishment of peatland vegetation if the water table level remains relatively high **(Fig. 4)**. In deeply drained sites any typical peat land vegetation never establishes. Besides the water table, the thickness and character of the remaining peat layer can also influence the course of succession (Salonen 1990; Rochefort & Campeau 1997). However, we do not have sufficiently detailed data to evaluate this phenomenon.

The impacts of all the natural disturbances on vegetation, i.e., fire, wind and the bark beetle outbreak, seem to be negligible in comparison to peat harvesting, as the samples appeared nearly in the same position as the undisturbed plots in **Fig. 4**. The sample score on the axis 1 in the figure can be considered as a relative measure of the severity of disturbance.

Finally, this research offers some implications for nature conservancy and restoration ecology regarding the studied varieties of peat bogs. If a disturbed site is not large, the water table remains untouched, and the original vegetation remains around, regeneration is rather fast. Ruderal species do not achieve a high importance and are followed soon by species typical for natural peatland vegetation. In the case of sites where peat was industrially harvested, we strongly recommend artificially increasing the water table up to the surface. This can induce a new peat-forming process and the re-establishment of typical peatland plant life, especially if at least some remnants of untouched peatlands are present in the surroundings (Neuhäusl 1992, Konvalinková 2006). To speed up the processes, some transplantation of constituent vegetation, both higher plants and cryptogams, may be helpful (Sliva 1997). We believe that such restoration projects will be considered soon, especially in the Protected Landscape Area and the Biosphere Reserve of the Třeboň Basin.

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Central European pine bogs changing along an altitudinal gradient

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Abstract

Vegetation analyses (phytosociological relevés) were performed in 20 peat bogs arranged along an altitudinal gradient in the southern part of the Czech Republic, Central Europe, to find relationships between vegetation and environmental gradients. Six of the peat bogs were investigated in detail. The bogs are dominated by *Pinus rotundata*, a species endemic to central Europe, and its hybridogenic populations with *P. mugo* (the hybrid is called *P.* × *pseudopumilio*), with increasing proportions of the latter towards higher altitudes. Data were processed by the methods of indirect (DCA) and direct (CCA) gradient analyses. Environmental variables (depth to the water table, mean and minimum temperatures, precipitation, pH, conductivity, NH_4 and PO_4 concentrations, total P, but not total N nor NO_3 concentration), as well as biotic characteristics of the sites, such as species composition, and growth form of the dominant pines, were closely correlated with the altitudinal gradient. Woody species, herbs and bryophytes, responded clearly to the altitudinal gradient and the trends were in principal the same. Results also indicate the uniqueness of each particular bog.

Keywords: *Pinus rotundata*, *P. uncinata*, mountain pine, *P. mugo*, *P.* × *pseudopumilio*, growth form, altitude, environmental gradients

Nomenclature: Kubát et al. (2002) for vascular plants and Kučera & Váňa (2003) for bryophytes.

Introduction

Central European ombrotrophic bogs and poor fens with bog pines are unique ecosystems, having persisted continuously in the same sites and approximately at the same extent since the early Holocene (Neuhäusl 1972, Jankovská 1980, Mikkola & Spitzer 1983, Steiner 1992, Svobodová et al. 2002). Continuity and stability at these timescales is unique among Central European ecosystems. Pine bogs can be considered as long existing habitat islands (Spitzer 1994), offering opportunities for micro-speciation and relictness, but being vulnerable to external disturbances. Their extrazonal character, occurring outside the main zone of peatlands in north and north-east Europe, makes the Central European peat bogs of interest in a wide biogeographical context (Dierssen 1996, Dierssen & Dierssen 2001).

A high similarity of environmental conditions among such bogs, especially with respect to water regime, low amounts of available nutrients, and low pH, facilitates comparison of vegetation among particular localities. The rather harsh environment restricts the number of biota in pine bogs. Consequently, factors responsible for biotic structure are easier to elucidate than in most other ecosystems (Økland 1992). The strong relations of the vegetation to environmental gradients, especially depth to the water-table and peat-nutrient concentrations, have been described from boreal peatlands (Malmer 1962, Damman 1986, Økland 1990, Jeglum & He 1995, Nordbakken 1996, etc.), from bogs in the southern Alps (Gerdol 1995, Bragazza & Gerdol 1999), and from some Central European bogs and peat fens (Neuhäusl 1972, Dierssen & Dierssen 1984, Navrátilová & Navrátil 2005, Grootjans et al. 2006, Hájek et al. 2006, Navrátilová et al. 2006). However, no detailed study has investigated changes in the environmental gradients and vegetation along the altitude in the central European pine bogs.

The Central European pine bogs possess an endemic species, *Pinus rotundata* Link., and its hybridogenic cline with *P. mugo* Turra (for taxonomical remarks see below). *Pinus rotundata* occurs in a small geographical range which includes parts of Germany, Austria, Poland and the Czech Republic (Jalas & Suominen 1973) with the centre of distribution in the southwestern part of the Czech Republic (**Fig. 1**). The typical tree-shaped *P. rotundata* occurs in submontaneous bogs only. Towards higher altitudes, it forms introgressive hybrids with *P. mugo* and the shape changes to shrub-like (Skalický 1988, Businský 1998).

Previous studies of Central European pine bogs have concentrated on one particular locality (Neuhäusl 1975, Münzbergová et al. 1999, Kučerová et al. 2008), a particular taxon, or special topics such as palynology (Jankovská 1980) or vegetation classification (Neuhäusl 1972). Only pine bog *Lepidoptera* (Spitzer 1994, Spitzer et al. 1999) have been studied in a broader geographical context.

The aims of this study were to describe, and as far as possible explain, the gradients in vegetation in relation to environmental factors. The following questions were especially addressed:

(a) How does vegetation pattern change along the altitudinal gradient?

(b) How are particular environmental factors related to altitude? to the mire?

(c) Do the particular vegetation layers respond to the environmental gradients in the same way?

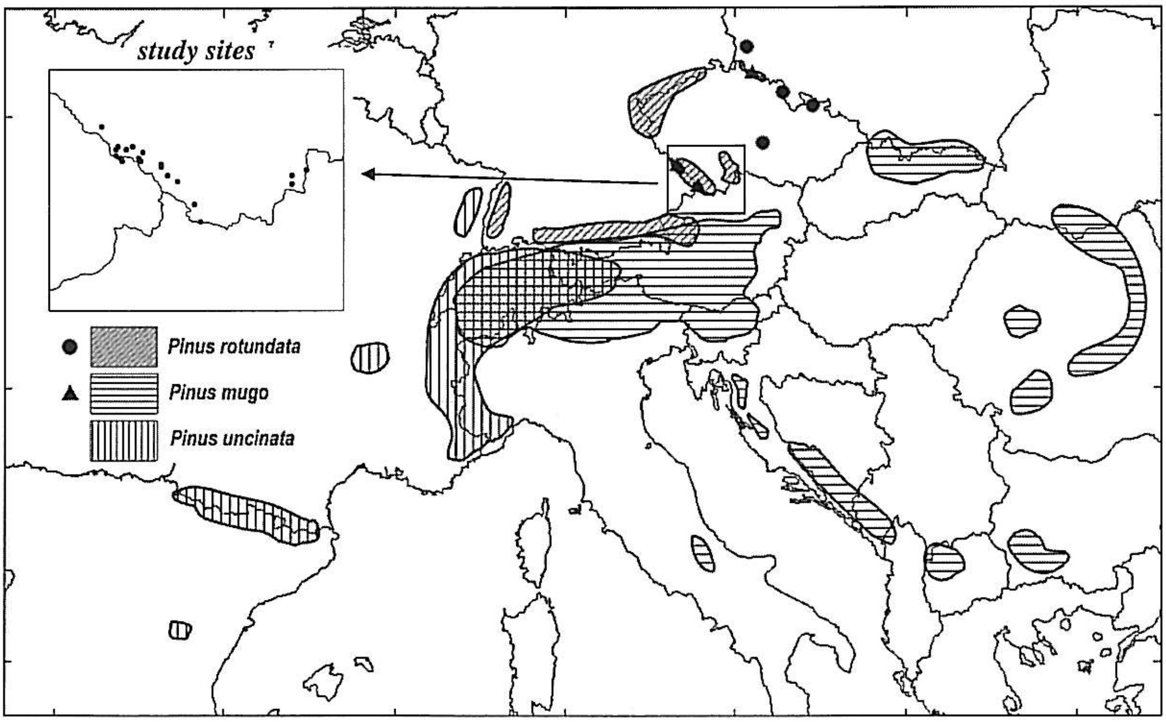

Fig. 1. Geographical range of *Pinus rotundata*, *P. uncinata*, and *P. mugo* with the location of the study sites. Adapted from Jalas and Suominen (1973).

Material and methods

Taxonomical and phytogeographical remarks on bog pines

There are several rather contradictory taxonomical views on bog pines. One, in our opinion an extreme approach, is to include all taxa into *Pinus mugo* Turra (Zoller 1981, Christensen 1987). Other approach is to accept *P. uncinata* Ramond in Lam. et DC., with two taxa: *P. uncinata* s.s. and *P. rotundata* Link at the subspecific level (Gaussen et al. 1993). *P. rotundata* is also often considered to be a polymorphous hybridogenous type between *P. mugo* and *P. uncinata* (e.g. Wisskirchen & Haeupler 1998, Fischer et al. 2005). Because of the relatively clear morphological, geographical, and ecological differentiation of the taxa, we have chosen to treat them as three separate species, i.e. *P. mugo, P. uncinata*, and *P. rotundata* (Skalický 1988, Businský 1998).

P. mugo is a typical shrubby species of the subalpine belt in central and southeastern Europe, rarely occurring at lower altitudes. *P. uncinata* is a tree-shaped species occurring mostly on mineral sites in western European mountains. *P. rotundata* is a tree-shaped species endemic to central European submontane peat bogs (**Fig. 1**). In our area, where *P. rotundata* grows with *P. mugo*, they have hybridized to form a hybridogenic cline with the shrubby growth form increasing in proportion with altitude. The hybrids are sometimes called *P.* × *pseudopumilio* (Willk.) Beck. Moreover, *P. rotundata* hybridizes with *P. sylvestris* L. (*P.* × *digenea* Beck) especially at the margins and disturbed sites of bogs (Skalický 1988).

Study sites

Twenty peat bogs were selected *a priori* for our study, based on the following criteria: a minimum area of 0.1 km^2, without evident human disturbances, with the aim to cover the whole altitudinal range of pine bogs in the studied area. The number of selected peat bogs resulted from administrative restrictions, accessibility, and undisturbed character of these strictly protected areas. The locations of the study sites are shown in **Fig. 1**; geographical coordinates, altitude, mean annual temperature and mean annual precipitation are listed in **Table 1**. We choose South Bohemian location because it is the centre of *P. rotundata* and *P. pseudopumilio* distribution range with the largest number of localities.

Table 1. Location, altitude, mean annual temperature and mean annual precipitation of the twenty peat bogs arranged according to increasing altitude. Six peat bogs studied in detail are indicated in bold. For details see the text.

Site	Site number	Latitude	Longitude	Altitude (m a.s.l.)	Mean annual temperature (°C)	Mean annual precipitation (mm)
Červené blato	**1**	**48°52' N**	**14°52' E**	**470**	**7.4**	**660**
Žofinka	2	48°49' N	14°52' E	474	7.4	675
Široké blato	3	48°54' N	14°59' E	495	7.3	680
Pěkná	4	48°50' N	13°57' E	735	5.5	795
Kyselov	**5**	**48°41' N**	**14°03' E**	**735**	**5.5**	**950**
Mrtvý luh	**6**	**48°52' N**	**13°52' E**	**740**	**5.2**	**900**
Malá niva	7	48°55' N	13°49' E	751	5.4	840
Velká niva	8	48°56' N	13°49' E	755	5.4	840
Multerberg	9	48°36' N	14°08' E	790	5.7	960
Novohůrecká slať	**10**	**49°09' N**	**13°20' E**	**865**	**5.5**	**1185**
Chalupská slať	**11**	**49°00' N**	**13°40' E**	**910**	**4.8**	**890**
Ždárek	12	48°57' N	13°39' E	985	4.9	980
Bukovská slať	13	48°58' N	13°38' E	987	5.0	985
Mlýnská slať	14	49°01' N	13°27' E	1050	2.6	1600
Jezerní slať	**15**	**49°02' N**	**13°35' E**	**1050**	**2.0**	**1090**
Tříjezerní slať	16	49°02' N	13°28' E	1066	2.7	1500
Tetřeví slať	17	49°01' N	13°32' E	1140	4.0	1200
Březina	18	48°58' N	13°29' E	1150	2.4	1800
Hraniční slať	19	48°57' N	13°30' E	1175	2.3	1720
Novohorský močál	20	48°59' N	13°27' E	1210	2.2	1860

Six out of the twenty studied peat bogs were selected for a more detailed study (protected areas where repeated sampling was enabled). This selection included two basic types of pine bogs:

a) Pine bogs with the tree-shaped *P. rotundata* - 3 localities (site number 1, 5, 10).

b) Pine bogs with the prevailing shrubby form of *P. rotundata* introgressively hybridized with *P. mugo* (called *P.* × *pseudopumilio*) - 3 localities (site number 6, 11, 15).

Another criterion for selection was the accessibility of the site to enable repeated sampling and monitoring. Sites selected for detailed study are marked bold in **Table 1**.

Field sampling

One 10 × 10 m plot was established in the centre of 14 studied bogs in 1997. In each plot, phytosociological relevés were surveyed (in 2001) using the Braun-Blanquet seven-degree scale (van der Maarel 1979), and maximum height of the shrub or tree layer (which was identical with the maximum height of bog pines) was measured.

In the centre of the 6 bogs studied in detail, one 50 × 50 m permanent research plot was established in 1997. One 10 × 10 m subplot was established in each of the four corners of the plot. In each subplot, phytosociological relevés were also surveyed (in 2001) using the same methods as above. The depth to groundwater table (measured in bore holes to the nearest 0.5 cm), maximum temperature and minimum temperature (both measured to the nearest 0.1 °C) were measured in the centre of each permanent plot every two weeks during the vegetation seasons (May – October) in 1998 and 1999, and average values were calculated. The reference level for the groundwater table position was the average bottom-layer surface in the plot. For temperatures, maximum and minimum thermometers were exposed 15 cm above the surface. Chemical analyses of ground water samples were performed eight times during the vegetation season in 1998. Conductivity and pH were measured and NH_4^+, NO_3^-, total N, PO_4^{3-} and total P were analyzed using flow injection analysis (FIA) (Tecator Inc; Sweden) and average values were calculated. The conductivity data were standardized to 20°C (variable EC), and the conductivity contributed by hydrogen ions (Sjörs 1950) was subtracted in order to eliminate the effect of varying acidity. Because the subtraction leads to negative values of corrected conductivity in some cases, correction of pH by adding of 0.2 according to Du Rietz (sec. Sjörs 1950) was applied previously to subtraction and resulting corrected conductivity (variable ECcorr) was used in all analyses. Mean height, trunk density and mean trunk diameter of the bog pines were measured for each permanent plot and average values were calculated. The trunk diameter was measured at DBH in trees and at 10 cm above the soil surface in shrubs.

Altitude for each plot was derived from detailed maps. Mean annual precipitation and mean annual temperatures for each locality were calculated by Czech Hydrometeorological Institute, branch office České Budějovice, in 2006.

Data analysis

Thirty-eight phytosociological relevés, including 92 species of vascular plants and bryophytes (63 bryophytes, 1 fern, 20 herbs and 8 woody species) were measured in 14 localities with one plot and the 6 localities studied in detail with 4 subplots. These data formed the first data set together with corresponding environmental data (see **Appendix** and **Table 1**).

The phytosociological relevés of the subplots from bogs studied in detail, with corresponding environmental data (see **Appendix**, **Table 1** and **Table 2**) formed the second data set (24 relevés, 76 species). Species cover was expressed as an ordinal transformation (1-7) of the Braun-Blanquet seven-degree cover-abundance scale (van der Maarel 1979).

Table 2. Site characteristics of the six peat bogs studied in detail (comp. Table 1) arranged according to increasing altitude. For details see the text.

Site number	1	5	6	10	11	15
Bog pine characteristics						
mean height (m)	6.11	5.36	0.78	4.31	1.98	0.76
trunk density (trunk.m^{-2})	0.27	0.35	2.09	0.63	3.30	1.84
mean trunk diameter (cm)	19.5	11.3	2.5	10.6	4.3	2.8
Abiotic factors						
altitude (m a.s.l.)	470	735	740	865	910	1050
groundwater table level (cm)	-25.8	-24.5	-9.2	-16.6	-9.6	-13.2
mean maximum temperature (°C)	29.9	31.1	34.3	35.9	33.2	31.9
mean minimum temperature (°C)	2.0	2.7	-2.9	-1.1	-3.2	-5.0
Chemical analyses						
pH	3.36	3.48	3.65	3.43	3.49	3.73
EC (µS)	164	114	93	120	93	80
ECcorr (µS)	73	46	47	45	27	42
NH_4 (µg.l^{-1})	1803	741	52	311	154	49
NO_3 (µg.l^{-1})	793	873	1524	1466	1052	467
total N (µg.l^{-1})	2183	3159	2528	2399	2347	1526
PO_4 (µg.l^{-1})	143	71	10	36	30	14
total P (µg.l^{-1})	207	98	53	48	57	37

Design of all tests did not treat the subplots as independent replicates because the environmental variables were collected at the plot level.

Detrended Correspondence Analysis (DCA) was used to compare species composition among the plots. The axes were interpreted by analysis of correlations between sample scores and recorded environmental variables.

The relationships of species composition to environmental variables were evaluated by Canonical Correspondence Analysis (CCA) in the species data set with all species included and also with all species from tree and shrub layer (E_{32}) excluded. Forward selection of environmental variables was performed.

The effect of woody species on ground layer vegetation was tested in CCA, where the particular woody species cover and composite variable for all trees and shrubs "Treeall3" (i.e., cover of all trees and shrubs), all pines "Pinuall3" (i.e., cover of all pines: *P. rotundata*, *P.* × *psedopumilio*, *P.sylvestris* and *P.* × *digenea*), and "Pinubog3"(i.e., cover of all bog pines: *P. rotundata*, *P.* × *psedopumilio* and *P.* × *digenea*) were used as environmental variables in the species data set where all species from tree and shrub layer (E_{32}) were excluded.

Significance was tested by the distribution-free Monte Carlo permutation test. In the test, the distribution of the test statistics under the null hypothesis was generated by restricted random permutations of cases in the environmental data (for details see ter Braak & Šmilauer 2002).

The DCA and CCA analyses were performed using the program package CANOCO for Windows version 4.5 (ter Braak & Šmilauer 1998).

The dependence of *P. rotundata* and *P.* × *pseudopumilio* cover and maximum height of bog pines on altitude was tested and visualized by generalized linear models (GLM, McCullagh & Nelder 1989) implemented in S-plus version 4.5 (Statistical Sciences 1999).

The matrix of Pearson correlation coefficients between the recorded variables and the matrix of Spearman correlation coefficients between recorded variables and sample scores on the DCA axes were calculated.

Table 3. Selected Spearman correlation coefficients between DCA axis and measured variables and Pearson correlation coefficients between measured variables for all studied plots (All) and plots studied in detail (Detail). Correlations marked bold are significant ($P < 0.05$). Significance levels: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, n.s. – non-significant.

Plots	Variable 1	Variable 2	r	p
All	DCA axis 1	altitude	**-0.83** ***	0.0003
All	DCA axis 1	maximum height	**0.92** ***	0.0001
All	DCA axis 1	precipitation	**-0.79** ***	0.0005
All	DCA axis 1	mean temperature	**0.87** ***	0.0002
Detail	DCA axis 1	maximum height	**1.00** *	0.0298
Detail	DCA axis 1	minimum temperature	**-0.89** *	0.0409
Detail	DCA axis 1	water level	-0.83 n.s.	0.0553
Detail	DCA axis 1	pH	**-0.94** *	0.0298
Detail	DCA axis 1	NH_4	**1.00** *	0.0298
Detail	DCA axis 1	PO_4	**0.94** *	0.0409
Detail	DCA axis 1	mean height	**1.00** *	0.0298
Detail	DCA axis 1	mean trunk diameter	**0.94** *	0.0409
Detail	DCA axis 1	mean temperature	**0.93** *	0.0444
All	altitude	maximum height	**-0.82** ***	0.0000
All	altitude	precipitation	**0.86** ***	0.0000
All	altitude	mean temperature	**-0.93** ***	0.0000
Detail	altitude	minimum temperature	0.78 n.s.	0.0652
Detail	altitude	water level	0.66 n.s.	0.1505
Detail	altitude	pH	0.66 n.s.	0.1530
Detail	altitude	EC	**-0.86** *	0.0265
Detail	altitude	ECcorr	**-0.83** *	0.0426
Detail	altitude	NH_4	**-0.86** *	0.0263
Detail	altitude	PO_4	**-0.84** *	0.0362
Detail	altitude	total P	**-0.90** *	0.0155
Detail	altitude	mean height	-0.70 n.s.	0.1216
Detail	altitude	mean trunk diameter	-0.79 n.s.	0.0591
Detail	altitude	temperature amplitude	0.75 n.s.	0.0835
Detail	altitude	precipitation	0.79 n.s.	0.0602
Detail	altitude	mean temperature	**-0.91** *	0.0118
Detail	minimum temperature	mean height	**0.94** **	0.0059
Detail	minimum temperature	trunk density	-0.78 n.s.	0.0647
Detail	minimum temperature	mean trunk diameter	**0.86** *	0.0298
Detail	water	mean height	**-0.92** **	0.0088
Detail	water	mean trunk diameter	**-0.90** *	0.0134
Detail	pH	NH_4	-0.73 n.s.	0.1023
Detail	pH	PO_4	-0.76 n.s.	0.0791
Detail	ECcorr	mean trunk diameter	0.79 n.s.	0.0593
Detail	NH_4	PO_4	**1.00** ***	0.0000
Detail	NH_4	total P	**0.99** ***	0.0003
Detail	PO_4	total P	**0.98** ***	0.0007

Results

The characteristics considered for all studied pine bogs generally exhibit a unidirectional trend in relation to the altitudinal gradient (**Fig. 2, Fig. 3**). A lot of correlations between the site characteristics and altitude were significant (**Table 3**).

The results of the DCA ordinations for 38 plots and all species are shown in **Fig. 2** and **Table 4**. The three inset diagrams in **Fig. 2** demonstrate the more or less constant position of the studied sites if the woody species were excluded from the ordination, only herbs (E_I) were included, and only bryophytes (E_0) were included.

Table 4. Results of DCA analyses of phytosociological relevés from the twenty study sites (38 relevés). Four variants (when the complete vegetation data set was used (E_{32}+E_I+E_0), when woody species were excluded (E_I+E_0), only herbs (E_I), and only bryophytes (E_0) were considered) are presented.

Species			DCA axis 1 explained variability (%)	DCA axis 1 λ_1	DCA axis 2 explained variability (%)	DCA axis 2 λ_2
E_{32}	E_I	E_0	26.5	0.432	8.4	0.137
–	E_I	E_0	25.1	0.397	7.5	0.118
–	E_I	–	35.5	0.468	7.6	0.100
–	–	E_0	22.3	0.395	9.6	0.172

Species are arranged along the first ordination axis in the main DCA diagram in a sequence approximately from a group of forest species (e.g., *Ledum palustre, Bazzania trilobata, Dicranum polysetum*) through species typical of all peat bogs (e.g., *Vaccinium uliginosum,*

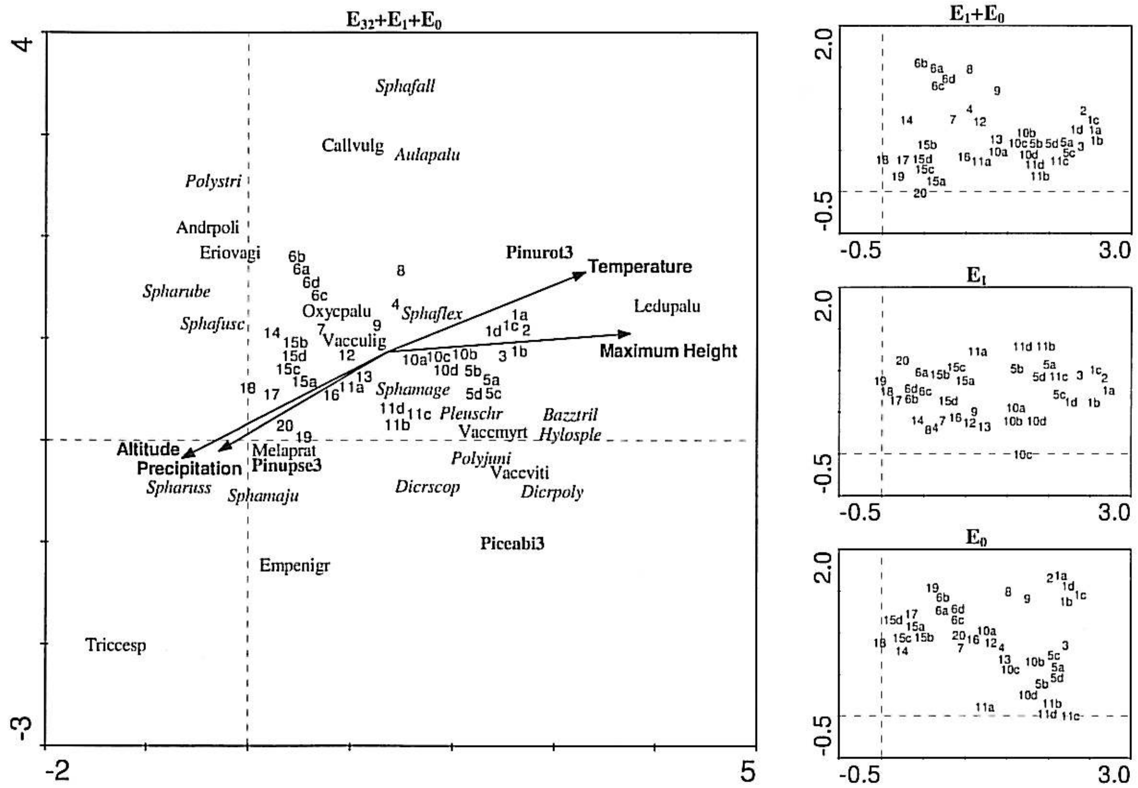

Fig. 2. Detrended Correspondence Analysis (DCA) of phytosociological relevés from the twenty study sites (38 relevés) with projection of passive variables. The main diagram represents the variant when the complete vegetation data set was used (E_{32}+E_I+E_0). Woody species are indicated in bold, herbs in normal font and bryophytes in italics. For abbreviations of the species names see Appendix. The inset diagrams correspond, from top to bottom, to ordination (a) when woody species were excluded (E_I+E_0), (b) only herbs (E_I), and (c) only bryophytes (E_0) were considered. For study sites, represented by numbers and lower case letters, see Table 1 and Table 2.

Oxycoccus palustris, Sphagnum magellanicum) located naturally near the diagram centre, to a group of species characterising open, mountain peat bogs (*Trichophorum cespitosum, Empetrum nigrum, Sphagnum fuscum, S. russowii*). The complete species list from the phytosociological relevés is given in the **Appendix**.

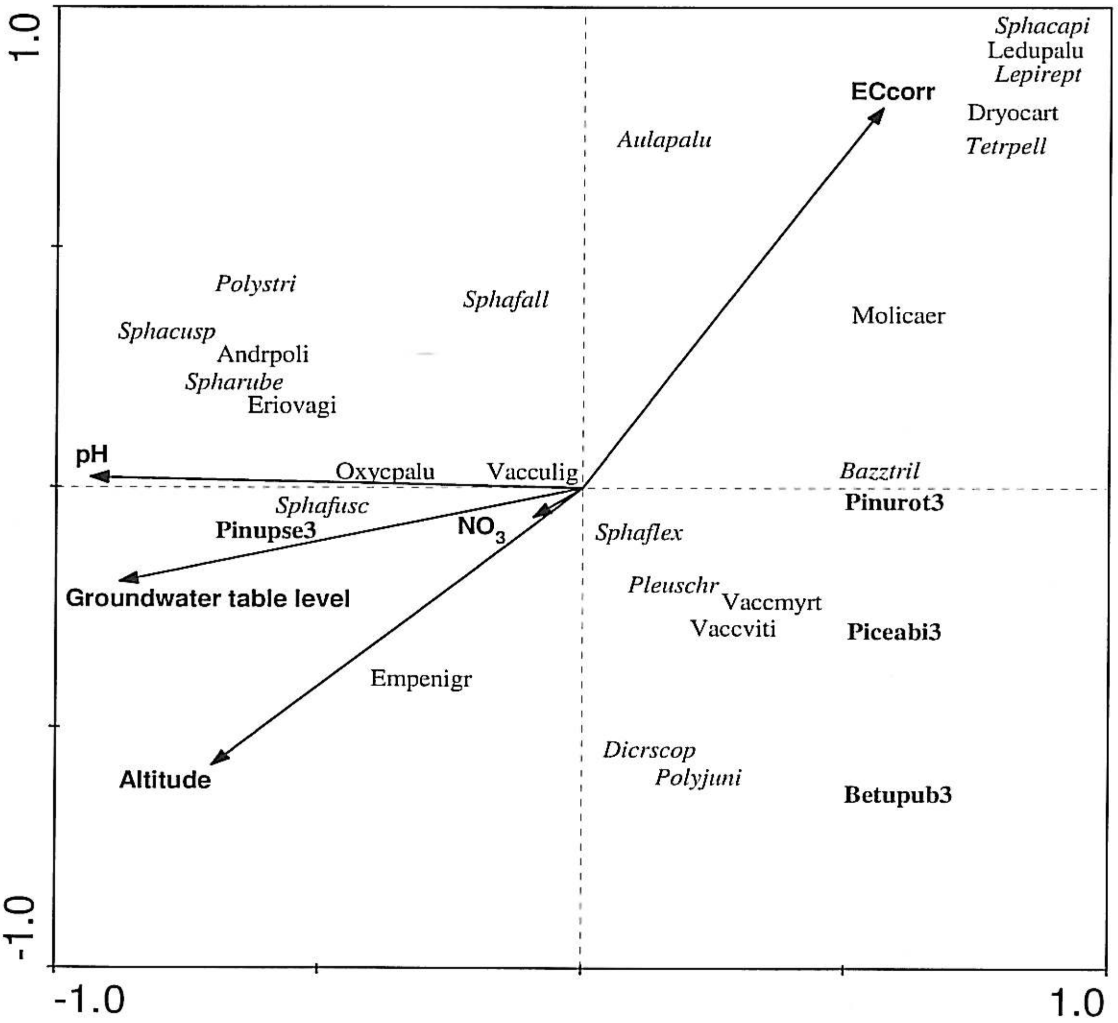

Fig. 3. Canonical Correspondence Analysis (CCA) of phytosociological relevés from the six sites studied in detail (24 relevés) and abiotic environmental characteristics chosen by forward selection of variables. For abbreviations of the species names see Appendix.

The studied sites are clearly arranged along the first ordination axis from the sites of lower altitudes (right side) to sites occurring in higher altitudes (left side) in all DCA diagrams (**Fig. 2**). But there are also some exceptions, for example site No. 6 (Mrtvý luh), which is a bog on the bottom of a distinct valley, with extreme climatic inversion situations. This site resembles in most characteristics those at higher altitudes, including the shrubby form of pine.

Results of correlation analysis of the scores on the DCA ordination axes and measured variables for all plots are showed in **Table 3**.

Results of correlation analysis of the scores on the DCA ordination axes and measured variables for the bogs studied in detail (the centroid position for each locality was used) shows that the first ordination axis was most correlated with biotic characteristics (**Table 3**).

Correlation analysis shown that most characteristics considered for the bogs studied in detail exhibited a unidirectional trend regarding the altitudinal gradient (**Table 3**). We also found rather surprising correlation between pH and PO_4 and pH and NH_4 (**Table 3**). Also the biotic characteristics of the dominant pines were related to altitude and to some other environmental factors (**Table 3**). The physiognomy of the site, which is determined by the growth form of the dominant pine, evidently influences some micro-climatic characteristics such as minimum temperature (**Table 3**). High mutual correlation were attained between the particular trophic factors, with only total N and NO_3 contents were not being well correlated to any other factor (**Table 3**).

We used forward selection in CCA (diagram not presented) to select the best explanatory variables for the vegetation composition in the pine bogs studied in detail. Significant explanatory variables (ordered by its importance) were: mean height, ECcorr, mean trunk density, altitude and maximum height. The first CCA axis (λ_1 = 0.437) was highly correlated with mean height, and explained 31.2% of the variability in the species data. The effect of mean height was highly significant (F=9.73; P=0.003; 9999 permutations) when analyzed separately. The second CCA axis (λ_2 = 0.229) was correlated with ECcorr and altitude and explained 16.3% of the variability in the species data. When we excluded all species from tree and shrub layer (E_{32}) from the analysis, most significant explanatory variable was maximum height.

When we excluded biotic characteristics, significant explanatory variables were (ordered by importance): pH, Eccorr, ground water table, NO_3 and altitude. The resulting CCA diagram (**Fig. 3**) shows practically the same pattern of species positions as for the previous CCA analysis. The first CCA axis (λ_1 = 0.437) was correlated with pH and explained 31.2% of the variability in the species data. The effect of pH was significant (F=8.59; p=0.01; 9999 permutations) when analyzed separately. The second CCA axis (λ_2 = 0.229) was correlated with ECcorr and altitude and explained 16.3% of the variability in the species data.

The effect of particular woody species cover or composite variable cover on vegetation with all species from tree and shrub layer (E_{32}) excluded tested in CCA shows **Table 5**. The highest effect in this analysis was shown by *P. rotundata* followed by cover of all trees and shrubs. High effect was also shown for *P.* × *pseudopumilio* cover. All other woody species had much lower explanation power.

Table 5. Results of Monte Carlo permutation tests (9999 permutations) in CCA analyses with species data set with all trees and shrubs excluded (only E_1 and E_0 species data included). Composite variables (Treeall3 – cover of all trees and shrubs; Pinuall3 – cover of all pines (*P. rotundata*, *P.* × *psedopumilio*, *P. sylvestris* and *P.* × *digenea*); Pinubog3 – cover of all bog pines (*P. rotundata*, *P.* × *psedopumilio* and *P.* × *digenea*)) are marked bold. For abbreviations of the other species names see Appendix.

Variable	F	p
Pinurot3	7.132	0.0001
Treeall3	4.848	0.0001
Pinuall3	4.511	0.0001
Pinubog3	4.206	0.0001
Pinupse3	3.297	0.0004
Piceabi3	2.141	0.0214
Betupub3	2.103	0.0246
Franaln3	1.698	0.0479
Pinusyl3	1.641	0.0995
Sorbauc3	1.583	0.1073
Pinudig3	0.993	0.5011

The dependence of *P. rotundata* and *P.* × *pseudopumilio* cover and maximum height of bog pines on altitude is shown in **Fig. 4**. Linear GLM showed highly significant dependence of *P. rotundata* cover on altitude ($p<0.001$) and maximum height of bog pines on altitude ($p<0.001$). Second order polynomial model showed also highly significant dependence of *P.* × *pseudopumilio* cover on altitude ($p<0.001$). *P. rotundata* dominates in altitudes under 700 m a.s.l. In the subsequent transitional zone from 700 to 900 m a.s.l. we can found both *P. rotundata* and *P.* × *pseudopumilio*, but the mixture of these species in the centre of one peat bog wasn't found in our study. *P.* × *pseudopumilio* dominates in altitudes over 900 m a.s.l. with maximum cover around 1000 m a.s.l. Maximum height of bog pines decreases continuously towards higher altitudes.

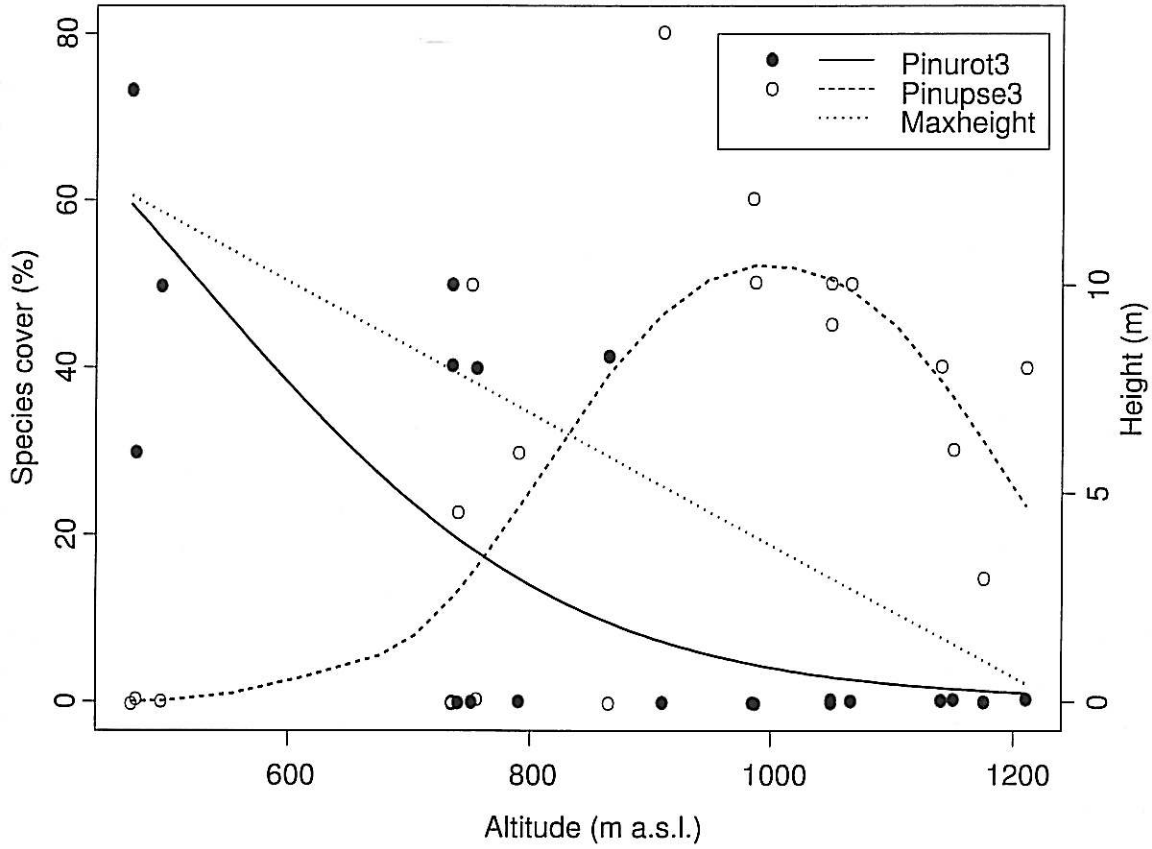

Fig. 4. The dependence of *P. rotundata* (Pinurot3) and *P.* × *pseudopumilio* (Pinupse3) cover and maximum height (Maxheight) of bog pines on altitude visualized by generalized linear models (GLM). Jittering (addition of random noise) was used to separate points with identical values.

Discussion

The results clearly demonstrate the importance of the altitudinal gradient, being closely linked to other environmental gradients, in influencing the distinct vegetation pattern (Peet 1978, Ellenberg 1988). The interesting aspect of the studied peat bogs is the close relation between altitude and the degree of hybridization and the resulting growth form (reflected in its height) of the keystone species (edificator). The growth form consequently determines some other abiotic and biotic characteristics of the site including species composition, which conclusion is supported by the fact that the growth form itself explained even more variability in vegetation data than the altitude. The fenotype plasticity of bog pine can be a partial reason of height and growth form changes along the altitude gradient. However, the other morphological characters (e. g. cone morphology) support old hybridization events between *P. rotundata* and *P. mugo*. The lower limit of transitional zone may indicate the lower distribution of *P. mugo* during the last cold climate period before the Holocene warming. We are not aware of any similar clear example of the relationship between altitude and growth forms of a taxonomic complex; the only partly comparable should be the cline in growth forms of *Betula pubescens* agg. in the Scandinavian mountains (Dierssen 1996). *P. rotundata* and *P.* × *pseudopumilio* only rarely coexist. It is probably because of different growth form which results in overshadowing of the shrubby hybrids by the tree-shaped *P. rotundata.*

The mutual relationships among the measured environmental factors are not surprising. Naturally, the sum of annual precipitation and site moisture are positively correlated with altitude, while mean annual temperature and trophic factors are negatively related (Peet 1978). Our study expands on the work by Kärstner & Flössner (1933) and Neuhäusl (1972) but they did not provide detailed data. Temperature amplitude (the difference between minimum and maximum temperatures measured at the ground) increased with altitude. Inside the closed forest stands, i.e. those sites with tree-shape pines in our case, the amplitude is generally lower (Stoutjesdijk & Barkman 1992). The maximum temperatures showed no clear trend in relation to altitude, because two opposite trends played role – lowering of temperature with increasing altitude and increasing maximum temperatures on more opened stands in higher altitudes.

Peat bog vegetation was studied in relation to environmental factors in other geographical regions, for example by Jeglum (1971), Pakarinen & Ruuhijärvi (1978), Karlin & Bliss (1984), Damman (1986), Malmer (1986), Økland (1990), Wassen et al. (1990), Gerdol (1995), Jeglum & He (1995), Bragazza & Gerdol (1999) and Hájková & Hájek (2003). The studies mostly illustrated the ecological importance of moisture and nutrient gradients. Their results are generally comparable with those presented in our study. The vegetation of peat bogs studied by us in detail was closely related to trophic factors such as pH and conductivity; groundwater table level was also an important factor.

The low correlation of total N with vegetation composition in bogs found in this study was also reported by Wassen et al. (1990), which is expected in the case of the organic sediment. The trend of increasing pH with altitude in our study and negative correlations of pH with most other trophic factors was rather surprising. However pH was low in all the sites with a small range of only 0.4 and the strongest correlations were only on the border of significance. Moreover, some long-distance atmospheric deposition, more intensive in the higher elevation, could influence the trend (Malmer 1986). But more probable is the effect of higher mineralization of the organic matter in sites with lower groundwater table, which is associated with proton release and acidification processes (Mitsch & Gosseling 2000).

Biotic characteristics of the pines, such as height and trunk diameter, are best correlated to both the altitudinal gradient and species composition of the sites (see the length and directions of arrows in the ordination diagram in **Fig. 2** and **Table 3**).

The resulting species patterns in the DCA and CCA diagrams are very similar, i.e. in both direct and indirect gradient analyses, which indicates the close relationships between the environmental and vegetation gradients and the fact that probably no other important environmental factors were missed in our sampling (see also Jongmann et al. 1987, Jeglum & He 1995). Position of the particular species is mostly well ecologically interpreted, considering the ecological behavior of the species. Results of the DCA analyses, considering all species together, excluding the woody species, including herbs only, or moss layer only, showed that all of the vegetation components reflected the environmental gradients generally in the same way, as the position of the vegetation samples in the ordination diagrams remained more or less the same in all calculations. The results also indicate a unique character of each peat bog as the respective four samples (relevés) from one site are not mixed with the other sites in DCA diagram even in the case of closely located sites. This is important for nature conservancy so to ensure an effective protection of all peat bogs.

The studied peat bogs provide a very illustrative example of close mutual relations between environmental and vegetational gradients, and taxonomical position of the dominant species. Considering the limited distribution range of the edificator *Pinus rotundata* (Jalas & Suominen 1973), relictness (Spitzer et al. 1999), sources of paleoecological information (Jankovská 1980), occurrence of rare and endangered species (Neuhäuslová et al. 1998), a continuous micro-evolution and interesting biogeographical relations (Mikola & Spitzer 1983), peat bogs are eminently important and valuable for scientific research, nature conservancy, and from a common cultural view.

Conclusions

The questions put in the Introduction can be answered in the following way:

(a) Species composition of the peat bogs and the growth form of the dominant pines, i.e. the transition from the tree-shape into the shrubby form as a result of hybridization, closely reflect the altitudinal gradient. The samples from the twenty studied sites were clearly arranged along the increasing altitude in the DCA diagram. The plots from one site were not mixed with plots from other sites in the DCA diagram, which indicates a specificity of even closely located bogs.

(b) Site moisture characteristics and temperature amplitude were positively correlated to altitude, while most trophic factors were negatively correlated.

(c) All vegetation components, i.e. woody species, the herb layer, and the moss layer, generally responded to the environmental gradients in the same way.

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Souhrn

Změny středoevropských rašelinišť s borovicí blatkou a jejími kříženci podél gradientu nadmořské výšky

Na dvaceti rašeliništích v různé nadmořské výšce v jižní části Čech byly provedeny vegetační analýzy (fytocenologické snímky) se snahou nalézt vztahy mezi vegetací a gradienty prostředí. Podrobně bylo sledováno šest rašelinišť. Studovaná rašeliniště jsou porostlá borovicí blatkou (*Pinus rotundata*), která je endemitem střední Evropy, a jejími hybridogenními populacemi s borovicí klečí (*P. mugo*). Zastoupení křížence *P.* × *pseudopumilio* vzrůstá směrem k vyšším nadmořským výškám. Data byla zpracována metodami jednorozměrné i mnohorozměrné statistiky. Proměnné prostředí (výška hladiny podzemní vody, průměrná a minimální teplota, srážky, pH, vodivost, koncentrace NH_4 a PO_4 a celkový P) i biotické charakteristiky lokalit (druhové složení, růstová forma dominantních borovic) byly často úzce korelovány s nadmořskou výškou. Tato korelace však neplatila pro koncentrace celkového N a NO_3. Významný byl rovněž vztah mezi růstovou formou dominantních borovic a abiotickými faktory i ostatními vegetačními charakteristikami. Druhové složení všech vegetačních pater (t.j. stromového a keřového, bylinného i mechového) se měnilo s nadmořskou výškou a hlavní trendy byly v podstatě stejné pro všechna vegetační patra. Z výsledků je mimo jiné patrná jedinečnost každého ze sledovaných rašelinišť.

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Appendix

Phytosociological relevés (10 x 10 m) from the studied peat bogs arranged according to increasing altitude. The seven-degree Braun-Blanquet scale was used.

Layer	Species	Abbreviation	Site number																																					
			1a	1b	1c	1d	2	3	4	5a	5b	5c	5d	6a	6b	6c	6d	7	8	9	10a	10b	10c	10d	11a	11b	11c	11d	12	13	14	15a	15b	15c	15d	16	17	18	19	20
E_{32}			80%	75%	60%	60%	55%	50%	50%	30%	50%	50%	40%	15%	10%	20%	25%	50%	40%	30%	35%	35%	40%	45%	70%	80%	75%	75%	60%	50%	50%	40%	40%	45%	40%	50%	40%	30%	20%	40%
	Betula pubescens agg.	Betupub3	+	+	.	.	+	.	.	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.
	Frangula alnus	Franaln3	+	+	+	+	+	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Picea abies	Piceabi3	+	1	+	+	.	.	.	1	+	1	1	.	.	.	.	.	.	.	+	+	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	1	.
	Pinus × digenea	Pinudig3	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Pinus × pseudopumilio	Pinupse3	.	.	.	.	.	.	.	.	.	.	.	2	2	2	3	3	.	3	.	.	.	.	4	5	5	5	4	3	3	3	3	3	3	3	3	3	2	3
	Pinus rotundata	Pinurot3	5	5	4	4	3	3	3	3	3	3	3	.	.	.	.	.	3	.	3	3	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Pinus sylvestris	Pinusyl3	.	+	.	+	2	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Sorbus aucuparia	Sorbauc3	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
E_1			40%	60%	50%	60%	60%	50%	50%	50%	50%	50%	55%	45%	50%	50%	45%	50%	50%	60%	50%	60%	55%	55%	50%	50%	50%	60%	60%	50%	40%	45%	40%	40%	50%	50%	50%	50%	60%	60%
	Andromeda polifolia	Andrpol	.	.	.	.	.	.	+	.	1	.	.	1	2	2	2	+	+	+	.	.	r	r	1	r	r	.	+	.	+	+	1	1	1	+	+	+	+	+
	Avenella flexuosa	Avenflex	+	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Betula pubescens agg.	Betupub1	.	+	+	.	+	.	.	+	+	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
	Calluna vulgaris	Callvulg	.	+	+	.	+	+	+	+	+	.	+	2	1	1	+	+	+	.	.	.	.	.	1	r	r	+	+	.	.	.	.	.	.	.	.	.	.	.
	Carex limosa	Carelimo	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+
	Carex pauciflora	Carepauc	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	r	.	.	.	+	+	.	.	.
	Drosera rotundifolia	Drosrotu	.	.	.	.	.	+	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	.	.	.	+
	Dryopteris carthusiana	Dryocart	1	2	+	1	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Empetrum nigrum	Empenigr	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	+	1	.	.	.	2	1	1	.	.	+	.	.	1
	Eriophorum vaginatum	Eriovagi	.	+	+	+	.	.	2	+	.	.	+	3	2	3	2	2	3	1	+	1	1	+	1	+	+	+	1	2	2	3	3	2	3	1	2	1	+	1
	Ledum palustre	Ledupalu	3	3	3	2	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Lycopodium annotinum	Lycoanot	+	+	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Melampyrum pratense	Melaprat	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	+	+	+	+	+	+	+	.	.	.	.	+	+	+	1	+	+	.	+	+	+	+	+
	Molinia caerulea	Molicaer	+	+	+	1	+	.	.	.	+	r	.	.	.	.	.	.	.	.	.	+	1	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Oxycoccus palustris	Oxycpalu	+	+	+	1	.	+	+	1	2	r	1	2	1	2	2	+	+	2	1	+	r	r	2	+	+	1	+	+	+	1	2	2	2	+	+	+	+	+
	Picea abies	Piceabi1	.	.	.	.	+	.	.	.	+	1	1	.	.	.	.	.	+	.	.	.	.	.	.	r	.	r	.	+	.	.	.	.	.	+	.	.	+	.
	Pinus rotundata	Pinurot1	.	.	.	.	.	.	.	1	+	1	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Pinus sylvestris	Pinusyl1	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Scheuchzeria palustris	Schepalu	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
	Stellaria longifolia	Stellong	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Trichophorum cespitosum	Triccesp	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	2	3	3	3
	Urtica dioica	Urtidioi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.
	Vaccinium myrtillus	Vaccmyrt	2	3	3	3	3	3	+	3	3	4	4	.	.	.	.	+	+	2	4	4	4	4	3	3	3	3	1	2	+	1	+	2	2	2	+	+	+	+
	Vaccinium uliginosum	Vacculig	1	2	+	2	+	+	2	1	1	2	1	1	2	2	2	3	2	3	2	2	2	2	2	1	2	1	3	2	2	2	2	2	2	3	2	2	2	2
	Vaccinium vitis-idaea	Vaccviti	1	1	1	2	+	+	.	2	2	2	2	.	.	r	.	+	.	.	1	+	+	+	+	2	2	3	+	+	.	1	+	+	+	.	.	.	.	.
E_0			80%	80%	85%	85%	65%	80%	85%	90%	93%	85%	85%	98%	99%	99%	99%	90%	90%	99%	98%	97%	95%	90%	93%	85%	83%	78%	90%	80%	90%	85%	88%	86%	85%	85%	65%	60%	10%	45%
	Aulacomnium palustre	Aulapalu	+	+	1	1	.	.	.	r	+	.	+	+	+	+	1	+	.	.	r	.	+	.	.	.	r	.	+	.	+	.	.	+	.	.	.	.	.	.
	Barbilophozia attenuata	Barbatte	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
	Barbilophozia floerkei	Barbfloe	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
	Bazzania trilobata	Bazztril	+	+	1	+	.	+	.	+	.	+	+	.	.	+	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
	Brachythecium salebrosum	Bracsale	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Calypogeia integristipula	Calyinte	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Calypogeia neesiana	Calynees	.	.	.	.	.	.	.	+	+	+	+	.	.	.	.	.	.	+	+	r	r	r	r	r	r	.	.	.	.	.	r	.	r	.	.	.	.	.
	Calypogeia sphagnicola	Calyspha	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	r	.	.	.	r	r	.	r	.	.	.	.	.
	Cephalozia connivens	Cephconn	+	+	+	+	.	+	.	+	r	+	+	r	r	+	r	.	.	.	r	r	r	+	.	r	r	.	.	.	.	r	r	r	r	.	.	.	.	.
	Cephalozia loitlesbergeri	Cephloit	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.
	Cephalozia lunulifolia	Cephlunu	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	r	.	r	.	.	.	r	.	.	.	+	.	.	.	.
	Cephaloziella rubella	Cephrube	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Dicranella heteromalla	Dicrhete	.	.	.	.	+	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Dicranodontium denudatum	Dicrdenu	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	r	+	.	.	r	r	.	.	.	+	.	+	+	.	.	.	+	.
	Dicranum bergeri	Dicrberg	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Dicranum flagellare	Dicrflag	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	r	.	.	.	.	.	.	.	.	.	.	.	.
	Dicranum montanum	Dicrmont	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Dicranum polysetum	Dicrpoly	+	+	+	1	+	1	.	.	.	.	.	.	.	+	+	.	.	.	.	+	.	.	.	2	+	1	.	.	.	.	.	.	.	.	.	.	.	.
	Dicranum scoparium	Dicrscop	.	.	.	.	.	.	.	+	+	+	+	.	.	.	.	.	.	+	1	1	+	1	+	1	+	+	.	.	.	r	+	.	.	+	.	+	.	+
	Dicranum undulatum	Dicrundu	.	.	.	.	.	.	.	.	.	+	.	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	+	1	+	.	.	.	.	.
	Gymnocolea inflata	Gymninfl	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	+
	Herzogiella seligeri	Herzseli	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Hylocomium splendens	Hylosple	+	1	1	+	.	+	.	1	.	+	.	.	.	.	.	.	.	+	.	.	1	r	.	.	2	.	.	.	.	+	.	.	.	.	.	.	.	.
	Hypnum cupressiforme	Hypncupr	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Hypnum jutlandicum	Hypnjutl	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Kurzia pauciflora	Kurzpauc	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	+
	Lepidozia reptans	Leprept	1	+	1	1	.	+	.	.	.	+	.	.	.	.	.	.	.	.	r	.	.	.	.	.	r	r	.	.	.	.	.	.	r	.	.	.	.	.
	Leucobryum glaucum	Leucglau	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Lophocolea heterophylla	Lophhete	+	+	+	+	.	.	.	r	.	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Mylia anomala	Mylianom	.	.	.	.	.	.	.	r	+	.	.	+	r	+	+	.	+	.	+	r	r	r	+	+	r	r	+	.	+	r	.	+	+	+	+	+	+	+
	Odontoschisma denudatum	Odondenu	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Plagiothecium curvifolium	Plagcurv	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.
	Plagiothecium denticulatum	Plagdent	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Plagiothecium laetum	Plaglaet	+	+	+	+	.	.	.	r	+	r	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Pleurozium schreberi	Pleuschr	+	1	1	2	2	+	1	+	1	2	2	+	1	1	+	+	+	1	+	1	1	+	1	2	2	2	+	1	+	+	r	+	+	2	+	+	+	+
	Pohlia nutans	Pohlnuta	+	+	+	+	+	+	.	r	+	r	+	.	.	.	.	+	.	.	r	.	.	r	r	r	r	+	.	.	.	.	r	r	r	.	.	.	.	.
	Polytrichum commune	Polycomm	+	+	1	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Polytrichum formosum	Polyform	.	.	.	.	+	.	.	r	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Polytrichum juniperinum	Polyjuni	.	.	.	.	.	.	.	1	2	+	1	.	.	.	.	.	.	.	1	2	2	2	2	1	1	1	.	.	.	.	.	.	+	.	.	.	.	.
	Polytrichum strictum	Polystri	+	+	+	1	.	.	1	.	.	.	.	2	3	2	2	2	+	+	.	.	.	.	.	.	.	.	+	+	2	2	1	1	2	+	.	+	+	.
	Ptilidium ciliare	Ptilcili	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.
	Ptilidium pulcherrimum	Ptilpulc	.	.	.	.	.	.	.	+	.	+	r	.	.	.	.	.	.	+	r	r	.	r	+	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.
	Ptilium crista-castrensis	Ptilcris	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Sanionia uncinata	Saniunci	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Sphagnum brevifolium	Sphabrev	.	.	.	.	.	.	+	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Sphagnum capillifolium	Sphacapi	1	2	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Sphagnum centrale	Sphacent	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Sphagnum compactum	Sphacomp	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
	Sphagnum cuspidatum	Sphacusp	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	+	1	+	+	.	.	+
	Sphagnum fallax	Sphafall	1	1	1	1	2	.	.	.	.	.	.	2	3	3	2	.	3	4	2	2	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
	Sphagnum flexuosum	Sphaflex	2	2	3	2	.	3	3	3	2	4	4	2	1	2	2	2	3	1	4	2	3	3	1	3	4	3	4	3	+	1	1	1	.	+	.	.	.	.
	Sphagnum fuscum	Sphafusc	.	.	.	.	.	.	+	.	.	.	.	2	1	2	2	2	.	.	.	.	1	1	4	1	1	1	+	.	3	1	2	3	1	+	.	1	.	+
	Sphagnum girgensohnii	Sphagirg	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
	Sphagnum magellanicum	Sphamage	3	3	2	3	2	2	1	3	4	2	2	2	1	2	2	2	+	1	2	3	3	3	1	2	+	1	1	+	+	2	3	2	3	3	2	+	+	3
	Sphagnum majus	Sphamaju	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	1	.	.	.	.	.	.	+	.	2	.	1	2	+	+	+	+	.
	Sphagnum palustre	Sphapalu	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Sphagnum rubellum	Spharube	.	.	.	.	.	.	.	.	.	.	.	2	1	1	1	.	.	.	2	.	+	.	+	+	.	.	+	.	2	2	2	1	1	.	2	3	+	.
	Sphagnum russowii	Spharuss	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	2	1	2	1	+	.	+	+	+
	Sphagnum tenellum	Sphatene	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	+
	Splachnum ampullaceum	Splaampu	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	+	.	.	.	.	.	.	.	.	.	.	.	.	.
	Tetraphis pellucida	Tetrpell	1	+	+	1	+	+	.	r	+	+	+	.	.	r	.	.	.	+	r	r	r	+	r	+	r	r	.	.	.	.	.	.	.	.	.	.	.	.
	Tetraplodon angustatus	Tetrangu	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Warnstorfia exannulata	Warnexan	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.

Disturbances on a wooded raised bog – how windthrow, bark beetle and fire affect vegetation and soil water quality?

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Abstract

A *Pinus rotundata*-dominated peatbog (Žofinka Nature Reserve) in the Třeboň Basin, Czech Republic, was affected by 'natural' disturbances: wind damage (in 1984), followed by a bark beetle attack, and fire (1994; 2000). Phytosociological relevés were used to document vegetation. Soil water chemistry was compared in three differently affected stands: (i) an undisturbed *Pinus rotundata* bog forest, (ii) a windthrow–bark beetle affected stand and (iii) a site burned by wildfire in 2000.

The species composition of the windthrow–bark beetle affected sites and the undisturbed *P. rotundata* bog forest differed mainly in the shrub and tree layers. Burned sites were partly colonized by anemochorous species (e.g. *Taraxacum* sp. div.) that disappeared within two or three years after colonization. Bare peat was colonized by bryophytes (e.g. *Marchantia polymorpha* and *Funaria hygrometrica*) typical of the disturbed sites, and by *Polytrichum* sp. div. and *Aulacomnium palustre*. Most plant species characteristic of the *P. rotundata* bog forest occurred at the burned sites eight years after the fire, but in different abundances. The edificator of the former community – *P. rotundata* – was mostly absent. Compared with windthrow followed by the bark beetle attack, fire promoted rapid expansion of *Molinia caerulea*.

Soil water in both the undisturbed *P. rotundata* bog forest and the windthrow–bark beetle affected sites had a similar composition: very low pH values, high P concentrations, low concentrations of cations (Ca^{2+}, Mg^{2+} and K^+) and inorganic nitrogen. The concentrations of soluble reactive phosphorus (SRP) and NH_4^+-N were negatively correlated with the groundwater table.

Total P, SRP and NH_4^+-N concentrations in the soil water at the burned site were by one order of magnitude higher than those in the *P. rotundata* bog forest, while concentrations of K^+, Mg^{2+} and Ca^{2+} were only about two times higher. High concentrations of P and N in the soil water found three years after the fire indicated a long-term elevated nutrient content in the soil water.

Keywords: Czech Republic, groundwater chemistry, nitrogen, phosphorus, *Pinus rotundata*, post-fire succession

Introduction

Windstorms, bark beetle infestation and fires are supposed as the natural processes in the long-term development of the northern taiga ecosystem (WEIN & MACLEAN 1983, FRELICH & REICH 1995). Understorey plant species of boreal forests are well adapted to frequent disturbances (ROWE 1983). However, such disturbances could have a strong effect on species diversity and ecosystem functions especially in size-limited protected areas. Nevertheless, natural long-term succession of wind- or fire-damaged forests was only rarely reported from Central Europe (cf. FISCHER et al. 2002, JONÁŠOVÁ & PRACH 2004).

The Central European *Pinus rotundata*-dominated bog communities (*Pino rotundatae-Sphagnetum* KÄSTNER & FLÖSSNER 1933 corr. NEUHÄUSL 1972) resemble the northern taiga ecosystem (JENÍK et al. 2002, for distribution see NEUHÄUSL 1972). The community occurs only as a relict on deep peatbogs up to 1000 m a.s.l (BUSINSKÝ 1998).

Windthrows create gaps that increase light and release other resources for understorey trees, herbs and seedling growth (MLADENOFF 1987). Both wind and insect infestations can alter competitive relationships between plants (i) directly through selective mortality, and (ii) indirectly because defoliation triggers carbon and nutrient release (BEUDERT 1999). Mosses without roots are mostly isolated from the groundwater table in *P. rotundata*-dominated peatbogs. This isolation occurs because of a regular drop in the groundwater table in summer (lowest groundwater table -65 cm below ground in late summer) and because the groundwater table never reaches the soil surface in this community (highest level -15 cm below ground in early spring, KUČEROVÁ et al. 2000). Therefore, precipitation remains the main source of nutrients for mosses. Obversely, vascular plants (ericoid shrubs, trees) could effectively absorb soil water nutrients through their roots. Therefore, any disturbance that increases the soil water nutrient concentration could change the competition pattern between vascular plants and mosses.

Fire induces drastic changes in the vegetation cover and the environment (e.g. changes in soil-moisture content, microclimate near the ground, irradiance). Burning could lead to increased nutrient levels, especially to extremely high peak concentrations for both P and K because of surface deposit of plant ash (TALLIS 1983). As a result, "nitrophilous" species or weedy plants dominate the initial recolonization stage. However, in a paleoecological study KUHRY (1994) suggested that the effect of local peat surface fires on vegetation cover is only short-term. Prefire conditions usually return within decades after the burning, and long-term vegetation development is not affected. It can be hypothesized that any nutrients released by burning are quickly leached out from permanently wet peatbogs.

In the 1970s the Žofinka peatbog was recognized as a well-preserved locality of the *P. rotundata* bog forest (KUČERA 1977). However, severe windthrows (in 1984) and a follow-up attack of insects destroyed most of the tree layer (LIŠKA et al. 1989). Further, two small fires affected the peatbog in 1994 and 2000. Approximately 3 ha were destroyed during each fire. Therefore, the locality offered an excellent opportunity to study the effects of different disturbance factors on initially similar sites. In this study, natural post-fire succession on a wooded raised bog was reported for the first time from Central Europe.

The objectives of this study were (i) to describe the post-fire colonization in the *P. rotundata*-dominated peatbog, and (ii) to compare vegetation and soil water quality at three differently disturbed sites on the peatbog – a burned site, a windthrow–bark beetle affected site, and an undisturbed *P. rotundata* bog forest.

Material and methods

Nomenclature

KUBÁT et al. (2002), KUČERA & VÁŇA (2003)

Study site

The study site (N 48°49‘, E 14°53’, 470–475 m a.s.l.) is located in the southern part of the Třeboň Biosphere Reserve in the Czech Republic, 22 km south of Třeboň (**Fig. 1**). The Žofinka peatbog (130 ha) is a continental raised bog (sensu NEUHÄUSL 1972) or treed bog. The tree layer consisted of uneven-aged stands of *Pinus rotundata* (monocormic species from the *Pinus mugo* complex, BUSINSKÝ 1998), with small admixture of *Pinus sylvestris* (max. 10%). The herb layer included ericoid dwarf shrubs (*Ledum palustre, Vaccinium myrtillus, V. vitis-idaea* and *V. uliginosum*) and the moss layer was dominated especially by *Sphagnum* species (e.g. *S. fallax* and *S. capillifolium*), *Dicranum polysetum, Polytrichum formosum* and *Pleurozium schreberi*.

Severe windthrow (in 1984) disturbed the most valuable stands of the *P.*

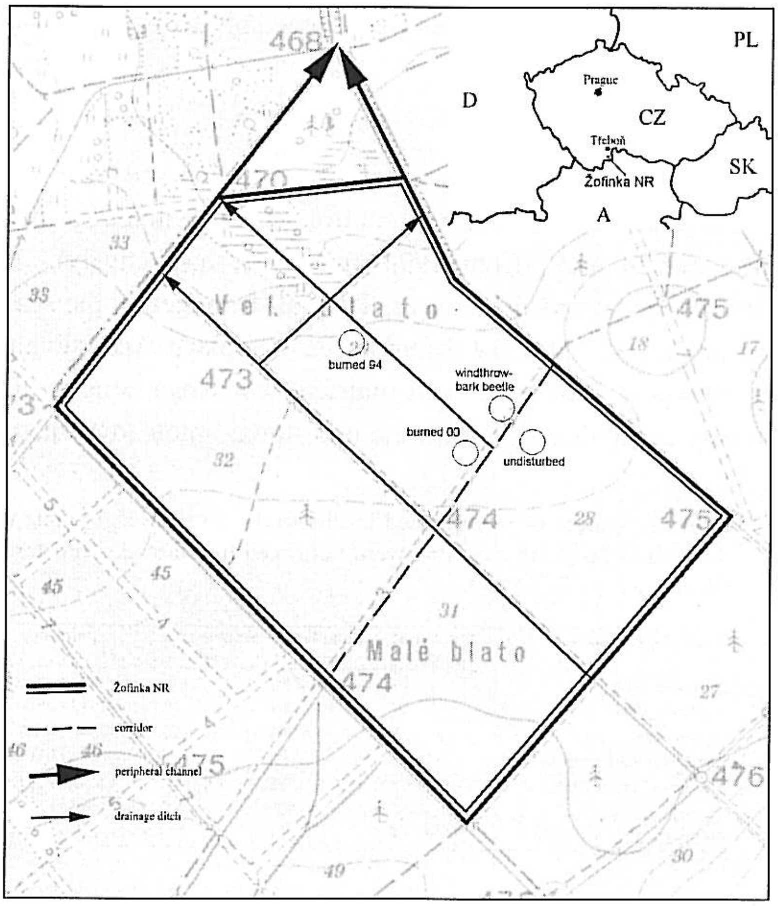

Fig. 1. Localization of plots burned in 1994 (burned 94), burned in 2000 (burned 00), windthrow-bark beetle affected (windthrow-bark beetle), and plots in undisturbed *P. rotundata* forest (undisturbed) in the Žofinka peatbog. For localization of the study site in Central Europe see the inset diagram.

rotundata bog forest. Many small- and large-scale windthrows became a food basis for the next bark beetle infestation. LIŠKA et al. (1989) reported the large-scale attack of different species of wood engraver on living *P. rotundata* trees in 1988. The former *P. rotundata* bog forest persisted only in fragments. Further, two small fires affected the peatbog in 1994 and in 2000.

The Žofinka peatbog is situated in a shallow depression of cretaceous bedrock. The bedrock is made up of sediments of the Klikov series – sand, clay and clayey sand (KOROŠ et al. 1998) and is very acidic and poor in nutrients. According to KOROŠ et al. (1998), the peatbog originated from a gradual local subsidence of the cretaceous bedrock, consequently followed by a local increase in the groundwater table. The bog surface is flat and maximum peat depth is about 4 m. Two deep drainage channels demarcate the Reserve in the NW and NE. Two shallow drainage ditches (ca. 0.5 m deep), penetrate the central part of the bog in the NW–SE direction.

Mean annual temperature is 7.8 °C in the Třeboň Basin (PŘIBÁŇ et al. 1992) and mean temperature in the vegetation period (April–September) is about 14 °C. Total annual precipitation is about 600–650 mm. Precipitation in summer is appreciably higher (400–450 mm) than in winter.

Vegetation data sampling

The following sampling sites were chosen for the comparison of vegetation and soil water chemistry: (i) an undisturbed *P. rotundata* bog forest site as control, (ii) the windthrow–bark beetle affected site, and (iii) the burned sites (from 1994 and 2000, respectively). All sampling sites were situated in the central part of the reserve. They all belonged to the same vegetation type – the *P. rotundata* bog forest – until the disturbances took place. According to terrain slope and hydrological situation, the water and nutrient exchange among the experimental plots were possible only in the direction from the undisturbed plots towards the burned plots (cf. **Fig. 1**).

Sampling plots **(Table 1)** were located in a subjective way to best represent the type of disturbance. At each plot, vegetation was recorded using the phytosociological relevé method. The nine-degree Braun-Blanquet cover scale as modified by VAN DER MAAREL (1979) was used.

Table 1. Sources of relevés used in this study. [a] – only eight plots were sampled in 2002, because two were destroyed by other experiments. [b] – relevé made by S. Kučera.

Type of disturbance	Number of samples	Sampling year	Sample area (m^2)	Reference
burned in 2000	10	2001, 2002	25	JAKŠIČOVÁ (2003)
burned in 1994 [a]	10	2001, 2002	25	JAKŠIČOVÁ (2003)
undisturbed	5	2002	25	JAKŠIČOVÁ (2003)
windthrow-bark beetle in 1984	5	2002	25	JAKŠIČOVÁ (2003)
windthrow-bark beetle in 1984	5	1998	400	KUČEROVÁ et al. (2000)
burned in 1994	1	1998	400	KUČEROVÁ et al. (2000)
undisturbed [b]	4	1971	500	KUČEROVÁ et al. (2000)

Chemical analysis

Test water sampling was made in all studied sites during 2001 (three samples in each site, incl. site burned in 1994). In June 2002 new dipwells (perforated PVC pipes, 1 m long, diameter 50 mm) were inserted into the peat to a depth of up to 70 cm in the following sampling sites: (i) the undisturbed *P. rotundata* bog forest site, (ii) the windthrow–bark beetle affected site, and (iii) the site burned in 2000. In each sampling site three dipwells were installed at a 10-m distance from the permanent plots. All dipwells were covered with small caps to prevent water contamination from litter or insects. Before the first sampling at the beginning of the growing season, all dipwells were emptied to clean them sufficiently. Two 100-ml samples were taken from the top of the groundwater table. After sampling the dipwells were emptied again. Groundwater table levels were measured before the water sampling. The sampling interval was ca 4 weeks during the growing season. In total nine samples were taken from each dipwell (four samples during 2002 and next five in 2003).

Water samples were stored in a refrigerator, while pH and conductivity were measured at 20 °C within 24 hours. The conductivity was reduced for H^+ activity according to SJÖRS (1952). The concentrations of NH_4^+-N, NO_3^--N, NO_2^--N, Cl^-, SO_4^{2-} and soluble reactive phosphorus (SRP) were determined in samples filtered through Whatman GF/C filters using a Tecator flow injection analyzer. The gas diffusion method was used to estimate NH_4^+-N (KARLBERG & TWENGSTRÖM 1983). The reaction of nitrite with sulfanilamide and N-(1-naphtyl)-ethylenediamine was used to determine NO_2^--N. NO_3^--N was determined as nitrite after reduction of the sample on the Cd-Cu column. The standard phosphomolybdenum complex method was used for SRP determination. The total N (TN) and total P (TP) values were determined as NO_3^--N and SRP respectively, after mineralization of samples using persulphate (GRASSHOFF et al. 1983). Cations (Ca^{2+}, Mg^{2+}, K^+, Al^{3+} and Fe^{3+}) were analyzed using an atomic absorption spectrophotometer Sectr AA640 (Varian Techtron, Australia) at the Chemistry Department of the Agricultural Faculty of the University of South Bohemia, České Budějovice.

Atmospheric deposition data was taken from the Lužnice station, ca. 20 km N of the Žofinka peatbog, which was reported annually in ANONYMOUS (1999–2003). Element concentrations represented bulk deposition (wet plus dry deposition).

Statistical analysis

Constrained ordination technique Redundancy Analysis (RDA) was used to analyze the vegetation composition relative to the time passed since the fire (36 relevés in total). Age since the fire (in years) was used as an environmental factor. Statistical significance of the age since the fire was tested using the Monte-Carlo permutation test (split-plot design for correction of repeatedly sampled plots). Only repeatedly sampled plots were used in this analysis (one 4-year-old and two 7-year-old burned plots that were destroyed in 2002 were excluded). Unconstrained ordination technique Principal Components Analysis (PCA) was used to analyze the vegetation composition of burned, windthrow–bark beetle and undisturbed sites (58 relevés in total). All relevés including ten older ones with different area (**Table 1**) were used in this analysis. Isolines of the Shannon-Weaver diversity index (SHANNON & WEAVER 1949) were projected onto the resulting graph. The Canoco for Windows 4.5 package (TER BRAAK & ŠMILAUER 2002) was used for all multivariate vegetation analyses.

Effects of disturbance type, sampling time and their interaction with water chemistry were tested using repeated measures ANOVA (Statistica 6 package; STATSOFT 2003) followed by the post-hoc comparison, Tukey´s test. Prior to the analysis, data were log-transformed ($\log_{10}[x+1]$) because of unequal group variance and to improve normality. Correlation analysis (Pearson r correlation coefficient) was applied to log-transformed data (except pH) to unravel patterns of variation in water chemistry. For the correlation analysis the data from the burned site and those unaffected by fire were treated separately.

Table 2. Comparison of water chemistry (means and standard deviations in parentheses) of the undisturbed *P. rotundata* forest, windthrow-bark beetle affected site and burned site on the Žofinka peatbog during 2002–2003. N = 27 for each site. The highest concentrations of all chemical variables were measured at the burned site. Means followed by the same letter within a row are not significantly different at $P = 0.05$ based on ANOVA and Tukey's HSD tests. Significantly different means are in bold. Electrical conductivity (ECcorr) is expressed as µS cm^{-1}, and element concentrations as mg l^{-1}.

	Undisturbed *P. rotundata* forest	**Windthrow– bark beetle site**	**Site burned in 2000**
ECcorr	2^{a} (42)	13^{a} (19)	**59^{b}** (65)
pH	**3.42^{a}** (0.20)	3.84^{b} (0.26)	4.00^{b} (0.81)
NH_4^+-N	0.93^{a} (0.64)	0.76^{a} (0.54)	**8.06^{b}** (10.31)
NO_2^--N	0.05^{a} (0.03)	0.04^{a} (0.02)	**0.12^{b}** (0.09)
NO_3^--N	0.19^{a} (0.22)	0.08^{a} (0.08)	**0.74^{b}** (1.73)
Total N	3.74^{a} (1.12)	3.44^{a} (1.19)	**15.03^{b}** (12.52)
Cl^-	**9.11^{a}** (4.41)	**5.63^{b}** (2.80)	**11.48^{c}** (3.88)
SRP	0.08^{a} (0.06)	0.11^{a} (0.07)	**1.38^{b}** (0.94)
Total P	0.16^{a} (0.05)	0.18^{a} (0.07)	**1.35^{b}** (1.09)
Na^+	0.75^{a} (0.40)	**0.48^{b}** (0.27)	0.84^{a} (0.29)
Mg^{2+}	0.42^{a} (0.12)	0.41^{a} (0.19)	**0.85^{b}** (0.35)
Ca^{2+}	2.70^{a} (2.60)	3.98^{a} (4.38)	**4.93^{b}** (4.38)
K^+	**0.92^{a}** (0.41)	**0.51^{b}** (0.18)	**2.44^{c}** (0.82)
Fe^{n+}	1.84^{a} (0.74)	1.71^{a} (1.21)	2.44^{a} (1.38)
Al^{3+}	0.96^{a} (0.48)	**0.61^{b}** (0.47)	1.08^{a} (0.58)

Results

Soil water chemistry of the undisturbed *Pinus rotundata* bog forest

The soil water was very acidic (mean pH = 3.42) with the lowest corrected conductivity (**Table 2**). The concentrations of all forms of inorganic nitrogen were low (inorganic N = 1.17 mg l^{-1}). Ammonium nitrogen predominated over the nitrate nitrogen. The concentrations of inorganic P (mean 0.08 mg l^{-1}) were half of the concentrations of TP. The ratio TN:TP was 23:1 indicating slight P deficiency in soil water (TN:TP > 16, AERTS et al. 1999). The Ca^{2+} concentrations ranged between 0.9-2.8 mg l^{-1} in 2003 (**Fig. 2d**). Cation sum ($Ca^{2+} + Mg^{2+} + K^+ + Na^+ + H^+$) was 459 µeq l^{-1}. The *P. rotundata* bog forest had the highest proportion of H^+ and the lowest proportion of Ca^{2+} and Mg^{2+} of the total cations (**Table 3**).

Table 3. Comparison of the ionic composition of rain and soil water (means and standard deviations in parentheses) on the Žofinka peatbog in equivalent charges of ions (µeq l^{-1}). N = 5 for rain water (1999-2003) and N = 15 for soil water for each site in 2003. The highest concentrations of almost all chemical variables were measured at the burned site. Means followed by the same letter within a row are not significantly different at P = 0.05 based on ANOVA and Tukey's HSD tests (only directly comparable values between study sites were tested). Significantly different means are in bold. The cation sum was calculated as sum of H^+, Na^+, Mg^{2+}, Ca^{2+} and K^+. Rainwater data were annually measured means taken from bulk collectors in the Lužnice station, ca. 20 km N of the Žofinka peatbog.

	Rainwater	**Undisturbed *P. rotundata* forest**	**Windthrow– bark beetle site**	**Site burned in 2000**
Cation sum	111 (69)	459^{a} (122)	**302^{b}** (106)	463^{a} (179)
H^+	12 (5)	322^{a} (114)	176^{ab} (89)	129^{b} (93)
Na^+	14 (6)	**21^{a}** (4)	**14^{b}** (4)	**34^{c}** (6)
Mg^{2+}	13 (10)	31^{a} (10)	37^{a} (19)	**81^{b}** (31)
Ca^{2+}	53 (38)	60^{a} (19)	61^{a} (24)	**145^{b}** (117)
K^+	19 (14)	**25^{a}** (10)	**14^{b}** (3)	**74^{c}** (17)
NH_4^+	39 (20)	84^{a} (50)	64^{a} (48)	**965^{b}** (794)
Cl^-	32 (30)	**208^{a}** (117)	**116^{b}** (39)	**315^{c}** (96)

The concentrations of H^+, NH_4^+, and Cl^- were elevated in soil water in comparison to rainwater (**Table 3**). The most pronounced difference was in H^+ concentrations (26.8× higher in soil water in the *P. rotundata* bog forest than in rainwater). Similarly, the mean Cl^- concentration in soil water distinctly exceeded the mean Cl^- concentration in rainwater (**Table 3**).

The concentration of the possibly toxic ion Al^{3+} was quite high in comparison with the base cation concentration.

Soil water chemistry of the windthrow–bark beetle affected site

The soil pH was slightly higher, but still very acidic (mean pH = 3.84) with low corrected conductivity (**Table 2**). No significant differences in forms of nitrogen and phosphorus were found between the undisturbed *P. rotundata* bog forest and the windthrow–bark beetle affected site. Cation sum (302 μeq l^{-1}) was lower than in the *P. rotundata* bog forest (**Table 3**). Considering the proportions of cations, K^+, Na^+ and Mg^{2+} were of a fairly equal importance. The concentrations of both Ca^{2+} and Mg^{2+} were low and similar to those measured at the undisturbed *P. rotundata* bog forest. The concentrations of Cl^-, Na^+, K^+ and Al^{3+} were significantly lower than at the previous site (**Table 2**).

Soil water chemistry of the burned site

The soil water was still very acidic (mean pH = 4.00) with medium corrected conductivity (**Table 2**). The concentrations of NH_4^+-N, SRP (soluble reactive phosphorus) and TP were by one order of magnitude higher at the burned site than those at stands unaffected by fire (**Table 2**). The concentrations of NO_2^--N, NO_3^--N, and TN were several times (2.5×, 4× and 4×, respectively) higher (**Table 2**). Similar to the stands unaffected by fire, ammonium nitrogen predominated over the nitrate nitrogen. Extremely high concentrations of SRP (max. 4.03 mg l^{-1}) and total phosphorus (max. 4.31 mg l^{-1}) were found in the soil water especially three years after the fire (see **Fig. 2b**). The concentrations of SRP and TP were rather similar indicating that most of P was in dissolved inorganic form in the soil water.

We also found similarly high concentrations of SRP and total P in both newly (burned in 2000, SRP 0.42 mg l^{-1}) and old burned sites (burned in 1994, SRP 0.37 mg l^{-1}) during test measurements of soil water quality in 2001 (**Fig. 2b**).

The concentrations of metallic cations (K^+, Mg^{2+} and Ca^{2+}) were significantly higher at the burned site than those at stands unaffected by fire, however, they reached only several mg l^{-1}. The proportion of bases was quite similar to the previous two stands, while NH_4^+-N represented a considerably higher proportion of cations (**Table 3**). No significant differences in concentrations of Fe^{n+} were found throughout all three sites.

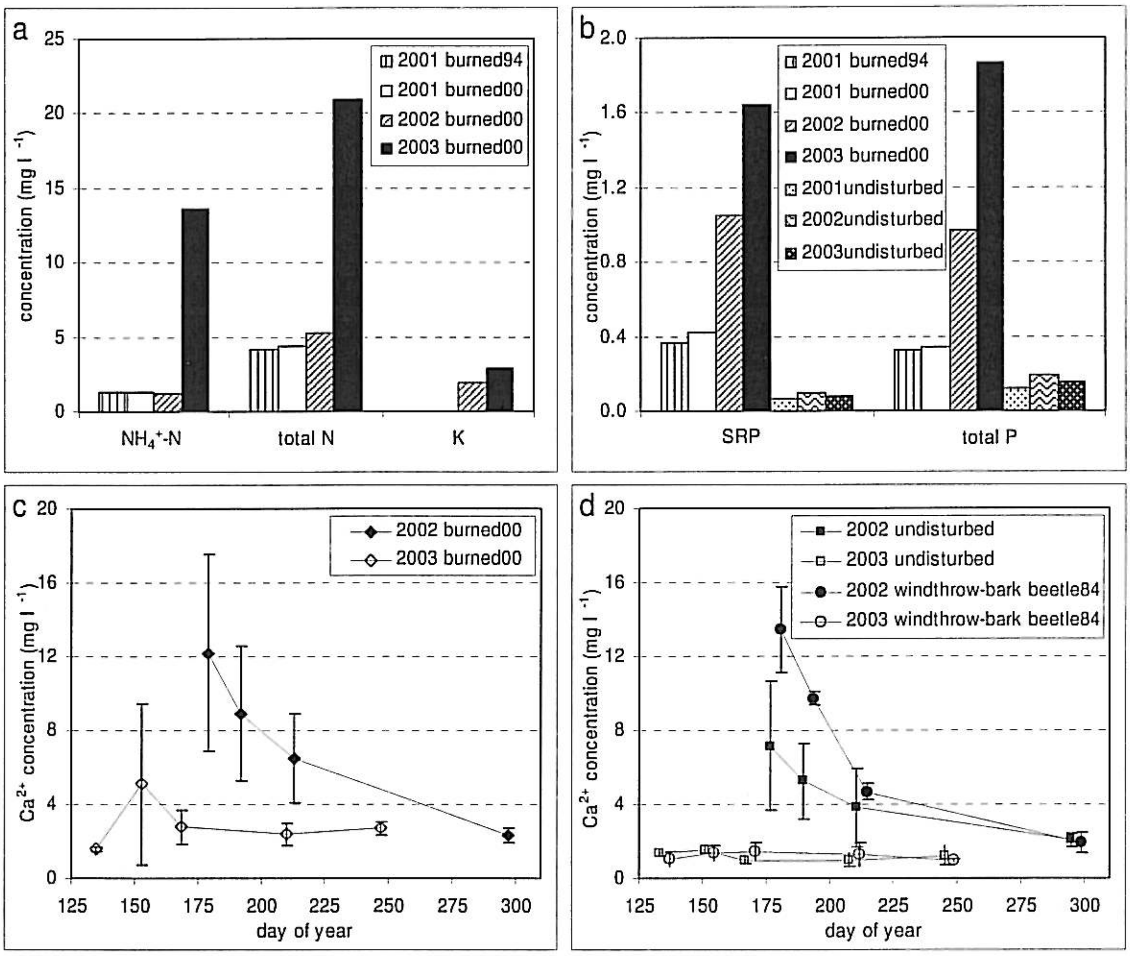

Fig. 2. (a) Increasing concentrations of NH_4^+-N, total N and K^+ at the site burned in 1994 (burned94) and 2000 (burned00) during three growing seasons (2001–2003). (b) Increase of soluble reactive phosphorus (SRP) and total P concentrations in soil water at the burned sites compared with soil water concentrations in the *Pinus rotundata* forest (undisturbed) during three growing seasons (2001-2003). In some cases concentrations of total P were ca 10% lower than the concentrations of SRP, which is in the range of analytical error. (c) Steadily decreasing Ca^{2+} concentrations at the site burned in 2000. (d) Decreasing Ca^{2+} concentrations in the *P. rotundata* forest and at the windthrow-bark beetle affected site (windthrow-bark beetle84) during the 2002 growing season, compared to the stable low Ca^{2+} concentrations in 2003. Points for the windthrow sites are slightly shifted (+3 days) on x-axis to reduce overlapping with undisturbed sites. The first four digits in the legend mean the year of soil water sampling.

Annual and seasonal variability in water chemistry

Statistically significant increases of mean concentrations of NH_4^+-N ($F = 71.05$, $P << 0.001$), NO_2-N ($F = 6.28$, $P = 0.02$), total P ($F = 9.43$, $P = 0.006$), total N ($F = 27.91$, $P << 0.001$), K^+ ($F = 11.67$, $P = 0.003$), Mg^{2+} ($F = 7.88$, $P = 0.01$), Fe^{n+} ($F = 20.00$, $P = 0.0002$) and Al^{3+} ($F = 14.28$, $P = 0.001$) were found at the burned site between 2002 and 2003 (repeated measures ANOVA, post-hoc comparison Tukey test). For example, the mean concentration was twofold higher for TP, almost 4 times as high for TN and 10 times as high for NH_4^+-N in 2003 than in 2002 at the burned site. Additionally, according to measurements of water quality done in 2001, the concentrations of SRP, total P and total N showed a steady increase between 2001 and 2003 at the burned site (**Fig. 2a, b**). At the same time, the mean concentrations of the above-mentioned nutrients were similar at both the *P. rotundata* bog forest and windthrow–bark beetle affected site, except for the Fe^{n+} increase at the windthrow–bark beetle affected site in 2003.

There was a marked decline, however, in concentrations of Ca^{2+} and Na^{+} throughout all sites from 2002 to 2003. Concentrations of Ca^{2+} steadily decreased during the 2002 growing period, being the highest at the burned site and windthrow–bark beetle affected site (**Fig. 2c, d**).

At both the *P. rotundata* bog forest and the windthrow–bark beetle affected site, the concentrations of SRP, NH_4^+-N, TP, and pH were negatively correlated with the groundwater table (**Table 4**). Corrected conductivity did not correlate with pH while it correlated positively with NH_4^+-N, SRP, NO_2^--N, Cl^-, TN and Fe^{n+}. At the burned site, only Fe^{n+} concentrations correlated significantly with the groundwater table (**Table 4**). Both corrected conductivity and pH correlated positively with the concentrations of NH_4^+-N, SRP, TP and TN.

Table 4. Correlation coefficients between chemical variables and groundwater table (GWT) for the undisturbed *P. rotundata* forest and windthrow–bark beetle affected site (part under diagonal), and for the burned site (part above diagonal), respectively. Log-transformation ($\log_{10}[x+1]$) was applied to all variables except pH. Correlations marked bold are significant ($P < 0.05$). N = 27 for each variable. Grey cells indicate pairs of significant-insignificant (or vice versa) correlation coefficients between the undisturbed plus windthrow–bark beetle affected site and the burned site, respectively.

	ECcorr	pH	NH_4^+-N	SRP	NO_2^--N	NO_3^--N	Cl^-	Total N	Total P	Na^+	Mg^{2+}	Ca^{2+}	K^+	Fe^{n+}	Al^{3+}	GWT
Eccorr		0.91	0.63	0.89	0.45	0.05	0.34	0.83	0.84	0.19	-0.10	-0.04	0.29	0.29	0.22	-0.17
pH	0.09		0.60	0.91	0.67	-0.21	0.50	0.75	0.90	-0.01	-0.35	-0.21	0.15	0.35	0.27	-0.09
NH_4^+-N	0.64	0.38		0.51	0.42	-0.28	0.54	0.40	0.45	0.16	-0.11	-0.03	0.21	0.47	0.24	-0.11
SRP	0.48	0.51	0.81		0.65	-0.08	0.46	0.84	0.95	-0.10	-0.31	-0.18	0.06	0.31	0.29	-0.16
NO_2^--N	0.36	-0.69	0.09	0.09		-0.45	0.65	0.59	0.70	-0.17	-0.53	-0.34	0.25	0.30	0.34	0.16
NO_3^--N	-0.03	-0.30	0.15	-0.21	-0.04		-0.84	0.05	-0.15	0.38	0.77	0.14	0.34	-0.51	-0.52	-0.10
Cl^-	0.59	-0.66	0.17	0.08	0.87	0.02		0.35	0.50	-0.24	-0.61	-0.13	-0.17	0.63	0.70	-0.08
Total N	0.57	-0.27	0.71	0.55	0.59	0.30	0.63		0.91	0.13	-0.27	-0.07	0.36	0.04	0.21	0.16
Total P	0.27	0.36	0.63	0.82	0.03	-0.08	0.03	0.55		-0.05	-0.44	-0.26	0.12	0.20	0.29	0.04
Na^+	0.33	-0.68	0.19	0.03	0.82	0.13	0.82	0.65	0.07		0.40	0.16	0.80	-0.19	-0.34	-0.06
Mg^{2+}	0.34	0.05	0.37	0.49	0.45	-0.25	0.37	0.50	0.42	0.49		0.26	0.27	-0.23	-0.23	-0.34
Ca^{2+}	0.32	-0.23	0.26	0.31	0.61	-0.24	0.58	0.48	0.19	0.70	0.79		0.01	-0.12	0.24	-0.06
K^+	0.35	0.01	0.60	0.20	-0.03	0.45	0.11	0.44	0.27	0.30	-0.15	-0.06		-0.15	-0.34	0.13
Fe^{n+}	0.37	-0.11	0.32	0.40	0.61	-0.25	0.53	0.55	0.30	0.60	0.92	0.82	-0.20		0.39	-0.70
Al^{3+}	0.26	-0.52	-0.03	-0.04	0.59	-0.18	0.58	0.39	-0.08	0.49	0.16	0.41	-0.13	0.37		-0.15
GWT	-0.36	-0.66	-0.66	-0.64	0.28	0.29	0.23	-0.21	-0.43	0.21	-0.26	-0.08	-0.21	-0.21	0.05	

Post-fire vegetation succession

Three categories of species could be distinguished from the burned sites (RDA analysis, **Fig. 3**): (i) initial colonizers – the species whose cover negatively correlated with the environmental factor "age = time after the fire" (left half of the RDA plot). The most common were anemochorous species (weedy species e.g. *Taraxacum* sp. div., *Epilobium* sp. div., *Conyza canadensis, Senecio* sp. div.), seedlings of *Populus tremula* and *Salix* sp. div., and the bryophytes typical for disturbed sites, e.g. *Marchantia polymorpha, Ceratodon purpureus, Pohlia nutans* and *Funaria hygrometrica*. Further, species typical for the *P. rotundata* bog forest – *Avenella flexuosa* and juveniles of *Frangula alnus* were among the first colonizers; (ii) the species whose cover positively correlated with "age = time after the fire". These are characteristic species of the wooded peatbogs, e.g. ericaceous dwarf shrubs (*Vaccinium*

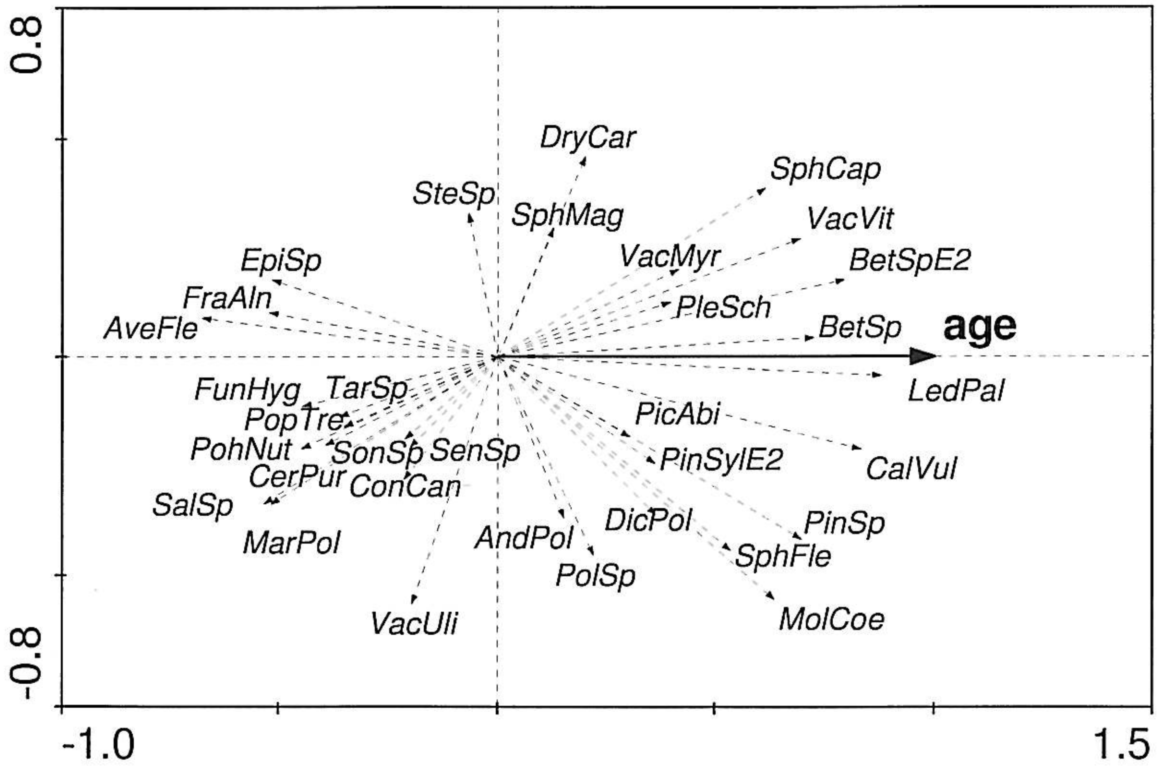

Fig. 3. Post-fire succession in the Žofinka peatbog with shrub and tree layers included in the analysis (species plot of the RDA analysis, sample plots from the sites burned in 1994 and 2000, respectively). Age of the burned site was used as an environmental factor. The first RDA axis explained 31% of the variability in the species data. The effect of age of the burned site was highly significant (Monte Carlo permutation test, N = 999, $P = 0.001$; F-ratio =15.25).

AndPol (*Andromeda polifolia*), *AveFle* (*Avenella flexuosa*), *BetSp* (*Betula* sp.), *BetSpE2* (*Betula* sp. E2), *CalVul* (*Calluna vulgaris*), *CerPur* (*Ceratodon purpureus*), *ConCan* (*Conyza canadensis*), *DicPol* (*Dicranum polysetum*), *DryCar* (*Dryopteris carthusiana*), *EpiSp* (*Epilobium* sp.), *FraAln* (*Frangula alnus*), *FunHyg* (*Funaria hygrometrica*), *HylSpl* (*Hylocomium splendens*), *LedPal* (*Ledum palustre*), *LeuGla* (*Leucobryum glaucum*), *MarPol* (*Marchantia polymorpha*), *MolCoe* (*Molinia caerulea*), *OxyPal* (*Oxycoccus palustris*), *PicAbi* (*Picea abies*), *PinSp* (*Pinus* sp.), *PinSylE2* (*Pinus sylvestris* E2), *PleSch* (*Pleurozium schreberi*), *PohNut* (*Pohlia nutans*), *PolSp* (*Polytrichum* sp.), *PopTre* (*Populus tremula*), *SalSp* (*Salix* sp.), *SenSp* (*Senecio* sp.), *SonSp* (*Sonchus* sp.), *SphCap* (*Sphagnum capillifolium*), *SphFle* (*Sphagnum flexuosum*), *SphMag* (*Sphagnum magelanicum*), *SteSp* (*Stellaria* sp.), *TarSp* (*Taraxacum* sp.), *VacMyr* (*Vaccinium myrtillus*), *VacUli* (*Vaccinium uliginosum*), *VacVit* (*Vaccinium vitis-idaea*)

myrtillus, V. vitis-idaea, Ledum palustre, Calluna vulgaris), *Betula* sp. div., *Picea abies* and bryophytes *Pleurozium schreberi, Dicranum polysetum* and *Sphagnum capillifolium*; (iii) the species whose cover did not correlate with "age = time after the fire", e.g. *Dryopteris carthusiana, Andromeda polifolia, Vaccinium uliginosum, Polytrichum* sp. and *Sphagnum magellanicum.*

The moss layer especially regenerated in the wet depressions. Ericoid shrubs regenerated quickly, mostly by resprouting from underground fragments but only seedlings of *Calluna vulgaris* were found more frequently. Seedlings of both Scots pine (*Pinus sylvestris*) and birch (*Betula* sp. div.) often occurred, however, the edificator of the former community – *P. rotundata* – was mostly absent.

Vegetation of disturbed sites

Vegetation relevés from differently affected stands (burned, windthrow–bark beetle and undisturbed, respectively) were analyzed using the PCA ordination with only species of the moss and herb layers included (both species from shrub and tree layers excluded, **Fig. 4a, b**). The stands were clearly distinguished according to the type of disturbance. The most similar sample plots were those from the first and second and those from the seventh and eighth year after the fire (**Fig. 4b**). The sample plot from the fourth year after the fire was closer to sample plots from the seventh and eighth year after the fire. Sample plots from the windthrow–bark beetle affected sites were most similar to the undisturbed *P. rotundata* bog forest. Few sample plots differing in their area did not affect this pattern and appeared mixed or close to the plots with the same type of disturbance.

Anemochorous species, indicating stands shortly after the fire (left half on the species plot, **Fig. 4a**) usually disappeared within two or three years. During the post-fire succession especially *Molinia caerulea* and saplings of *Betula* sp. started to dominate in the understorey (upper part on the species plot, **Fig. 4a**).

A luxuriant herb layer of ericoid dwarf shrubs (*Ledum palustre, Vaccinium myrtillus, V. vitis-idaea,* and *V. uliginosum*), low scattered trees (up to 8 m), dead trees and snags were the characteristic feature of the stands disturbed by wind or by both wind and insect infestation. *Sphagnum flexuosum* or *S. fallax* and some dwarf shrubs (*Oxycoccus palustris*) occurred in wet depressions created by uprooted trees (right half on the species plot, **Fig. 4a**). Compared to the undisturbed *P. rotundata* forest, *Frangula alnus, Betula pendula,* and *Pinus sylvestris* occurred often in the lower tree layer. Therefore, sample plots from the windthrow–bark beetle affected sites were mixed-up with sample plots from the undisturbed *P. rotundata* bog forest only when both species from shrub and tree layers were excluded from the ordination (**Fig. 4b**).

Understorey plant communities of undisturbed *P. rotundata* forest and that developed after fire and windthrow followed by bark beetle attack shared all herb species and ca. 65% of moss species, even if the total cover of herb and tree layer was quite different. *Frangula alnus* occurred in highest abundances in windthrow–bark beetle affected sites (1% mean coverage in 18-year-old plots) followed by old burned plots (mean coverage 0.4% in 7- and 8-year-old plots) and was absent in undisturbed plots. Fire promoted a rapid expansion of *Molinia caerulea* (mean coverage 27% in 7- and 8-year-old burned plots in comparison with 4.7% in the 18-year-old windthrow–bark beetle affected plots). *Molinia caerulea* had very low coverage in undisturbed plots (mean coverage 0.1% in relevés from 2002).

The lowest species diversity indicated by Shannon's index (**Fig. 4b**) was found for 1-year-old burned plots. After that there is a growth of diversity towards wind-damaged and undisturbed *P. rotundata* forest.

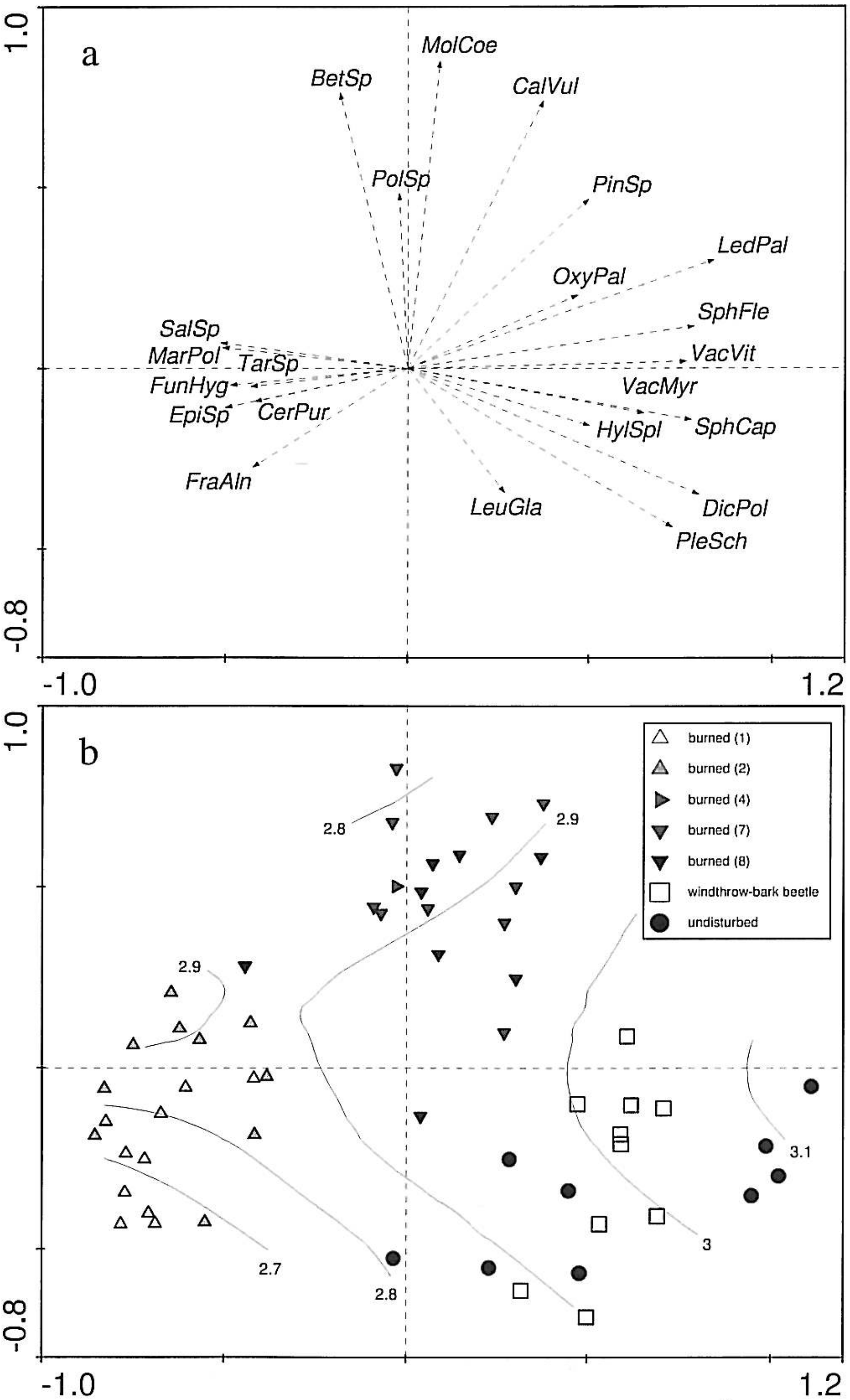

Fig. 4. Increasing species diversity from differently affected to undisturbed plots in the Žofinka peatbog with shrub and tree layers excluded from the analysis. Species (a) and samples (b) plot of the PCA analyses are depicted, with samples from burned (number in brackets indicates time since burning in years), windthrow–bark beetle affected and undisturbed *P. rotundata* sites. Isolines correspond to Shannon-Weaver index of species diversity. The first and second PCA axes explained 30.7% and 15.0% of the variability in the species data, respectively. For explanation of species abbreviations see Fig. 3.

Discussion

Vegetation of windthrow–bark beetle affected and undisturbed sites

Unlike fires, both windthrow and bark beetle outbreak directly affected only canopy trees. Therefore, the species composition at windthrow–bark beetle affected sites and at undisturbed *P. rotundata* bog forest differed mainly in shrub and tree layers. A new tree layer was established especially by young individuals of *P. rotundata* (partly also by *P. sylvestris*), which were already present as saplings in the stands prior to the disturbance (KUČEROVÁ, unpubl. data). Similarly, FISCHER et al. (2002) documented a successful regeneration of the spruce tree layer from the young spruce saplings already present on plots destructed by windstorm in the Bavarian National Park.

However, *P. sylvestris* saplings became more abundant than *P. rotundata* saplings at the windthrow–bark beetle affected sites. Higher admixture of *P. sylvestris* in the new tree layer would increase the possibility of the next introgressive hybridization of the *P. rotundata* population with *P. sylvestris* on the locality – the process already documented for several *P. rotundata* populations in the Třeboň Basin (BUSINSKÝ 1998, REKTORIS et al. 2003). Therefore, further long-term prosperity of the *P. rotundata* population seems quite uncertain in the Žofinka peatbog.

Almost all species of both herb and moss layer successfully survived (or recolonized the site) 18 years after canopy break-up. Nevertheless, some species (especially *Frangula alnus* and *Molinia caerulea*) occurred in higher abundances at the windthrow–bark beetle affected sites. Both species could be positively affected by disturbance event (soil disturbance, higher light levels) or by higher nutrient concentrations. However, no differences were found in N and P soil water concentrations at the undisturbed *P. rotundata* bog forest and at the windthrow–bark beetle affected site. Release of nutrients from fallen trees has been rather slow in contrast to fire. Released nutrients were probably incorporated into the already present ericoid shrubs and mosses, allowing them to expand their coverage. Both species (*Frangula alnus* and *Molinia caerulea*) probably expanded from the already present individuals to the places with low herb and moss coverage in between former trees being supported by higher light levels. As the stands were not cleared after the windstorm the soil disturbance was restricted to the pit-and-mound system created by uprooted trees. Such places were colonized by several pioneer species (*Rubus idaeus*, *Betula* sp., etc.) in mountain spruce forests in the Bavarian Forest National Park (FISCHER et al. 2002). In our case the pits were primarily suitable for the colonization of *Sphagnum* sp. due to the high groundwater table while dry-tolerant mosses and lichens especially colonized mounds.

Post-fire vegetation succession

HOLUBIČKOVÁ (1960) reported surface peat fires from the Mrtvý luh peatbog (Upper Vltava river valley) in the 20th century. The post-fire vegetation was similar to that in undisturbed stands, only trees and some sensitive species were absent (e.g. *Andromeda polifolia* and *Oxycoccus palustris*). This record corresponded with our findings. JANKOVSKÁ

(1980), however, found evidence of the effect of periodic fires on the *P. rotundata*-dominated peatbogs in the Třeboň Basin during the Subatlantic period (charcoal layers in peat sediments in Červené blato bog, 10 km from the study site, and Borkovická blata bog). Those probably deep ground fires temporarily increased the cover of the *Rhynchosporion albae* KOCH 1926 communities, especially of *Scheuchzeria palustris*. The former *P. rotundata*-dominated communities regenerated during the time.

In some aspects, the post-fire succession in the *P. rotundata* bog forest seems to resemble the post-clearing succession in mountain spruce forests (FISCHER et al. 2002, JONÁŠOVÁ & PRACH 2004). Fire created large-scale open habitats very suitable for invading species similar to that usually made during forest clearing. During succession weeds quickly disappeared and the grasses (*Calamagrostis villosa* in spruce forest, FISCHER et al. 2002, compared to *Molinia caerulea* in the *P. rotundata* bog forest) started to dominate in the herb layer. Both vascular plants and mosses characteristic of the *P. rotundata* bog forest steadily increased their abundance during the post-fire succession. However, the abundance of light- and nutrient-demanding species increased markedly in comparison to the former *P. rotundata* bog forest. Additionally, the edificator of the former community – *P. rotundata* – decreased considerably in favour of *P. sylvestris* and *Betula* sp. div.

Soil water was still very acidic and deficient in cations even after total mineralization of surface organic matter by burning and subsequent increase of nutrient concentrations for plant growth (especially N and P, see **Table 2**). This corresponded with the post-fire vegetation succession. During a very short period (2-3 years) the present species were mostly the same as those at the unaffected stands, i.e., acidophilous species tolerating low cation saturation.

Almost all dissolved phosphorus in the soil water was present in inorganic form indicating low microbial activity. The excess of N and P in soil water could result from a relatively low uptake of these nutrients by sparse vegetation in the beginning of the post-fire succession. Additionally, the species present probably could not use all available nutrients because of their slow growth, high nutrient reutilization or a relative unavailability of these nutrients due to low pH as speculated for bog plants by several authors (WAUGHMAN 1980, AERTS et al. 1999).

However, high concentrations of both inorganic N and P available in both soil surface and soil water along with the effect of disturbance probably had a positive effect on the growth of some plants (e.g. vigorous growth of *Molinia caerulea* and *Betula* sp.). LOACH (1968) documented very large growth increases of *Molinia caerulea* after P additions in combination with other elements (N, K). *Molinia caerulea* is even tolerant of burning (TAYLOR et al. 2001), so it could very rapidly colonize the burned sites. Similarly, growth of *Betula pendula* was positively affected by N additions with simultaneous high P loads (TOMASSEN et al. 2003).

High concentrations of inorganic P at the burned soil surface could promote colonization of *Sphagnum* from spores together with many other bryophytes (e.g. *Pohlia nutans, Polytrichum strictum*) as reported by RYDIN (1986) and SUNDBERG & RYDIN (2002). Actually, we reported successful colonization of wet depressions by several *Sphagnum* species (e.g., *S.*

capillifolium, S. flexuosum, and *S. fallax*) at the site burned in 1994. The site burned in 2000 was colonized by several bryophytes typical for the *P. rotundata* bog forest (*Polytrichum* sp. div., *Aulacomnium palustre*) during one year.

Soil water chemistry of the *P. rotundata* bog forest

Two interesting results in soil water chemistry of the *Pinus rotundata* bog forest were found during the study.

(i) Very low pH, in comparison with the studies made in similar vegetation (cf. NEUHÄUSL 1975, BUFKOVÁ et al. 2005), the lowest pH values were measured directly in the *P. rotundata* bog forest in the Žofinka peat bog;

(ii) Rather high concentration of SRP (soluble reactive phosphorus) even in the undisturbed *P. rotundata* bog forest (cf. GORHAM et al. 1984, TAHVANAINEN et al. 2002, BRAGAZZA et al. 2003). Similar high concentrations of both H^+ and SRP were measured simultaneously in the *P. rotundata* bog forest in the Červené blato peatbog (KUČEROVÁ, unpubl. data), 10 km from the Žofinka peat bog;

Because the area receives little pollution (cf. ANONYMOUS 1999-2003, POKORNÝ & KUČEROVÁ 2000), there are two possible explanations. First, the Žofinka peatbog is situated in the lowest altitude in the *Pino rotundatae-Sphagnetum* range with rather low precipitation and rather high air temperature during the vegetation period. According to GORHAM et al. (1984) very low pH values in soil water are typical for such continental bogs. The mineralization could proceed here faster than in mountain peatbogs because of the higher temperature and higher groundwater fluctuation. Additionally, the soil profile was not so intensively washed by rainwater. Therefore, the mineralization products (especially H^+, coloured humid acids, but also SRP, NH_4^+-N) could accumulate in the soil water while most cations were incorporated in the biomass. This corresponded with the negative correlation of the concentrations of NH_4^+-N, SRP and total P to groundwater table (see **Table 4**) in both *P. rotundata* bog forest and windthrow–bark beetle affected site. Similarly, WILSON & FITTER (1984) documented fast P mineralization under conditions of low pH and low groundwater table. High values of available P in soil solution could be ensured by high turnover rates even though P inputs may be low (KELLOGG & BRIDGHAM 2003). Nevertheless, P availability for plants could be reduced by changes in Fe and Al dynamics in soil water through complexation of dissolved phosphate (DARKE & WALBRIDGE 2000, PANT & REDDY 2001).

Second, high acidity, elevated concentrations of dissolved P and simultaneously low availability of cations could be a consequence of the long-term influence of previous drainage (in the beginning of the 20th century). Similarly, SENGBUSCH & BOGENRIEDER (2001) found acidification of the upper peat horizon along with the lower groundwater levels and the decreased availability of both calcium and magnesium in previously drained *P. rotundata* forests in the south of the Black Forest, Germany.

Small-scale dust pollution from the burned site could be a reason for the relatively high soil water concentrations of Ca^{2+} throughout all sites in June 2002 (i.e., 10 months after the fire, **Fig. 2c, d**). The pronounced decrease of Ca^{2+} concentrations during 2002, and almost equal concentrations in 2003 could correspond to a rapid uptake of Ca^{2+} by vegetation or to its adsorption to soil particles. The mean Ca^{2+} concentrations in 2003 were close to the values given for mountain peatbogs (mean 0.9 mg l^{-1} in *Pinus mugo-Sphagnum capillifolium* community, RYBNÍČEK 2000). Al concentrations, however, were quite high in comparison with the base cation concentrations. In the Žofinka peatbog, the molar ratio of $Ca:Al_{total}$ was never lower than 0.3, which is considered as 'critical thresholds' below which damage to temperate tree species is frequent (CRONAN & GRIGAL 1995).

Several authors (e.g. CLYMO 1983, TALLIS 1983) reported extremely high peak concentrations of both P and K after fire. Contradictory to these studies, we did not find extremely high peak concentrations of K^+. We measured a gradual increase in concentrations of all dissolved forms of N and P after fire (see **Fig. 2a, b**) probably resulting from a dissolution and redistribution of released N and P from the soil surface towards soil water. Additionally, P adsorption in the peat soil could be saturated three years after the fire, resulting in higher P concentration in soil water (RICHARDSON 1985).

The similarly high concentrations of SRP and total P in both newly and old burned sites could indicate the long-term persistence of higher phosphorus levels in the soil water at the old burned site. However, according to terrain slope (KOROŠ et al. 1998), small distance and relatively high mean saturated hydraulic conductivity (0.176 m day^{-1}, KUČEROVÁ, unpubl. data), there was a possibility of subsurface flow of soil water in the direction from the newly burned site towards the old one associated with nutrient flux (see **Fig. 1**).

Conclusion

Only low differences were found in the soil water chemistry between windthrow-bark beetle affected and undisturbed *P. rotundata* forest sites. The species composition of the moss and herb layer after 18 years of natural succession was similar to the vegetation without wind damage. However, the documented long-term changes of the tree and shrub layer could be partly irreversible (increase in *P. sylvestris* density). Even if the natural succession after wind damage maintained most of the species diversity in the peatbog, the accumulation of highly flammable dead wood increased the probability of a fire. Occasional fires could substantially change both the species composition and the soil water chemistry. A short-term increase of weeds was followed by a decrease in species diversity and by an increase in dominance of some competitive species (*Molinia caerulea*). However, a temporary higher groundwater table after canopy break-up could positively affect regeneration of the moss layer. The species composition of the tree and herb layer changed more after the fire than after the wind damage, probably with long-term consequences. Concentrations of nutrients released by burning (especially N and P) increased markedly in soil water compared to stands affected by both windthrow and bark beetle attack.

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Mire vegetation gradient established by interaction with water reservoir

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Abstract

The peatbog complex Kyselovský les in the Czech Republic was flooded on 85% of its original area by water of the Lipno reservoir in 1958. A new vegetation pattern has spontaneously developed in the newly established shoreline and replaced the original peatbog vegetation dominated by bog pine (*Pinus rotundata* Link) forest. This vegetation pattern consists of zonal strips with relatively sharp borders. This zonation is a mosaic of sedge fens, reed canary grass (*Phalaris arundinacea* L.) beds, tussock cottongrass (*Eriophorum vaginatum* L.) stands and a community dominated by ericaceous shrubs. The study focused on the vegetation development of this zonal vegetation. Measurements of water table level, groundwater pH and conductivity, together with terrain microtopography, were done in order to estimate the ways how the water reservoir influences the mire vegetation. The most important factor is lake water fluctuation, which explained most of the vegetation gradient variability. Lake water fluctuations were represented by lake water levels, which directly flooded a certain part of the gradient from 1990 to 2006 for an exactly known number of days.

Keywords: sedge fen, raised bog, waterlogging, flooding, *Eriophorum vaginatum*, *Pinus rotundata*

Nomenclature: Rothmaler (1986) for vascular plants, Skalický (1988) for the genus *Pinus* and Kučera and Váňa (2003) for bryophytes.

Introduction

The floristic variation of mire vegetation is closely related to ecological gradients. The most serious attempt for classification and synthesis of variation along such gradients was a comprehensive study of Wheeler and Proctor (2000). This study was followed by critical comments from Økland et al. (2001). Wheeler and Proctor (2000) agreed with their critics on existence of at least two gradients of general importance: a poor-to-rich gradient (alkalinity, Ca and N availability) and the gradient of depth to water table. Other gradients (mire margin-mire expanse, salinity, open mire-swamp forest, snow-cover stability) were also discussed, but they seem either to have more limited geographical relevance (regional or local importance) or they are not widely accepted (mineral water limit, deep peat-mineral soil gradient). The definitions of these ecological gradients can be applied at least to the mires in north-western Europe (Scandinavia, Britain, Ireland, and northern Germany). Other studies have shown that the translation of these gradient definitions to distant regions has strong limitations (Nakamura et al. 2002). Numerous studies focused on local species distribution and vegetation patterns along the gradients (Bragazza and Gerdol 1999; Glaser et al. 1990; Økland 1989), most frequent approach is to examine the relationship between vegetation and hydrology in the study area. Hydrology is usually characterized by measurement of various factors – groundwater pH (Asada 2002), conductivity (Asada et al. 2004), concentration of major ions - H^+, $Ca^{2+,}$ K^+, Mg^{2+}, Na^+, Cl^- , total N, total P (Bragazza and Gerdol 1999; Hájek and Hekera 2004) and water level (Bragazza and Gerdol 1996). Studies using the gradients as a background for explanation of dynamic vegetation processes are not as frequent. Among processes studied so far were for example the impact of periodical river flooding (Wassen et al. 1990) , historical development of peat mounds (Glaser et al. 1990), impact of atmospheric deposition (Bragazza et al 2003), or the effect of cleat-cut and mounding (Asada et al. 2004).

One factor that can form the vegetation gradient is a surplus of mineral water from the mire's neighbourhood. This surplus of mineral water can originate from running water, and it is quite frequent, because mires are often formed as part of a wetland mosaic in river basins (Asada 2002; Bufková et al. 2005). The occasional flooding by river water can play an important role in the vegetation gradient in mires (Wassen et al. 1990). Not only streams, but also standing water bodies can influence mire vegetation. Studies were published that focused on the influence of eutrophic artificial ponds (Navrátilová and Navrátil 2005) or natural shallow ponds in a glacier formed landscape (Whitehouse and Bayley 2005).

Our study site is a special case of mineral water influence on mires. The peatbog Kyselovský les developed as part of a wetland mosaic in a river basin that was occasionally flooded by the Vltava River. The mire was permanently flooded in part by the newly built Lipno dam in 1960. In 1995, it was discovered that a new vegetation developed between the bog and lake. This new vegetation does not consist of continuously changing vegetation, but of discrete zones with narrow borders between them. The question that we wanted to address was: Why and under which conditions has this zonality developed? We also wanted to study the zonation variability and thus we compared the sequence of plant communities in various parts of the shoreline.

Material and methods

Site description

The study site Kyselovský les is situated in the southeastern part of the Šumava Mountains in the Czech Republic near the border with Austria (48°41´N, 14°3´E). The altitude is relatively low, at only 740 m a.s.l. The peatbog was part of a large complex of peat bogs that developed (due to good natural conditions) in the Vltava River basin between Černý Kříž and Lipno during the Holocene. This part of the basin is 44 km long, wide and shallow with an acidic geological base (oligotrophic ground conditions) with a stream slope of 0.04-0.7%

(Nowak et al. 1937), mean annual precipitation of about 800 mm, and mean annual temperature of 6 °C (Syrový 1958).

The historical status of the peatbog vegetation before the first human impacts can be estimated from the study by Schreiber (1924). Central parts of the peat bog consisted of open vegetation dominated by *Pinus* × *pseudopumilio* (Willk.) G. Beck. and sedge communities with *Betula nana* L. This type of vegetation is typical for true raised bogs at the higher altitudes of the Šumava Mountains. Large areas surrounding the central part were covered by typical bog pine (*Pinus rotundata* Link) woods (*Pino rotundatae-Sphagnetum* Kästner and Flössner 1933 corr. Neuhäusl 1972), with the occurrence of *Ledum palustre* L., which is a typical community of mires of lower altitudes from the Šumava Mountains and the Třeboň basin. This peatbog provided suitable environment for endemic plant species (*Pinus rotundata*) and for boreal species (*Oxycoccus palustris* Pers., *Andromeda polifolia* L., *Ledum palustre*), which are supposed to be relic from last glacial period. The phytogeographic and ecological value of the peatbog is thus evident. A large part of the peatbog was also damaged by peat mining (**Fig. 1**).

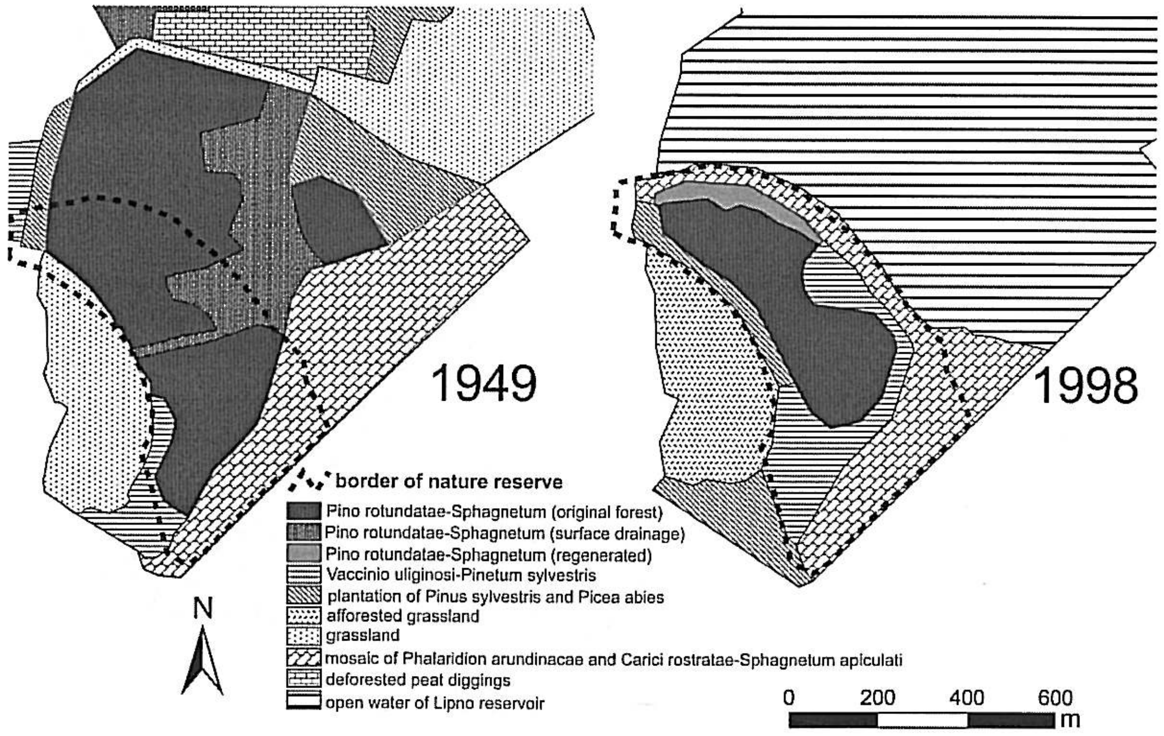

Fig. 1. Vegetation changes in the Kyselovský les during 50 years.

Building of the new Lipno water reservoir started in 1953. The lake above the newly built dam flooded 4870 ha of land in 1958. A 48 km long section of the Vltava River floodplain disappeared under the reservoir's water level. Among other wetlands, the new dam affected also the Kyselovský les peatbog, flooding 85 % of its original area.

Before the Lipno dam was filled, whole forests in the area of the planned reservoir were felled to the elevation of the proposed highest water level. Tree felling on the peatbog was done in winter, when they were accessible to heavy machines, because the peat was frozen. All trees in the flooded area were cut and the material that could not be processed (mostly branches) was burned in place (Kotlaba 1956).

Unflooded remains of the peat bog had been without direct human influence since 1958, because access to the area has been strictly controlled by the military administration (J Grohman, personal communication, 2006). The peatbog became protected by National Park Šumava Administration in 1995 and the protected area has National reserve status. The national reserve protects two main types of communities in the shoreline. The first is a regenerated bog pine woods, phytosociologically classified as *Pino rotundatae-Sphagnetum.* The second protected plant community is a poor sedge fen along the shoreline, dominated by *Carex lasiocarpa* Ehrh. with a large population of in Central Europe endangered species *Lysimachia thyrsiflora* L.

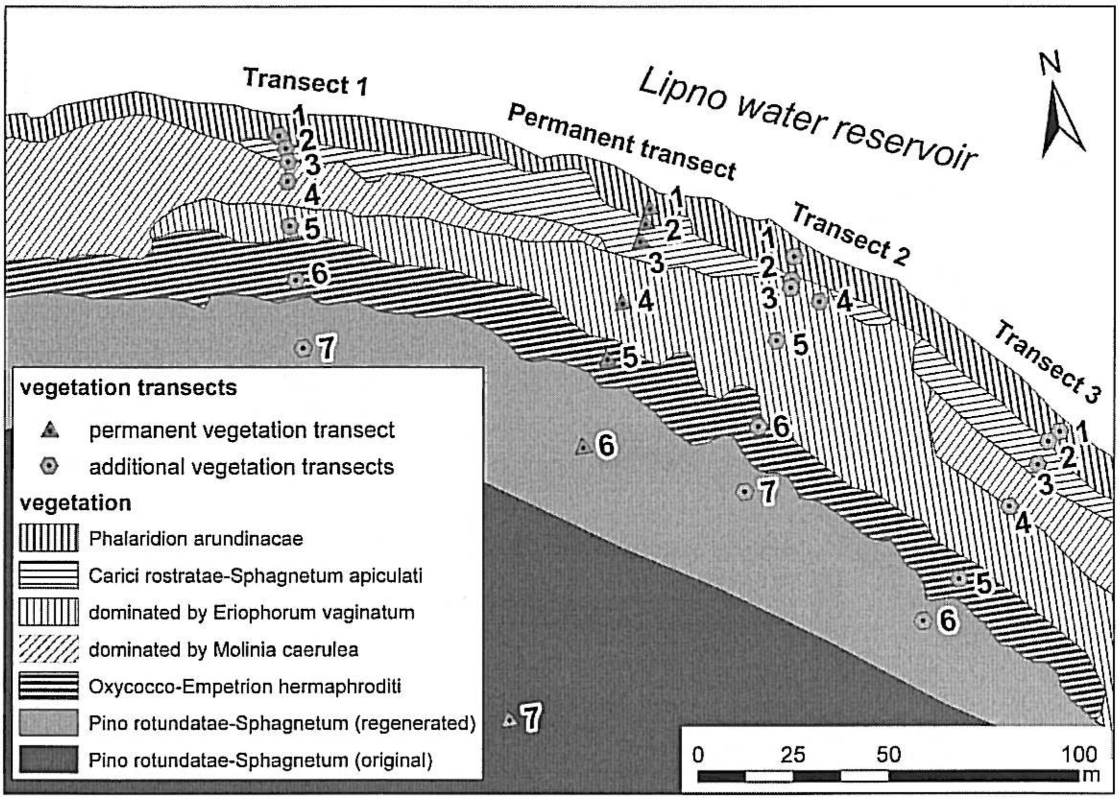

Fig. 2. Vegetation map of the Kyselovský les with transects.

Transects

We made one permanent transect consisting of 7 plots in 1997. The transect started at the bank of the Lipno dam (plot No. 1), through herb communities (plots 2-5) and young *Pinus rotundata* forest (plot 6) to the original *Pinus rotundata* forest (plot 7). The plots were situated in the centre of each initially-distinguished type of vegetation (**Fig. 2**). The standard size of each permanent plot was 5 × 5 m. Plots along the shoreline were resized due to the smaller width of their vegetation zone; plot 1 was resized to 2 × 12.5 m and plot 2 to

8 × 3.125 m, both of them with the same total area as the standard plots. The permanent plots were established to study the vegetation changes in the lakeshore. Phytosociological releves were taken in each plot in 1997 and 2006. East from each plot a dipwell was made using a perforated PVC pipe that was inserted down to a 1 m depth. We made in the dipwells 51 measurements of water table level during the study period 1997-2006. Measurements were made approximately once a month especially in the periods 1996-1998 and 2005-2006. Water pH and conductivity were also measured in the field by portable instrument (WTW multiline P3) 10 times inside the dipwells. Measurements (the number of measurements is in brackets) were made during the growing seasons 1996 (4), 1997 (3), 1998 (1) and 2006 (2). The measured values of electrical conductivity were corrected for the effect of hydrogen ions.

Three additional vegetation transects were established in 2005. The additional transects were positioned in order to cover the variability of the zonal vegetation between the intact peatbog and lake, according to the results of recent vegetation mapping. Plots on the transects were situated in the centre of each initially-distinguished type of vegetation. Their geographic positions are shown in **Fig. 2**. Geographical positions of the plots on the transects were measured using a GPS receiver (Trimble Pathfinder and Trimble Geo XT) with submeter accuracy. Elevation measurements of the plot centres and dipwells were made by surveyor's level with centimetre accuracy on both the new vegetation transects and the permanent transect in August 2005. The relative horizontal positions of the plots were recalculated to absolute height level above sea in winter 2005, using the known level of the water reservoir in absolutely calm weather. Results of the height measurements are shown in **Fig. 3**.

Daily measurements of the Lipno dam water level from January 1990 to January 2006 (5861 measurements) were obtained from the Vltava River Administration Authority (Povodí Vltavy s.p.). These data were used for computing flooding duration of each plot in the studied period.

The depth of the peat was determined using a 3 meter long peat corer in September 2005. The thickness of the peat layer was determined in the beginning and at the end of each vegetation transect.

Mapping of recent vegetation and reconstruction of historical status of vegetation

A black and white aerial photograph from 1949 was used for the reconstruction of the vegetation status before flooding by the Lipno reservoir. Black and white aerial photographs from 1959, 1962, 1974, 1982 and 1996 taken by the Czechoslovak army were used as background material for estimating the vegetation changes along the shoreline. A rectified colour aerial photograph from 2004 was used as background for the mapping of recent vegetation status. Vegetation in the lake shore was mapped between the bog pine forest and shoreline in July 2005. Vegetation units that were distinguished on the permanent transect were used for the mapping. One of the aims of the recent mapping was to investigate how far the zonal vegetation from the transect could be applied to the situation in the whole lake shore between the peatbog and the Lipno dam.

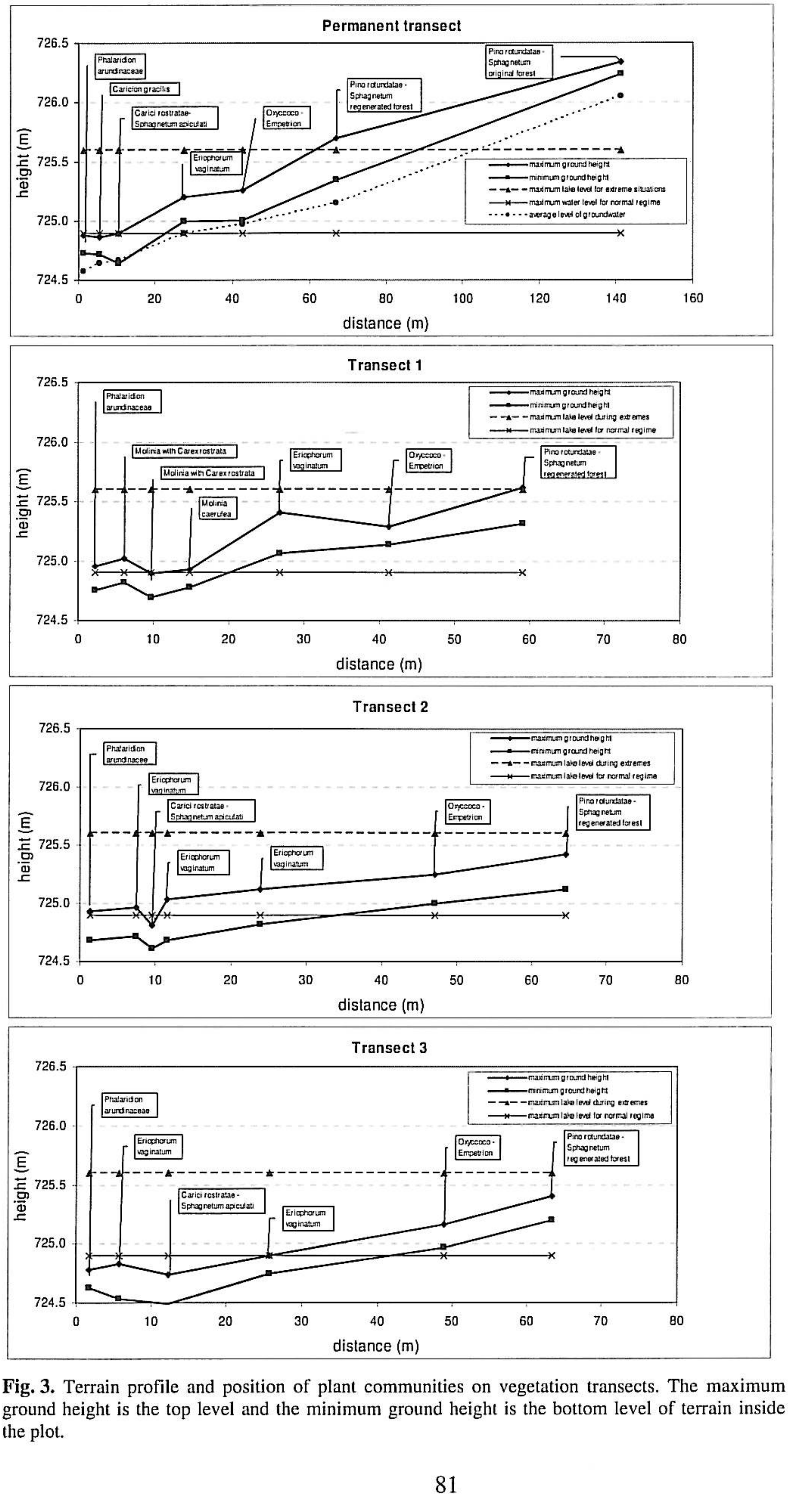

Fig. 3. Terrain profile and position of plant communities on vegetation transects. The maximum ground height is the top level and the minimum ground height is the bottom level of terrain inside the plot.

Data analysis

34 phytosociological relevés of the permanent plots were made in 1997 and 2006. A total of 86 species formed the first data set. Detrended Correspondence Analysis (DCA) was used to compare species composition among the plots. The phytosociological relevés of all plots made in 2006 with the corresponding environmental data formed the second data set (27 relevés, 86 species). Species cover was expressed in percentage in both data sets and was log transformed (ln(x+1)) before analysis. The relationships of species composition to environmental variables in the second data set were evaluated by Canonical Correspondence Analysis (CCA). Forward selection of environmental variables was performed. Significance was tested by the distribution-free Monte Carlo permutation test. In the test, the distribution of the test statistics under the null hypothesis was generated by random permutations of cases in the environmental data (for details see ter Braak and Šmilauer 2002). All plots were treated as independent replicates because the transects were close to each other, plots on each transects were not direct neighbours, and the similarity of plots in the same community between transects was much higher than the similarity of neighbours belonging to different communities in the transect. Therefore, restricted Monte Carlo permutation scheme was not required. The DCA and CCA analyses were performed using CANOCO for Windows version 4.5 (ter Braak and Šmilauer 2002).

Table 1. Characteristics (mean ± SD) of the plots on permanent transect.

Plot No.	Plant community	dominant vascular plants	succesion of trees	water pH	water conductivity ($\mu S.cm^{-1}$)	water table level (cm)	max. flood depth (cm)	flood days (%)	max. flood length (days)
	water of Lipno lake			6.43 ± 0.18	50.27 ± 6.04				
1	*Phalaridion arundinacae* Kopecký 1961	*Phalaris arundinacea* *Peucedanum palustre* *Galium uliginosum*	*Salix pentandra* *Frangula alnus*	4.27 ± 0.30	51.71 ± 33.31	-33.48 ± 16.15	81.3	6.01	59
2	*Caricion gracilis* Neuhäusl 1959 em. Balátová-Tuláčková 1963	*Carex gracilis*	*Betula pendula* *Frangula alnus*	4.37 ± 0.23	34.53 ± 13.17	-15.14 ± 12.93	82.8	6.55	59
3	*Carici rostratae-Sphagnetum apiculati* Osvald 1923	*Carex rostrata* *Carex nigra*	*Betula pendula* *Pinus sylvestris*	4.21 ± 0.12	40.29 ± 13.45	-8.22 ± 10.93	84.8	7.98	103
4	*Eriophorum vaginatum* (dominant)	*Eriophorum vaginatum*	*Pinus sylvestris* *Pinus rotundata*	3.86 ± 0.20	35.22 ± 17.17	-7.38 ± 7.86	52.3	0.17	10
5	*Oxycocco-Empetrion hermaphroditi* Nordhagen 1936	*Vaccinium uliginosum* *Vaccinium myrtillus* *Calluna vulgaris*	*Betula pubescens* *Pinus rotundata* *Frangula alnus* *Picea abies*	3.78 ± 0.21	38.1 ± 11.57	-8.98 ± 7.36	48.8	0.15	7
6	*Pino rotundatae-Sphagnetum* (regenerated forest)	*Pinus rotundata*	*Pinus rotundata*	4.07 ± 0.20	30.61 ± 12.09	-22,91 ± 10.55	9.8	0.03	2
7	*Pino rotundatae-Sphagnetum* (original forest)	*Pinus rotundata*	*Pinus rotundata* *Picea abies*	3.93 ± 0.13	37.13 ± 15.94	-21.06 ± 10.07	0	0.00	0

Results

Habitat conditions on transects

Terrain profile in the studied transects has some common characteristics as shown in **Fig. 3**. The bank is upright, 0.5-1 m high and continues under the artificial lake as a flat bottom, which can be seen when the water level is below 723.5 m a.s.l. The terrain from the shoreline gently rises towards the northern mire margin, with a slope of 0.7%-1%. This shallow slope corresponds to the original surface profile of the peatbog before flooding. The slope is interrupted at a distance of 5-12 meters from the lake by a shallow depression. This sharp bank edge and depression are most probably caused by surface erosion of peat. First-hand observations in 2005-2006 gave evidence of the erosion. A long winter with a lot of snow was followed by strong storms in the spring and summer. Strong surf, together with a high lake level eroded several decimetres of the peat from the bank edge. Part of the eroded peat was transported up into the sedge zone and covered the original vegetation, especially mosses. On the permanent transect, the layer of washed peat could be estimated by measuring the change in the distance between the top of the PVC pipe and the newly established ground level. The peat was eroded in the area of plots 1-3, the thickness of washed peat varied from 6 to 9 cm. This rapid change demonstrated the intensity by which wave erosion could change the microtopography of peatbog, forming local depressions and elevations along the shoreline. Thus, the coastal zone is very rapidly influenced by water erosion during certain periods, up to a maximum distance of 15 m from the shoreline.

The water reservoir also influences low parts of the peat bog through occasional flooding of the shore (**Table 1**, **Fig. 3**).

All peat cores did not contain any traces of mineral substrate to a maximum depth of 3 m. The measurements of water tables showed that the water table in the peatbog margin has a convex shape (fitted by the second order polynomial regression) (**Fig. 4**).

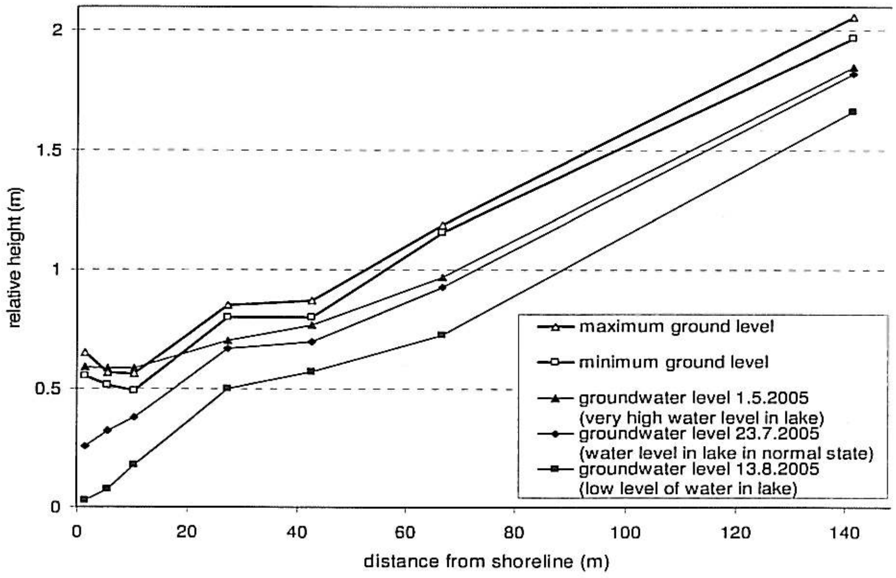

Fig. 4. Measurements on the permanent transect, and fluctuations of the water table.

When the water level in the lake is high, the water table becomes flat or concave in shape, especially at the beginning of the transects (**Fig. 4**).

The measurements of water pH and conductivity showed that acidity is the main difference between lake water and mire water; lake water always has a pH greater than 6, while the average pH in the peatbog was less than 4 (the acidity-alkalinity gradient can be seen in **Table 1**). Influence of lake water, which should increase the pH, can be observed only in the first 3 plots of the permanent transect, covered by reed canary grass and sedge fens, which are very often directly flooded by the water reservoir. The corrected electrical conductivity has relatively low levels in both the mire and lake. These facts support the theory that the vegetation gradient developed mostly due to the differences in water table regime.

Spatial vegetation pattern

The results of elevation measurements are put together with the vegetation mapping of the transects in profiles in **Fig. 3**. These profiles show the basic situation of the vegetation in the border zone between the lake and peatbog in summer 2005.

The additional vegetation transects proved that the sequence of plant communities in the contact zone is relatively stable, with some exceptions. The major exception from the permanent transect is the position of the community dominated by *Eriophorum vaginatum* L. This community occurred between *Phalaris arundinacea* dominated stands (as. *Phalaridion arundinacae*) and sedge communities dominated by *Carex rostrata* (as. *Carici rostratae-Sphagnetum apiculati*) in transects 2 and 3, which is closer to the shoreline than in the permanent transect and transect 1.

The results of DCA for plots sampled in 1997 and 2006 are shown in **Fig. 5**. The first ordination axis explained 21.7% and the first two ordination axes explained 28.8% of the variability in the vegetation data. The samples from the plots on transects formed a clear sequence in the ordination diagram corresponding to their distance from the Lipno reservoir, from plots on the bank of the Lipno reservoir (left side) to plots at the end of the transects with undisturbed *Pinus rotundata* forest (right side). Plots with a lower water table, and subsequently more advanced succession of woody species, are in the upper side, while plots with higher water table are in the bottom. Plots closer to the Lipno reservoir are more variable than plots in the bog pine forest. Successional changes on the permanent transect are evident from the drift of the repeatedly sampled plots to the upper part of **Fig. 5**. *Phalaris arundinacea* L., *Sphagnum teres* (Schimp.) Ångström, and *Lysimachia thyrsiflora* occur in the plots closer to Lipno reservoir. Typical species for the undisturbed *Pinus rotundata* forest are *Pleurozium schreberi* (Brid.) Mitt., *Vaccinium myrtillus* L., *Vaccinium vitis-idaea* L., and *Vaccinium uliginosum* L. The lower water table is indicated by *Pinus sylvestris* L., *Betula pendula* Roth., and *Calamagrostis canescens* (Weber) Roth. The species that occur in higher water levels are *Carex rostrata* Stokes, *Carex vesicaria* L., and *Sphagnum cuspidatum* Ehrh. ex Hoffm.

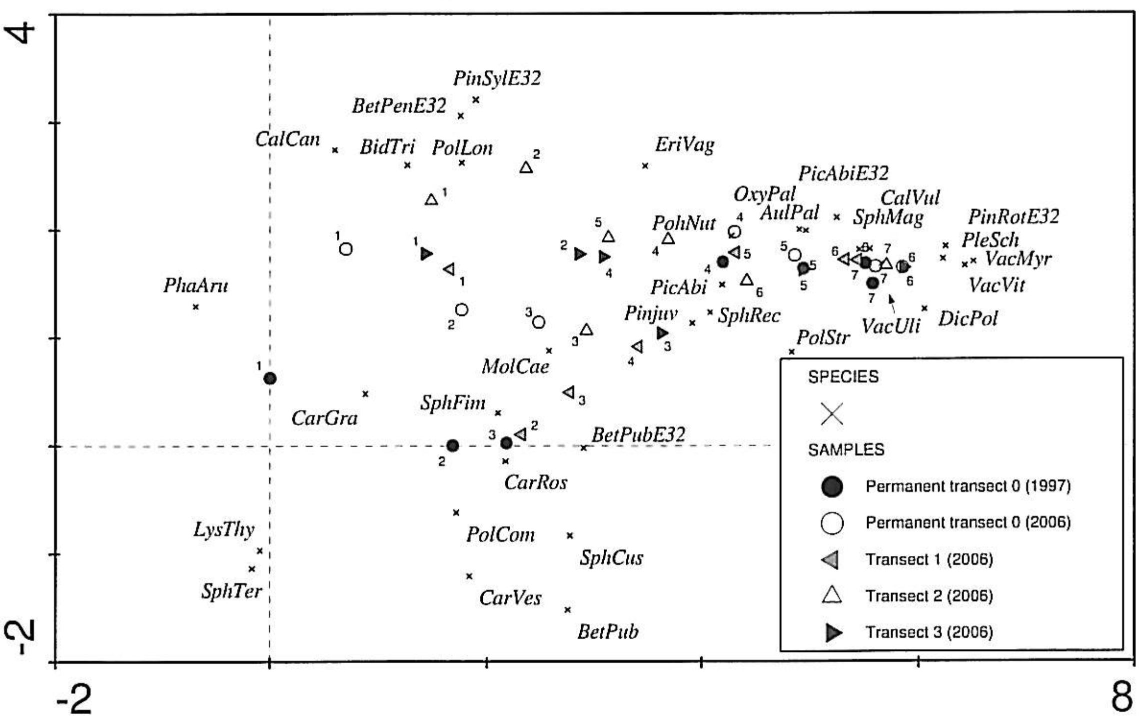

Fig. 5. Sequence of plots in the ordination diagram corresponding to their distance from the Lipno reservoir. Results of DCA (Detrended Correspondence Analysis) for phytosociological relevés. The sample number in ordination diagram is the position of sample on particular transect (see Fig. 2). The number in legend in brackets is the year of sampling.

AulPal (*Aulacomnium palustre* (Hedw.) Schwägr.), *BetPenE32* (*Betula pendula* E3+E2), *BetPub* (*Betula pubescens juv.*), *BetPubE32* (*Betula pubescens* E3+E2), *BidTri* (*Bidens tripartita*), *CalCan* (*Calamagrostis canescens*), *CalVul* (*Calluna vulgaris*), *CarGra* (*Carex gracilis* Curtis), *CarRos* (*Carex rostrata*), *CarVes* (*Carex vesicaria*), *DicPol* (*Dicranum polysetum* Sw.), *EriVag* (*Eriophorum vaginatum*), *MolCae* (*Molinia caerulea*), *LysThy* (*Lysimachia thyrsiflora*), *OxyPal* (*Oxycoccus palustris*), *PhaAru* (*Phalaris arundinacea*), *PicAbi* (*Picea abies juv.*) , *PicAbiE32* (*Picea abies* E3+E2), *PinRotE32* (*Pinus rotundata* E3+E2), *Pinjuv* (*Pinus sylvetris juv. and Pinus rotundata juv.*), *PinSylE32* (*Pinus sylvestris* E3+E2), *PleSch* (*Pleurozium schreberi*), *PohNut* (*Pohlia nutans* Lindb.), *PolCom* (*Polytrichum commune* Hedw.), *PolLon* (*Polytrichastrum longisetum* (Sw. ex Brid.) G. L. Sm.), *PolStr* (*Polytrichum strictum* Brid.), *SphCus* (*Sphagnum cuspidatum*), *SphFim* (*Sphagnum fimbriatum*), *SphMag* (*Sphagnum magellanicum* Brid.), *SphRec* (*Sphagnum recurvum* s.l.), *SphTer* (*Sphagnum teres*), *VacMyr* (*Vaccinium myrtillus*), *VacUli* (*Vaccinium uliginosum*), *VacVit* (*Vaccinium vitis-idaea*)

The results of DCA for plots sampled in 2006 with corresponding environmental variables passively projected onto ordination plot are shown in **Fig. 6**. The first ordination axis explained 25.2% and the first two ordination axes explained 33.4% of the variability in the vegetation data. **Fig. 6** clearly shows mutual relationships between environmental variables. Close positive correlation between altitude and distance from the Lipno reservoir and its negative correlation to maximum flood depth and water table deviation is apparent. We can also find positive correlation among maximum flood length, sum of flood depth and water table. The positive relationship between mean flood depth and altitude is not so close but interesting. Plots in relatively low altitudes are frequently flooded with relatively low mean flood depth and vice versa.

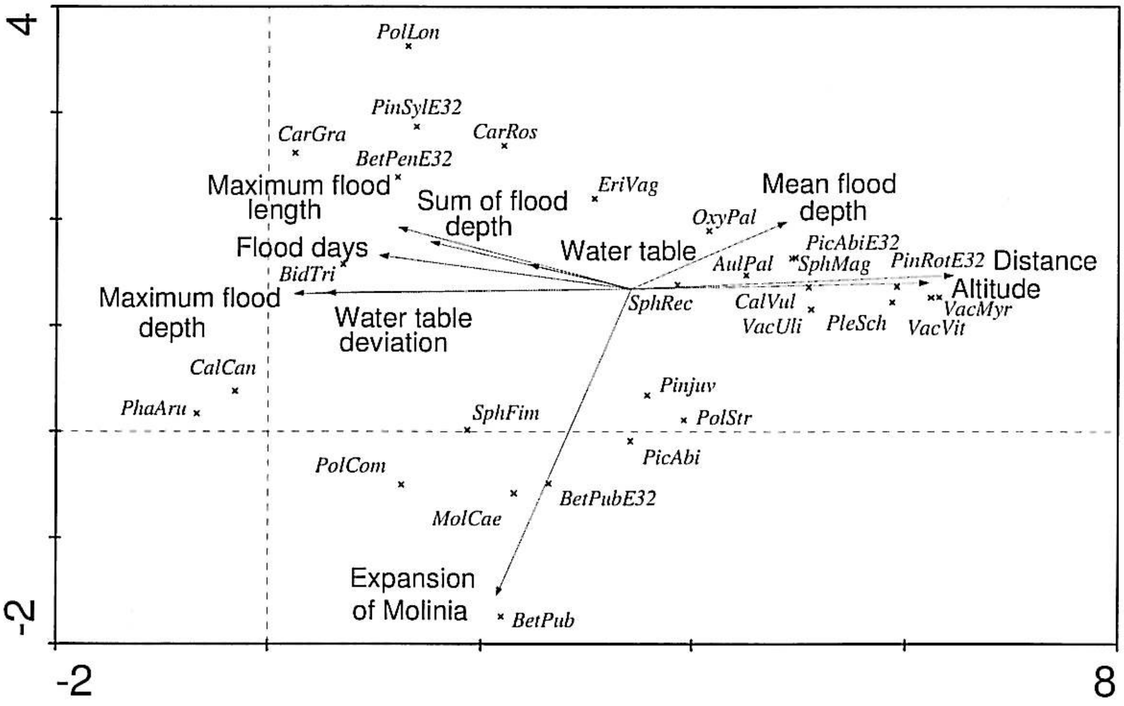

Fig. 6. Species in the ordination diagram and their relationship to environmental variables. Results of DCA (Detrended Correspondence Analysis) for phytosociological relevés with passive environmental variables projected onto the resulting ordination plot. For explanation of species abbreviations see Fig. 5.

The most important significant explanatory variables selected by forward selection in CCA for plots sampled in 2006 were maximum flood depth and water table deviation. These were followed by mean flood depth, maximum flood length, flood days and water table. The CCA analysis, with environmental variables maximum depth of flooding and water table deviation, is presented in **Fig. 7**. The first ordination axis explained 22.1% and the first two ordination axes explained 32.7% of the variability in the vegetation data. The effect of both canonical axes considered together was highly significant (MCPT, 9999 permutations, F=5.83, p=0.0001). *Carex rostrata, Sphagnum fimbriatum* Wilson and juvenile *Betula pubescens* Ehrh. occur in the plots most affected by flooding. On the opposite side of the gradient were found e.g. *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and *Picea abies* (L.)Karsten. Species typical for high water table fluctuations are *Calamagrostis canescens* and *Phalaris arundinacea*. In contrast, species such as *Oxycoccus palustris*, *Calluna vulgaris* (L.)Hull and *Sphagnum recurvum* s.l. *(S. fallax* (H. Klinggr.) H. Klinggr. and *S. flexuosum* Dozy et Molk.*)* are in plots with a relatively stable water table.

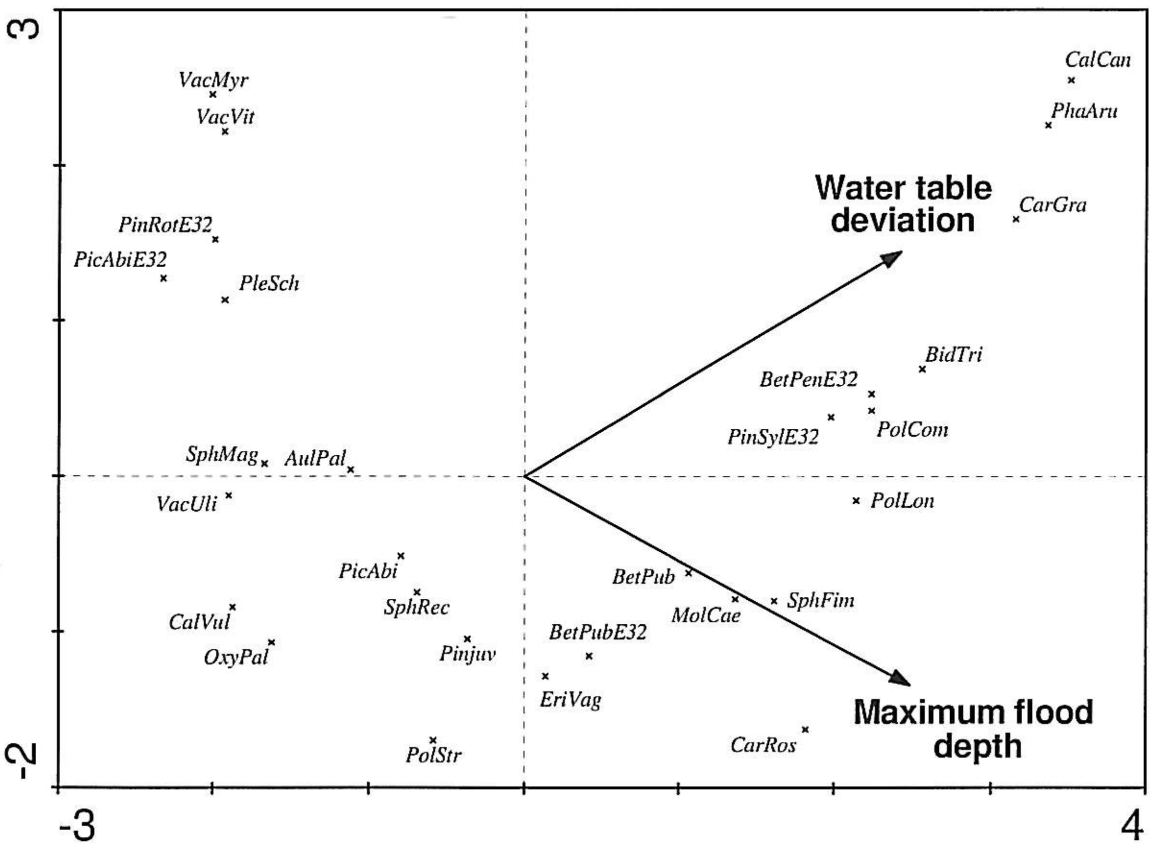

Fig. 7. Species in the ordination diagram and their relationship to maximum flood depth and water table deviation. Results of CCA (Canonical Correspondence Analysis) for phytosociological relevés. For explanation of species abbreviations see Fig. 5.

Temporal vegetation development

The schematic map of the reconstructed vegetation in 1949 is shown in **Fig. 1**. The water reservoir was completely filled with water in 1962 and the new reservoir shoreline established. A new non-forest area appeared between the lake's shoreline and the remains of the original bog pine vegetation. It was 50-80 m wide, with an area of 5.4 ha. The initial status of the vegetation in this area can be reconstructed as bog pine forest with a completely removed tree layer. The community was probably dominated by *Vaccinium* sp. shrubs and was probably very similar to the recent ericaceous shrub community documented on the vegetation transects (as. *Oxycocco-Empetrion hermafroditii*).

The first scattered trees in the non-forest area can be seen in aerial photo from 1974. Massive regeneration of *Pinus rotundata* is evident in the 1982 aerial photo. The former large non-forest area was split into 2 parts. One part, 20-40 m wide along the border with the old growth bog pine forest, has regenerated back to bog pine forest (**Fig. 1**). The second part of the shoreline has stayed unforested with only scattered trees.

Mapping of the recent vegetation has documented the zonal vegetation along the shoreline since 1997. The vegetation zones have developed typically in the places between intact old growth or regenerated *Pinus rotundata* forest and the lake. The vegetation changes as one moves towards the edges of the peatbog, with a higher percentage of sedge and reed communities and signs of peat degradation: expansion of *Molinia caerulea* (L.) Moench, and decreasing *Eriophorum vaginatum* and *Vaccinium uliginosum*. This vegetation occurs on places that were historically influenced by surface drainage. Results of the recent vegetation mapping are shown in **Fig. 2**.

Tree succession is the most visible vegetation change along the shoreline since 1997. The most successful tree species is *Betula pendula*, which has formed compact stands in some parts of the shore. The composition of young trees and seedlings differs between communities, as can be seen in the characteristics of the permanent transect in **Table 1**. Lake water fluctuations can also rapidly influence tree succession. Norway spruce seedlings were relatively frequent in tussock cottongrass stands before 2002. Most seedlings and young trees of *Picea abies* died out during summer 2002, when the water table level in the Lipno reservoir was extremely high and lake water flooded most of the shoreline for a long time. *Picea abies* saplings are mostly present only in vegetation zones that are more distant from the shore, e.g. in the ericaceous shrub community (see **Table 1**), since summer 2002.

Another short term vegetation change occurred in summer 2006 as a consequence of surface erosion of peat near the shoreline. The bare peat layer was colonized by species such as *Taraxacum* sp., *Plantago major* L., *Bidens tripartita* L., *Ranunculus repens* L., and *Polygonum lapathifolium* L. The new colonizers occurred in large numbers of seedlings with small coverage.

Discussion

Results of this study must be first interpreted in the context of the very extensive discussion about ecological gradients in European mires (Wheeler and Proctor 2000; Økland et al. 2001), a theme that is especially important for the fennoscandian region. All plots on the permanent transect have water pH lower than 5; according to the classification of Wheeler and Proctor (2000), hence all communities can be classified as bogs. This evidence is in contrast with the species composition in the reed canary grass beds community, which contains a majority of species that are supposed to be fen indicators in the region of Central Europe: *Phalaris* *arundinacea, Lysimachia thyrsiflora, Salix pentandra* L., *Lysimachia vulgaris* L., *Peucedanum palustre* (L.) Moench, and *Gallium uliginosum* L. There is also a visible difference in pH between the sedge fens and tussock cottongrass stands in the permanent transect (see **Table 1**). These results indicate that there may be a mineral soil water limit in our gradient (Du Rietz 1949). Whether it can be determined as a narrow borderline zone as presented in many fennoscandian studies (Økland et al. 2001) will be the subject of further chemical analyses.

Water table level, together with the rising terrain profile, indicates that the peatbog can be classified as a raised bog (Ingram 1982; Bragazza et al. 2005). The convex shape of the water table level also indicates that the main surface water flow leads from the mire expanse to the shoreline. The character of peatbog water can be considered as strongly acidic in comparison with other studied mires (Bragazza and Gerdol 1999; Bragazza et al. 2005; Whitehouse and Bayley 2005).

Fishpond mires were studied by Navrátilová and Navrátil (2005) in the geographically and ecologically similar area of the Třeboň basin. They concluded that nutrient rich waters and a high water table enrich the fen areas that are distant from the pond edges. They assumed that mean pH and maximum water table level were the most significant environmental factors explaining the vegetation variation. Our results conform to the significance of the above mentioned environmental factors, although the influence of the Lipno reservoir is not as intensive as with the compare interaction between fens and fishponds, for various reasons. The water from the lake, which is used for recreational purposes, has lower nutrient content and is more acidic than water in the fishponds, which are intended for fish farming. The thick peat layer of Kyselov also has a much higher buffering capacity than the shallow fen organic soils of the fishpond mires. Based on the thick peat layer at Kyselov, the pedological conditions in all transects are probably similar and the vegetation in the coastal zone is not influenced at all by mineral material.

The most significant and visually apparent change to the vegetative communities of Everglades peatlands has been an increased dominance of cattails (*Typha domingensis*), at the expense of the dominant sawgrass (*Cladium jamaicense*). This change is favoured by the enrichment of the peat with P loadings from agricultural drainage, pumped into the peatland area (Craft and Richardson 1997). When wastewater was applied to an acidic, nutrient-poor peatland, the peatland's capacity to retain phosphorus was exhausted after a few years of application (Nicols and Higgins 2000). Increased pH, nutrient availability, and water levels altered the peatland vegetation community. The *Sphagnum* ground cover was reduced or eliminated in many places, and dense stands of cattail (*Typha sp.*) developed in some areas (Nicols and Higgins 2000). In extreme situations, peatland vegetation can be directly damaged by high nutrient concentrations. During dry season 1997 the high content of NH_4^+ in fishpond's water killed all trees and reduced *Sphagnum* carpets in the shoreline zone of peatbog Rod in Třeboň basin area in Czech republic (Matějka and Rajchard 1997). If our peatland was in a permanent contact with nutrient rich water, the intensity of interaction would be higher, peat chemistry would be altered more dramatically, and the changes of vegetation would be more apparent.

Comparison of the sequence of plant communities between transects raises the question of the position of stands dominated by *Eriophorum vaginatum.* This community differs from the others because it has more than one possible position in the vegetation sequence. Its occurrence between the reed canary grass beds and sedge fens near the shoreline of transects 2 and 3 can be due to disturbance, because these habitats are influenced by surface erosion of peat; *Eriophorum vaginatum* is an extremely successful colonizer of bare peat under certain conditions. In North America, *Eriophorum vaginatum* colonizes disturbed sites including burns, frost boils, and gravel pits (Howard 1993). *Eriophorum vaginatum* formed monodominant stands in the mined Wendlinger Filz peatbog in the foothills of the Alps (Maas and Poschlod 1991). Monodominant stands of *Eriophorum vaginatum* also are part of natural succession in the mined Soumarský Most peatbog, which is only 30 km from our study site.

Surface erosion changes the microtopography in the shoreline area and also promotes the establishment of new plant species. How long these newly established species will stay in the shore vegetation will be an important subject of further vegetation mapping on the vegetation transects. Whether the change of microtopography leads to permanent vegetation change in the shoreline will be also the subject of further research.

The zone between the sedge fens and ericaceous shrubs has, in many ways, the most extreme environmental conditions: low pH, highest water table level, and lowest nutrient content (see **Table 1**). The successful establishment of *Eriophorum vaginatum* is probably the result of its tolerance to waterlogging together with its physiological adaptations to nutrient deficiency, such as efficient uptake of nutrients under anaerobic conditions (Gore and Urquart 1966). This ecological plasticity of *Eriophorum vaginatum* is the main reason for it having the widest distribution on the gradient among the vascular plants; this situation was also reported from Staller Loch in the Southern Alps by Bragazza and Gerdol (1996).

The border between the tussock cottongrass stands and ericaceous shrubs occurs in all transects at a similar level, as shown in **Fig. 3**. Ericaceous shrubs are probably limited by lake flooding, because their associated mycorrhizal fungi do not endure waterlogging (Miller 1982; Lindholm and Markkula 1984; Wallén 1987).

For *Vaccinium* species, *V. uliginosum* dominates open areas, while *V. vitis-idaea* and *V. myrtillus* are more successful in shaded areas under the bog pine forest canopy. This evidence is inconsistent with the results from other studies, which showed that *Vaccinium vitis-idaea* occurs more in open areas (Økland 1989; Bragazza and Gerdol 1996). Its absence in our case is most probably due to a too high water table or occasional flooding.

The Kyselov peatbog is an important example of the impact of flooding by a large artificial water reservoir. Our findings will be useful for predicting the damage of mire ecosystems due to planned water reservoirs. The new Lipno reservoir flooded at least 85% of the original peatbog area, and caused a reduction in biodiversity: the loss of most endangered communities and species (e.g. *Betula nana, Ledum palustre*). On the other hand, the rest of the peatbog does not show any signs of rapid degradation and biodiversity of the non-forest communities has even locally increased in the coastal zone.

Conclusion

Our research has shown that water table position and fluctuation are key factors that produce vegetation gradients between an artificial lake and mire. The influence of lake water is strongest in extreme situations, when mire plant communities are directly flooded by mineral waters.

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Successional changes of vegetation at the "Multerberské rašeliniště" peat bog during the last 50 years, the Šumava Mts.

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Abstract

Vegetation changes at the "Multerberské rašeliniště" peat bog during the last 50 years were studied using a comparison of two black and white aerial photographs from 1949 and 1996. Massive successional changes leading from the original open peat bog vegetation to dense *Picea abies* forest were observed at the site. In the same time influence of a deep drainage to the hydrology of peat bog was studied along a transect. Dam was built in a draining ditch after the monitoring of a groundwater table level during 1996–1997 to study the potential success of amelioration of the site.

Keywords: *Pinus × pseudopumilio*, *Pinus mugo*, *Pinus rotundata*, peat bog, hydrology, succession, restoration, Czech Republic

Nomenclature: VÁŇA (1997) for bryophytes, ROTHMALER et al. (1988) for vascular plants, HEJNÝ & SLAVÍK (1988) for woody plants

Introduction

Nature conservation institutes often have to deal with dynamics of vegetation in protected areas. There are many examples of endangered species retreat in non-forest communities. This study is aimed at a similar problem in peat bog communities. The population of the hybrid *Pinus × pseudopumilio* (*Pinus mugo × P. rotundata*) developed under the conditions including a very high groundwater table in the center of an intact raised bog. The lagg of the peat bog was converted into grassland in the past and it was deeply drained for forest cultivation later. Some of the draining ditches disturbed also those parts situated near former lagg. *Picea abies* invaded the peat bog, because its growth is probably supported by changed hydrological conditions.

Site description

The site of "Multerberské rašeliniště" (48°36'N, 14°03'E) is a small raised bog situated 1 km from Czech-Austrian state border in an extensive area on the right bank of the Lipno water reservoir. The center of the peat bog is dominated with open shrubby community which can be classified as association *Pino rotundatae-Sphagnetum* KÄST. & FLÖSS. 1933 (corr.

NEUHÄUSL 1967). For a better description of the vegetation see **Table 1** and BASTL & HORN (1997). The site is protected for its hybrid population of *Pinus* × *pseudopumilio* (*Pinus mugo* × *P. rotundata*) with continuous habitual transitions between both parents (KUČERA 1973).

A village 'Multerberger Waldhäuser' was founded nearby the peat bog in the 18th century (KOVÁŘ & KOBLASA 1996). People kept cattle there and so they cut most of the forest that surrounded the peat bog and converted this area into grasslands. It is possible that they used also the vegetation of the central peat bog as a pasture. They disturbed the southern part of the peat bog. There are traces of a surface drainage and peat cutting at least 50 years old (KUČERA 1973). The original German inhabitants were transferred mostly to Germany after the World War II. Abandoned farmhouses were destroyed and Forestry Management changed the grasslands into the *Picea abies* plantations. The peat bog was suggested for potential peat exploitation with about 120 000m^3 of peat in 1963 (WAIS et al. 1963) but there was no further interest of peat mining company 'Rašelina Soběslav'.

Table 1. Plant species found along a transect at the "Multerberské rašeliniště" peat bog in 1997. Cross indicates presence of species.

	Site No.						
	1	2	3	4	5	6	7
E_2+E_3							
Picea abies			×	×			
Pinus × *pseudopumilio*					×		×
Pinus sylvestris			×				
E_1							
Andromeda polyfolia						×	
Carex canescens	×						
Eriophorum vaginatum	×				×	×	×
Melampyrum pratense					×	×	×
Oxyccocus palustris					×	×	×
Vaccinium myrtillus		×	×	×	×		
Vaccinium uliginosum		×	×	×	×		×
Vaccinium vitis-idaea		×	×	×			
E_0							
Aulacomnium palustre				×			
Bazzania trilobata			×				
Cladonia sylvatica				×			
Dicranella heteromalla			×				
Dicranum polysetum		×	×	×			
Hylocomium splendens			×	×			
Lepidozia reptans			×				
Pleurozium schreberi		×	×	×			
Pohlia nutans			×				
Polytrichum strictum							×
Sphagnum capillifolium			×				
Sphagnum cuspidatum	×						
Sphagnum flexuosum				×	×	×	×
Sphagnum magellanicum				×	×	×	×
Sphagnum fallax	×				×	×	×
Sphagnum russowii		×					

KUČERA (1973) proposed this site for protection (9 ha) in 1973. Protected area of "Multerberské rašeliniště" was declared in 1991. Unfortunately, Forestry Management disturbed the hydrology of this peat bog in 1980's, when the nearby grassland was drained for *Picea abies* cultivation.

Methods

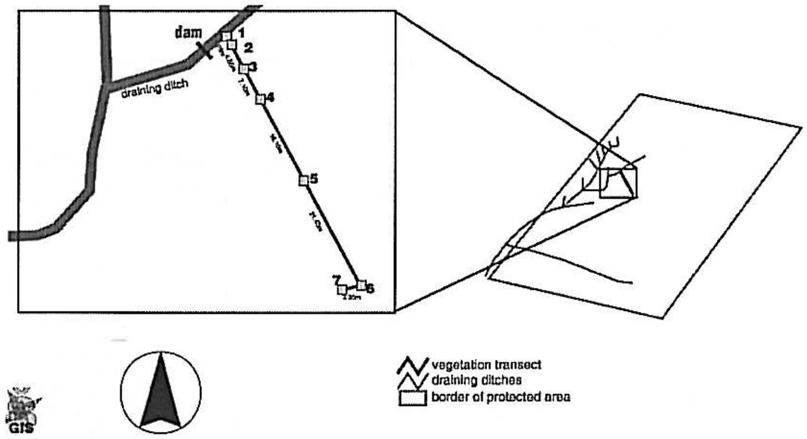


Fig. 1. Map of the transect at the "Multerberské rašeliniště" peat- bog.

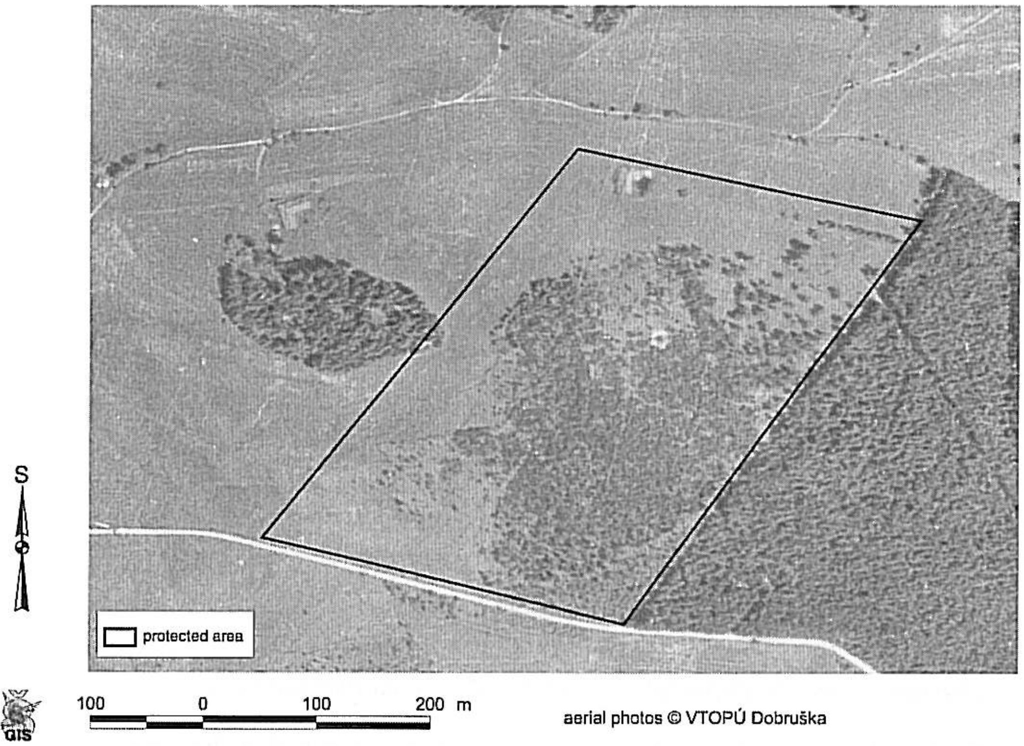
Paper black-and-white positive aerial photographs in scale 1 : 5000 were used as a background for mapping of the vegetation. Aerial photograph from 1949 was made by Military Topographic Institute, aerial photograph from 1996 was made by Argus Geo System. Both photographs were made for cartographic purposes. Original photographs were scanned in resolution 300 DPI and then transformed to coordinate system Gauss Kruger S-42 using points with known cartographic position. Data were processed in program ARC-INFO 7.0.4 with GRID commands. Field investigation of dead wood remains (most probably *Pinus × pseudopumilio*) in forest understorey was also used for reconstruction of vegetation state in 1949.

The groundwater table variation was monitored during 1996–1999 along the transect using plastic tubes (1.5 m long, 6 cm in diameter). The groundwater table level was measured manually approximately twice a month during vegetation season and in winter irregularly. The transect (**Fig. 1**) leads from the draining ditch (site No. 1), through the group of *Picea abies* trees (sites No. 2–4), to open peat bog with scattered trees and shrubs (sites No. 5–7). The draining ditch (site No. 1) is 3m wide, 80 m long, average depth is 1 m and maximum depth is 1.5 m. The draining ditch was probably dug before the World War II (according to the age of the oldest trees growing right on the edges of the ditch). In the 1970's the ditch was partly functionless (KUČERA 1973), but in the middle of 1980's it was again connected to a new drainage system of the surrounding grasslands.

In September 1997 wooden dam (5 m wide and 1.5 m high) was build in the draining ditch (site No. 1) as an attempt to restore original level of groundwater table.

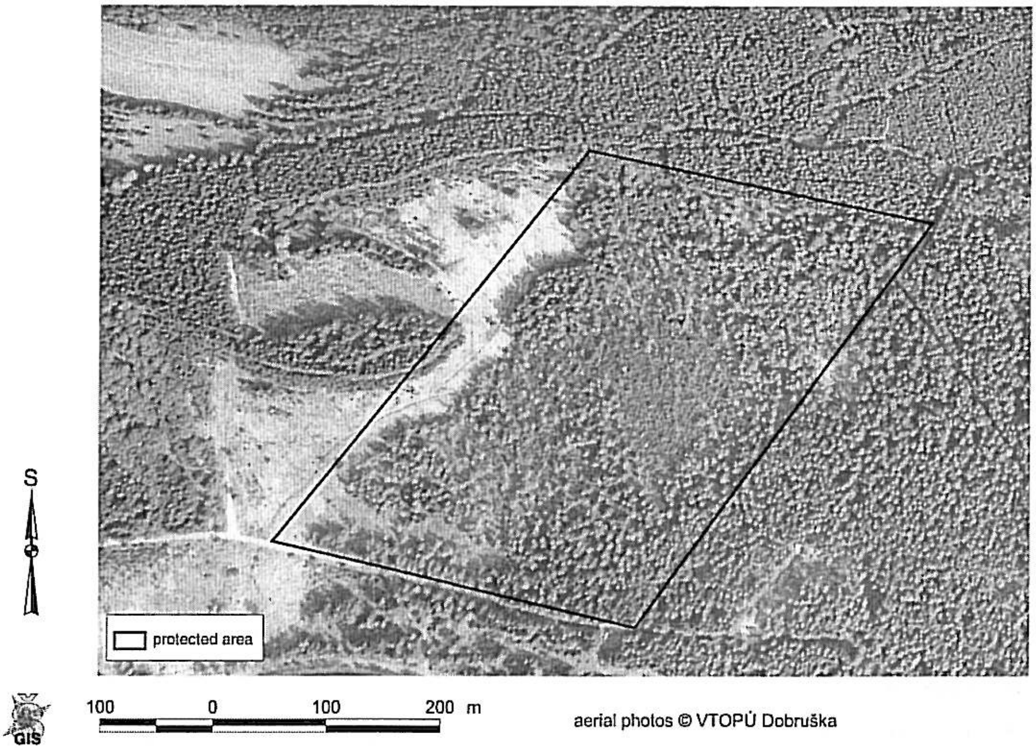
Results

The aerial photographs (**Fig. 2**, **Fig. 3**) show the wide reforestation that occurs in the surroundings during the last 50 years. Comparison of both vegetation maps (**Fig. 4**) has also shown rapid successional changes leading to *Picea abies* forest and retreat of *Pinus × pseudopumilio*.



aerial photos © VTOPÚ Dobruška

Fig. 2. – Rectified aerial black-and-white photograph of the "Multerberské rašeliniště" peat bog. State in 1949.



aerial photos © VTOPÚ Dobruška

Fig. 3. Rectified aerial black-and-white photograph of the "Multerberské rašeliniště" peat bog. State in 1996.

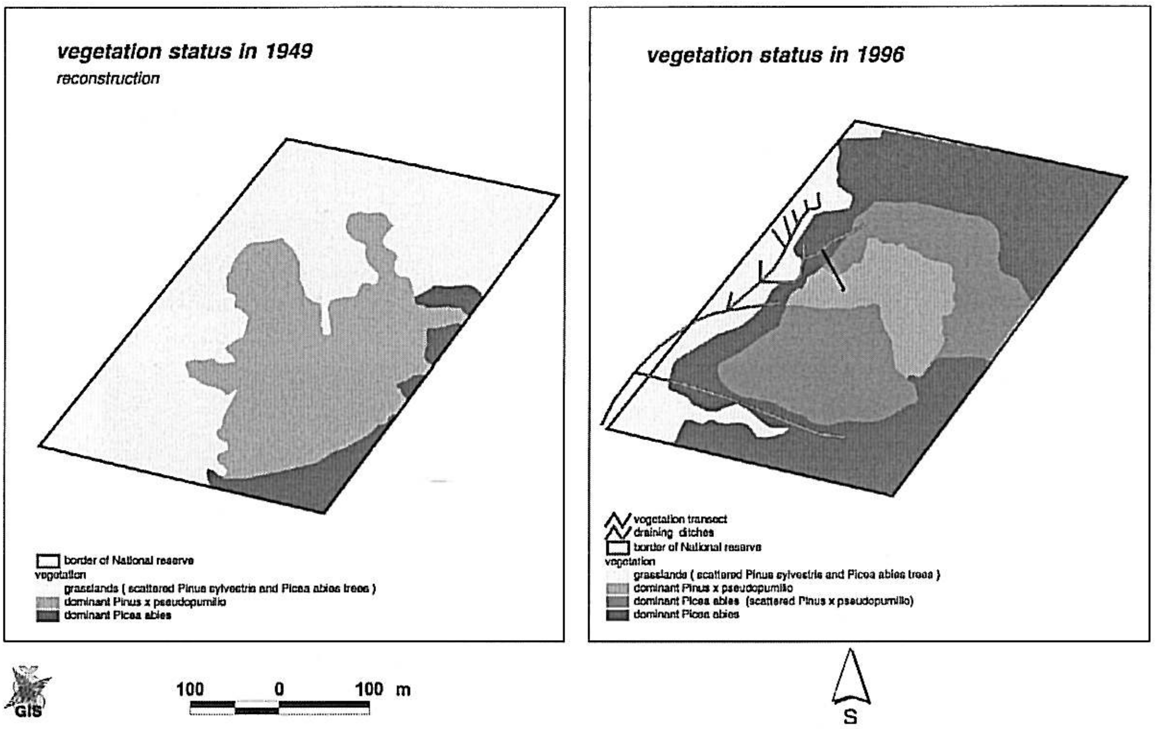


Fig. 4. Vegetation maps of the " Multerberské rašeliniště" peat bog from 1949 and 1996.

The measurements of groundwater table level (**Fig. 5**) have shown that the drainage directly influences groundwater table level in the distance of 13 m. The damming caused a rise of water (0.5 m) during periods with higher precipitation, in drier periods the groundwater table level decreases to 5–10 cm above the level before damming.

Discussion

The biggest change that occurred at the study site is depends on construction of draining ditches in 1980's. It caused increase of a lateral seepage and so most of the rainwater is nowadays very quickly taken away by drainage. According to the groundwater mound theory this leads to increase of a

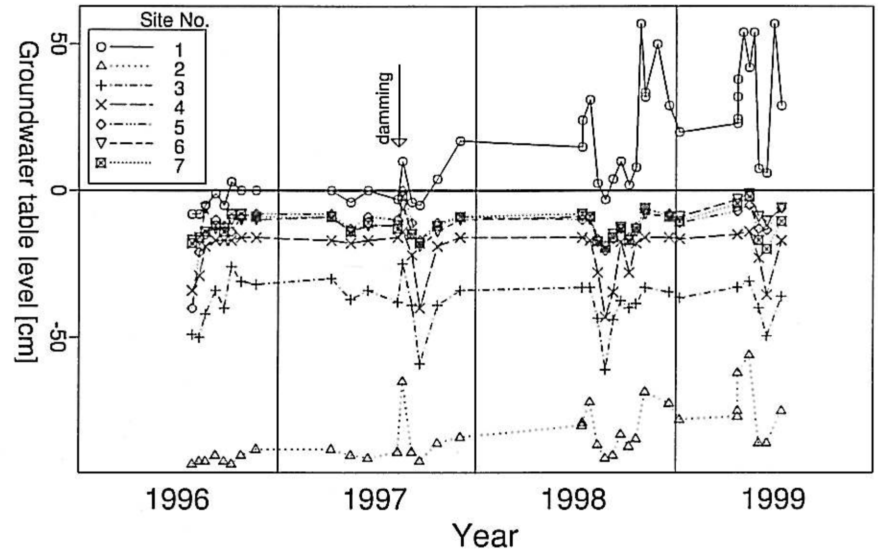


Fig. 5. Fluctuations of groundwater table level on transect at the "Multerberské rašeliniště" peat bog during 1996–1999.

groundwater table fluctuation that results in a deepening on the acrotelm (BRAGG 1995). Although there is no evidence of initial hydrology on the site, we can make the same conclusions as BRAGG (1995) from our measurements along the transect.

Similar study by BRAGG and STEINER (1995) dealt with the development of 'Puergschenmoos' vegetation. Vegetation records from 1947 indicated that the drainage of marginal parts of peat bog resulted in reducing of the hollows in the center and that *Pinus mugo* became taller and denser. This conclusion is consistent with our comparison of aerial photographs. However, the major difference is invasion of *Picea abies* in this case. Changed site conditions (a drainage and may be also absence of an original inhabitants impact) probably favour *Picea abies* to *Pinus* × *pseudopumilio*. The research on the age structure of newly established *Picea abies* patches is planned to characterize the rate of succession.

Conclusion

It is evident that for further survival of the unique hybrid population of *Pinus* × *pseudopumilio* amelioration of marginal parts of the peat bog is necessary. If the actual state remains unchanged, *Picea abies* could overgrow the rest of the site. The damming of draining ditches will be complicated by the fact that there are no permanent springs strong enough to fill the ditches for longer dry periods. The improvement of this state could be possible after natural regeneration of *Sphagnum* mosses in dammed ditches.

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Souhrn

Sukcesní změny vegetace na Multerberském rašeliništi během posledních 50 let na Šumavě

Na lokalitě Multerberské rašeliniště byly za pomoci černobílých leteckých snímků vyhodnoceny změny vegetace mezi lety 1949 a 1996. Srovnání ukázalo ústup křížence *Pinus* × *pseudopumilio* a mohutný nástup sukcese smrku ztepilého směrem do centra rašeliniště, který je zřejmě způsoben zejména odvodněním a pravděpodobně i částečnou eliminací vlivu původních obyvatel. Zároveň byl sledován vliv odvodnění na vodní režim rašeliniště v transektu mezi odvodňovacím příkopem a centrálními partiemi rašeliniště. V druhém roce monitoringu byla v odvodňovacím příkopu postavena hráz. Tento experiment měl ukázat praktickou účinnost hrazení odvodňovacích příkopů na změnu vodního režimu. Hráz je schopna v deštivých obdobích zadržovat až 0,5 m vody, v suchých obdobích hladina podzemní vody postupně klesá 5–10 cm nad původní úroveň v nehrazeném příkopu. Postupného výraznějšího zvyšování průměrné hladiny podzemní vody lze pravděpodobně dosáhnout až s pomocí přirozeného růstu rašeliníku. Sledování vývoje na lokalitě bude pokračovat i v dalších letech.

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Shrnutí

Borovice blatka (*Pinus rotundata* Link) je ohrožený středoevropský druh, s přirozeným výskytem vázaným pouze na rašeliniště. Vyskytuje se v relativně širokém rozmezí nadmořských výšek, přičemž s rostoucí nadmořskou výškou začínají převažovat hybridy s *P. mugo* nazývané *P.* × *pseudopumilio*. Vlastní přítomnost a růstová forma *P. rotundata* případně *P.* × *pseudopumilio* závisí na nadmořské výšce a ovlivňuje složení vegetace jednotlivých lokalit. Vegetace jednotlivých lokalit s borovicí blatkou je vždy do značné míry specifická a poukazuje na unikátnost každého ze sledovaných rašelinišť.

V současné době je zaznamenán ústup *P. rotundata* ve většině areálu. Populace buďto hromadně vymírají nebo postupně ustupují v závislosti na intenzitě disturbance. Míra přirozeného zmlazení *P. rotundata* je většinou velmi nízká.

Hlavními důvody ústupu jsou zřejmě změněné stanovištní podmínky. Změna podmínek byla vyvolána především lidskou činností, ať již přímou (těžba, odvodňování, ale i ústup od tradičního obhospodařování), tak pravděpodobně i nepřímou (atmosférické depozice, změna klimatu).

Úspěšné uchycení semenáčků borovice blatky a jejich přežívání v konkurenci smrku ztepilého a borovice lesní záleží především na těchto faktorech:

a) dostatečná výška hladiny podzemní vody

V podmínkách vysoké hladiny podzemní vody vykazují semenáčky *P. rotundata* nejlepší růst v porovnání s hlavními konkurenčními druhy, jimiž jsou *Picea abies* a *P. sylvestris*. Při snížené hladině podzemní vody sice rostou semenáčky blatky lépe, ale ještě lepší růstové výsledky vykazuje postupně *P. sylvestris* a *P. abies*.

b) nízká hladina dostupných živin

Rašeliniště s výskytem životaschopných populací blatky se vyznačují relativně nízkým obsahem živin. Nízký obsah dostupných živin je podmínkou existence samotného ekosystému, v kterém jsou schopné přežívat jen druhy adaptované na tyto extrémní podmínky. Zvýšený obsah živin sice podporuje růst *P. rotundata*, ale především i ostatních druhů, s kterými je borovice blatka v konkurenčním vztahu.

c) dostatečná hladina osvětlení

Dynamika růstu borovice blatky v případě stínění se velmi snižuje především v porovnání se smrkem ztepilým, pokud ten nachází ostatní podmínky příznivé pro svůj růst (což je především nižší hladina podzemní vody). Smrk ztepilý je navíc schopen dosahovat daleko větších výšek než borovice blatka, takže populaci blatek postupně přeroste a zastíní. Tím prakticky znemožní přirozené zmlazení a stíněné starší stromy odsoudí k postupnému zániku.

Jednotlivé výše zmíněné faktory jsou různou měrou ovlivněny v případě různých disturbancí, což následně určuje pravděpodobnost návratu borovice blatky na narušená místa. Na narušených lokalitách se navíc *P. rotundata* může křížit s *P. sylvestris* což může být zvláště pro malé populace zničující.

Nejpříznivější z hlediska následné pravděpodobnosti úspěšné regenerace jsou přirozené disturbance. Při polomu není nepříznivě narušen vodní režim, spíše naopak dochází k mírnému zvodnění stanoviště v důsledku poklesu transpirace a otevře se prostor pro růst původně podúrovňových stromů. Požár má podobné důsledky pro vodní režim, ale likviduje i podúrovňové stromy a navíc po něm dochází k zvýšení obsahu dostupných živin, takže se regenerace o nějaký čas oddaluje.

Z lidských zásahů má nejméně negativní vliv prostá těžba dřeva, po níž je porost schopen opět zregenerovat, pokud nedojde k narušení vodního režimu. Těžba rašeliny zasahuje do ekosystému vždy velmi radikálně. Původní způsob těžby borkováním většinou nepostihl kompletně celou lokalitu a po ukončení těžby začaly vytvořené sníženiny, které jsou většinou dobře zásobené vodou, opět postupně regenerovat. Na příhodných místech pak dochází k opětovnému uchycování borovice blatky. Vyloženě nepříznivé jsou pro ni většinou pouze příliš zvodnělé či naopak přesychavé části. Moderní velkoplošná těžba (na našem území především frézováním) je spojena s důkladnějším odvodněním než v případě borkování a navíc většinou na lokalitě neponechává významnější zbytky původních porostů, které jsou jako zdroj semen borovice blatky i ostatních druhů základní podmínkou možné kolonizace uvolněného prostoru. Zbytková vrstva rašeliny je minimální a navíc byla hlavně v minulosti rašeliniště lesnicky rekultivována, což většinou znamenalo jejich definitivní zánik. I na nerekultivovaných plochách těžených rašelinišť je velmi obtížné zvýšit a hlavně stabilizovat výšku hladiny podzemní vody. Krajně obtížné je vůbec uchycení rašeliništních druhů a nastartování opětovného ukládání humolitu. Úspěšná a udržitelná přirozená kolonizace borovicí blatkou je v tomto případě ze střednědobého hlediska (desetiletí) málo pravděpodobná.

Z hlediska populací blatky je nepříznivým lidským zásahem pravděpodobně i opuštění tradičního využívání rašelinišť k pastvě či selektivní těžbě, které udržovaly na lokalitách méně zapojený porost. Vliv klimatických změn (zvyšování průměrné teploty) a atmosférické depozice (formy dusíku) pravděpodobně také přispívají k většímu zapojování porostů, což opět znevýhodňuje blatku.

Pro zlepšení stavu populací *P. rotundata* a blatkových rašelinišť jako celku je pravděpodobně první a nejdůležitější podmínkou udržení optimální hladiny podzemní vody a celková stabilizace vodního režimu. V naprosté většině případů totiž trpí lokality narušením vodního režimu v důsledku odvodnění. Přílišné a náhlé zvýšení hladiny však může vést až k odumírání původního porostu, proto je dobré provádět manipulaci pozvolně. Dlouhodobější nepřiměřené zvýšení hladiny či opakované zaplavování lokalit minerálně bohatší vodou může způsobit úplné vymizení blatky a významné změny původních rostlinných společenstev. Efekt stabilizace a optimalizace vodního režimu bude pravděpodobně relativně dlouhodobý.

V případě akutního ohrožení stávajících populací borovice blatky kompeticí se smrkem ztepilým, s nemožností rychlé úpravy vodního režimu, lze zřejmě použít i selektivní kácení smrku ztepilého. To sice zlepší světelné i vlhkostní podmínky pro borovice blatky, ale je bohužel zároveň doprovázeno větší náchylností uvolněných starších jedinců k vývratům a polomům. Efekt takového zásahu je však pravděpodobně relativně krátkodobý a nenahrazuje vlastní úpravu vodního režimu.