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Dynamika horského smrkového lesa

Dynamics of mountain Norway spruce forest

Disertační práce

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Abstrakt

Narušení hrají nezastupitelnou roli v dynamice lesa tím, že ovlivňují strukturu a druhové složení lesa. Nicméně role disturbancí v lesích střední Evropy je do současnosti málo probádanou oblastí navzdory důležitosti, kterou tyto znalosti mají pro hospodaření v lesích. Tato práce se zabývá dendrochronologickou analýzou historického vývoje, historie a režimu narušení horského smrkového lesa na Šumavě. 24 studijních ploch bylo rozmístěno ve starých porostech horských smrčin Šumavy, které se v současnosti rozpadly na rozsáhlých plochách. Na studijních plochách byly získány základní údaje popisující strukturu porostu a navíc byly odebrány vývrty nejméně z 35 kmenů na každé ploše. Letokruhové série byly použity pro rekonstrukci historického vývoje porostu a výskytu historických narušení v prostorovém měřítku od jednotlivého stromu až po krajinu. Na přírůstových sériích byly hledány události, které indikují historická narušení: 1) náhlé, setrvalé a výrazné zvýšení přírůstu (uvolnění z potlačení) a 2) rychlý počáteční přírůst (stromy vzniklé v otevřených podmínkách porostní mezery). Silná narušení, která odpovídají mortalitě více než poloviny stromů, byla identifikována v historii všech analyzovaných porostů. To znamená, že porosty, které se v současnosti rozpadly, vznikaly po podobných narušeních v minulosti. Historická silná narušení se vyskytovala především před 130 – 230 lety v období 1780 – 1880. Nejrozsáhlejší disturbance se vyskytla kolem roku 1820 a narušila více než polovinu studijní oblasti. Narušení byla synchronizována napříč celým pohořím a mezi vzdálenými lokalitami. Většina rekonstruovaných narušení byla vysvětlitelná známými historickými vichřicemi a gradacemi lýkožrouta smrkového. Došli jsme k závěru, že přirozená narušení (včetně rozsáhlých, silných a málo častých narušení) přispívají k široké variabilitě středoevropských horských smrčin. Udržitelný management lesů by měl zahrnout popsaný režim narušení a jeho biologické dopady, protože mnoho druhů je na těchto přirozených strukturách závislých. Popsané vývojové trendy po disturbanci mohou navíc pomoci při předpovídání budoucího vývoje porostů, které se rozpadly v současnosti.

Klíčová slova:

Narušení, režim disturbancí, vichřice, lýkožrout smrkový, Šumava

Abstract

Disturbances play a major role in shaping forest structure and composition. Despite the importance of the knowledge to forest management, their effects on forest ecosystems in central Europe are poorly understood. Using a dendrochronological approach, this research investigates the past development, disturbance history and disturbance regime of the old mountain Norway spruce (Picea abies) forest in the high elevation Bohemian Forest of the National Park and Protected Landscape Area Šumava. A total of 24 study plots were established across the old mountain spruce stands in Bohemian Forest, which were recently broken-up in large extent. Stand structure data was measured and increment cores were collected from at least 35 stems for each plot. Tree ring chronologies were used to reconstruct past stand development and disturbances across scales, from individual trees up to a landscape scale. Growth series were surveyed for events indicative of past tree mortality: 1) abrupt, sustained and rapid increases in growth (releases from suppression), and 2) rapid early growth rates (gap origins). High-severity disturbances, defined as the indication of dieback of at least half of tree population in a given period, were identified in the history of all stands. This finding indicates that stands that were severely broken-up recently were established after similar disturbances in the past. The most severe disturbance periods occurred 130 – 230 years ago during the period of 1780 – 1880. The most extensive disturbance occurred around the year 1820 and affected more than half of the study area. The disturbances were synchronized across whole mountain range. Most disturbances were explained by known historical windstorms and bark beetle outbreaks. We conclude that disturbances, including large, high-severity and low-frequency disturbances, contribute to the broad range of variability of central European mountain spruce forests. Sustainable management strategies should therefore incorporate disturbances of various severities and their biological legacies, as many species likely depend on them. In addition, the development trajectory of stands following stand-replacing disturbance, as described here, can be used to predict future development of recently disturbed stands.

Key words:

Disturbance, disturbance regime, windstorm, bark beetle, Bohemian Forest

Obsah

1. Úvod

Druhá polovina dvacátého století přinesla zásadní změnu v chápání dynamiky vegetace a potažmo přirozených lesů (White, 1979; Wu and Loucks, 1995). Původní představa byla reprezentována například teorií klimaxu a popisovala přirozený les jako vysoce stabilní samoregulující se entitu (Clements, 1916). V tomto pojetí byly disturbance chápány jako vzácné události, které iniciují sukcesi směřující ke klimaxu. Teorie klimaxu byla zavržena na základě zjištění, že věková, druhová a prostorová struktura lesa je v dominantní míře formována variabilními typy narušení (Henry and Swan, 1974; Oliver and Stephens, 1977; Pickett and White, 1985; Johnson and Miyanishi, 2007) a že existují typy krajin, ve kterých les v důsledku rozsáhlých narušení nedosahuje rovnovážného stavu ani na velkých prostorových škálách (Turner et al., 1993).

Přestože znalosti o charakteru (tj. struktuře a dynamice) přirozených lesů jsou v současnosti poměrně dobré v Severní Americe, ve střední Evropě jsou stále značně neúplné z několika důvodů. Zaprvé, přírodní lesy (nebo dokonce krajiny přírodních lesů) jsou vzácné po rozsáhlé exploataci těchto zdrojů. Zadruhé, význam stanoviště pro charakter vegetace byl v minulosti nadhodnocen pravděpodobně proto, že většina lesů ve střední Evropě má velice stabilní druhové složení (Splechtna et al., 2005). Zatřetí, chráněné pralesovité zbytky byly pravděpodobně zakládány na chráněných místech, kde síla a frekvence disturbancí byla menší a kde se vyskytovaly heterogenní porosty s obdivuhodnými velkými stromy (Angelstam and Kuuluvainen, 2004). Tím pádem začtvrté, byl malý zájem o studium role disturbancí v lesích a historické studie (např. dendrochronologické) byly málo prováděny.

V současnosti je poznání dynamiky přirozených horských smrkových lesů a jejich přirozené struktury zásadním a aktuálním tématem v několika oblastech střední a východní Evropy. Tyto znalosti jsou nutné při rozhodování o managementu lesů. Problematika režimu disturbancí, přirozeného vývoje porostů a jejich přirozeného rozsahu variability je podkladem např. při hospodaření v ochranných lesích v Alpách. Je snaha odpovědět na otázky jak se budou porosty vyvíjet v budoucnosti, jaký vliv na ně budou mít přirozená narušení a jaký efekt to bude mít na plnění ochranných funkcí těchto lesů (Bebi et al., 2001; Dorren et al., 2004; Kulakowski and Bebi, 2004; Krumm et al., 2011; Kulakowski et al., 2011). Tato oblast by se koneckonců dala zobecnit. Společnost v současnosti požaduje od lesů plnění také dalších funkcí než jen produkci dřeva. Pro plnění těchto dalších funkcí jsou pak často důležité znalosti o přirozených strukturách lesa a režimu narušení, protože využívání přirozených procesů pro plnění hospodářských cílů vede k vyšší efektivitě a nižším nákladům (Bengtsson et al., 2000). Jedním z hlavních cílů Evropské unie do budoucna je zastavit vymírání druhů a snižování biodiverzity, které postihlo také středoevropské horské smrčiny zejména díky způsobu hospodaření (Foley et al., 2005). Imitování přirozené variability lesa při hospodaření je cestou jak zajistit rozličným druhům prostor pro život a zajistit udržitelnost našeho počínání v krajině (Franklin et al., 2002; Lindenmayer et al., 2006). V neposlední řadě jsou znalosti o přirozené dynamice lesů důležité v chráněných územích pro formulaci zásad jejich managementu, resp. pro vylišení zásahových a bezzásahových území. Pro takové úvahy je nutné odhadovat budoucí vývoj zájmových porostů.

Oblastí zájmu v této práci bude zejména horský smrkový les v NP a CHKO Šumava tedy oblast, kde je možné (díky tomu, že se jedná o území zaměřené na ochranu přírody) jednak studovat přirozenou strukturu a dynamiku lesních porostů a jednak jsou zde tyto informace potřebné v praktickém managementu. Díky tomu, že lidská kolonizace dosáhla k horským hřbetům Šumavy relativně pozdě, až v 18. století (Beneš, 1996), existují v oblasti ještě porosty s přirozeným nebo polopřirozeným původem (Čada, 2009; Hubený, 2010a; Hubený, 2010b; Janda et al., 2010; Svoboda et al., 2010). Horské smrčiny jsou podstatným základem bohatství Šumavy, a jako takové jsou samozřejmě předmětem nekončících diskusí. Nedostatek podložených znalostí v takovém případě situaci ještě zhoršuje. Základním předpokladem pro pochopení dynamiky (a potažmo charakteru) lesů je obsažení co největšího časového a prostorového rámce vzhledem k dlouhověkosti stromů a lesů. Jinými slovy situace, která v lese nastala před stovkami let, může ovlivnit jeho dnešní charakter. V šumavských národních parcích (NP Bayerischer Wald v Bavorsku a NP Šumava v Čechách) postupně docházelo během posledních třech dekád k rozsáhlým narušením lesa zejména vlivem vichřic a gradací lýkožrouta smrkového (Lausch et al., 2011; Fischer et al., 2002). Zásadní otázkou pro management je, zaprvé, zda tyto události jsou přirozené pro středoevropské horské smrkové lesy a, zadruhé, jakým způsobem se budou narušené plochy vyvíjet v budoucnosti. Popsané výzvy budou řešeny v rámci této disertační práce.

2. Rozbor problematiky

2.1 Šumavský problém – historie se (ne)opakuje

Kolonizace Šumavy byla dokončena poměrně pozdě. Její poslední etapa (tzv. dřevařská kolonizace) vrcholila v 18. století (Beneš, 1996). V polovině 18. století byly založeny Stožec, Borová Lada, Prášily a další v současnosti často již zaniklé vsi. Obyvatelé těchto vesnic těžili dřevo zejména ve svém okolí, proto nepřekvapí, že i v 19. století byly zejména vrcholové vzdálenější partie šumavského hvozdu pokryty původním lesem. V těchto lesích ve vysokých nadmořských výškách dominoval smrk ztepilý. Takové smrkové pralesy mohl (vzhledem k jejich odlehlosti) v minulosti člověk využívat pouze k pastvě dobytka a lovu (Macar and Maršík, 2005).

Teprve od poloviny 19. století se začínají lesy ve vyšších partiích Šumavy intenzivně využívat k těžbě dřeva. Většinu lesů tehdy vlastnily šlechtické rody Schwarzenbergů a Hohenzollernů, které měly zájem na jejich hospodářském využití. V té době tedy proběhlo první zařízení lesů pro hospodářské účely, jejich rozdělení na porosty a také jejich důkladné zmapování (Jelínek, 2005; Macar and Maršík, 2005). Díky tomu se do současné doby dochovaly poměrně podrobné údaje o charakteru tehdejších lesů, z nichž významná část byla do té doby minimálně ovlivněna činností člověka (Jelínek, 2005). Představu o fungování přírodních lesů mohou poskytnout také další historické materiály o výskytu vichřic a kůrovcových gradací, které ovlivňovaly historické lesy (Zatloukal, 1998; Skuhravý, 2002; Schelhaas et al., 2003; Brázdil et al., 2004).

Z historických materiálů je patrné, že se v minulosti na Šumavě vyskytovaly silné vichřice téměř v každém desetiletí, a že se minimálně jednou za století vyskytla vichřice schopná působit silné polomy na větších plochách (tab. 1; Zatloukal, 1998; Brázdil et al., 2004; Jelínek, 2005). Dynamiku středoevropských horských smrkových lesů však může navíc výrazně ovlivňovat lýkožrout smrkový (*Ips typographus*). Druh, který je schopný se ve vhodných podmínkách rapidně množit a působit rozsáhlá narušení přesahující dopad původního větrného polomu (Skuhravý, 2002; Okland and Bjørnstad, 2006). Vhodnými podmínkami, které zejména působí pozitivně na populaci lýkožrouta, jsou teplota, sucho a polomy (Marini et al., 2012). První podmínka působí přímo na rychlost vývoje lýkožrouta. Další dvě podmínky ovlivňují obranyschopnost jeho potravy, smrku ztepilého, a tím nepřímo opět zvyšují jeho úspěšnost (Marini et al., 2012). Lýkožroutové gradace byly na Šumavě zaznamenány v průměru asi dvakrát za století (tab. 1; Zatloukal, 1998; Jelínek, 2005). Zajímavá je synchronizace gradací na evropské úrovni. Schelhaas et al. (2003) zdokumentovali pro oblast Evropy nahodilé těžby způsobené lýkožroutem smrkovým a zjistili jejich výrazný dopad ve shodných obdobích, které udává tab. 1 pro Šumavu. To by nahrávalo tvrzení, že převažující vliv na vznik gradace mají klimatické podmínky, což potvrzuje i Aakala et al. (2011) z boreálních smrčin na severozápadě Ruska, kde došlo k žíru lýkožrouta bez výrazného polomu.

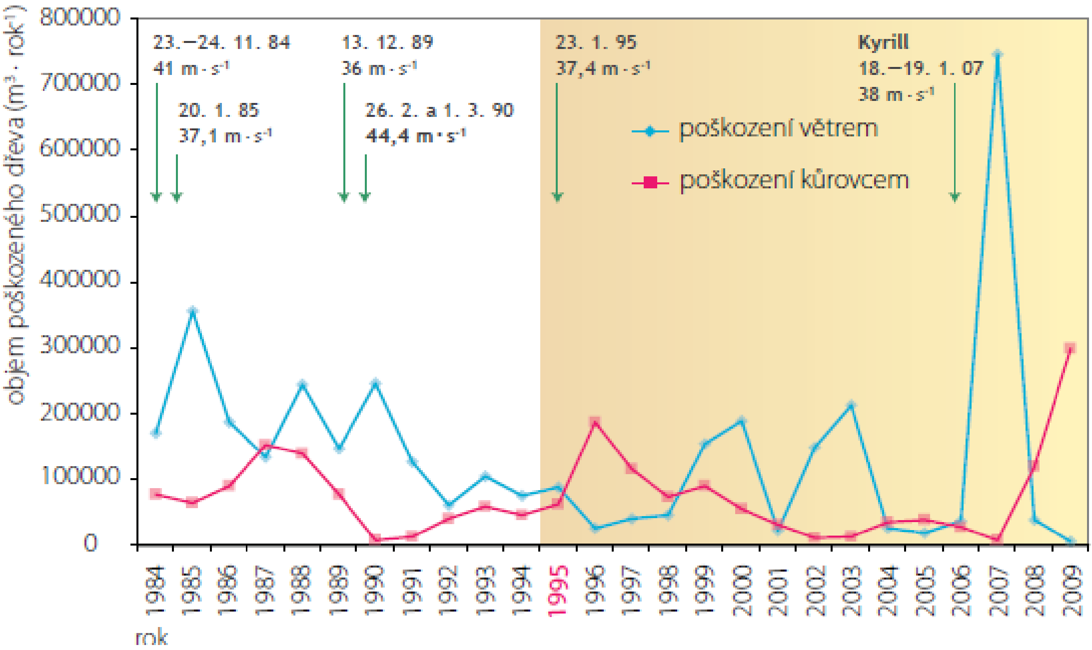
V polovině 19. století, v době zařizování lesů a vytvoření prvních lesnických porostních map, byl podíl starých porostů (>120 let) na Schwarzenberském panství na Šumavě asi 25% (Jelínek, 2005; Svoboda, 2006). Tyto porosty tedy vznikaly před kolonizací Šumavy a byly většinou klasifikovány jako původní pralesy (Jelínek, 2005; Svoboda, 2006). Tuto hodnotu lze brát spíše jako minimální, protože zbývající část plochy byla výsledkem spolupůsobení přírodních narušení (tab. 1) a těžební činnosti člověka (Svoboda, 2006). Do popsané situace přinesla razantní změnu série vichřic z období 1859-1870, která vyvrcholila „mocným orkánem ze 7. prosince 1868“ (Macar and Maršík, 2005). V 70. letech 19. století za ní následovala gradace lýkožrouta smrkového. Tato narušení postihla odhadem 5-7 mil. m^3 dřeva (Zatloukal, 1998). Nejvíce a nejintenzivněji byly postiženy právě staré lesy. Disturbance narušily 85% porostů starších 120 let. Z původního podílu 25% tak na konci 19. století zbylo v zájmovém území pouhých ca 5% starých porostů (Svoboda, 2006). Z těchto informací vyplývají dvě skutečnosti. Zaprvé, že narušením v podobě vichřic a kůrovcové gradace ve druhé polovině 19. století nebyly schopné odolat ani původní porosty. Zadruhé, že tyto disturbance zásadně změnily strukturu lesa na Šumavě (Svoboda, 2006).

Popsaná narušení byla samozřejmě hospodářsky zpracovávána. Proto v současné době není možné určit, jak velká část lesa v období 1870-1880 byla narušena přirozeně, a jak velká část byla následně vytěžena (Jelínek, 2005; Svoboda et al., 2010). I v následujících několika desetiletích podléhaly šumavské lesy bezesporu hospodářskému využití. V tomto období, jak se domnívám, tím pádem pravděpodobně došlo k zásadnímu ovlivnění struktury krajiny horského smrkového lesa činností člověka. Došlo pravděpodobně ke zjednodušení krajinné mozaiky, protože již na přelomu 19. a 20. století byly pravděpodobně vytěženy zbývající přeživší porosty, které by přirozeně přežívaly do následující vlny disturbancí.

Tab. 1: Přehled historicky známých vichřic a gradací lýkožrouta smrkového (*Ips typograhpus*) na Šumavě. Informace byly získány z prací Zatloukala (1998), Brázdila et al. (2004) a Jelínka (2005).

období	**typ disturbance**
1710	vichřice
1720-1730	vichřice a gradace lýkožrouta
1740	vichřice
1778	vichřice
1801	vichřice
1812-1813	vichřice
1818	vichřice
1821-1822	vichřice
1830	vichřice
1833-1840	vichřice a gradace lýkožrouta
1853	vichřice
1859-1863	vichřice
1868-1877	vichřice a gradace lýkožrouta
1903-1906	vichřice
1921-1922	vichřice
1929	vichřice
1939-1940	vichřice
1946-1954	gradace lýkožrouta
1955	vichřice
1957	vichřice
1960	vichřice
1967	vichřice
1976	vichřice
1983-1989	vichřice a gradace lýkožrouta

V novodobé historii od roku 1984 po sérii vichřic docházelo opět k rozsáhlým rozpadům horských smrkových lesů na Šumavě (obr. 1; Zatlouhal, 1998). Dynamické období na české části Šumavy vyvrcholilo orkánem Kyrill z 18.-19. ledna 2007. Ještě větší vliv než vítr měly gradace lýkožrouta smrkového se třemi vrcholy aktivity v období 1984-1989, 1995-1999 a 2007-2012 (Šantrůčková et al., 2010). Popsané disturbance razantně změnily obraz a strukturu horských smrkových lesů na Šumavě a odstranily naprostou většinu starých porostů (Lausch et al., 2011). Moderní narušení za posledních 30 let postihly asi 4,5 milionu m^3 dřeva (obr. 1; Klewar ústní sdělení, Zatloukal, 1998; Šantrůčková et al., 2010).



Obr. 1: Graf vývoje objemu poškozeného dřeva větrem a lýkožroutem smrkovým (Ips typographus) v NP Šumava za období 1984-2009 s uvedením vyskytnuvších se vichřic o síle orkánu. Převzaté z práce Šantrůčkové et al. (2010).

Na základě historických materiálů lze říci, že současný rozpad porostů horských smrčin na Šumavě měl mnohé paralely se známými událostmi z minulosti. Minimálně lze říci, že silné přirozené disturbance v podobě větru a gradací lýkožrouta smrkového se vyskytovaly také v minulosti. Byly však zjištěny některé odlišnosti současného rozpadu od minulosti: 1) krajinná mozaika lesa mohla být zjednodušena těžebními aktivitami na přelomu 19. a 20. století, 2) fitness lýkožrouta smrkového mohlo být vyšší díky klimatické změně a vyšším teplotám (Seidl et al., 2011) a 3) obranyschopnost smrku mohla být nižší v důsledku znečištění ovzduší a měnícího se klimatu (Šantrůčková et al., 2007; Seidl et al., 2011).

2.2 Dynamika výzkumu

Snaha o poznání zákonitostí, které formují přirozené lesy, sahá na Šumavě hluboko do historie. Již z roku 1846 pochází údaje od lesmistra Seidla o struktuře pralesního porostu ze šesti výzkumných ploch na svahu Černé hory (Bečka, 2012). Nedlouho poté byly založeny i věhlasné výzkumné plochy lesmistra Johna v Boubínském pralese (Macar and Maršík, 2005; Vrška et al., 2012). Kromě strukturních zákonitostí se John zajímal i o věkovou strukturu porostu. Nejstarší nalezený strom dosahoval v roce 1864 věku 580 let a nejvíce stromů bylo asi 280 let starých (Nožička, 1959).

Podobně také ve světě dochází od 19. století k využívání informací obsažených v letokruzích pro různé vědecké úkoly. K zásadnímu převratu však dochází na počátku 20. století, kdy Andrew Ellicott Douglass, „otec dendrochronologie“, objevuje princip křížového datování, tedy principu, kdy na základě shodné meziroční variability v růstu a vzájemného porovnávání je možné přiřadit každý letokruh konkrétnímu kalendářnímu roku (Douglass, 1929; Speer, 2010).

Na začátku 20. století se formuje také představa přírodních ekosystémů jako stabilních, vyvážených a harmonických systémů v poslední fázi sukcese. Takové představy jsou reprezentovány např. teorií klimaxu (Clements, 1916). V tomto pojetí jsou přírodní disturbance vnímány jako externí faktor vychylující systém z rovnováhy, kam se posléze opět sekundární sukcesí navrací. Častým problémem při studiu zákonitostí fungujících v přírodních ekosystémech je zahrnutí nedostatečného časového a prostorového rámce nebo využívání metody chronosekvencí (tj. substituce času prostorem; Johnson and Miyanishi, 2007). S využitím dendrochronologických metod bylo možné obsáhnout daleko větší časový rámec a sledovat tak, jakým způsobem vznikaly v současnosti staré porosty (Henry and Swan, 1974; Oliver and Stephens, 1977). Průkopníkem nejen v oblasti výzkumu dynamiky lesa s využitím dendrochronologie ve střední Evropě byl Bohuslav Vinš (1961), který rekonstruoval minulý vývoj porostu smrko-jedlo-bukového pralesa. V historii porostu zjistil dlouhodobé kolísání v intenzitě růstu a náhlá zvýšení přírůstu, což je v současné době dáváno do souvislosti s historickým narušením porostů (Vinš, 1961). Výsledkem těchto pionýrských prací bylo zjištění, že přírodní disturbance jsou přirozenou a nedílnou součástí dynamiky lesa, protože 1) existuje gradient od slabých po silné události, které formují strukturu lesa, a 2) některé disturbance jsou iniciovány nebo podporovány biotickými komponenty systému (White, 1979).

V současnosti se pomocí konceptu narušení popisuje historický vývoj porostu. Koncept režimu disturbancí se, ve finále, stal velice užitečným pro definici celkového charakteru, dynamiky a rozsahu variability lesa v krajině (Frelich, 2002; Kulakowski and Bebi, 2004). Narušení je „jakákoliv relativně samostatná událost v čase, která poruší strukturu ekosystému, společenstva nebo populace a změní zdroje, dostupnost substrátu nebo fyzikální prostředí“ (Pickett and White, 1985). Výhodou tohoto konceptu je jeho jednoduchost a obecná použitelnost. Narušení je možné kvantifikovat poměrně jednoduše s minimalizací subjektivního přístupu. Teze, že narušení se vyskytuje v každém lese, je obdobná té, že stromy umírají. Narušení se vyskytne v čase izolovaně, tj. jedná se z pohledu vývoje lesa o událost; poruší předchozí stav, tj. jedná se o relativní změnu; ale také podnítí další vývoj (Pickett and White, 1985; Frelich, 2002). Koncept režimu narušení je popis všech typů narušení, které se v krajině vyskytují (tj. popis faktoru narušení, frekvence výskytu, síly a rozsahu; Frelich, 2002). Odpovědí na režim narušení je rozsah variability, tj. struktura lesa v krajinném měřítku, která je výsledkem působení narušení (Kulakowski and Bebi, 2004).

Právě díky relativně radikálnímu efektu, který narušení v lese má, je možné rekonstruovat narušení v minulosti. Nejen tím se zabývá obor zvaný dendroekologie, který na základě dendrochronologického přístupu (studia charakteristik letokruhů a jejich časových řad) získává znalosti o ekologii druhů stromů, jejich populací a společenstev. Retrospektivní sledování pomocí letokruhových sérií hraje nezastupitelnou roli při studiu dynamiky lesa, neboť ta se odehrává v daleko delších časových měřítkách, než které lze zachytit studiem na trvalých výzkumných plochách či dokonce lidskou pamětí (Vinš, 1961; Henry and Swan, 1974; Cook and Kairiukstis, 1990).

Obr. 2: Uvolnění (náhlé a setrvalé zvýšení přírůstu po odstranění konkurence)

Pomocí konceptu narušení lze studovat různé typy narušení od přírodních disturbancí větrem, gradacemi různých druhů hmyzu apod. (Frelich and Lorimer, 1991; Swetnam and Lynch, 1993; Eisenhart and Veblen, 2000; Firm et al., 2009; Fraver et al., 2009), přes různé typy požárů (Niklasson and Granström, 2000; Gutsell and Johnson, 2002; Peters et al., 2002; Wallenius et al., 2005; Lilja et al., 2006), až po rekonstrukci minulých historických těžeb (Motta et al., 1999; Storaunet et al., 2000; Groven et al., 2002) nebo vypalování (Ruffner and Abrams, 2002).

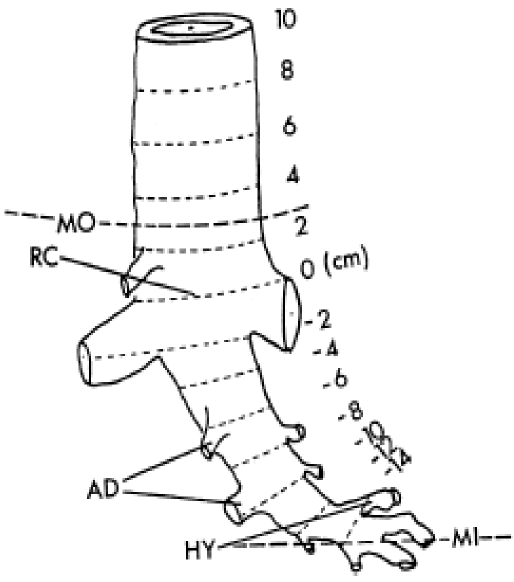
Výskyt takových narušení se rekonstruuje pomocí efektu, který tato narušení měla na porost a přeživší stromy, neboť disturbance (jak bylo zmíněno) působí relativně radikální změnu a podněcují další vývoj. Odstraněním stromů, které byly vyvráceny větrem, podlehly ataku lýkožrouta smrkového, byly spáleny požárem nebo vytěženy, dochází k uvolnění zdrojů na stanovišti. Stromy, které přežily, reagují na snížení kompetice náhlým a setrvalým zvýšením přírůstu. Taková událost v letokruhové sérii se nazývá uvolnění (obr. 2; Lorimer and Frelich, 1989). Další jedinci v uvolněných podmínkách klíčí nebo dorůstají do výšky odběru vzorků. Jejich růst je od počátku rychlý a jeho trend je rovný, klesající nebo parabolický (Frelich, 2002). Pokud byla obnova pod disturbancí odstraněným porostem málo početná, malá nebo byla také odstaněna, lze pak rekonstruovat výrazný pulz v obnově. Takto vzniklé porosty jsou výrazně stejnověké a poukazují na to, že vznikly po silném narušení (Gutsell and Johnson, 2002; Peters et al., 2002; Lilja et al., 2006). V některých studiích, které se zaměřují na dataci pouze silných narušení výrazně devastujících porost, se disturbance datují pomocí doby, kdy stromy dosáhly korunové klenby. V korunové klenbě je každý strom, který dostává přímé sluneční záření (tj. i malé stromky v porostních mezerách). Doba dosažení korunové klenby je počátek růstu pro stromy vzniklé v porostní mezeře nebo doba prvního velkého uvolnění (Frelich and Lorimer, 1991).

Některá narušení zanechávají na přeživších stromech další stopy svého výskytu. Gradace defoliátorů působí výrazné snížení přírůstu u hostitelských stromů (Swetnam and Lynch, 1993), požáry vytváří na popálených stromech ohnivé jizvy (Wallenius et al., 2002; Wallenius et al., 2005), stromy přeživší vichřici mohou vytvořit reakční dřevo nebo zvýšené množství pryskyřičných kanálků (Zielonka and Malcher, 2009).

2.3 Dynamika obnovy – věk

Ekologické chování obnovy lesa může být částečně popsáno jednoduše pomocí věkové struktury populace (Agren and Zackrisson, 1990; Hofgaard, 1993; Engelmark et al., 1994; Brumelis et al., 2005). Znalosti o vztahu obnovy (věková struktura) a minulých narušení jsou poměrně důležitá. Nicméně zjistit skutečný věk stromu je náročné (DesRochers and Gagnon, 1997; Niklasson, 2002). Běžná praxe odebírání vývrtů ve výšce pařezu nebo prsní výšce vede k podhodnocení věku stromu a, co je podstatnější, k rozptylu věkové distribuce v řádu desetiletí (DesRochers and Gagnon, 1997; Parent et al., 2000; Gutsell and Johnson, 2002; Niklasson, 2002; Peters et al., 2002). Tyto problémy v minulosti vedly k chybným interpertacím věkové struktury lesa. Bylo zjištěno, že (oproti dosavadním představám) se stromy v severní Americe obnovovaly ihned po požáru a nikoliv se zpožděním. Podhodnocení věku bylo tím vyšší, čím byl vyšší věk stromu, a podhodnocení bylo vyšší u druhů, které z počátku života rostou pomaleji. To např. vyvrátilo domněnku, že listnaté stromy nalétávají na lokalitu dříve, a teprve v jejich podrostu se obnovuje smrk a další druhy. Rozdíly existovaly pouze v intenzitě výškového přírůstu v mládí (DesRochers and Gagnon, 1997; Gutsell and Johnson, 2002; Peters et al., 2002). Niklasson (2002) zjišťoval skutečný věk stromů u smrku ztepilého v severním Švédsku, které se uchytily po přízemním požáru v podrostu borovic. Skutečný věk byl v průměru o 20-26 let vyšší oproti počtu letokruhů při zemi. O podobnou hodnotu byl navíc zvýšen rozptyl výsledné distribuce věků. Nejstarší část stromu (místo vyklíčení) se většinou nacházelo pod zemským povrchem pod nejvýše položenými kořeny (obr. 3; Niklasson, 2002). U smrku často dochází v mládí k ohýbání kmínku vlivem např. sněhu. Tento je následně přitlačen k zemi, v důsledku čehož vytváří výše položené adventivní kořeny (Niklasson, 2002).

V závislosti na cíli konkrétní studie někdy není třeba znát přesný věk stromu. Při datování minulých narušení pomocí obnovy porostu je dobré dostat se v čase co nejblíže době disturbance. V případě lesů ovlivňovaných požáry, kdy nové stromky klíčí až po požáru, je důležité zjistit věk stromu co nejpřesněji (viz předchozí odstavec). Nicméně v případě vlivu větru nebo hmyzu, kdy po narušení dochází k uvolnění již existující obnovy v podrostu, často není nutné zjišťovat přesný věk stromů (Fraver and White, 2005a; Splechtna et al., 2005).



Obr. 3: Schématické znázornění části kmene a kořene smrku ztepilého s označením sekcí po 2 cm. MO: horní okraj přízemní vrstvy mechu; RC: nasazení nejvýše položeného kořene; AD: adventivní kořeny; HY: hypokotyl, nejstarší část stromu, který byl často velmi malý a umístěný paralelně k mnohem většímu „hlavnímu" kořeni, a proto byl často považován za kořen a ztracen; MI: minerální půda (převzato z práce Niklasson, 2002).

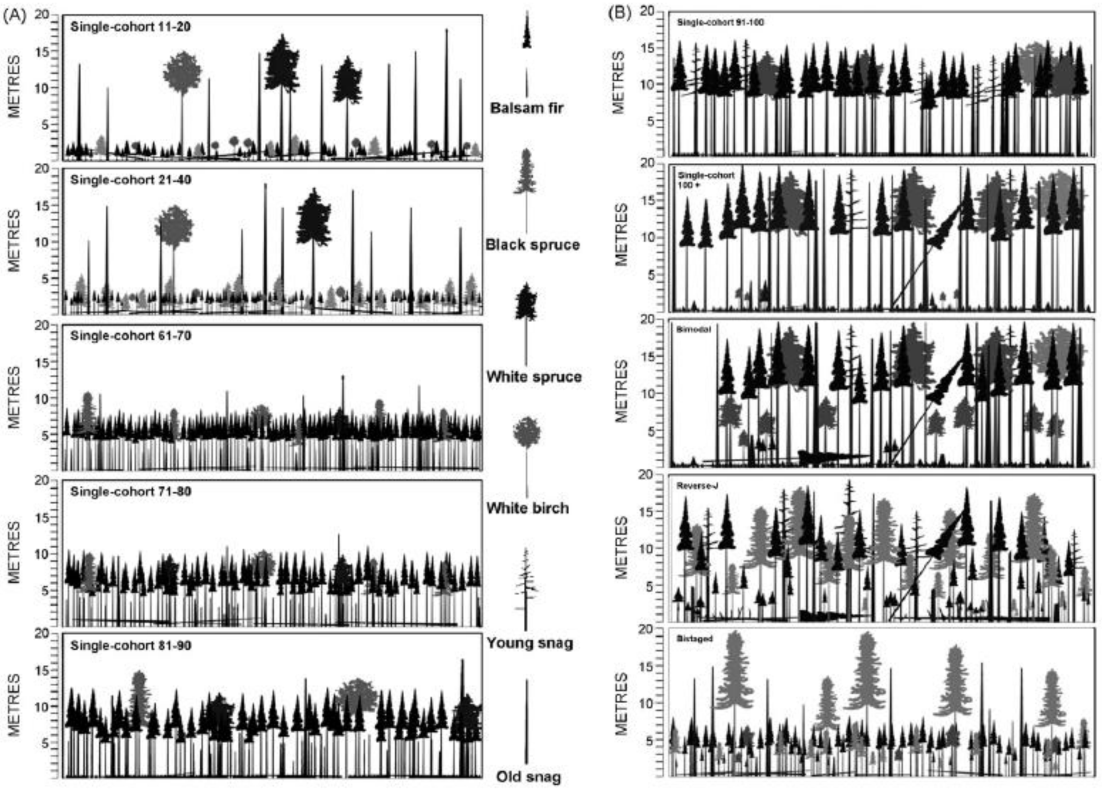
V případě horského smrkového lesa střední Evropy jsou po narušení větrem nebo lýkožroutem smrkovým uvolněni malí jedinci (Jonášová, 2001; Jonášová and Prach, 2004; Ulbrichová et al., 2006; Svoboda, 2007; Svoboda and Zenáhlíková, 2011; Zenáhlíková et al., 2011). Zmlazení je pod zapojenou korunovou klenbou výrazně limitováno nedostatkem světla, takže často není schopné dosáhnout větší výšky než 0,5 metru (Holeksa et al., 2007; Saniga, 2007). Z toho důvodu se domníváme, že je vhodné odebírání vývrtů při zemi ve výšce pařezu – v souladu s dalšími autory (Veblen et al., 1994; Motta et al., 1999; D'Amato and Orwig, 2008).

Fischer and Fischer (2012) sledovali dynamiku obnovy po rozpadu vichřicí v roce 1983 (dorůstání do výšky 1 m). Zjistili, že podíl vzrostlejší obnovy z podrostu předchozího porostu je relativně menší (100-650 smrků/ha). Většina nové generace dorostla do výšky 1 metru v období 1988-1998. Celková početnost smrku dosahovala v roce 2008 v průměru asi 3000 ks/ha. U smrků, které dorostly v roce 2003 (20 let po disturbanci), už byla vysoká úmrtnost (ca 80%). V období 1988-1998 byl také zaznamenán výrazný pulz v obnově břízy. Po roce 1998 již začala ustupovat a úmrtností ca 50% trpěly i nejstarší jedinci. V roce 2008 však ještě stále rostla v hustotě ca 3000 ks/ha a zaujímala asi polovinu dřevní zásoby (Fischer and Fischer, 2012).

Dynamiku obnovy ovlivňuje typ a síla narušení (tj. podíl odstraněných stromů) a struktura předchozího porostu (Ulbrichová et al., 2006; Čada, 2009). Zde existuje gradient od 1) slabšího narušení, které ponechá část předchozího porostu, ale umožní dorůstání obnovy do korunové klenby; přes 2) porosty, které byly před narušením rozvolněné, a proto v nich existovala i relativně starší obnova; 3) porosty, kde sice byla obnova mladá, ale kde zbyly některé plodící stromy; po 4) porosty, kde byly odstraněny všechny dospělé stromy a následný porost může pak být (podle charakteru obnovy) oproti předchozím případům dosti řídký (Jonášová and Prach, 2004; Ulbrichová et al., 2006; Čada, 2009). Hustota stromků se pohybuje od nuly až přes 15000 ks/ha, přičemž podíl ploch s hustotou 0-500 ks/ha je 7 %, stejně jako podíl ploch s hustotou přes 15000 ks/ha. Největší počet ploch byl v kategorii 1000-3000 ks/ha (Čížková et al., 2011).

2.4 Dynamika disturbancí

V části lesů Newfoundlandu (Severní Amerika) dominuje jedle balsámová (Abies balsamea). Na této jedli se živí obaleč Choristoneura fumiferana a píďalka Lambdina fiscellaria fiscellaria, kteří jsou schopni kalamitního namnožení a „likvidace“ rozsáhlých porostů této jedle. Gradace byly dobře zdokumentovány a ve dvacátém století se opakovaly u obaleče každých 30 let a u píďalky každých 13-27 let. V těchto podmínkách je zřejmé, že jedle, které se dožijí 200 let, jsou vzácností. I přesto si však jedle udržuje svou dominanci v těchto lesích, protože jako jediná dokáže vytvořit početné zmlazení (až několik stovek tisíc na ha), které odrůstá po odstranění mateřského porostu a vytváří další hustý porost této jedle (McCarthy and Weetman, *2007). Zajímavé srovnání s problémy s gradací lýkožrouta smrkového v horských smrkových lesích střední Evropy poskytne možná také studie Parent et al. (2001), která potvrdila masivní produkci semen, potažmo obnovu, u jedle balzámové těsně před a na začátku gradace zmíněného obaleče.*



Obr. 4: Schématické znázornění vývoje porostu v jedlo-smrkovém lese ovlivňovaném hmyzími gradacemi (převzato z práce McCarthy and Weetman, 2007).

Dalším příkladem může být vztah požárů a některých druhů přizpůsobených jim, např. vytvářením tzv. serotinních šišek, které se otvírají po požáru a umožňují obnovu (např. borovice banksova, Pinus banksiana, nebo smrk černý, Picea mariana; Frelich, 2002). Tyto druhy zároveň lépe hoří než druhy bez přizpůsobení k požárům, čímž se zvyšuje pravděpodobnost výskytu požáru, a tím se udržuje dominance zmíněných druhů (Frelich, 2002). U jiného druhu smrku sivém (Picea glauca) byla zdokumentována za příznivých podmínek masivní obnova, která byla nejvyšší v prvním roce po požáru a zcela ustala do pěti let po požáru (Peters et al., 2002). Frekvence korunových požárů má razantní vliv na druhové složení lesa. V průměru se vyskytne *požár každých 20-120 let. V takovém případě dominuje porostu borovice banksova. V případě, že se však vyskytne požár dříve než za 20 let, borovice nemá ještě vytvořenou zásobu semen a následnému porostu dominuje osika (Populus tremuloides). Naopak, pokud se požár nevyskytne déle než 200 let, zvyšuje se podíl smrku (Picea mariana), který v porostu často v menší míře existoval již po požáru, a jedle (Abies balsamea), bříza (Betula papyrifera) a zerav (Thuja occidentalis) začínají odrůstat v porostních mezerách vznikajících odumíráním borovice (Frelich, 2002).*

Smrkové lesy celosvětově podléhají velice různorodým režimům disturbancí – od systémů, které jsou formovány silnými korunovými požáry (např. *Picea mariana* v boreálních lesích severní Ameriky; Frelich, 2002), silnými vichřicemi a gradacemi hmyzích parazitů (např. *Picea engelmani* v horském pásmu amerických Skalistých hor; Veblen, 2000; nebo *Picea glauca* v boreálních lesích severní Ameriky; Berg et al., 2006), až k systémům s převažujícími starými pralesovitými porosty podléhajícími maloplošné dynamice porostních mezer (např. *Picea rubens* v severovýchodní Americe; Fraver and White, 2005a). V boreálních lesích Evropy je smrk ztepilý (oproti borovici lesní) považován spíše za druh stíntolerantní a pozdně sukcesní a předpokládá se, že v dynamice boreálních smrkových lesů převažuje spíše dynamika na menších plochách a oheň v ní je méně důležitým faktorem (Shorohova et al., 2009; Kuuluvainen and Aakala, 2011).

Jaké typy disturbancí jsou typické pro horské smrkové lesy střední Evropy, je aktuálním tématem současného výzkumu. Je to také podstatné pro rozhodování o managementu chráněných území a přístupu k současným rozsáhlým disturbancím (Vacek and Podrázský, 2008; Prach et al., 2009). Historické znalosti a souvislosti z prostoru Šumavy byly rozebrány v části 2.1 Šumavský problém – historie se (ne)opakuje. V této části byla zanedbána diskuse nad problematikou sekundárního ovlivnění lesa lidskou činností před obdobím intenzivní těžařské aktivity (tj. před rokem ca 1850). Bylo často spekulováno, že pastva dobytka, aktivity uhlířů, smolařů a popelářů, či možné toulavé těžby ovlivnily les natolik, že přestal být odolný vůči přirozeným narušením (v moderní terminologii: změnil se jeho režim disturbancí; Zatloukal, 1998; Jelínek, 2005). Problémem je, že bližší lokalizaci těchto aktivit (tedy zda a v jaké míře se týkaly i vrcholových partií Šumavy), jejich intenzity a vlivu na dynamiku lesa v současnosti již pravděpodobně není možné zjistit. Popisovaný postoj reprezentuje i následující citát: „Významná je skutečnost, že již v letech 1833-39 (po relativně malém polomu) a znovu v letech 1868-1878 selhaly samoregulační mechanismy v lesích, pokud nebyla předchozí větrná kalamita včas zpracována. Pod tlakem přemnoženého kůrovce se hroutily i porosty ve stavu nepochybně lepším a přírodnímu bližším, než lesy současné. Roli zde hrál evidentně „dominový efekt“, kdy kůrovci namnoženému v lidskou činností pozměněných porostech neodolaly následně ani porosty relativně zachovalé“ (Zatloukal, 1998). Ve světovém měřítku nejsou neznámé krajiny, které přirozeně podléhají rozsáhlým, málo častým a silným disturbancím v podobě větru nebo hmyzích gradací (Turner and Dále, 1998; Frelich, 2002; Kulakowski and Bebi, 2004). Takové krajiny se dochovaly zejména v Severní Americe – severoamerických Skalistých horách (Veblen et al., 1991; Eisenhart and Veblen, 2000; Veblen, 2000; Kulakowski and Veblen, 2003), a také v dalších boreálních a temperátních lesích (Frelich, 2002; Kramer et al., 2001; Berg et al., 2006).

Vstupní branou do problematiky moderního pojetí dynamiky horského smrkového lesa ve střední Evropě může být práce Holeksy et al. (2007). Autoři této práce analyzovali poměrně velkou plochu horského smrkového pralesa v pohoří Zadná Poľana na Slovensku. Pokud by se les vyvíjel podle tzv. teorie malého vývojového cyklu (Korpeľ, 1989), muselo by docházet k relativně maloplošnému střídání ploch různého stáří (tj. v různém stádiu vývoje). Nicméně i přes fakt, že studovaná plocha byla relativně rozsáhlá a vysoce variabilní pokud jde o faktory prostředí, a že porostní zásoba, prostorová struktura a výška stromů prokázaly výraznou variabilitu podél nadmořské výšky, tloušťková struktura porostu a charakteristiky zmlazení byly uniformní. Výsledky naznačují, že dorůstání nových stromů do porostní klenby nebylo v čase kontinuální dokonce ani v měřítku několika čtverečních kilometrů (Holeksa et al., 2007).

Moderní předpoklady o dynamice středoevropského horského smrkového lesa byly vzneseny v práci Kulakowski and Bebi (2004), kteří předpokládají, že zdejší přírodní lesy jsou pod výrazným vlivem silných a málo častých disturbancí podobně, jako v severoamerických Skalistých horách. V případě absence častých požárů je dynamika lesa řízena větrem (Frelich, 2002; Panayotov et al., 2011). Vichřice působí nepravidelně rozmístěné polomy a vytváří porostní mezery o velikosti jediného stromu až po stovky hektarů. Dopad vichřice je zásadně ovlivněn topografií a dalšími faktory

(Frelich, 2002; Kulakowski and Bebi, 2004; Zielonka et al., 2010). Smrk ztepilý však může odumírat také v důsledku napadení lýkožroutem smrkovým (viz část 2.1 Šumavský problém – historie se (ne)opakuje). Lýkožrout smrkový může mnohonásobně rozšířit původně vichřicí narušenou plochu, a tak zasáhnout celou krajinu (Økland and Bjørnstad, 2006). Další faktory narušení jsou méně, nebo pouze lokálně důležité – laviny, patogenní houby a herbivorní zvířata (Frelich, 2002; Kulakowski and Bebi, 2004).

Předpokládá se, že doba opakování požárů v horských lesích střední Evropy je dlouhá řádově dosahující stovky až tisíce let (Tinner et al., 1999; Beer and Tinner, 2008). Vichřice schopné rozvrátit větší plochy lesa a gradace lýkožrouta smrkového se podle historických materiálů vyskytovaly na Šumavě asi jednou, resp. dvakrát za století (Zatloukal, 1998; Brázdil et al., 2004; Jelínek, 2005; Svoboda, 2006). Moderní výzkum dlouhodobých vývojových procesů a role disturbancí v horském smrkovém lese začal poměrně nedávno (Motta et al., 1999; Zielonka and Malcher, 2009; Zielonka et al., 2010; Janda et al., 2010; Svoboda et al., 2010; Panayotov et al., 2011; Svoboda et al., 2012). Zielonka and Malcher (2009) a Zielonka et al. (2010) rekonstruovali za posledních 150 let tři intenzivní vichřice, po kterých vznikal porost ve Vysokých Tatrách, který byl znovu rozvrácen vichřicí v roce 2004. Byly to vichřice z roku 1868, 1915 (nebo 1919) a 1941. Rozsah polomů byl minimálně desítky hektarů. Dále vyvozují, že popsaný režim disturbancí může mít na svědomí koexistenci smrku a modřínu v těchto podmínkách (modřín je v Tatrách častější na místech vystavených větru), protože modřín je schopný lépe přežít silný vítr, a také intenzivně odrůstat v otevřených podmínkách (Zielonka and Malcher, 2009; Zielonka et al., 2010). Vítr byl za posledních 150 let nejpodstatnějším faktorem narušení také ve smrkovém pralese v Bulharsku (Panayotov et al., 2011). Panayotov et al. (2011) popsal v tomto období několik silných vichřic, které vytvářely polomy v rozsahu 1-10 ha. Také ve zbytku horského smrkového pralesa na Trojmezné na Šumavě byla na ploše 20 ha rekonstruována nerovnovážná dynamika porostu. Porost byl pravděpodobně utvářen málo častými, středně až hodně silnými narušeními. Vliv minulých narušení vrcholil asi před 200 lety. Popsaný porost se v současnosti rozpadl vlivem gradace lýkožrouta smrkového. Odumřely téměř všechny stromy přesahující výšku 6 metrů (Svoboda et al., 2011).

2.5 Dynamika růstu

Menší pozornost byla věnována dendrochronologické rekonstrukci chování individuálních stromů v rámci režimu narušení. Heterogenita růstových reakcí stromů na disturbanci a jejich následná vývojová trajektorie je poměrně neznámá (Canham, 1990; Wu et al., 1999; Rentch et al., 2003; Doležal et al., 2004; Weber et al., 2008; Doležal et al., 2009). Vývoj lesa byl popsán na úrovni porostu (Korpeľ, 1989; Oliver, 1980/1981). Ve světě nejuznávanější je práce Olivera (1980/1981), který rozdělil vývoj porostu po silném narušení do čtyř stádií. Ihned po disturbance ve fázi iniciace porostu dochází k obnově porostu a exponenciálnímu růstu stromů v otevřených podmínkách. Toto stádium je následováno fází redukce kmenů, kdy se uzavírá korunová klenby, intenzita růstu se snižuje, zvyšuje se asymetrická kompetice a dochází k samozřeďování. Větší stromy jsou během stádia redukce kmenů zvýhodněny. Během třetí fáze dochází k druhé obnově porostu, hustota korunové klenby se snižuje díky odumírání dominantních stromů a nové zmlazení má opět prostor odrůstat (Oliver, 1980/1981; Doležal et al., 2009).

Za účelem interpretace historie narušení Frelich (2002) popsal několik typů růstových trendů, které se u stromů obecně vyskytují. 1) Uvolnění, tj. náhlé radikální a setrvalé zvýšení přírůstu, jako reakce na odstranění konkurence narušením. Uvolnění se vyskytuje typicky u stromů potlačených v podrostu po odstranění horní úrovně, nebo u úrovňových stromů po odstranění jednoho nebo více sousedících stromů. 2) Rychlý počáteční růst se vyskytuje u stromů, které začaly růst v již otevřených podmínkách po disturbanci. Jejich následný růstový trend je buď rovný, klesající nebo parabolický. 3) Nejednoznačný trend růstu má většinou poměrně dlouhou počáteční zónu, při které strom postupně zvyšuje intenzitu růstu. V případě nejednoznačného trendu se vstup do hlavní úrovně interpretuje v době, kdy intenzita růstu překročí kritérium používané pro rychlý počáteční růst. 4) Nepravidelný trend růstu je takový trend, který není zahrnut do žádné z předchozích kategorií. Tyto růstové křivky většinou nemají žádný jednoznačný dlouhodobý trend, vyskytují se v něm často náhlé pulsy a propady v přírůstu, jejich hodnocení nemá obecná pravidla a záleží na individuálním posouzení hodnotitele. Obvykle však lze většinu růstových křivek zahrnout do kategorií 1 nebo 2 (Frelich, 2002).

Pro stíntolerantní dřeviny popsal Canham (1990) tři typy růstových strategií, pomocí kterých stromy dosahovaly hlavní korunové úrovně: 1) rychlý růst od počátku bez období potlačení, 2) jediné počáteční období potlačení, po kterém následovalo uvolnění v porostní mezeře, která umožnila odrůst kontinuálně do korunové klenby, a 3) několik period potlačení a uvolnění před závěrečným uvolněním, během kterého strom dosáhl korunové klenby. Asi 80% buků velkolistých (*Fagus grandifolia*) a javorů cukrových (*Acer saccharum*) rostoucích v pralese ve státě New York (USA) bylo potlačeno před dosažením korunové klenby (typy 2 a 3), přičemž dominoval typ s několikanásobnými potlačeními (ca 60% stromů). Stromy zaznamenaly v průměru 2-3 periody potlačení. Finální uvolnění se průměrně objevilo ve věku 60-130 let s tloušťkou 6-12 cm (Canham, 1990). Podobné hodnoty se objevili i u smrku červeného (*Picea rubens*). 72% stromů bylo potlačeno před dosažením korunové klenby a počet period potlačení byl v průměru 1,43 (Wu et al., 1999).

Obrácený poměr byl zjištěn u několika druhů dubů na severovýchodě Spojených států (Rentch et al., 2003), a také u smrku ztepilého v horské smrčině na Šumavě (Svoboda et al., 2011). Tyto druhy jsou obvykle považovány za středně tolerantní k zástinu. Rentch et al. (2003) pro duby popsal tři strategie pro dosažení hlavní korunové úrovně na základě počáteční intenzity růstu, celkového charakteru přírůstové křivky a výskytu výrazných uvolnění. První strategie se v podstatě shoduje se strategií 2 podle Frelich (2002), viz výše. Jedná se o stromy bez výrazného uvolnění s intenzivním počátečním růstem a rovným, klesajícím nebo parabolickým celkovým trendem. Druhá strategie je podobná předchozí, nicméně u těchto stromů byl přírůst po několika desetiletích potlačen v důsledku uzavírání korunové klenby tak, že strom potřeboval následně uvolnění pro dosažení hlavní korunové vrstvy. Třetí skupina stromů vykazovala pomalý potlačený růst již od počátku a potřebovala jedno (zřídka dvě) uvolnění pro dosažení hlavní korunové vrstvy (Rentch et al., 2003). Polovina dubů pocházela z velkých porostních mezer, které umožnily okamžité dosažení horní úrovně (první strategie). 38% dubů vzniklo v menších mezerách (druhá strategie). Zatímco zbylých 13% zaznamenalo zpočátku delší období potlačení. Podobně 74% smrků v horském smrkovém pralese na Trojmezné bylo klasifikováno jako vzniklé v porostní mezeře (intenzivní počáteční růst; Svoboda et al., 2011).

3. Cíle práce

Disertační práce je zaměřena na popis vývojových procesů v horském smrkovém lese na Šumavě. Soustředí se zejména na historické souvislosti dynamiky lesa na místech, kde v současnosti došlo k zásadním narušením (rozpadu lesa), což platí pro většinu starých porostů horských smrčin Šumavy. Historie porostů byla zkoumána pomocí letokruhové analýzy, která umožňuje analyzovat vznik a vývoj porostu a historii narušení (Lorimer, 1985). V případě, že bude potvrzena hypotéza o přirozeném, či polopřirozeném původu významné části porostů na Šumavě, bude možné studovat dynamiku lesa v krajinném měřítku, což je potřebné pro kompletní pochopení fungování lesa (Frelich and Lorimer, 1991). Práce řešila tři hlavní části:

1) Cílem v první části bylo na třech lokalitách v CHKO Šumava a) popsat porostní strukturu před aktuálním rozpadem a b) zjistit, jak předchozí porosty vznikaly a srovnat to s aktuální situací. Byly kladeny otázky, zda tyto porosty vznikaly během krátké doby po silném narušení, nebo během delšího období? Byly stejnověké, nebo různověké? Jsou aktuální narušení unikátní z historické perspektivy, nebo je současná situace srovnatelná s minulými narušeními? Cílem bylo také diskutovat, které faktory způsobily nalezená historická narušení. Byla testována hypotéza tvrdící, že šumavské horské smrčiny vznikly uměle na vytěžených plochách (Zatloukal, 1998; Vacek and Podrázský, 2008).

2) Druhá část řešila otázku vývojových procesů a historie narušení na mikroúrovni porostu a jednotlivých stromů na lokalitě Jezerní hora. Cílem bylo a) rekonstruovat minulá narušení (jejich načasování, frekvenci a sílu) v porostu na Jezerní hoře v severní části Šumavy, b) popsat věkovou strukturu (obnovu) stromů a její reakci na narušení a c) popsat vývojové trendy jednotlivých stromů po narušení (s použitím přírůstových sérií).

3) Cílem ve třetí části bylo popsat co nejpodrobněji režim narušení v krajinném měřítku horské smrčiny na Šumavě (sedm lokalit). Cílem bylo testovat hypotézu Müllera et al. (2008), která tvrdí, že rozsáhlá a silná narušení jsou pro studovaný typ lesa typická. Tato hypotéza byla založena na zjištění, že většina druhů horských

smrčin reagovala pozitivně na aktuální silná a rozsáhlá přirozená narušení v Národním parku Bavorský les. Konkrétně bylo cílem a) rekonstruovat načasování, frekvenci a sílu (částečně také rozsah) historických narušení a b) vysvětlit rozdíly v historii narušení podmínkami prostředí.

4. Metodika

4.1 Studijní oblast

Disertační práce byla zpracována v oblasti Šumavy, v NP a CHKO Šumava. Zde se v nadmořské výšce nad ca 1150 metrů ve vrcholových partiích hor vyskytují přirozené horské smrčiny. Ve stromovém patře výrazně převládá smrk ztepilý (*Picea abies*) s téměř stoprocentním zastoupením s malou příměsí dalších dřevin (*Sorbus aucuparia, Acer pseudoplatanus, Abies alba, Fagus sylvatica* a další; Neuhäuslová and Moravec, 1998).

Geologicky Šumava patří ke krystaliniku Českého masivu (Moldanubikum) s poměrně pestrým zastoupením hornin. Převažujícími horninami jsou ruly, svory a diority (Cháb et al., 2007). Půdy jsou slabě vyvinuté s převažujícími podzoly a rankery (Kozák, 2010). Klima je studené s průměrnou roční teplotou asi 4 °C. Kontinentalita podnebí se zvyšuje od západu k východu. Zatímco v západní části (např. Jezerní hora) dosahují roční srážkové úhrny přes 1400 mm/rok, ve východní části (např. Boubín) je to pouze 800-1000 mm/rok (Tolasz, 2007).

V pohoří Šumavy byly vytipovány staré porosty horských smrčin, které vznikaly před rokem 1850. Výběr probíhal na podkladě historických lesnických map (které na Šumavě vznikaly po roce 1860; Jelínek, 2005; Státní oblastní archiv Plzeň), literatury, leteckých snímků a současných lesnických map. Biotop horské smrčiny byl rámcově ohraničen vrstevnicí 1150 m. n. m. Následně však byly zahrnuty i některé další lokality s neznámou minulostí, pro něž neexistovali historické mapy (Můstek). Zde je nutné upozornit, že vybrané lokality pokrývaly většinu horských smrčin Šumavy. Sedm lokalit bylo vybráno pro tuto studii (obr. 5, postupně od severozápadu k jihovýchodu): Ostrý, Jezerní hora, Můstek, Polom-Ždánidla, Boubín, Plechý a Hraničník. Dvě zbývající lokality byly shledány jako nevhodné, neboť se zde vyskytovaly pouze mladší porosty. Byly to lokality Březník a Poledník.

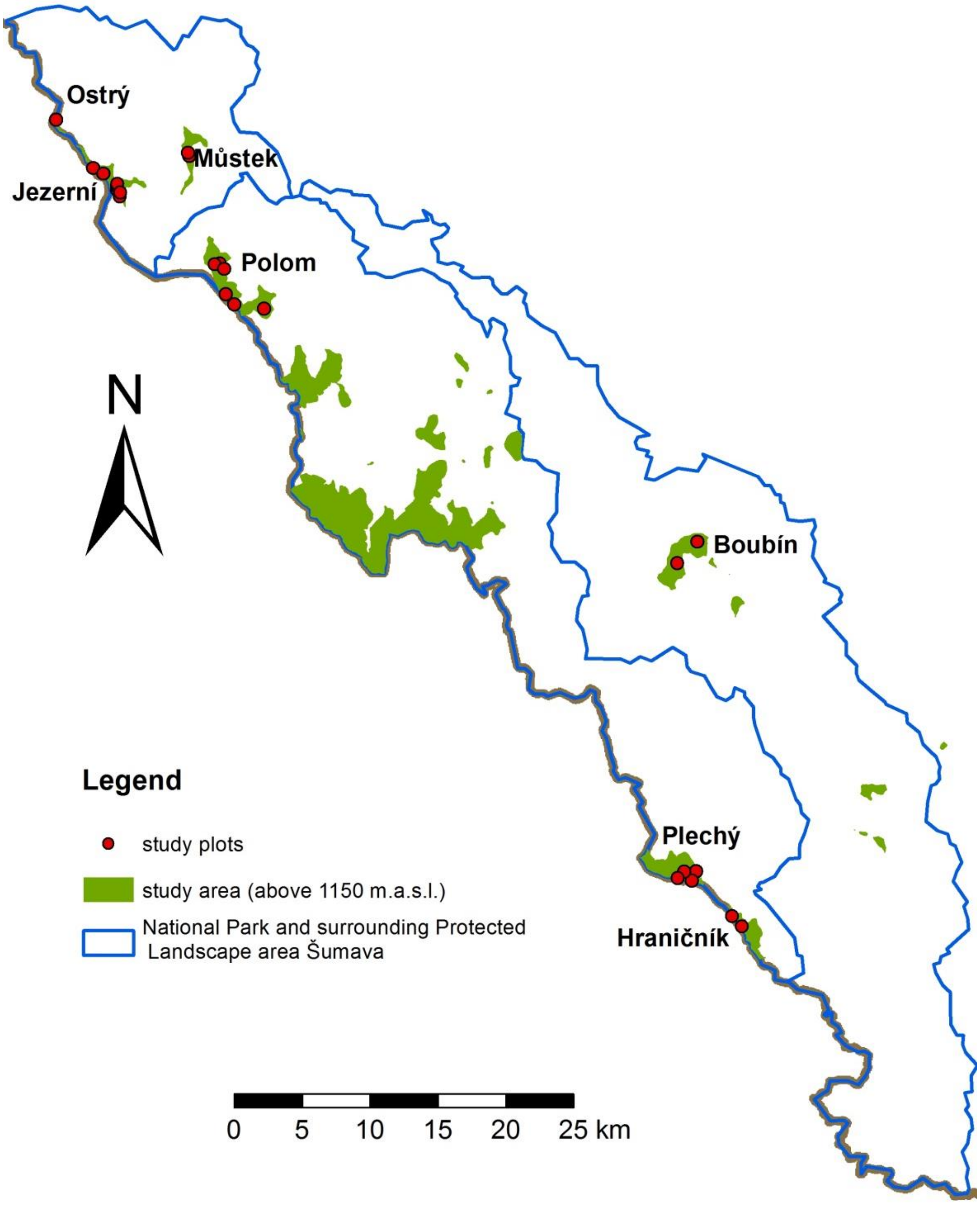
Většina starých porostů horských smrčin Šumavy se postupně rozpadala od 80. let 20. století vlivem vichřic, žíru lýkožrouta smrkového (*Ips typographus*) a asanačních těžeb, což kulminovalo vichřicí Kyrill v lednu 2007.

4.1 Sběr dat

Celkem 24 studijních ploch bylo na Šumavě založeno pro studium krajinného měřítka disturbancí (obr. 5). Počet ploch na každé lokalitě (v rozsahu od jedné do osmi) závisel na rozloze lokality. Plochy byly vybírány tak, aby pokryly co největší variabilitu porostů (většinou na základě historických porostních map). Na každé lokalitě byla snaha založit alespoň dvě plochy, což se nepodařilo pouze na lokalitě Ostrý díky její malé rozloze. Plochy byly vybírány tak, aby byly homogenní a reprezentativní co se týče stanovištních podmínek. Byly zakládány v místech, která se rozpadla v důsledku vichřice Kyrill, nebo později tak, aby bylo možné z ještě nezetlelých kmenů odebírat vzorky.

Výchozí velikost studijní plochy byla 50 x 50 metrů. Na vybraných lokalitách (Ostrý, Jezerní hora, Můstek, Boubín) byla struktura porostu na ploše geodeticky zaměřována pomocí systému Field Map (Field-Map®, Monitoring and Mapping Solutions, Ltd.; www.fieldmap.cz). Byly zaměřeny pozice všech živých a mrtvých stromů (s průměrem nad 10 cm) na ploše. Pro každý kmen byl zaznamenán jeho druh, tloušťka ve výšce pařezu (ca 30 cm) a třída rozkladu pomocí klasifikace Grovena et al. (2002). Groven et al. (2002) použil osmistupňovou škálu na základě přítomnosti kůry, tvrdosti bělového a jádrového dřeva a viditelnosti struktury dřeva. K této škále byla přidána třída 0 pro živé stromy. Stromy, které odumřely při vichřici v roce 2007 či později byly zařazovány do třídy rozkladu 2.

Na třech plochách na lokalitě Jezerní hora byly následně odebrány vývrty Presslerovým nebozezem ze všech zaměřených kmenů, z kterých to bylo možné. Vývrty byly odebírány ve výšce pařezu (30-40 cm nad zemí) z mrtvých stromů (pařezů, vývratů, souší; viz výše výběr ploch). Cílem bylo získat vývrt s reprezentativním růstem (v případě excentrického středu) a neovlivněný kořenovými náběhy. Posléze byla vyhodnocena věková struktura porostů na plochách na Jezerní hoře a bylo zjištěno, že rozdíly v distribuci věků mezi celým souborem dat a výběrem z něho klesají při použití 30-40 vzorků. Bylo tedy usouzeno, že pro popis věkové struktury porostu na ploše je dostatečný odběr alespoň 35 vývrtů. Toto číslo je konzistentní s dalšími podobnými studiemi (Frelich and Lorimer, 1991; Veblen et al., 1994; D’Amato and Orwig, 2008; Fraver et al., 2009). Proto byl na každé ploše vytvořen transekt středem plochy (tj. dlouhý 50 metrů), který byl široký tak, aby na něm bylo možné odebrat vzorky minimálně z 35 kmenů. Následně byly odebrány vý点vrty ze všech kmenů v transektu na lokalitách Ostrý, Můstek a Boubín stejným způsobem jako na Jezerní hoře.



Obr. 5: Lokalizace studijních ploch na Šumavě. Vrstevnice 1150 m.n.m. rámcově ohraničuje studijní lokality.

Na zbývajících lokalitách (Polom-Ždánidla, Plechý, Hraničník) bylo pracováno již pouze s popsaným transektem (50 m dlouhý a široký tak aby zahrnul alespoň 35 vhodných kmenů) bez geodetického zaměřování. Na každé ploše byla vytyčena čtvercová síť 5 x 5 metrů pomocí kompasu a dálkoměru Vertex (Haglof, www.haglof.se). Pomocí této sítě byla určena přibližná pozice každého živého a mrtvého stromu, určen jeho druh, tloušťka a třída rozkladu. Z každého kmenu na transektu byl opět odebrán vývrt.

V laboratoři byly vývrty vysušeny, nalepeny do dřevěných prken s drážkami a seříznuty žiletkou. U takto připravených vývrtů byl pod binolupou počítán počet letokruhů a měřena jejich šířka pomocí posuvného stolku LINTAB připojeného na počítač s programem TsapWin (RINNTECH, Inc., Heidelberg, Germany, www.rinntech.com) s přesností na 0,01 mm. Hranice letokruhů byly lokalizovány s využitím mikroskopu Olympus se záměrným křížem.

Získané letokruhové série byly sledovány metodou křížového datování tak, aby každá informace o šířce letokruhu byla přiřazena ke specifickému kalendářnímu roku, ve kterém byl vytvořen (Douglass, 1929). Pomocí této metody je možné opravit problematické přírůstové série s chybějícími letokruhy (chybějícími na vývrtu, viz např. Peters et al., 2002) a posunout série z mrtvých stromů a stromů, u kterých nebylo možné získat celou sérii v důsledku hniloby bělového dřeva. Křížové datování bylo provedeno v programu Past4 s použitím vizuálního hodnocení (Yamaguchi, 1991), a také statistických testů – Gleichlaufigkeit a *t*-test transformovaných sérií (Knibbe, 2007). Několik sérií, které nebylo možné spolehlivě datovat, byly vyloučeny. Zakřivení a průměrná šířka prvních pěti letokruhů byla použita pro určení počtu chybějících letokruhů v případě, že vývrtem nebyl trefen střed (Duncan, 1989). Zde je nutné podotknout, že zjištěné věky nejsou věky absolutní, nýbrž věky dorostu do výšky odběru vzorků (30-40 cm nad zemí), viz část 2.3 Dynamika obnovy - věk.

4.1 Zpracování dat

Letokruhové série a věk byly využity k analýze toho, jak porost vznikl a jak se dále vyvíjel. Pro potenciálně stinné lesy mírného pásma, které nejsou pod vlivem silných požárů, platí, že distribuce věků nemusí dobře vypovídat o vzniku porostu, protože stromy mohou existovat dlouhou dobu v podrostu. Lepší charakteristikou proto bývá okamžik, kdy strom začal intenzivně odrůstat (Oliver, 1980/81). Takové okamžiky je možné nalézt na přírůstových sériích. Začátek intenzivního růstu indikuje otevřené podmínky pro růst stromu, které bývají vytvořeny úmrtím stromů v okolí. Tímto způsobem se dají odhalit minulá narušení, která se v porostu vyskytla. Na letokruhových sériích byly hledány dva typy událostí: 1) rychlý počáteční růst – strom začal růst v otevřených podmínkách, 2) uvolnění – náhlé, setrvalé a výrazné zvýšení přírůstu. Pokud jsou takovéto události v čase synchronizovány u více stromů, značí to důležité narušení, které se v porostu v minulosti vyskytlo.

Strom byl označen jako „vzniklý v mezeře" (s rychlým počátečním růstem) v případě, že jeho průměrný přírůst mezi 6. a 15. letokruhem byl větší než 1 mm a následující trend přírůstu byl rovný, klesající nebo parabolický (Frelich, 2002; Splechtna et al., 2005; Jönnson et al., 2009; Svoboda et al., 2011). Svoboda et al. (2011) a Janda (nepubl.) sledovali počáteční růst mladých stromů v porostních mezerách a zjistili, že maximálního růstu (>1,88 mm) dosahují stromy v porostní mezeře větší než 1000 m^2. A minimální hranice pro strom rostoucí v otevřeném zápoji v porostní mezeře byla 1,06 mm.

Uvolnění byla v letokruhových sériích odhalována tzv. metodou absolutní růstové změny (Fraver and White, 2005b). Pro každý rok každé přírůstové série, vyjma prvních a posledních deseti let, byly spočteny růstové změny odečtením předchozího desetiletého průměru od následujícího desetiletého průměru. Pokud růstová změna byla větší než +0,55 mm byla označena jako uvolnění v případě, že byla zároveň maximální změnou v intervalu ±10 let (Jönnson et al., 2009). Na závěr byly růstové série prohlédnuty vizuálně a subjektivně vyřazena uvolnění, která nebyla zřejmá – např. krátkodobé pulzy nebo propady v přírůstu.

Dále byla provedena analýza dynamiky přírůstu. Růstové série byly standardizovány ve třech krocích. Nejprve byla data transformována mocninou transformací. Optimální exponent, p, byl vypočten podle vzorce: $p = 1 - m$, kde m je sklon regresní křivky vztahu logaritmovaného průměrného přírůstu a rozdílu mezi kvartily pro nepřekrývající se desetiletí (Emerson, 1983). Výsledná hodnota p se rovná 0,3. Následně byl odfiltrován vliv věku na přírůst metodou RCS (Grudd et al., 2002). Tato metoda zavádí jedinou křivku věkového trendu získanou regresní analýzou vztahu přírůst vs. věk z mnoha stromů. Ve třetím kroku byla odstaněna vysokofrekvenční variabilita proložením každé individuální série 40tiletou spline funkcí (Cook and Kairiukstis, 1990). S výslednými spline funkcemi (růstovými trendy) byla provedena clusterová analýza pomocí metody „average linkage“ s „Euclidean distance“.

Vztahy mezi nejrůznějšími popisovanými proměnnými (tloušťka, věk, třída rozkladu, počet událostí indikujících narušení, typy růstových trendů) byly testovány pomocí jednoduché neparametrické statistiky (Spearmanův korelační koeficient, Kruskall-Wallis ANOVA).

5. Výsledky

5.1 Čada, V., Svoboda, M., 2011. Structure and origin of mountain Norway spruce in the Bohemian Forest. J. For. Sci. 57, 523–535.

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Structure and origin of mountain Norway spruce in the Bohemian Forest

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ABSTRACT: Information on the historical background of the present forest conditions is needed for proper decisions on forest management. Disturbances play a major role in the formation of forest structure and composition. This paper compares the present break-up of mountain spruce stands in the Bohemian Forest (in the Šumava Protected Landscape Area) with conditions during their initiation using dendrochronological techniques. On three selected localities we established two study plots within relatively old stands of unknown origin. Stands were recently broken up by a windstorm. The present situation was described by diameter and decay class distribution. To describe the situation at the stand initiation, we cored at least 40 stems on each plot to get the age structure and growth series of trees. Disturbances were marked by discovering synchronous releases on tree-ring series. Main population waves were initiated in association with severe disturbances during a relatively short period, leading to the establishment of relatively even-aged, homogeneously looking stands. The disturbancees were synchronized between plots and accounted for by historically known windstorms or bark beetle outbreaks; notwithstanding, logging as a disturbance factor is also particularly possible.

Keywords: dendroecology; natural disturbance; *Picea abies* (L.) Karst.; regeneration; stand dynamics; disturbance history

Understanding the forest dynamics (and its structural effects) is greatly needed for proper management of protected areas as well as for effective utilization of commercial areas (Kimmins 2004). The definition of a natural range of variability is still missing for mountain Norway spruce forests in Central Europe (Kulakowski, Bebi 2004). This is a problem because the degree of naturalism (based on structural attributes) is used for managing the existing protected areas and establishing or excluding others (Míchal, Petříček 1999). The disagreement about protected mountain spruce stands in the Bohemian Forest (Šumava National Park and Protected Landscape Area) is partly based on the problems raised by the relative homogeneity of these stands and their present relatively large break up (Fischer et al. 2002; Jonášová, Prach 2004; Vacek, Podrázský 2008; Prach et al. 2009), which is not consistent with the original idea of what constitutes a virgin forest.

The initial description of forest dynamics in Central Europe arises from the work of Korpeľ (1989, 1995). His model of a small developmental cycle was developed mainly by studying stand structures on study plots and was used for all forest types in a similar manner. But even this author accepts the possibility of "catastrophic break up" in mountain spruce forests. Not until the last decade was it discovered – based on studies of historical documents (Svoboda 2006), extensive structural work (Holeksa et al. 2007) and dendroecology (Motta et al. 1999; Zielonka, Malcher 2009; Zielonka

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et al. 2010; Svoboda et al. submitted 2011) – that this type of disturbance could naturally cause a large break up on the landscape level. Other than repeated measurements on study plots (which lasts for many decades), only reconstruction by a dendrochronological tree-ring analysis could describe the past stand development (Vinš 1961; Henry, Swan 1974; Oliver, Stephens 1977). Wave-regenerated stands initiated after severe disturbances in the past have subsequently a relatively homogeneous structure versus continually regenerated stands affected by disturbances of low severity (Frelich 2002).

Disturbances play a fundamental role in vegetation dynamics. They have become the basic part of the vegetation dynamics in the last 50 years (Pickett, White 1985). The disturbance is defined as any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment. The mentioned change (resource openness) is usually followed by a release of smaller trees from suppression (growth increase) or establishment of new cohorts (Lorimer, Frelich 1989). A few main disturbance factors exist in studies of tree population dynamics – fire, wind, insects, other pathogens and animals, including man-made harvesting (Frelich 2002). But the attributes of a concrete disturbance regime remain unanswered – the rotation period, severity and extent of different types of disturbances occurring in a landscape (Frelich 2002).

A part of the regeneration ecology of species could be described by the age distribution of a population (Ågren, Zackrisson 1990; Hofgaard 1993; Engelmark et al. 1994; Brumelis et al. 2005). The knowledge of its relationship to disturbances is vital, but it is very difficult to determine the real age of a tree (DesRochers, Gagnon 1997; Niklasson 2002). Taking increment cores in higher parts of stems (stump or breast height) leads to an underestimation of tree age and dispersion of age distribution in degree of decades (DesRochers, Gagnon 1997; Parent et al. 2000; Gutsell, Johnson 2002; Niklasson 2002; Peters et al. 2002). But instead, the aim could be to describe the origin of a stand (relationship of forest regeneration and disturbances). For this purpose, it is not necessary to obtain the real ages of trees, but it needs to get as close as possible (in time) to the disturbance. It is possible to sample trees at breast height in forest types where higher advanced regeneration is released after removing the overstorey (Fraver, White 2005a; Splechtna et al. 2005). In the case of mountain Norway spruce in the Bohemian Forest, mainly small regeneration is released after disturbance (Jonášová 2001; Jonášová, Prach 2004; Ulbrichová et al. 2006; Svoboda 2007; Zenáhlíková, Svoboda 2011), so we feel it is important to core trees as low as possible at stump height consistently with other authors (Veblen et al. 1994; Motta et al. 1999; D'Amato, Orwig 2008).

In the Bohemian Forest almost all old mountain Norway spruce stands were broken up since the end of the 1980's due to windstorms and attacks of bark beetle. A notable proportion was broken up by the Kyrill windstorm in January 2007. The goal of the work was therefore 1) to describe the structure of those disturbed stands immediately before the windstorm, and 2) to describe its origin and to compare it to the present situation. Are these stands wave regenerated or not, even-aged or multi-aged? Are present disturbances historically unique, or is the present situation comparable to the past? In particular, we will solve what may be the cause of the found disturbances, whether wind, bark beetle or human activities. We will discuss the hypothesis about the artificial origin of these forests (Zatloukal 1998; Vacek, Podrázský 2008).

MATERIAL AND METHODS

This work was conducted within selected mountain Norway spruce stands of the Protected Landscape Area (CHKO) Šumava located in the south-western Czech Republic in central Europe (Fig. 1). Pure Norway spruce woods occur mainly in isolated upper parts of this section of the mountain range. The tree layer is strongly dominated by Norway spruce (*Picea abies* [L.] Karst.) with only an admixture of other species (*Sorbus aucuparia* [L.], *Acer pseudoplatanus* [L.], *Abies alba* [Mill.], *Fagus sylvatica* [L.] and others) (Neuhäuslová, Moravec 1998).

Three separated localities of the Šumava Protected Landscape Area were selected for this study: (1) Jezerní Mt. (1,343 m a.s.l., plots JEZ1 and JEZ2) on the top of the Královský hvozd ridge, and (2) Můstek Mt. (1,235 m a.s.l., plots MUS1 and MUS2) on the top of the Pancíř ridge in the north-western range of the Bohemian Forest, and (3) Boubín Mt. (1,362 m a.s.l., plots BOU1 and BOU2) on the top of the Boubín highlands in the central part of the Bohemian Forest (Table 1). Geologically, the Bohemian Forest is a crystalline complex – the

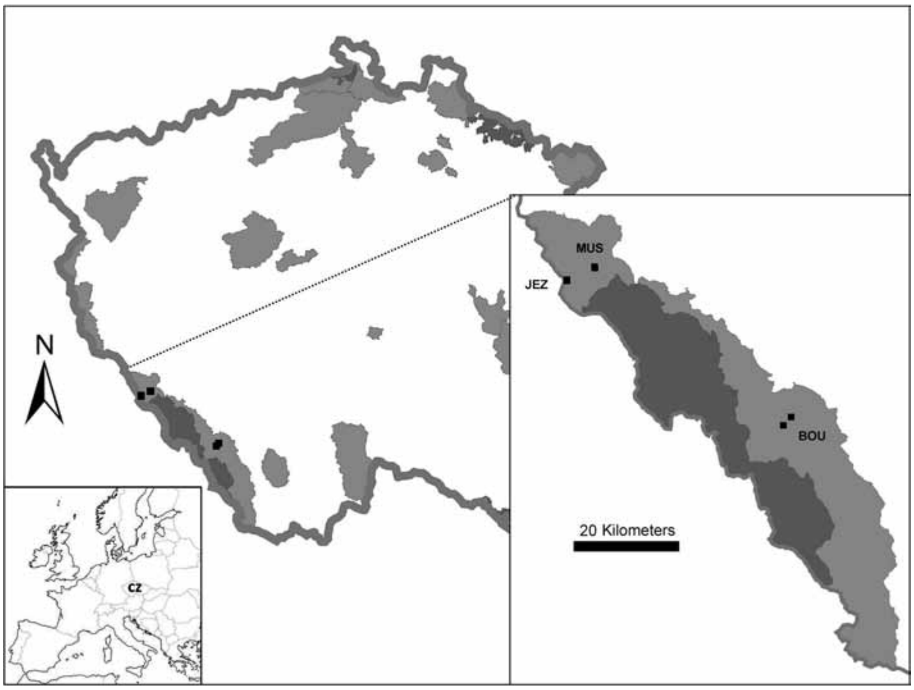

Fig. 1. Location of the study area in the Czech Republic. The Šumava Protected Landscape Area is in light grey (CENIA© ČSÚ, ARCDATA, AOPK ČR, MŽP; geoportal.cenia.cz). Positions of the study plots (Jezerní Mt. – JEZ, Můstek Mt. – MUS, and Boubín Mt. – BOU – see Methods) are shown by black squares

oldest (Hercynian) part of the Bohemian Massif is called Moldanubicum. This complex consists mainly of Eastern schist. Jezerní Mt. and Můstek Mt. are pure (mica schist) and Boubín Mt. is richer (gneiss) (Cháb et al. 2007). The same situation is found within the soil cover – from stony soil on Jezerní Mt. to podsol on Boubín Mt. (Kozák 2010). The climate is cold with mean annual temperature of about 4°C. The continentality increases from west to east. Mean annual precipitation

Table 1. Basic characteristics of the plots

		Locality (plot)					
		Jezerní Mt.		Můstek Mt.		Boubín Mt.	
		JEZ1	JEZ2	MUS1	MUS2	BOU1	BOU2
Altitude (m)		1,337	1,321	1,200	1,175	1,280	1,317
Longitude (m)	SJTSK	−846,106	−846,082	−840,861	−840,750	−804,794	−803,310
Latitude (m)	SJTSK	−1,131,124	−1,131,368	−1,128,668	−1,128,916	−1,158,897	−1,157,324
Spruce (percentage by number/basal area)		99.61/98.99	100	100	99.43/98.83	100	100
Additional species		rowan			fir, beech		
Living trees	density of trees (ha^{-1})	516	316	608	348	348	284
	mean diameter (cm)	35	40	32	40	46	51
	basal area (m^2·ha^{-1})	50.65	41.45	54.82	48.18	55.58	60.31
Dead trees	density of trees (ha^{-1})	512	448	80	244	100	144
	mean diameter (cm)	26	31	24	22	37	33
	basal area (m^2·ha^{-1})	30.36	36.64	3.93	10.17	12.63	13.25
Sum	density of trees (ha^{-1})	1,028	764	688	592	448	428
	mean diameter (cm)	30	35	31	32	43	45
	basal area (m^2·ha^{-1})	81.01	78.09	58.75	58.35	68.21	73.57

Positions of the study plots (Jezerní Mt. – JEZ, Můstek Mt. – MUS, and Boubín Mt. – BOU – see Methods) reaches about 1,400 mm·year^{-1} on Jezerní Mt., over 1,200 mm·year^{-1} on Můstek Mt. and 800–1,000 mm·year^{-1} on Boubín Mt. (Tolasz 2007). Vegetation communities are described as *Calamagrostio villosae-Piceetum* (with transition to *Calamagrostio villosae-Fagetum* on Můstek Mt.; Neuhäuslová, Moravec 1998).

A few authors postulated the unnatural planted origin of mountain spruce stands of the Bohemian Forest (Zatloukal 1998; Vacek, Podrázský 2008). But in fact no direct evidence exists before the 1860s when the first management plans for large land owners of forests were made (Jelínek 2005). Hardly any stands older than 80 years, which were described as virgin forests on these maps, have survived to the present. And there exists a high uncertainty about the way of the origin and historical management of stands younger than 80 years on these maps.

For our study we selected forest stands of unknown origin on the three localities. Two study plots were analyzed on each locality. For Jezerní Mt. a 41–60 years old patch was found surrounded by more than 80-years-old stands on the first map from 1876 (State Archive SOA Plzeň, VS Železná Ruda, map 2). Boubín Mt. is a part of the protection forest where no logging has been set in prescription since 1858 (Vaněk 1985). The first plot on Boubín Mt., BOU1, was placed into a stand younger than 20 years on the first map from 1868. This stand was next to an area affected by the bark-beetle outbreak in the 1870's, which was subsequently logged (Jelínek 2005). It was not possible to find the boundary in the field. The second plot on Boubín Mt., BOU2, was placed into a stand described as being older than 80 years in 1868 (Jelínek 2005). Můstek Mt. was owned by the village of Javorná and no direct evidence of management exists from the 19th century (Jelínek 2005).

Data collection

Two 50 × 50 m study plots were established at each locality (i.e. 6 plots in total). Plots were selected in an area that was fully replaced after the Kyrill windstorm from January 2007. Salvage logging was done at all localities after the windstorm. There was an effort to meet the requirement for homogeneity and representativeness of each plot.

Electronic and laser measuring devices linked to a GIS (Field-Map®, Monitoring and Mapping Solutions, Ltd.; www.fieldmap.cz) were used to measure the stand structures. All live and dead trees (diameter at stump height over 10 cm) were positioned. For each tree we recorded its species, dia-meter at stump height (about 30 cm) and decay class based on the classification of Groven et al. (2002). Groven et al. (2002) used an eight-class scale based on the presence of bark, solidity of sapwood and heartwood and visibility of wood structures. We added to the scale the class 0 for living trees. Unlike Groven et al. (2002) we were not able to find any trees that could be listed in class eight (totally decayed, found by pigmented soil) due to the dense vegetation cover and soil disruption by disturbances (windstorm as well as subsequent logging). This problem is also likely responsible for the slight underestimation of further classes. Trees that died due to the windstorm in January 2007 or later were included in class 2.

The aim was to describe the state of the stands before break-up. Thus, trees in class 2, together with classes 0 and 1, were further specified as "living trees" and trees in higher decay classes were further specified as "dead trees".

We extracted one core at stump height from each possible bole on the plots on Jezerní Mt. After salvage logging we could almost always view the pith of a stump, we focused on taking cores from the side with representative growth (in cases with exocentric growth) and not affected by root swellings. We then evaluated the age structure from Jezerní Mt. and found that the average differences between all ages of the sample and subsamples diminished more slowly after taking 30–40 samples. Thus, we realized (taking the plot as a point in space) that it was sufficient to core about 30–40 trees. This number is consistent with other studies (Frelich, Lorimer 1991; Veblen et al. 1994; D'Amato, Orwig 2008; Fraver et al. 2009). We established a transect through the centre of each plot (i.e. 50 m long) and wide enough to include about 40 boles from which it was possible to take a core. We then extracted a core from each bole inside the transect on Můstek Mt. and Boubín Mt. in the same way as described for Jezerní Mt.

Increment cores were air-dried, attached to a wooden mount and cut with a razor-blade. The contrast was improved by moistening and impressing the chalk. Ring widths on all cores were measured to the nearest 0.01 mm using the LINTAB measuring device connected to a computer with TsapWin programme (RINNTECH, Inc., Heidelberg, Germany). Ring borders were localized using an Olympus stereomicroscope with a cross.

To append the width of each measured ring to an absolute year, it is necessary to do cross-dating

(Douglass 1929). This can solve the problem of partially missing rings (missing on the core, for example Peters et al. 2002) and move series from dead trees or trees with decayed sapwood. Cross-dating was done in Past4 programme using visual cross-dating as well as statistical tests – Gleichlaufigkeit and *t*-test of transformed series (Knibbe 2007). Sample chronologies were plotted against the mean chronology made of series of well growing trees with wide rings (Yamaguchi 1991), against the mean chronology from Trojmezná Mt. in the southern part of the Bohemian Forest (Janda et al. 2010) and verified by the light ring of 1912 (Gindl 1999) and marked rings found by Čejková and Kolář (2009). Final verification was done in COFECHA (Holmes 1983; Grissino-Mayer 2001). A few series which did not fit well were excluded. Missing rings were inserted and given the lowest measurable value of 0.01 mm.

To evaluate tree age, we estimated the number of rings missed in cases when the core did not pass through the pith. We estimated the distance between the first measured ring and expected pith by placing a transparent sheet with concentric circles. The number of missed rings was then acquired by dividing this distance by the mean ring width of the five rings closest to the centre.

Data analysis

There was a total of 281 series for Jezerní Mt. (plot JEZ1 – 168, plot JEZ2 – 113), 89 series for Můstek Mt. (plot MUS1 – 43 series, plot MUS2 – 46 series) and 90 series for Boubín Mt. (plot BOU1 – 46, plot BOU2 – 44). A total of 23 series of the Jezerní Mt. had rotten centres and therefore it was not possible to calculate their age. Of the remaining 258 series, 19% passed through the pith, 90% were within 14.30 mm of the pith and the maximum distance to the pith was 39.90 mm. For Můstek Mt. and Boubín Mt., 10 series had rotten centres. For the other 171 series, 51% passed through the pith, 90% were within 6.73 mm and the maximum distance to the pith was 30.45 mm.

Ring width series were used for the dating of past disturbance events. These methods are based on the knowledge that a tree accelerates its growth after its competitors are removed by a disturbance. This is called a release and is defined as a rapid, sudden and sustained growth increase. Synchronized release events indicate a relevant disturbance (Lorimer, Frelich 1989). To filter out other changes in growth, releases are usually computed from 10-year running means and only changes over a subjectively assessed threshold are marked (Lorimer, Frelich 1989). We used the "absolute increase" method to determine releases (Fraver, White 2005b). Absolute growth changes were calculated for each year of each series except the first and the last 10 years by subtracting the prior 10-year mean from the subsequent 10-year mean. A year was marked as a release if the value was the maximum of a 20-year interval (±10 year) and exceeded the threshold of +0.55 mm (Jönsson et al. 2009). This threshold was specified directly to Norway spruce based on experience with its growth variation (Jönsson et al. 2009). This threshold is equivalent to 24% of the boundary lines used for Norway spruce averaged across all prior growth classes (Splechtna et al. 2005; Zielonka et al. 2010). Finally we checked all series and their releases visually. Releases were excluded if the growth acceleration was not obvious (the average percentage among plots was 18.4% of cases excluded) – for example growth restoration after short-term growth reduction, short-term pulses etc. Releases were also added in obvious cases (the average percentage among plots was 11.8% of cases added). Visual checking is vital in this type of work, because growth fluctuations due to environmental variation (climate, injuries, mast year etc.) have a high effect close to the specified threshold. Basically it is always a trade-off between positive and negative errors. Non-release growth changes are not related only to climate variations, which is usually used to test the criteria (Nowacki, Abrams 1997; Black, Abrams 2003). There exists a great overlap with changes caused by injuries, reaction wood etc. (Fraver, White 2005b; Fraver personal communication). To overcome the problem of subjectivity, we also defined more strict criteria to detect higher magnitude and longer duration releases (15-year means, absolute increase threshold +0.75 mm) where little subjectivity was used (on average 2.3% of cases excluded). Results (Fig. 4) showed that the dating of major disturbances was little affected by a specified threshold. Releases connected to major disturbances were both of higher magnitude and longer duration.

All releases were then counted every year and plotted proportionally to the sample depth in each year. We wanted to show the real distribution of releases and date the disturbances as closely as possible by peaks in distribution. We wanted also to determine the rate of past break-up (immediate or slower origin of stands). It is important to note that mathematically derived criteria and tree reaction delay (mainly 1–5 years) could cause a few-year dispersion of releases in time (Nowacki, Abrams 1997; Rentch et al. 2002; Jones, Thomas 2004). Nevertheless, we found that releases were clustered on the time axis. We then calculated also the percentage of all older trees released in specified periods and showed it above the chronology. The chronology was truncated when the sample depth dropped below 10 and the time axes were restricted to the period of main tree establishment on the plots, i.e. 1750–1929.

Nonparametric methods were used to test our results. Spearman's correlation coefficient was used to test relationships between basic characteristics from Table 1 and the Kruskal-Wallis test (subsequently also post-hoc multiple comparison tests) was employed to compare the distributions of diameters, decay classes and ages. We used the 0.05 significance level to reject the null hypothesis.

RESULTS

Structure of the tree layer

Forest stands on all plots consisted of nearly 100% Norway spruce. Basic characteristics are shown in Table 1. A relatively high variation of values was found in the case of tree densities (316 to 608 trees per hectar). If we incorporate data from the mountain spruce locality Trojmezná in the Bohemian Forest (Svoboda 2007; Janda et al. 2010; Svoboda et al. 2010) and also the historical situation (i.e. dead trees), then the range is from 200 to 1,600 trees per hectare. Basal area showed less variation (note that our data were taken at stump height) – i.e. from 40 to 60 $m^2 \cdot ha^{-1}$. This dispersion is attributable to recent mortality before the windstorm on plots JEZ2 and MUS2 and less on plot JEZ1 (Fig. 3). In these cases, it is probable that the population of trees did not fill in the space re-

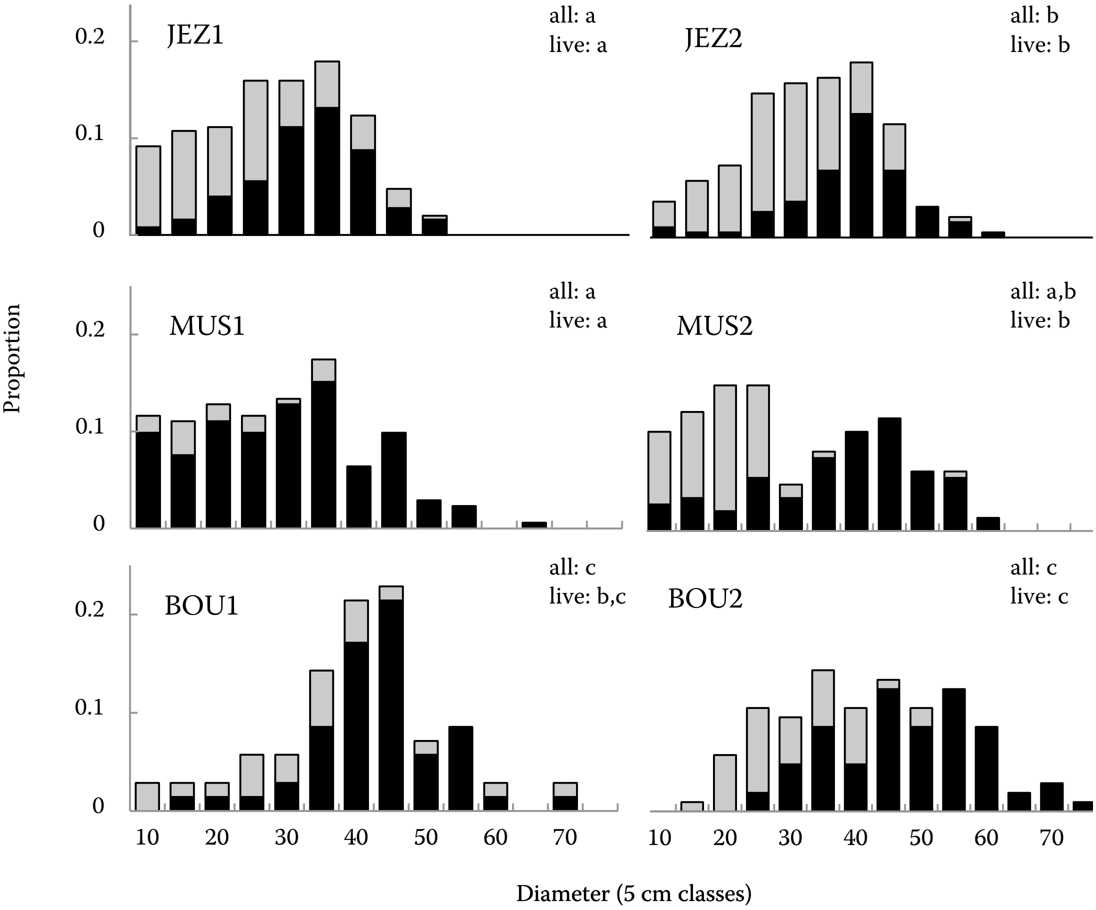

Fig. 2. Diameter distribution of living (black columns) and dead trees (grey columns) before the stand replacing windstorm from January 2007. Results of the Kruskal-Wallis test, comparing distributions of all trees and live trees between plots, are shown on the right sides of the graphs (all: $H_{5, N=936} = 127.23$, $P < 0.001$; live: $H_{5, N=56} = 141.23$, $P < 0.001$). Distributions with different letters differed significantly ($P < 0.05$)

leased by this mortality before the windstorm. After exclusion of these plots, the range of basal areas narrowed to 55–60 $m^2 \cdot ha^{-1}$. The proportion of dead trees was higher if we used the tree number, but it was lower if we used basal areas for the computation. This means that dead trees had smaller diameters than living trees. The largest differences were on Můstek Mt. and Boubín Mt., while differences were less notable on Jezerní Mt. (Figs 2 and 3). This indicates recent mortality of thick dominant trees caused by recent disturbances before the windstorm at the latter locality and only recent self-thinning at the other localities.

Spearman's correlation coefficients were calculated for the variables in Table 1 ($n = 6$, $P < 0.05$). Trees had larger diameters on Boubín Mt. (mean diameter vs. longitude, $r = 0.83$), while more trees grew on Jezerní Mt. and Můstek Mt. A significant negative relationship was found between the tree number and their mean diameter (living as well as all trees, $r = -0.90$ and $r = -0.83$, respectively). This is probably related to the differences in environmental conditions (Material and Methods). There was a higher proportion of dead trees on Jezerní Mt. (basal area of dead trees vs. altitude, $r = 0.89$). A positive relationship was found between the basal area of all trees and that of dead trees ($r = 0.89$). There was a negative, non-significant relationship between the basal area of living trees and the number of dead trees ($r = -0.60$).

The diameters of living trees generally showed a modal type of distribution (Fig. 2). This distribution shows a tendency to the left asymmetry on all plots. The distributions of all trees among plots differed significantly (Kruskal-Wallis test, $H_{5,\ N=936} = 127.23$, $P < 0.001$). A distinct diameter structure was found on Boubín Mt. with hardly any proportion of stems below 10 cm. The result evolve if we use only living trees (Kruskal-Wallis test: $H_{5,\ N=56} = 141.23$, $P < 0.001$). The exclusion of thin stems and development of a classical modal type continued also at the other localities. The modes developed in

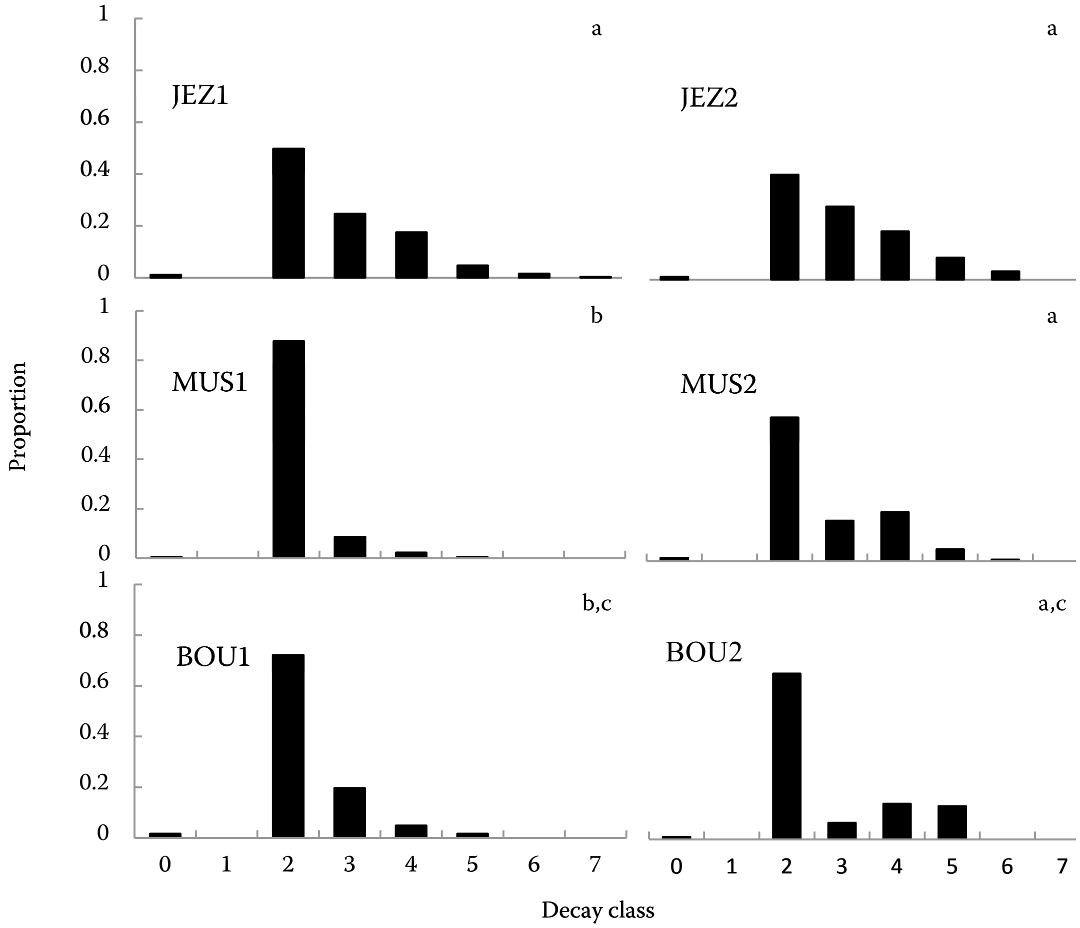

Fig. 3. Distribution of decay classes, after Groven et al. (2002), which show recent stand dynamics and lasting of break-up. Trees died after the windstorm in January 2007 are in class 2. The break-up was more rapid when the dominance of class 2 was stronger. Results of Kruskal-Wallis tests comparing distributions between plots are shown on the right sides of the graphs ($H_{5,\ N=923} = 95.56$, $P < 0.001$). Distributions with different letters differed significantly ($P < 0.05$)

the 45–50 cm class on Boubín Mt. and Můstek Mt. and in smaller classes on Jezerní Mt.

The decay class distribution shows recent stand dynamics (Fig. 3). Forests with continuous dynamics usually show a dominance of decay class 3 (Groven et al. 2002), however this was not attained on the study plots. Instead, we found a high dominance of class 2 on all plots (i.e. mainly trees destroyed by the Kyrill windstorm or after it), which indicates the unstable dynamics of these stands. The strength of this instability is described by the magnitude of the dominance of decay class 2. The distributions among plots differed significantly (Kruskal-Wallis test: $H_{5,\ N=923} = 95.56$, $P < 0.001$). There was a low amount of dead wood on Můstek Mt. and Boubín Mt. before the windstorm. Recent higher mortality (before the windstorm) was found on Jezerní Mt. This area was broken up more slowly.

Age structure and disturbances

Age distributions on the plots are closer to the modal type of distribution than to the exponential type of distribution (Fig. 4). This shows an unstable type of forest dynamics. Peaks in age distributions are quite narrow and located in only a few decades. On the other hand, the age range is from 85 to 215 years. Other smaller peaks in tree establishment could be found on four plots. The main peaks of tree establishment occurred in the 1820s on plots JEZ2 and BOU2, in the 1850s on plot BOU1, in the 1860s on plots JEZ1 and MUS1, and in the 1870s on plots MUS2 (and smaller ones also on plot BOU1). Smaller peaks occurred also in the 1780's on plots JEZ1 and BOU2, and the 1910's on plot MUS1.

Release events are clustered on the time axis (Fig. 4). Continuous polygons of release events are separated by periods with no releases. The peaks in tree establishment are closely connected with peaks in releases (i.e. with disturbances), occurring mainly in the same decade. In a few cases on Můstek Mt., the peak in ages preceded the disturbance by one decade. In one case, the peak in tree establishment was delayed one decade after the disturbance (plot BOU1, 1840–1850). Also, regeneration stopped 2 or 3 decades after the disturbance, with the exception of two plots (MUS1 and BOU1), where the origin was connected with more and separate disturbances.

The majority of trees which established before major disturbances showed suppressed growth and accessed the canopy through release. Only a few trees were left from the overstorey of the previous stand and showed no release in the time of the main tree establishment. The proportion of trees older than the main population wave (main peak in age distribution) highly differs from 5 trees to a half of all trees. 71–94% of these older trees showed synchronized release events in the period of the peak in age distribution (Fig. 4). Sometimes it is probable that two or several close disturbance events in time caused the stand initiation. For example, there are two separated peaks on plot BOU2 in the years 1812 and 1824 or prolonged releases over more than a twenty-year period on plot JEZ1. Peaks in release chronologies were synchronized to the early 1820s (JEZ2, BOU2), early 1860s (JEZ1, BOU1), 1870s (MUS1, MUS2) and early 1920s (MUS1). Additional peaks were created in the early 1780s (JEZ1) and between the years 1836 and 1843 (BOU1).

DISCUSSION

We found structurally relatively homogeneous stands of mountain Norway spruce on the microscale level at the three selected localities at higher elevations of the Bohemian Forest. The tendency to the left asymmetry of diameter distributions is also a tendency towards heterogeneity. This tendency was found in more uneven-aged stands and younger stands. The distribution could also be decreasing if the regeneration could grow to the canopy in recent decades (Korpeľ 1989; Motta et al. 1999; Janda et al. 2010). This occurs in cases of two-layered stands (Korpeľ 1989; Janda et al. 2010), regenerated stands (Korpeľ 1989) or early successional stands (Motta et al. 1999). This pattern was not attained on our study plots, so that no regeneration growing up to the canopy occurred since the 1920s. This is probably the cause of the visual homogeneity of these stands.

As the dynamics of dead wood follows the dynamics of living trees (Svoboda, Pouska 2008), we can describe recent dynamics by the distribution of the decay classes. Two different types of pattern were found. A small portion of dead wood occurred at two localities (Můstek Mt. and Boubín Mt.) suggesting that the windstorm was the only big disturbance event which caused the present break up. On the other hand, stands were breaking up more slowly on Jezerní Mt., which lasted for about two decades (Fig. 3). This was even more evident in the work of Janda et al. (2010) from Trojmezná Mt. in the southern part of the Bohemian Forest.

The detected origins of the stands show rather convergent than divergent character compared to

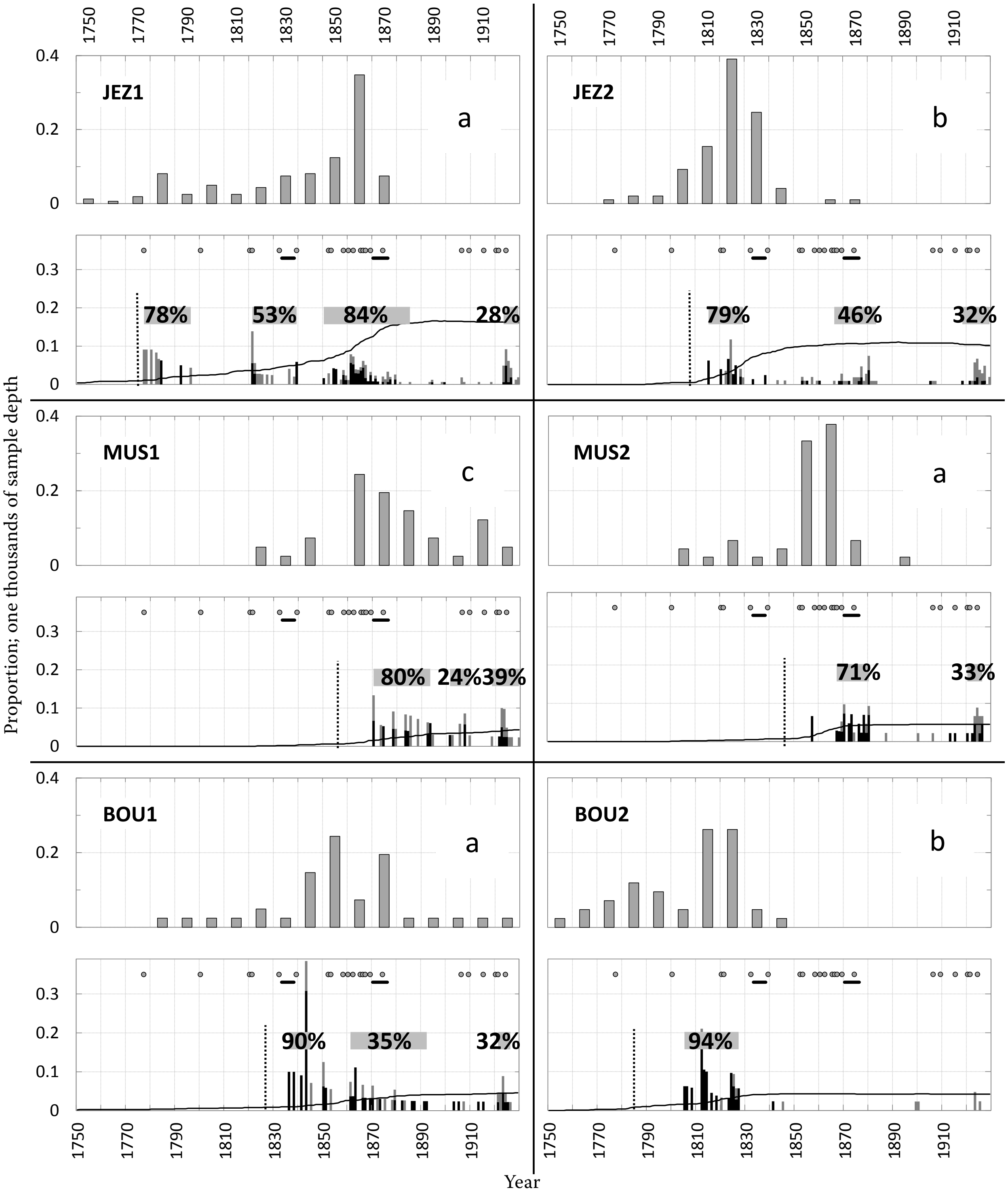

Fig. 4. Distribution of ages and release events in the period of stand establishment. Ages are summarized in 10-year classes (upper graphs, grey columns). For every year, the number of released trees is shown proportionally to the sample depth in that year (lower graphs, columns). Black columns are releases of higher magnitude and longer duration (see methods). Releases are clustered on the time axis to separated periods. The percentage of released trees in these periods is shown above. One thousandth of the sample depth is shown as lines on lower graphs. Release chronology was truncated when the sample depth dropped below 10 (indicated by a vertical dotted line). Time axes are restricted to the period of main tree establishment on the plots, i.e. 1750–1929. 5 individuals (3.11%) on plot JEZ1 and 2 individuals (4.88%) on plot BOU1 established before the year 1750. Circles on the lower graphs indicate known historical windstorms (Brázdil et al. 2004) and bold lines indicate known historical bark-beetle outbreaks (Skuhravý 2002). Results of the Kruskal-Wallis tests comparing age distributions between plots are shown on the right side of the graphs ($H_{5, N=427} = 154.12$, $P < 0.001$). Distributions with different letters differed significantly ($P < 0.05$)

the present situation. The main population waves were relatively even-aged (two to three decades). The proportion of trees older than the main waves is dependent on the character of the preceding stand (Frelich 2002). Only a few trees existed in the preceding understorey for more than a decade on four of the six plots. Our opinion is that this ratifies the situation known in the present structures. New, relatively even-aged stands grow up from small individuals after the breakup. These individuals have already been mainly in the understorey. Some regeneration is possible also shortly after a disturbance, but the delay is not more than a few years. A smaller proportion of individuals could be described as advanced regeneration, being higher than 0.5–1 m (Jonášová 2001; Ulbrichová et al. 2006; Svoboda 2007; Zenáhlíková, Svoboda 2011). Some exceptions do exist. This could be the case for the more heterogeneous, multiple-origin stands. We found populations with clearly two peaks in the age distribution on two plots. Secondly, the present modal age distribution does not necessarily mean that no regeneration occurred after. Younger trees often experience a higher probability of mortality, thus they may not survive to the present (Johnson et al. 1994). This could be the explanation for the peak of dead trees in diameter distribution on plot MUS2 (Fig. 2), which could be younger trees that regenerated later. We reconstructed a disturbance from the 1920s on this plot, which caused regeneration on the first plot of this locality, MUS1.

Periods with increased numbers of release events are coincident with periods of increased recruitment and therefore the initiation of stands. These periods are separated on the time axis, which indicates that high severity disturbances regenerated these stands. Consistent with the present situation, the break-up of a preceding stand could sometimes be caused by temporally closer disturbances, and could last for two decades. But the stand initiation connected with one disturbance event was also recognized. It is important to note that small understorey saplings could increase their growth (show release) after a small canopy opening preceding the main, severe disturbance (Bače et al. 2009).

Using only tree ring data, we could not determine which factor caused the past stand breakups. We could not distinguish between windstorm, bark beetle outbreak or harvesting. But we can use other information to make one interpretation more probable. Most disturbances were closely (scale of years) synchronized between plots and localities. And most of them are clearly accounted for by historical evidence (Fig. 4). These include the windstorms of 1778, 1821 or 1822, 1833 and a subsequent bark beetle outbreak in 1840, several windstorms in the 1850s and 1860s, 1870 and subsequent bark beetle outbreak in 1921 or 1922 (Skuhravý 2002; Brázdil et al. 2004). As an example, all three plots (JEZ1, JEZ2, BOU2), which were old enough to experience the early 1820s windstorms, indicated a disturbance during this time. Disturbances in the 1780s and 1820s initiated also the stand on Trojmezná Mt. (Svoboda et al. unpublished 2011). Less synchronized is the origin of plot BOU1 in the 1840s.

It is more difficult to analyze the possible logging of windthrows, bark beetle infested trees or survived trees, which could come after the natural event. We could perhaps get help from the information that present logging usually destroys advanced regeneration (Jonášová 2001; Jonášová, Prach 2004). Since the second half of the 19th century, forests have been managed intensively in the Czech part of the Bohemian Forest, including the harvesting of left virgin forest (Beneš 1996; Jelínek 2005). We have evidence of the logging of trees after the bark beetle attack on Boubín Mt. (plot BOU1) in the 1870s (Jelínek 2005), which may also be the cause of the release peak on plot MUS1 in 1884.

Neither could we solve if all the trees regenerated naturally or were planted. Based on historical evidence the planting was carried out in the Bohemian Forest since the second half of the 19th century (Jelínek 2005). Therefore the regeneration of JEZ2 and BOU2 was probably fully natural. Many trees regenerated before the disturbance on the rest of plots. Underplanting is not probable on these inaccessible sites. The natural regeneration was therefore important but we do not know to what extent.

Furthermore, we were not able to solve the issue of secondary interference of the forest dynamics by humans. This interference is highly probable, but it is not clear how strongly it could affect the main pattern of the stand break up and initiation. In the past, this was mainly livestock grazing, selective logging, management of the state frontier, roads and so on (Jelínek 2005). Presently, human interference consists in thinning, harvesting in the neighbourhood, logging of bark-beetle infested trees, pollution and so on, some of which could increase the stand homogeneity.

CONCLUSIONS

Severe natural disturbances have played a fundamental role in forest dynamics in the upper parts of the Šumava Protected Landscape Area. This type of stand initiation results in a relatively homogeneously looking structure, which is not a sign of planted origin. The described structure and dynamics could therefore be probably taken as a part of the range of natural variability of mountain Norway spruce forests. This knowledge is important in natural conservation and ecological forestry. The information about regeneration ecology and natural hazards of these forests could be applied also in strictly commercial forests. But more research is needed to make these issues more clear and to support our preliminary results with more replications and also to improve our knowledge of human interference.

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Dendrochronological reconstruction of the disturbance history and past development of the mountain Norway spruce in the Bohemian Forest, central Europe

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ABSTRACT

Disturbances play a major role in shaping forest structure and composition. However, the effects of disturbances on forest ecosystems in central Europe are poorly understood, despite the importance of this information for forest management (e.g., for managing recent, large-scale, high-severity disturbances in the region). Using the tree-ring approach, this work investigates the past development, disturbance history and historical range of variability of the old mountain Norway spruce (*Picea abies*) forest stand in the high elevation Bohemian Forest (Protected Landscape Area Šumava) in the Czech Republic.

The goals of the study were threefold: (1) to reconstruct the historical disturbances of the forest, (2) to describe the recruitment strategy of trees in response to disturbance, and (3) to describe the subsequent development of trees by their growth trends.

We cored all stems within three 0.25 ha plots. The growth series were surveyed for events indicative of past tree mortality: (1) abrupt, sustained and rapid increases in growth (releases from suppression) and (2) rapid early growth rates (gap origins). We then conducted a cluster analysis of individual growth trends by fitting splines to the power-transformed and age-filtered (RCS-method) tree ring series.

High-severity disturbances were identified in the 1820s and 1860s. Less severe disturbances also occurred every 10–50 years. The disturbances were synchronised among plots and consistent with data from distant locations in the Bohemian Forest. Most disturbances were explained by known historical windstorms; some by bark beetle outbreaks. Most trees regenerated shortly before or after disturbance and exhibited evidence of 1–3 disturbance events in their growth chronologies. A smaller proportion of trees was suppressed before disturbance for more than 10 years. The cluster analysis of growth trends revealed five types of tree behaviour classified according to their growth rate during (1) stand initiation and (2) later development.

We conclude that disturbances (including large, high-severity and low-frequency disturbances) contribute to the broad range of variability of central European mountain spruce forests. Sustainable management strategies should therefore incorporate described disturbances and their biological legacies, as many species likely depend on them. In addition, the development trajectory of stands following stand-replacing disturbance, as described here, can be used to predict future development of presently disturbed stands.

1. Introduction

An understanding of forest dynamics is vital for the effective management of both commercial and protected forests. Mimicking the natural range of variability has become an important concept in ecological forestry (Franklin et al., 2002; Kulakowski and Bebi, 2004) but the knowledge is also important for the effective utilisation of natural resources in commercial forests (Kimmins, 2004). In the last half-century, disturbances have become integral to our view of forest development and dynamics (Pickett and White, 1985) and have been used to describe forest history. Ultimately, the concept of the disturbance regime has become useful for describing entire forest dynamics and the range of variability of a forest (Frelich, 2002). While the knowledge is now good in North America, it is still limited in central Europe for several reasons. First, natural forests and forest landscapes are scarce, having experienced extensive exploitation. Second, the role of disturbance was not fully appreciated in the past, reflecting the existing paradigms in forest ecology at the time (Splechtna et al., 2005). Third, conserved remnants were likely often established in locations

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protected from disturbances, containing heterogeneous old-growth stands and large trees (Angelstam and Kuuluvainen, 2004). Consequently, disturbances were rarely studied and historical studies (e.g., dendrochronological) rarely conducted.

Less attention has been paid to the dendrochronological reconstruction of the behaviour of individual trees within the framework of disturbances. The heterogeneity of tree reactions to disturbance and subsequent developmental trends and pathways are relatively unknown (but see Canham, 1990; Wu et al., 1999; Rentch, 2003; Doležal et al., 2004, 2009; Weber et al., 2008). Forest development after a major disturbance has been described at the stand scale. The authoritative work of Oliver (1980/1981) divided the stand development following severe disturbance into four stages. The general model suggests that regeneration and exponential growth occur in the open condition during stand initiation, immediately after a major disturbance. This stage is followed by a stem-exclusion stage, where the canopy closes, growth slows and asymmetric competition and self-thinning increase. Larger trees are favoured during the stem-exclusion stage. During the third phase (i.e., understory reinitiation), the density of the canopy decreases due to the dieback of dominant trees, and regeneration is again favoured (Oliver, 1980/1981; Doležal et al., 2009).

How should we view the natural dynamics of mountain Norway spruce forest in central Europe? This is a fundamental question of conserved forest management efforts in central Europe, and the absence of an answer is problematic for the National Park Šumava (the Czech part of the Bohemian Forest), Tatra National Park (Carpathians, Slovakia) and other conserved areas (Fischer et al., 2002; Jonášová and Prach, 2004; Vacek and Podrázský, 2008; Prach et al., 2009; Jonášová et al., 2010). Korpel̆ (1995) work was authoritative in describing forest dynamics in the Czech Republic. His developmental cycles were primarily developed by studying forest structure on study plots and were similarly applied to all forest types. Modern methods (which often use dendrochronology to reconstruct forest history) have revealed the importance of disturbances (moderate as well as wide-spread and severe) to the dynamics of mountain Norway spruce forests in central Europe (Zielonka and Malcher, 2009; Zielonka et al., 2010; Panayotov et al., 2011; Svoboda et al., 2012).

Globally, spruce forests exhibit heterogeneous disturbance regimes, ranging from systems created by frequent and severe crown fires (e.g., *Picea mariana* in the boreal zone of North America; Frelich, 2002), those subject to severe windstorms or insect outbreaks (e.g., *Picea engelmani* in the subalpine zone in the Rocky Mountains of North America; Veblen, 2000; *Picea glauca* in the boreal zone of North America; Berg et al., 2006) to those with prevailing old-growth stands and patch or gap dynamics (e.g., *Picea rubens* in eastern North America; Fraver and White, 2005b). *Picea abies* is considered a shade-tolerant, late-successional species in the European boreal zone (Shorohova et al., 2009; Kuuluvainen and Aakala, 2011). Gap dynamics were most commonly reported forest dynamics in boreal Fennoscandia (Kuuluvainen and Aakala, 2011). In contrast, in central Europe, *P. abies* is classified as mid-tolerant species that can dominate already during stand initiation following extensive disturbance (Fischer et al., 2002; Jonášová and Prach, 2004; Jonášová et al., 2010).

Initial assumptions about the dynamics of central European mountain spruce forest were described by Kulakowski and Bebi (2004), who postulated that the natural variability of the forest is largely determined by strong, infrequent disturbances. In the absence of frequent disturbances by fire, forest stand disturbances are generally driven by wind (Frelich, 2002; Panayotov et al., 2011). Windstorms cause irregularly spaced windthrows, creating gaps ranging in size from the area of a single tree to several hundred hectares. The severity of a windstorm is highly influenced by stand location (e.g., topography) and other factors (Frelich, 2002; Kulakowski and Bebi, 2004; Zielonka et al., 2010). In addition, Norway spruce can also die due to the attacks by the bark beetle *Ips typographus*, which can rapidly increase in number under suitable conditions. When occurring along with windstorm disturbances, *Ips typographus* outbreaks can affect entire landscapes (Økland and Bjørnstad, 2006). Other disturbance agents are less or only locally important, such as avalanches, fungi and other pathogens and herbivorous animals (Frelich, 2002; Kulakowski and Bebi, 2004).

The natural recurrence period of fire in central European mountain spruce forests is expected to range from several hundred to several thousand years (Tinner et al., 1999; Beer and Tinner, 2008). Windstorms that can kill a tree and increase forest heterogeneity can occur yearly. Severe windstorms that can cause stand break-up over large areas have occurred every century, based on historical evidence (Brázdil et al., 2004; Svoboda, 2006). The recurrence period for severe windstorms can be approximately 100 years at exposed sites (Zielonka and Malcher, 2009; Zielonka et al., 2010). The impacts of bark beetle outbreaks often exceed those of wind in global forests (Eisenhart and Veblen, 2000; Berg et al., 2006). There is some (weak) historical evidence to suggest that bark beetle outbreaks occurred approximately twice a century in the Bohemian Forest (Zatloukal, 1998; Skuhravý, 2002).

Despite these observations, knowledge of disturbances in the European mountain Norway spruce forests remains qualitative and general. Modern research on long-term developmental processes and the impact of disturbances on mountain spruce forests has only begun recently (Motta et al., 1999; Zielonka and Malcher, 2009; Zielonka et al., 2010; Janda et al., 2010; Svoboda et al., 2010, 2012; Panayotov et al., 2011), and further research is needed. In addition to repeated measurements on study plots (which take many years) and chronosequencing, reconstruction of forest development using dendrochronological tree-ring analysis is important for progress in this field (Vinš, 1961; Henry and Swan, 1974).

Extensive forest disturbances have occurred during the past several decades in the national parks of the Bohemian Forest (Bayerischer Wald in Bavaria and Šumava in the Czech Republic; Lausch et al., 2011; Fischer et al., 2002). These disturbances were primarily caused by windstorms and bark beetle outbreaks. Therefore, the question is whether these events are naturally occurring; i.e., are within the boundaries of the historical range of variability for central European mountain spruce forest. The second question is how the disturbed stands will develop in the future. Several recent studies address these topics in the Bohemian Forest (Janda et al., 2010; Svoboda et al., 2010; Čada and Svoboda, 2011; Svoboda et al., 2012). Svoboda et al. (2012) studied the disturbance history of one old-growth fragment on a 20-ha study plot and concluded that the forest was historically shaped by infrequent, moderate-to-high severity natural disturbances.

The present study focuses on the developmental processes and disturbance history at the micro-scale and is conducted at another old forest stand (65 km away from Svoboda's et al. (2012) study site) to extend the current evidence. The goals of this study are to

(1) reconstruct the past disturbances in the mountain Norway spruce forest at Jezerní Mt. in the Bohemian Forest of central Europe; i.e., to determine the timing, frequency and severity of past disturbances;
(2) identify the population development (primarily the pattern of tree recruitment) of Norway spruce, with attention to the response to disturbances; and
(3) using growth histories, describe the developmental trends of individual trees after establishment.

2. Methods

2.1. Study area

This work was conducted within the National Natural Reserve (NNR) of Černé and Čertovo Lakes (I. zone of CHKO Šumava – Czech part of the Bohemian Forest) on the mountain plateau of Jezerní Mt. (1343 m; 49°10′8″N, 13°11′4″E), located in the south–west of the Czech Republic in central Europe (near the state boundary with Bavaria, Germany). These nearly monospecific Norway spruce woods are primarily restricted to isolated upper parts of the mountain range. The tree layer is strongly dominated by Norway spruce (*P. abies* L. (Karst.)), with minimal admixture with other species (e.g., *Sorbus aucuparia* L., *Acer pseudoplatanus* L., *Abies alba* Mill., *Fagus sylvatica* L.; Neuhäuslová and Moravec, 1998; Čada and Svoboda, 2011).

The vegetation community is described as *Calamagrostio villosae-Piceetum* (with patches dominated by *Calamagrostis villosa*, or *Deschampsia flexuosa*, or *Vaccinium myrtillus* on more stony soils; Sofron, 1981; Koutecký, 2005). The geological substrate is pure mica schist (Cháb et al., 2007), and the soil is stony (Kozák, 2010). The climate is cold and humid, with a mean annual temperature of approximately 4 °C and a mean annual precipitation of approximately 1400 mm/year (Tolasz, 2007). The site is exposed to west winds and is located at the end of a valley that rises parallel to the prevailing western winds, creating an environment similar to an anemo-orographic system (Jeník, 1998).

Human settlement began below the tops of the mountain ridges in the Bohemian Forest in the 18th century (Beneš, 1996). Felling by man may have subsequently potentially occurred in the study area. Historical documents indicate a younger patch at this location in the 1870s; this has been interpreted as logging activity (Sofron, 1971), but in fact, there was no direct evidence. The specification of forest damage due to grazing is vague. The reserve was founded in 1911, but exploitation had already decreased following a bark beetle outbreak in the 1870s (Sofron, 1971). Stands at Jezerní Mt. have been breaking up due to wind, bark beetles and subsequent clearance since the 1990s (Koutecký, 2005). This break-up culminated in a windstorm, named Kyrill, in January 2007, which resulted in stand break-up over most of the Jezerní Mt. plateau and surrounding area. Approximately half of the spruce stands in the reserve were affected by a stand-replacing disturbance covering an area of approximately 55 ha. An additional 65 ha was severely disturbed near the Reserve. Reserve practices include active management to avoid bark beetle outbreaks; therefore, all affected trees were logged for the sanitation reasons, with most of the wood left in the reserve.

2.2. Data collection

We established three 50 × 50 m study plots in the area where the stands had been totally affected by windstorm and subsequent sanitation logging. All stems thicker than 10 cm were positioned (i.e., stumps, snags, uprooting and alive trees). Stem thickness at stump height (30–40 cm) and species were identified for each stem. For more details of stand structure, see Čada and Svoboda (2011).

Subsequently, we took one increment core from each possible stem thicker than 10 cm at stump height. We focused on taking cores from the side with the most representative growth (in cases with exocentric growth) and not affected by root swellings. Increment cores were air-dried, attached to a wooden mount and cut with a razor blade. Contrast was improved by moistening and impressing with chalk. Ring widths were measured to the nearest 0.01 mm using a sliding table, TimeTable (Vienna Institute of Archaeological Science), which was connected to a personal computer running Past4 software (Knibbe, 2007). Each tree-ring series was cross-dated following the procedure of Yamaguchi (1991) and using statistical tests implemented in Past4 (Knibbe, 2007) and COFECHA (Holmes, 1983; Grissino-Mayer, 2001). A few series that did not fit well were excluded from all further analyses. The curvature and mean width of the five tree rings closest to the centre were used to estimate the number of rings missed in cases where the core did not pass through the pith (Duncan, 1989). We did not correct for bias caused by coring height (Niklasson, 2002); therefore, "ages" referred to hereafter are not true ages but recruitment ages at coring height.

A total of 382 growth series (168, 113 and 101 from plots 1, 2 and 3, respectively) were obtained. Twenty-six had rotten centres and therefore, it was not possible to calculate their ages. Of the remaining 356 series (161, 97 and 98), 28% passed through the pith, and 90% were less than 12.6 mm from the pith. Additional cores were rotten on the outside area beneath the bark. Thus, 323 series (150, 81 and 92) were terminated after 1955.

2.3. Data analysis

2.3.1. Analysis of disturbance events on growth series

Two types of events on the 382 growth series were assumed to indicate past disturbance: (1) release from suppression (abrupt, sustained and large increase in growth) indicates the death of surrounding trees and (2) gap origin (rapid early growth rate) indicates the existence of a tree in open conditions during its recruitment (Lorimer and Frelich, 1989). Gap-originating trees were defined as those trees whose mean width of the 6–15 ring exceeded 1.0 mm (Splechtna et al., 2005; Firm et al., 2009; Jönsson et al., 2009) and whose subsequent growth pattern was declining, parabolic, or flat (Frelich, 2002).

We used the "absolute increase" method to identify releases from suppression (Fraver and White, 2005a) because it is simple, clear and poses no problems regarding the definition of the upper boundary (Splechtna et al., 2005; Zielonka et al., 2010). Absolute growth changes were calculated for each year of each series (except for the first and last 10 years) by subtracting the prior 10-year mean from the subsequent 10-year mean. A release year was identified by a growth change value that was the maximum of the surrounding 20-year interval (±10 years) and that exceeded the threshold of +0.55 mm (Jönsson et al., 2009). This threshold was specified for the Norway spruce, based on experience with its growth variation (Jönsson et al., 2009). Finally, we visually checked all of the series and their releases. Releases were excluded if the growth acceleration was not obvious (24.2% cases excluded). For example, growth restoration after short-term growth reduction or short-term pulses were excluded. Releases were also added in obvious cases (18.7% cases added). Visual checking is vital in this type of work because growth fluctuations due to environmental variation (climate, injuries, mast year, etc.) have a great effect near the specified threshold. Basically, there is always a trade-off between positive and negative errors. Non-release growth changes are not only related to climate variation, which is usually used to test the criteria (Nowacki and Abrams, 1997; Black and Abrams, 2003), but there is also a large overlap with changes caused by injury, reaction wood and other factors (Fraver and White, 2005a; Fraver, pers. comm.; personal observation).

To mitigate the influence of subjectivity, we also defined stricter criteria to detect "intense releases": releases higher in magnitude and longer in duration (15-year means, absolute increase threshold +1.00 mm) than standard releases. They were defined such that a subjective approach was little used (on average, 2.4% of cases were excluded and no cases were included).

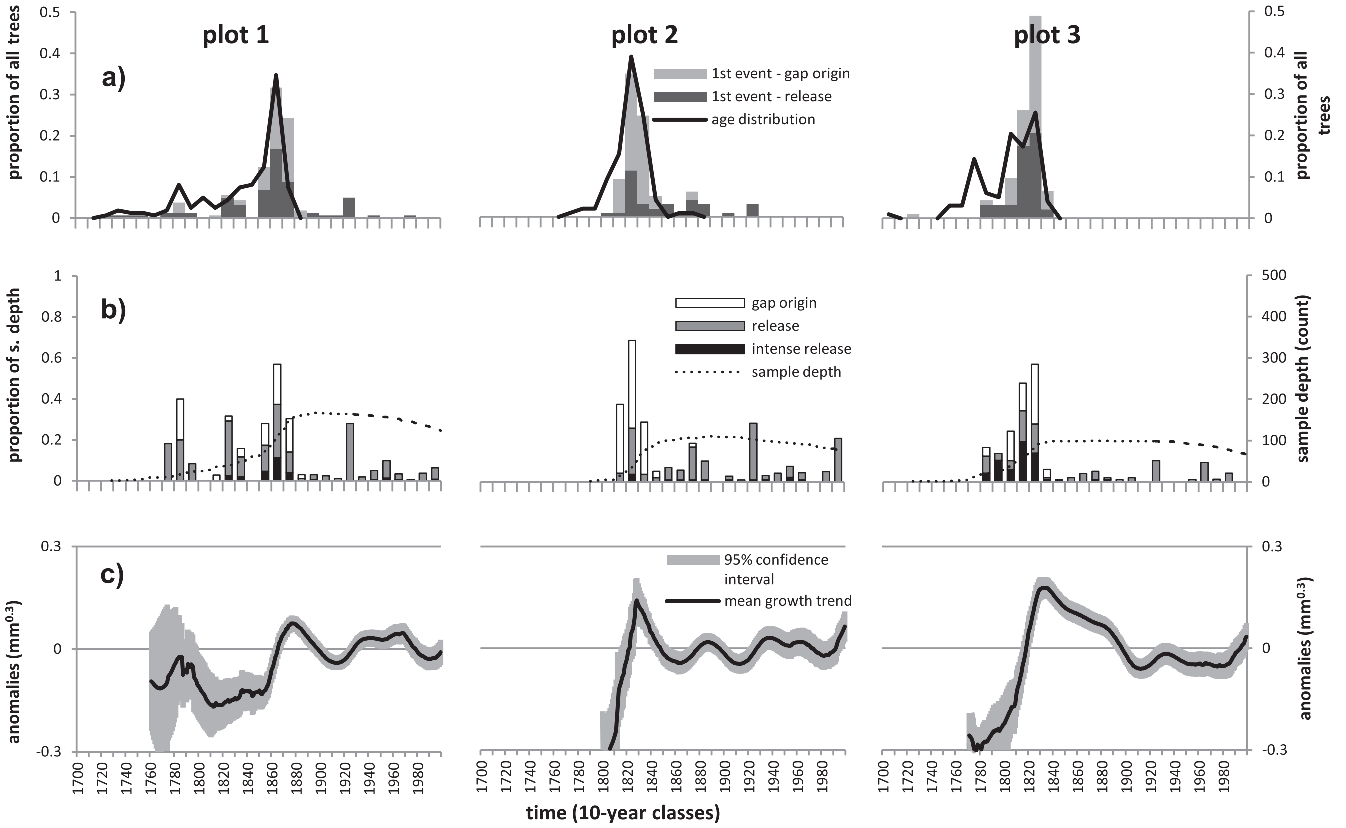

Fig. 1. (a) The distributions of ages (lines) and first disturbance events in growth series (columns), summarised into 10-year classes. Two types of events indicative of past disturbances were investigated: releases from suppression and gap origin events (see Section 2.3.1 of Methods). One main disturbance period, which initiated the stands, was identified for each plot. (b) Disturbance chronologies. For each decade, the number of disturbance events is shown proportional to the sample depth at the end of the decade. In this case, releases were categorised into two classes: higher magnitude, longer duration releases ("intense releases") and ordinary releases (see Section 2.3.1 of Methods). Chronologies were truncated when the sample depth dropped below 10. Several peaks, reflecting both low- and high-severity disturbances, were reconstructed. (c) The mean growth trend (and its 95% confidence interval), calculated as the average value of the growth trends of individual trees (see Section 2.3.2 of Methods). Note the rapid change and subsequent above-average growth rates during the establishment of the stands.

We then calculated the disturbance chronology (Fig. 1b) following Lorimer and Frelich (1989) and Frelich (2002). All release and gap-origin events were summarised into decades and plotted proportional to sample depth at the end of the decade. The chronology was truncated when sample depth dropped below 10. The resulting chronology, called a "tree-population-based" chronology by Frelich (2002), shows the proportion of the population affected by a disturbance within a given decade. The effect of an individual tree is not weighted by its size. The calculated proportion does not fully correspond to the affected area, because of the different areas occupied by individual trees. However, we believe that this method poses no problems for interpretation because the tree layer in our study site was largely uniform, lacking any cohort of small trees (Čada and Svoboda, 2011).

It is believed that this type of chronology overestimates some disturbances because subdominant trees bordering the created gap could show releases (Lorimer and Frelich, 1989; Svoboda et al., 2012). Therefore, we also show the real distribution of first events (gap-origin or release) on the growth series (Fig. 1a), without plotting them proportionally to sample depth (Svoboda et al., 2012). We used only 356 trees of known age. This distribution should more accurately depict the origin of the stand. The time when the trees started to grow faster towards the canopy is shown. This distribution is more informative than simple age structure because the time of release better approximates the recruitment of advanced regeneration than does the time of germination (Oliver, 1980/1981; Lorimer and Frelich, 1989). We do not use Lorimer and Frelich's (1989) term "canopy accession" because we do not determine whether the first event is the "major" event.

2.3.2. Analysis of growth trends

We investigated the growth trends of trees to describe stand development from this point of view. For this analysis, we used 323 series of known ages that terminated after 1955. For computations, we used the statistical software R (version 2.10.1, R Development Core Team, 2009) and the package "dplr" (Bunn, 2008). Growth series were standardised in three steps to obtain growth trends:

(1) The data were power transformed. The optimal power, p, for transformation was computed as

$$p = 1 - m \tag{1}$$

where m is the slope of a regression of the log10 median ring width against the log10 interquartile range ring width of non-overlapping, 10-year segments (Emerson, 1983). Medians below 0.1 mm were excluded from this relationship. The resulting power, p, is equal to 0.3.

(2) The age trend of the transformed data was excluded using the RCS method (Grudd et al., 2002). The transformed series were scaled by their biological age, and the mean value for each year was calculated. The trend displayed a linear pattern between the approximate ages of 5 and 229 years (beyond which the sample depth dropped to low values). Therefore,

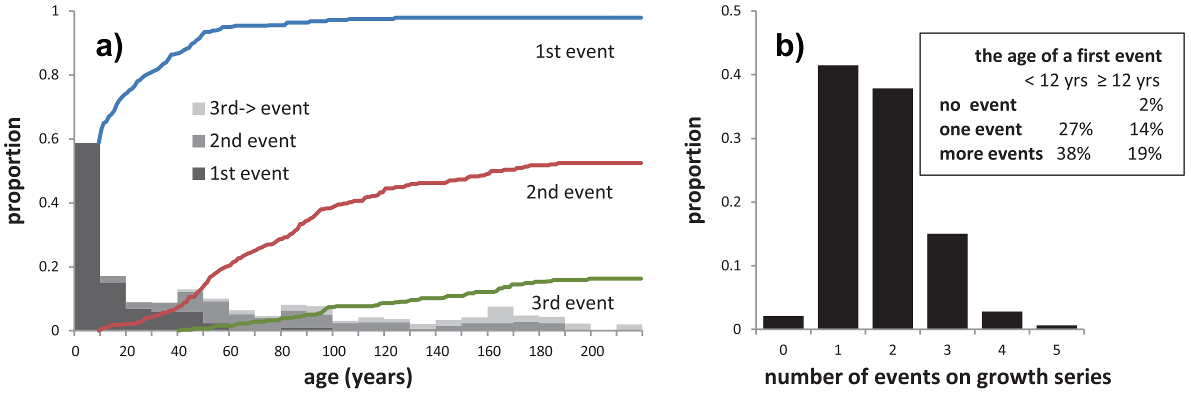

Fig. 2. (a) The frequency of a disturbance event in the growth chronologies of individual trees by tree age. Lines depict cumulative values. First, second and subsequent events in the growth chronologies are distinguished. Events are significantly associated with ages <12 years, with the probability slowly decreasing thereafter. (b) The frequency of the number of events in individual chronologies. Typically, 1–3 disturbance events were identified. Data from both graphs are combined in the table to describe several tree behaviour types; i.e., the number of trees exposed to disturbance before or after age 12 and the total number of events observed per tree.

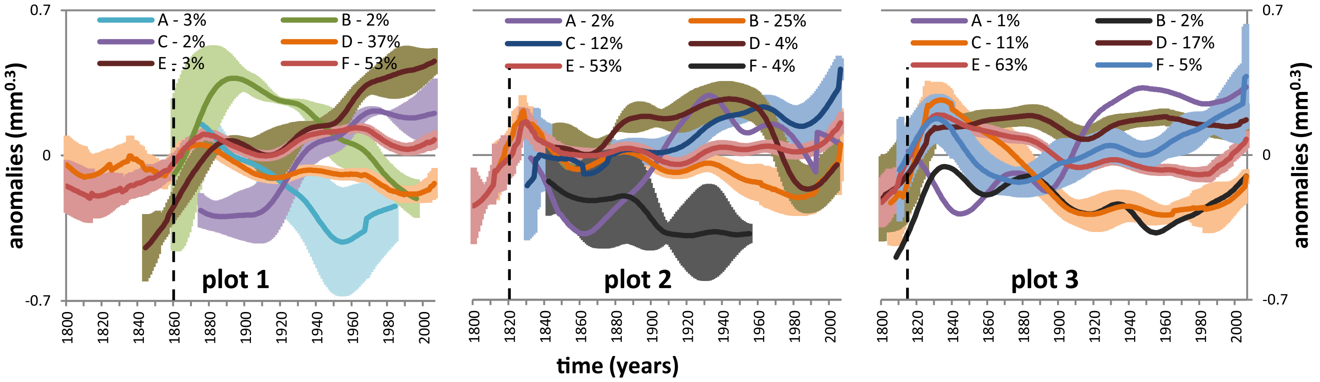

Fig. 3. Mean growth trends (and 95% confidence intervals) calculated as the average values for groups identified by cluster analysis. For each group, the designation and percentage of all trees in the plot are included in the legend. Graphs show the differentiation of growth rates after stand initiation following severe disturbance. The approximate timing of the severe disturbance is indicated by the vertical dashed line. Five types of tree behaviours were interpreted based on two measures: the occurrence of rapid growth during stand initiation and the occurrence of rapid growth during later development. Later development was affected by less severe disturbance.

we fitted the line of the intercept equal to 1.093 and the slope equal to −0.017 ($r^2 = 0.16$; $p < 0.001$) for all of the transformed data in the interval of 5–229 years. Subsequently, the fitted line was subtracted from all the transformed values. Data from before the age of 5 years were eliminated.

(3) High-frequency variability was excluded using 40-year spline functions individually fitted to each series (Cook and Kairiukstis, 1990). Gained splines are used in further analysis and referred to as trees' "growth trends".

Finally, all growth trends were entered into the cluster analysis separately on three plots. We used the average linkage method of Euclidean distances. Based on the resulting dendrograms, six groups were distinguished on each plot. Each group was marked by the capital letter (group A–F on each plot), and its proportion, mean growth trend and 95% confidence interval were calculated (Fig. 3). Based on the interpretation of the Fig. 3, we described five types of tree behaviour following the stand-replacing disturbance (Types 1–5, see Section 3.2 of Results).

Nonparametric statistical tests (Spearman's correlation coefficient, *r*; Kruskal–Wallis ANOVA, H) were used to identify relationships among the four different variables used in the paper to describe the origin, past development and structure of the forest and, therefore, to link up the different aspects of the stand dynamics. We tested the four variables: age, diameter, number of events per growth chronology and group (as identified by the cluster analysis). Additionally, Spearman's correlation coefficient was used to test for a relationship between age and the frequency of disturbance events in growth chronologies, and nonparametric Friedman's ANOVAs were used to test for differences in the length of intervals between disturbance events in the growth series.

3. Results

3.1. Stand initiation and disturbance history

Each plot was dominated by one dominant population wave. The predominant peaks in age distribution (Fig. 1a) occurred in the 1860s (in plot 1) and 1820s (plots 2 and 3). The proportion of trees older than the main population wave ranges from only a few trees in plot 2 to one half of the population in plot 1. The distributions of first disturbance events in the growth series (see Section 2.3.1 of Methods for definition; Fig. 1a) indicate more precisely the origins of the stands. The distributions show a few separated periods when trees started to grow towards the canopy. Peaks in this distribution indicate past disturbances and the time of stand origin. The period corresponds also to peaks in the age distribution. These data suggest the occurrence of severe disturbance in approximately 1860 (in plot 1) and 1820 (in plots 2 and 3). These disturbances led to the initiation of the stands in our study plots. The

Table 1

Nonparametric statistics (Spearman's correlation coefficient, *r*, and Kruskal–Wallis ANOVA, H) of the relationships among age, tree diameter, number of events in the growth chronology and group (as identified through cluster analysis of individual growth trends, Fig. 3). Kruskal–Wallis ANOVA was computed for the variable "group" separately on each plot (H1, H2 and H3 refer to plots 1, 2 and 3, respectively). *p*-Values appear in brackets after the statistics, and values below 0.05 are in boldface.

	Diameter (*N* = 323)	Age (*N* = 323)	Group (*N* = 6)	No. events (*N* = 5)
Diameter (*N* = 323)		**r = 0.38 (<0.001)**	**H1 = 49.12 (<0.001);** **H2 = 17.08 (0.004);** **H3 = 23.15 (<0.001)**	**H = 22.00 (<0.001)**
Age (*N* = 323)	**r = 0.38 (<0.001)**		H1 = 8.23 (0.14); H2 = 8.65 (0.12); H3 = 1.47 (0.92)	H = 6.39 (0.27)
Group (*N* = 6)	**H1 = 49.12 (<0.001);** **H2 = 17.08 (0.004);** **H3 = 23.15 (<0.001)**	H1 = 8.23 (0.14); H2 = 8.65 (0.12); H3 = 1.47 (0.92)		**H1 = 20.69 (<0.001);** **H2 = 15.25 (0.009);** H3 = 8.69 (0.12)
No. events (*N* = 5)	**H = 22.00 (<0.001)**	H = 6.39 (0.27)	**H1 = 20.69 (<0.001);** **H2 = 15.25 (0.009);** H3 = 8.69 (0.12)	

events in the growth series during those periods are spread across 2–3 decades.

The disturbance chronologies (Fig. 1b) reveal distinct periods of disturbance that are synchronised among plots. In addition to the one severe disturbance period on each plot described above, there are additional, less severe disturbances. The significant peaks in the chronologies (i.e., with more than 10% of trees indicating disturbance) occurred in the 1780s, 1810–1830s, 1850–1870s, 1920s, 1940–1960s and the 1990s.

During the severe disturbances that initiated the stands, 85%, 82% and 94% of the existing trees displayed the disturbance event in plots 1 (1850–1889), 2 (1810–1849) and 3 (1800–1830), respectively. Releases were of higher magnitude and longer duration during severe disturbances. During this period, 72%, 17% and 76% of all intense releases occurred in plots 1, 2 and 3, respectively. The relatively low percentage of intense releases in plot 2 reflects the small number of trees that were older than the disturbance.

All plots exhibited above-average growth during stand initiation (Fig. 1c), indicating open conditions and minimal competition during this time. The above-average growth lasted 33 years (1865–1897) in plot 1, 26 years (1822–1847) in plot 2 and 79 years (1818–1896) in plot 3. Before this period, growth was below average, with subsequent rapid change. Growth gradually declined to average values after the peak, fluctuating around the average thereafter.

We can distinguish three categories of trees based on age structure and the timing of disturbances (Fig. 1a): (1) trees that attained coring height more than a decade before a disturbance, survived in the understory and were released by the disturbance, (2) trees that attained coring height shortly before or after (±10 years) a disturbance and grew rapidly thereafter (the majority of trees fell into this category), and (3) trees that also attained coring height shortly before or after a disturbance but were then suppressed, experiencing the first event (release) decades after stand initiation, during a less severe disturbance.

3.2. Stand development

Stand development was characterised by the occurrence of events (as signs of disturbance) in the growth chronologies and by the heterogeneity of growth trends. Typically, 1–3 events occurred within an individual chronology (Fig. 2B). These events occurred mainly at younger ages. Sixty-five percent of trees experienced their first event before age 12. After age 20, the frequency of events slowly decreased with increasing age (Spearman's $r = -0.765$, $p < 0.01$). First events are, therefore, concentrated at younger ages (the median interval to the first event is 3 years). Subsequent intervals between first and following events and between the last event and the end of the series did not differ from random (median = 61 years; Friedman's nonparametric ANOVA (52, 2) = 1.05, $p = 0.591$). Twenty-seven percent of all trees registered only one disturbance event occurring before age 12 (Fig. 2).

Based on cluster analysis results, which distinguished six groups of trees with similar growth trends (Fig. 3), we identified five types of spruce behaviour occurring from stand initiation to the present. Two factors were important: the rate of tree growth during stand initiation and the rate of tree growth during later development. Therefore, the five types of behaviour are (1) rapid growth through stand initiation, with subsequent slowing to average values (groups B and F on plot 1, E on plot 2 and E on plot 3); (2) rapid growth through stand initiation, with subsequent slowing to below average values due to suppression (groups A and D on plot 1, B on plot 2 and C on plot 3); (3) rapid growth both through and after stand initiation due to release during a less severe disturbance (groups E on plot 1, D on plot 2 and D and F on plot 3); (4) slow growth through stand initiation followed by rapid growth due to release during a less severe disturbance (groups C on plot 1, A and C on plot 2 and A on plot 3); and (5) slow growth both through and after stand initiation (groups F on plot 2 and B on plot 3). The border between groups is understandably not sharp, preventing calculations of the proportion of trees that is classified into each type. Type 1 is the most common, with a modal type of growth trend, exhibited by approximately half the population. The second most common type of behaviour is Type 2 (approximately a quarter of the population). Only 2% of trees were classified as Type 5.

Statistical results are shown in Table 1. Tree diameter is age-dependent. Tree diameter and the number of events within individual chronologies varied among groups identified through the cluster analysis. Post-hoc testing indicated that, in general, trees of Types 1 and 3 were thicker than trees of Types 2 and 5. Tree diameter significantly increased with number of disturbance events. Age was not correlated with either groups or the number of events. Only trees with no event were slightly (not significantly) younger. Interestingly, the fastest growing younger trees ($N = 18$, median age = 157 years, median diameter = 41 cm) attained diameters similar to those of oldest trees in plot 1 ($N = 6$, median age = 251 years, median diameter = 36 cm).

4. Discussion

As we have presently realized, severe natural disturbances strongly affect mountain spruce forest dynamics in central Europe

(Fischer et al., 2002; Jonášová and Prach, 2004; Jonášová et al., 2010; Lausch et al., 2011). Recent data suggest that this pattern of stand dynamics was also present in the past (Zielonka and Malcher, 2009; Zielonka et al., 2010; Panayotov et al., 2011; Svoboda et al., 2012). We reconstructed one severe disturbance period that initiated the stand in each plot. The disturbance in the 1820s was similar between plots 2 and 3. The data suggest that the disturbance in plot 2 could be stand-replacing or major (sensu Oliver, 1980/1981) because all the mature trees may have been removed and "most trees beginning growth after the disturbance do not encounter competition from surrounding, undisturbed trees" (Oliver, 1980/1981). The disturbance in plot 1 did not remove all mature trees, but the developmental pattern was otherwise relatively similar (Figs. 1 and 3), indicating identical open conditions after the disturbance. Widespread, advance regeneration (at heights above the coring height) occurred on plot 3 before the disturbance period, but the severity of the disturbance was likely comparable to that of the other two plots. The long periods of release in plots 1 and 3 suggest that previous stands were likely removed by more than one disturbance event (Fig. 1). The stand may have been successively broken up by a several disturbance events over two to three decades, similar to the current break-up (Janda et al., 2010; Čada and Svoboda, 2011). This type of stand initiation resulted in a relatively homogeneous stand structure (Holeksa et al., 2007; Svoboda and Pouska, 2008; Svoboda et al., 2010; Čada and Svoboda, 2011).

Using only tree ring data, we could not directly identify the causal factor behind past stand break-ups. However, we deduced from the synchronisation of the disturbances among distant locations in the Bohemian Forest and the explanations of historically known disturbances that the pattern was caused by windstorms or bark beetle outbreaks; i.e., natural disturbances (Čada and Svoboda, 2011; Svoboda et al., 2012). Svoboda et al. (2012) found similar peaks in the disturbance chronologies in the 1780s and 1820s in an old growth fragment 65 km away. The disturbances we identified in the 1780s, 1820s, 1860s–70s and 1920s are supported by the findings of Čada and Svoboda (2011) in two other locations. The peaks in our disturbance chronologies could be related to the known windstorms of 1778, 1812–13, 1821–22 and 1833 (the latter followed by a bark beetle outbreak in 1834–1840); the numerous windstorms from 1853–1870, followed by a bark beetle outbreak in the 1870s; the windstorms of 1921–22; the low-severity bark beetle outbreak in the late 1940s or the windstorm in 1955 (Skuhravý, 2002; Schelhaas et al., 2003; Brázdil et al., 2004; see Table 2 in Svoboda et al. (2012) for a summary of historically known disturbances). A secondary interference of man on the natural pattern of forest dynamics is likely throughout the whole period investigated here (Jelínek, 2005); however, it is unknown whether and how human activity affected the predominant pattern of stand break-up and initiation. These stands were likely used for livestock grazing, and some unknown management practices may have occurred due to the management of the nearby state boundary. Selective logging or logging of dead or surviving trees after natural disturbances may also have occurred, although the site is relatively inaccessible (Jelínek, 2005).

As in the present, the initiation of the main population waves was likely related to windstorms, which were most likely more important in wind-exposed locations (in accordance with Zielonka et al., 2010). The stand in plot 2 was likely initiated after the windstorm of 1821 or 1822, which potentially removed as much as 100% of mature trees, leaving only seedlings behind. A smaller proportion of trees surviving the windstorm may have been killed by the bark beetle, which can greatly increase in number in windthrows and then attack live trees (Økland and Bjørnstad, 2006). This scenario could potentially explain the extension of some releases in the 1830s (Fig. 1b). The stand in plot 1 was likely initiated after a windstorm in approximately 1860. This disturbance did not remove all the mature trees and released the advanced regeneration, which attained a wide range of ages. This pattern is the most likely cause of the heterogeneity in the preceding stand (Frelich, 2002; Kulakowski and Veblen, 2003; Fraver and White, 2005b; Nagel et al., 2006). The releases again extended into the 1870s from the peak of the 1860s in plot 1, and there is a distinct peak in plots 2 and 3 (Fig. 1b). The "big bark beetle outbreak" of the 1870s is widely known from historical material, and it affected large areas of spruce stands in the Bohemian Forest (Skuhravý, 2002; Jelínek, 2005; Svoboda, 2006).

The range of variability of the central European mountain Norway spruce forest should, therefore, include the effects of infrequent severe windstorms. We detected intervals of approximately 150 and 190 years between severe windstorms that initiated stands (i.e., between reconstructed and present windstorms). We also found intervals of 10–50 years between less severe disturbances. The extent of severe disturbances can be estimated from forestry maps from the 1870s (Jelínek, 2005; state archive: SOA Plzeň, VS Železná Ruda, map 2). There is a 53.4 ha patch at our location and a 100.4 ha patch at the Trojmezná site (Svoboda et al., 2012) depicted on old maps (state archive: SOA Plzeň, VS Železná Ruda, map 2), suggesting that the high-severity disturbances occurring at the beginning of 19th century ranged in size from tens to hundreds of hectares. This pattern is not unknown in global forests (Turner and Dale, 1998; Frelich, 2002; Kulakowski and Bebi, 2004). In the absence of frequent fires, wind disturbances play a major role in forest dynamics (Frelich, 2002), but in some forest types, insect outbreaks can even exceed the influence of wind. Large, infrequent disturbances by windstorms and bark beetle outbreaks have been historically reconstructed in the Rocky Mountains of North America (Veblen et al., 1991; Eisenhart and Veblen, 2000; Veblen, 2000; Kulakowski and Veblen, 2003) and in other boreal and temperate forests (Frelich, 2002; Kramer et al., 2001; Berg et al., 2006).

The disturbance regime of the studied forest is different from some other forest types that contain spruce. Spruce is often recognised as a shade-tolerant tree species that can form typically shady, old-growth forest. Examples include *P. rubens* forest in northeastern USA (Fraver and White, 2005b; Fraver et al., 2009), the mixed spruce-fir-beech, lower altitude forest containing *P. abies* in Europe (Splechtna et al., 2005; Motta et al., 2011) and European boreal *P. abies* forests (Shorohova et al., 2009; Kuuluvainen and Aakala, 2011). Gap dynamics are most commonly reported in *P. abies* forests of boreal Fennoscandia (Kuuluvainen and Aakala, 2011). In contrast, *P. abies* in the study region highly dominates the landscape, which is shaped by large, infrequent and severe disturbances. Norway spruce can colonise disturbed sites and dominate even during stand initiation (Fischer et al., 2002; Jonášová and Prach, 2004; Jonášová et al., 2010). The different behaviours between boreal and temperate populations of *P. abies* could be explained only by the different disturbance regime; i.e., different frequency and intensity of windstorms, which also influence the quantity of food available to the bark beetle (Økland and Bjørnstad, 2006). Different climatic and bedrock conditions could also explain some differences among spruce populations (Holeksa et al., 2007).

In mountain Norway spruce forests, trees are unlikely to grow up under a dense canopy because spruce saplings have high light requirements (Holeksa et al., 2007). Our results are consistent with this hypothesis, as most trees experienced the first event in their chronologies at a young age (Svoboda et al., 2012). Regeneration is therefore controlled by disturbances, peaks during disturbance and grows up within the gaps (Holeksa et al., 2007). In such conditions, spruce typically enter the canopy via a single event (Svoboda et al., 2012), unlike spruce in lower altitude forests (Splechtna et al., 2005) or typical shade-tolerant species (Canham, 1990; Wu et al., 1999). Canham (1990) identified several periods of release, which allowed canopy recruitment of *Fagus grandifolia* and *Acer saccharum* in north-eastern USA, attained at an average age of approximately 70 years. Similarly, 72% of *P. rubens* trees underwent episodes of radial growth suppression and release before reaching the forest canopy (Wu et al., 1999). On the other hand, our results resemble the pattern found by Rentch (2003) in oaks, which are typically classified as mid-successional species of intermediate shade tolerance. Sixty-two percent of oak individuals were gap-originated, and the rest were considered to be suppressed before canopy recruitment. Excepting species requirements, the observed pattern can be affected by the disturbance regime of the studied forest. We emphasise that slow growth does not say much about the light conditions separately. Slow growing trees, particularly of mid-tolerant species, can be supported by a small gap or a sparse overhead canopy.

The present study and that of Zielonka et al. (2010) were conducted on wind-exposed sites and identified more release events per individual growth chronology than did Svoboda et al. (2012). In the former two studies, less severe disturbances influenced stands that were relatively even-aged. These releases are less likely due to the loss of older, large overstory trees and more likely due to the death of a same-aged neighbouring (and likely larger) tree. Therefore, two or three events in the chronology are also often on those exposed sites, but no new regeneration reached the canopy, and trees that would otherwise be excluded by self thinning are released.

We observed heterogeneous patterns of growth trends in individual trees, both increasing and decreasing. This heterogeneity may reflect variation among trees in position in the canopy, competition status and reaction to disturbance. We described the diversification in growth rates following the initiation of the stand by severe disturbance. As expected, the most common pattern observed was the modal pattern with a peak during stand initiation; however, other types are also indispensable. The lower proportions of suppressed trees (Types 2, 4 and 5) are likely due to higher mortality relative to other types (Johnson et al., 1994). Our results demonstrate the high plasticity and tolerance of Norway spruce to different light conditions, which can be used to alter the management practices. Our data suggest that Norway spruce can sustain the period of slow growth in lower parts of the canopy and can again greatly accelerate growth upon release even at older ages. Age was uncorrelated with the type of growth following major disturbance and the number of disturbance events (Table 1).

The open conditions occurring during stand initiation lasted approximately 30 years (Fig. 1c). Most trees surviving to the present had above-average growth. During stand initiation, competition is weak and regenerated trees grow faster than surviving older trees, as described by Doležal et al. (2004, 2009). In contrast, even during stand initiation, some trees were suppressed. This observation suggests that, even during this phase, competition may vary spatially, having locally significant effects. Such competition could occur in dense clusters of young trees. After the peak in the decade of the disturbance, the number of newly recruiting trees decreased abruptly (Fig. 1a).

By definition, no regeneration can reach the canopy during the second phase (i.e., the stem-exclusion phase) (Oliver, 1980/1981). This is true for the rest of the study period because no regeneration taller than 1 m was found in our plots (pers. obs.). The stem-exclusion phase may continue: Lilja et al. (2006) found that an even-aged cohort of Norway spruce could dominate a stand for up to 300 years if it is not disrupted by disturbance. The diversification of growth magnitudes occurred during the stem-exclusion phase (Fig. 3). Due to asymmetric competition, the growth of many trees was suppressed by the dominant trees, whose growth rates were roughly average (Doležal et al., 2004, 2009). This general pattern was disrupted by less severe disturbances, which released some of the trees; these released trees then abruptly increased their growth to above-average rates. Disturbances altered stand development, even during the stem-exclusion phase. Large individuals that would dominate the stand were regularly removed. However, this type of low-severity disturbance did not cause regeneration because the moderately tolerant spruce could sustain suppression and filled the released space. Trees that were suppressed during stand initiation (as described above) were now released by less severe disturbances and therefore survived. It could be possibly the interesting explanation of the differences in diameter distributions between wind-exposed and non-exposed sites (Čada and Svoboda, 2011). The lower severity disturbances caused mortality, increased heterogeneity and created deadwood during even the early stages of stand development, a process that could be important for biodiversity.

5. Conclusions, generalisations and management implications

Severe natural disturbances play and have played a fundamental role in mountain Norway spruce forest dynamics in central Europe. We detected intervals between severe disturbances of approximately 15 and 19 decades, as stands matured. Severe windthrows occurred at these intervals in our study area. However, we reconstructed a relatively regular occurrence (mean interval: approximately 35 years) of disturbances of varying severity at the study site. These data are consistent with other studies from central Europe (Zielonka and Malcher, 2009; Zielonka et al., 2010; Panayotov et al., 2011; Svoboda et al., 2012). The sensitivity of the stand likely influences disturbance severity (Frelich, 2002). After windthrows and under suitable climatic conditions, the bark beetle can increase in abundance and attack live mature trees and stands. Under such conditions, the extent of the disturbance can increase greatly (Økland and Bjørnstad, 2006). Our data suggest that bark-beetle induced mortality occurred at the study site during past outbreaks. We therefore contend that stands of these forest types over the age of approximately 150 years are highly susceptible to disturbance, with a low probability of survival to older ages in an undisturbed state (Lausch et al., 2011). Conversely, many species are favoured by conditions created by these types of disturbances (Müller et al., 2008), which have likely occurred naturally for hundreds of years. These conditions, such as openness, increased quantities of dead wood of various types, and ground disruption are legacies of disturbances. The effective management of protected areas, where these species should find space for life, requires an understanding of these properties (Franklin et al., 2002). We also found that some important structures can naturally develop even in the early stages of stand development due to low severity disturbances. Finally, the observed growth patterns could be the impetus for managing forests in a more heterogeneous manner. We confirmed that the Norway spruce is a very plastic species that can grow and produce biomass under various light conditions (i.e., densities) and can also react positively to canopy openings even at older ages.

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Disturbance regime of the mountain Norway spruce forest landscape in the Bohemian Forest, central Europe

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1. Introduction

The decisive influence of disturbances on forest structure and dynamics is widely accepted (e.g. Kimmins, 2004; Johnson and Miyanishi, 2007). The frequency, severity and extent of disturbances affect species composition and the spatial horizontal and vertical distribution of trees (Frelich, 2002). All disturbances occurring in the landscape can be described by the concept of disturbance regime, which contain all kinds of disturbances occurring in all time and spatial scales. Disturbance regimes describe patterns of disturbance over time characterized by the frequency (probability), severity and extent of the disturbances (Frelich, 2002). The importance of disturbances in forest structure and dynamics imply that the description of disturbance regime of the forest landscape is crucial for many purposes. Prevailing disturbance regimes are closely associated with the natural communities, and forest species are dependent or adapted to the specific disturbance regime (Lindenmayer et al., 2006). Even in forests oriented on wood production, managing more closely to the natural disturbance regime is more cost effective from long perspective (Bengtsson et al., 2000). Understanding of natural disturbance regimes is also useful for managing other ecosystem services important for society, such as carbon sequestration, soil and avalanche protection, water and nutrient cycling etc. (Bebi et al., 2001; Dorren et al., 2004).

In areas with wind as a dominant disturbance agent, landscape level studies revealed high heterogeneity of disturbance severities. Wind disturbances are spatially irregularly distributed and influenced also by stand age and structure (Frelich, 2002). Disturbance regimes are usually characterised by often low severity disturbance and less frequent pulses of moderate severity disturbances. Low severity windthrow events that create small-scale canopy gaps are most common, but less frequent moderate severity disturbances are more important drivers of forest structure across the landscape (Frelich and Lorimer, 1991; D'Amato and Orwig, 2008; Fraver et al., 2009; Aakala et al., 2011). For example Fraver et al. (2009) found no evidence of stand replacing disturbance in the old-growth landscape over last 120-280 years with maximum of 55% disturbed canopy area. This kind of disturbance regime favours the dominance of shade tolerant species, which form advance regeneration in the understorey already before the disturbance (Metslaid et al., 2005). However, in other forest types, severe windthrow events may remove up to 100% of trees on areas across tens of hectares (Veblen et al., 2001), which similarly allow for the release of advanced regeneration and following stand often consists mostly of shade tolerant species (Kulakowski and Veblen, 2003). The pulses of moderate severity disturbances are of greater importance, extent and severity in forests dominated by tree species that host insects (e.g. bark beetles or budworms) that may form outbreaks (Fraver et al., 2009). Moreover, bark beetle outbreaks could be triggered by windthrow events (Økland and Bjørnstad, 2006; Temperli et al., 2013). The landscape-level mosaic resulting from these disturbance regimes consists of patches in various stages of structural development, rather than various stages of compositional succession (Fraver et al., 2009).

In central European mountain Norway spruce (*Picea abies*) forests, extensive and severe disturbances occurred recently with wind and bark beetle as the most important disturbance agents (Grodzki et al., 2006; Lausch et al., 2011, 2013). Interestingly a lot of native species react positively on these natural disturbances in Bavarian Forest National park (Müller et al., 2008; Lehnert et al., 2013). Based on this knowledge, Müller et al. (2008) hypothesized that extensive and severe disturbances have been typical for the forest for long time and, therefore, are within the natural range of variability of the central European mountain spruce forest. Later, several historical studies found that extensive and severe disturbances occurred also in the past (Schelhaas et al., 2003; Zielonka and Malcher, 2009; Zielonka et al., 2010; Panayotov et al., 2011; Svoboda et al., 2012; 2014; Čada et al., 2013; Brůna et al., 2013). Zielonka et al. (2010) described the occurrence of a windthrow event 140 years ago on the area of 100 ha, which experienced similar disturbance again in the year 2004. Panayotov et al. (2011) determined that wind was the most important disturbance agent over the last 150 years and evidenced mosaic of patches with high-severity blowdowns ranging from 0.16 to 10 ha. Disturbance regime of mountain Norway spruce forest of Eastern Carpathians has been described as highly heterogeneous, because historical disturbances varied from low to high severity disturbances, including stand replacing disturbances tens of hectares in extent (Svoboda et al., 2014; Trotsiuk et al., submitted). Janda et al. (submitted) in Bohemian Forest and Trotsiuk et al. (submitted) in Ukrainian Carpathians both described complex spatiotemporal pattern of forest dynamics created by a combination of frequent small scale low severity disturbances combined with peaks of disturbances of moderate severity. Disturbances often affected large areas, but its severity was spatially variable and lacked delineable borders of gaps or patches (Svoboda et al., 2012; Janda et al., submitted; Trotsiuk et al., submitted). Brůna et al. (2013) analysed archive information and described extensive landscape scale wind and bark beetle disturbances in late 19th century in Bohemian Forest; they determined that disturbances were mainly associated with the age of previous stand. Despite these observations central European mountain Norway spruce forest out of Carpathians is lacking the description of the landscape scale variability of disturbance regime and also understanding of what influence the disturbance regime of a stand. Existing studies described only limited time and spatial scales, what asks for more research in this field.

Knowledge of natural forest dynamics is of great importance for the management of commercial as well as conserved forests (Kimmins, 2004). In natural forest landscapes with extensive old-growth forests that escaped or experienced little human influence, a more complete understanding of disturbance regimes can be attained (Frelich, 2002). In areas such as highly populated central Europe, where old-growth forests are highly uncommon and natural forest landscapes are lacking, we often have an incomplete understanding of forest dynamics (Splechtna et al., 2005). In addition, much of the remaining old-growth forest occurs on inaccessible or specific locations that are hardly representative of the surrounding landscapes (Angelstam and Kuuluvainen, 2004). In this context, the Bohemian Forest offers a unique opportunity to study natural forest dynamics at a landscape scale in central Europe. The history of this mountain range (see below) has preserved relatively large forest areas with limited human influence (Beneš, 1996). Recent studies indicated that significant portion of the landscape in high elevation was under the control of natural disturbances (Svoboda et al., 2010; Čada and Svoboda, 2011; Svoboda et al., 2012; Brůna et al., 2013; Čada et al., 2013).

The present study focuses on the description of the disturbance regime of the mountain Norway spruce forest of the Bohemian Forest in central Europe. We would like to test Müller’s et al. (2008) hypothesis that extensive and severe disturbances are typical for this forest type. Our specific goals include: 1) reconstruction of the timing, frequency and severity (particularly extent) of past disturbances, and 2) explain differences in disturbance histories based on site conditions. We will use the advantages of dendrochronological methods to reconstruct forest disturbance histories (Lorimer, 1985), and conduct the study at the landscape level to fully evaluate disturbance patterns (Frelich and Lorimer, 1991) in the area, where much of the forest has been controlled by natural disturbances.

2. Methods

2.1. Study area

2.1.1. Location and site conditions

The work was conducted in the mountain Norway spruce forest in the mountain range called Bohemian Forest. The mountain range is situated in central Europe on the border of three countries, Czech Republic, Germany (Bavaria) and Austria, and host two national parks (Šumava National Park and Bavarian Forest National Park). Our study was arranged in Czech part of the mountain range (fig. 1). Nearly monospecific Norway spruce forest grow in the high elevations (>1150 m.a.s.l.) of the mountains; forest is dominated by Norway spruce with minor components of *Sorbus aucuparia* L., *Acer pseudoplatanus* L., *Abies alba* Mill. and *Fagus sylvatica* L. (Neuhäuslová and Moravec, 1998).

Vegetation communities are mostly of two types: *Calamagostio villosae-Piceetum* (with patches dominated by *Calamagrostis villosa*, *Deschampsia flexuosa*, or *Vaccinium myrtillus* on more stony soils) and *Athyrio alpestris-Piceetum* (Neuhäuslová and Moravec, 1998). Geological substrate belongs to the crystalline complex of the Bohemian massive and consists of three main types – mica schists, gneisses and granites (Cháb et al., 2007). Soils are shallow and poor, dominated by podsols and stony soils (Kozák, 2010). Climate is cold with mean annual temperature of about 4°C. Continentality increases from west to east and, therefore, mean annual precipitation decreases from about 1400 mm to 800 mm per year (Tolasz, 2007).

2.1.2. History of the territory

The Bohemian Forest was historically relatively protected from deforestation. Prehistoric and early medieval colonization did not affect the mountain range except small areas along the trade and communication trails. One explanation is that the forest acted as a barrier against Germanic expansion (Beneš, 1996). The Bohemian Forest also escaped the pastoral colonisation, unlike the Alps or Carpathians, likely because it lacks an alpine zone. The colonization of mountain foothills started during the main medieval colonization in the 12th and 13th centuries; this period of colonization did not affect higher altitudes except for trade and communication trails (Beneš, 1996). The last and most extensive period of deforestation peaked in late 18th century (Beneš, 1996) after a period of demographic recovery following the severe loss of population during The Thirty Years' War in 17th century. Most of the villages in the central part of the mountains were founded in the mid-18th century or later with an emphasis on glassworks and ironworks. People often established their houses directly in the forest and then harvested neighbouring forest. They logged a lot of mostly hardwood species, particularly beech, which largely affected the hardwood forest zone below the main ridges (Beneš, 1996). Forests that were difficult to access in higher elevations were used only for cattle grazing and hunting (Macar and Maršík, 2005). The significant interest of main landowners in timber harvesting is dated since the early 19th century with attention also to spruce wood in high elevations (Beneš, 1996; Brůna et al., 2013). That's why they developed detailed forest management maps with forest age structure and species composition in the mid-19th century (Brůna et al., 2013). At that time, more than 39% of the forest stands at elevations above 1150 m.a.s.l. were >120 years old and were mostly described as primary forest (based on database of Brůna et al., 2013); the proportion of primary forest was probably even higher because younger stands could also have originated after severe natural disturbances (Čada and Svoboda, 2011). However, during the period 1868-1870, large scale wind and bark beetle disturbances substantially altered the forest in the study area; two thirds of stands older than 120 years were removed (based on database of Brůna et al., 2013). Most of the wood was likely logged after disturbance (Brůna et al., 2013). Logging activity decreased in the 20th century related to societal changes in the country associated with WWI and WWII, the establishment of Czechoslovakia, displacement of German inhabitants and establishment of inaccessible state border zone. Since the 1980s, most of the old stands in the mountain spruce zone of the Bohemian Forest were broken up by windstorms, bark beetle outbreaks and salvage logging. The break-up culminated by severe windstorm in January 2007 (Lausch et al., 2011; 2013). In neighbouring Bavarian Forest National Park, a total of 5800 ha of Norway spruce stands died off because of bark beetle infestations between 1988 and 2010 (Lausch et al., 2013).

2.2. Data collection

We limited the study area to forest above 1150 m.a.s.l. because it roughly fit the distribution of the community of mountain Norway spruce in the Bohemian Forest. Then we selected old stands that were likely established before 1850 based on historical forestry maps (see above; Brůna et al., 2013; State Archive SOA Plzeň), local literature, aerial photographs and present forestry maps. We also considered stands of unknown ages not listed on the historical forestry maps. We selected seven out of nine localities existed in the Bohemian Forest (fig. 1). One of the two remaining localities had to be removed because the forest was broken up already in 90s and it would be impossible to extract increment cores.

We established 24 plots across the study area in homogeneous and representative stand and site conditions. Plots were limited to stands that had experienced severe disturbance events from 2007 or later to ensure we could get the increment cores from fresh wood. The number of plots per locality varied (range of 1 – 7) proportionally to the extent of the locality. In the smallest locality, Ostrý, where just one plot could be established, we took twice more cores. Plots were 50 meters long transects that varied in width according to stem density to get at least 35 increment cores. All stems thicker than 10 cm at stump height (30 cm above ground) were recorded (i.e., stumps, snags, uprooting and alive trees). Stem thickness at stump height and species were identified for each stem (Čada and Svoboda, 2011). We used also the data published by Čada et al. (2013) from one locality, where three 50x50 meter plots were analysed.

We extracted one increment core from each possible stem on the plot. We also extracted cores from trees near the plot that were deemed to be very old because they are potentially very valuable for disturbance reconstruction. We focused on extracting cores from the side with the most representative growth (in cases with exocentric growth) and not affected by root swellings. Increment cores were air-dried, attached to a wooden mount and cut with a razor blade. Contrast was improved by moistening and impressing with chalk. Ring widths were measured to the nearest 0.01 mm using a sliding table LINTAB and TsapWin software (www.rinntech.com). Each tree-ring series was cross-dated following the procedure of Yamaguchi (1991) and using statistical tests implemented in Past4 (Knibbe, 2007). A few series that did not fit well were excluded from all further analyses. The curvature and mean width of the five tree rings closest to the centre were used to estimate the number of rings missed in cases where the core did not pass through the pith (Duncan, 1989). We did not correct for bias caused by coring height (Niklasson, 2002); therefore, "ages" referred to hereafter are not true ages but recruitment ages at coring height.

2.3. Data analysis

2.3.1 Analysis of disturbance events on growth series

Two types of events on growth series were assumed to indicate past disturbance: 1) release from suppression (abrupt, sustained and large increase in growth) indicated the death of surrounding trees, and 2) gap origin (rapid early growth rate) indicated the existence of a tree in open conditions during its recruitment (Lorimer and Frelich, 1989). Gap-origin trees were defined as those trees whose mean width of the 6-15 ring exceeded 1.0 mm (Splechtna et al., 2005; Firm et al., 2009; Jönsson et al., 2009) and whose subsequent growth pattern was declining, parabolic, or flat (Frelich, 2002).

We used the “absolute increase” method to identify releases from suppression (Fraver and White, 2005; Čada et al., 2013) because it is simple, clear and poses no problems regarding the definition of the upper boundary (Splechtna et al., 2005; Zielonka et al., 2010). Absolute growth changes were calculated for each year of each series (except for the first and last 10 years) by subtracting the prior 10-year mean from the subsequent 10-year mean. A release year was identified by a growth change value that was the maximum of the surrounding 20-year interval (±10 years) and that exceeded the threshold of +0.55 mm (Jönsson et al. 2009). This threshold was specified for the Norway spruce, based on experience with its growth variation (Jönsson et al. 2009). Finally, we visually checked all of the series and their releases. Releases were excluded if the growth acceleration was not obvious. For example, growth restoration after short-term growth reduction or short-term pulses were excluded. Releases were also added in obvious cases. Visual checking is vital in this type of work because growth fluctuations due to environmental variation (climate, injuries, mast year, etc.) have a great effect near the specified threshold. Basically, there is always a trade-off between positive and negative errors. Non-release growth changes are not only related to climate variation, which is usually used to test the criteria (Nowacki and Abrams, 1997; Black and Abrams, 2003), but there is also a large overlap with changes caused by injury, reaction wood and other factors (Fraver and White, 2005; Fraver, pers. comm.; personal observation).

To mitigate the influence of subjectivity, we also defined stricter criteria to detect "intense releases": releases higher in magnitude and longer in duration (15-year means, absolute increase threshold +1.00 mm) than standard releases. They were defined such that a subjective approach was little used.

Disturbance chronologies of ten and one year time steps were used following Lorimer and Frelich (1989) and Frelich (2002). All release and gap-origin events were summarised by decades (resp. individual years) and plotted proportional to sample depth at the end of the decade (resp. in specific calendar year). Chronologies were truncated when sample depth dropped below 10. The resulting chronology, called a "tree-population-based" chronology by Frelich (2002), shows the proportion of the population affected by a disturbance within a given decade. The effect of an individual tree is not weighted by its size. The calculated proportion does not fully correspond to the affected area, because of the different areas occupied by individual trees. However, we believe that this method poses no problems for interpretation because the tree layer in our study site was mostly uniform, lacking any cohort of small trees (Čada and Svoboda, 2011). We calculated the average disturbance chronology from individual plot chronologies for each locality and the entire mountain range. Peaks in disturbance chronologies of one year time step were used for calculation of disturbance frequencies and severities. The individual disturbance was defined as a peak in 10-year running sum if it exceeds proportion of 0.1 (resp. 0.5 for severe disturbances). Similar analyses were done for testing the synchronicity of disturbances over the mountain range. To evaluate synchronization between plots, only part of the chronology based on releases from suppression were used because the time dispersion of releases is substantially lower compared to gap origin events (Čada and Svoboda, 2011). Based on the obtained severities and frequencies of disturbances on individual plots, we calculated the rotation period for disturbances of different severity classes following the method of Frelich and Lorimer (1991). Rotation period refers to the average time interval between disturbances of similar severity in a given stand, and also to the time it would take on average for all plots in the mountain range to experience a given disturbance rate (Frelich and Lorimer, 1991).

We attempted to explain the reconstructed disturbances using historical evidence of windthrows and bark beetle outbreaks based on archived documents within the region, i.e. from nearby villages or forests mostly in lower elevations. We summarised data published in works of Zatloukal (1998), Brázdil et al. (2004) and Jelínek (2005).

Multivatiate Ripley's K-function for one-dimensional data was used to test synchronisation of reconstructed disturbances and historical records (Gavin et al., 2006; Bigler et al., 2007; Gavin, 2010). This method was simplified for one-dimensional data from widely used method of spatial point pattern analysis. In our work, we tested the association (coincidence) between two time-series of events. We used the forward selection method expecting the delay of tree responses (disturbance reconstructions) after real events. The K-function was transformed to L-function and Monte Carlo simulations were used to evaluate statistical significance (Gavin, 2010).

2.3.1 Statistical analyses

Decadal scale disturbance chronologies for each plot were grouped using cluster analysis. The disturbance severity of each decade represented one variable. We used the average linkage method of Euclidean distances. Based on the resulting dendrograms, three groups of disturbance histories were distinguished. Mantel test were performed to answer the question if Euclidean distances between disturbance histories of plots are related to its geographical distances. All analyses were done using the statistical software R (version 2.10.1, R Development Core Team, 2009) and the Mantel test was performed in the package „ade4“ (Dray and Dufour, 2007).

Nonparametric statistical tests (Spearman's correlation coefficient, r; Kruskal-Wallis ANOVA, H) were used to explore the differences in disturbance histories between plots. As dependent variables we used the frequency of disturbances, severe disturbances and disturbances in 20th century, and maximal and average severity of disturbances. Environmental variables such as longitude, latitude, altitude, aspect, slope, slope position, locality, vegetation community and geological substrate were used as independent variables. Geographical data were obtained from global positioning systems measurements and a 30 meter digital elevation model. Aspect was transformed by cosine transformation. The rest of environmental data were obtained mostly using published maps corrected by visual assessment in the field (Neuhäuslová and Moravec, 1998; Cháb et al., 2007; Kozák, 2010). Slope position was described based on the altitudinal distance of the plot from closest ridge. Based on the low variability of temperatures across the study area and close relationship of precipitations to longitude, we did not use climatological data because sufficiently high resolution data was unavailable.

3. Results

Norway spruce represented 99.9% (98.9 – 100%) of all individuals measured in the study area. Relatively high variation was found in the case of tree densities. Average density of live trees before actual disturbance was 345 (148 – 608) trees per hectare. The density of all stems was 593 (296 – 1028) per hectare. Average basal area of live trees before actual disturbance was 55 (34 – 96) m^2/ha. Together all stems averaged at 74 (57 – 117) m^2/ha.

Age distribution of trees on individual plots show rather homogeneous even-aged pattern, which already indicate the occurrence of severe disturbance. On average, 70% of trees on plots recruited to coring height in relatively short period of 30 years. On the other hand, mean range of ages was 141 years. Most trees recruited to coring height in the period of 1750 – 1880. Trees older than 1750 reached the proportion of 3.5%. Between 1750 – 1800, 17.3% of all trees were recruited; in the period of 1800 – 1880, 74.4% were recruited, and only 4.8% of trees were recruited after 1880 (fig. 2).

Disturbance chronologies indicated each plot experienced at least one severe disturbance (1-3). Time since the most severe disturbance varied from 133 to 261 year (on average 177 years). Maximal severity was on average 79% of removed population with a range of 50 – 100%. Frequency of all disturbances (severity > 10%) was 29 years (range of 20 – 47 years). Fig. 2 shows the proportion of population affected each decade by disturbance on each location and together across the mountain range. Serious disturbances occurred in the period of 1780 – 1880. Forest stands of our study area were established mostly in this period after severe disturbances. In the decade after 1820, extensive disturbance removed more than half of the population in the entire study area. This decade was the most severe at all localities (there is no data at one locality) suggesting that this disturbance occurred across the whole region. The severity and extent of disturbances varied between localities. More extensive localities (such as Jezerní or Polom) recorded broader range of disturbance histories than less extensive localities (such as Ostrý, Boubín and Můstek).

Disturbances were generally synchronized between plots and locations. Yearly disturbance chronologies were in most cases significantly correlated to each other. Mean correlation between disturbance chronologies was 0.21 (range of -0.07 – 0.57). Sixty-eight percent of correlations (188 out of 276) were significant at the level of 0.05. Fig. 3 shows the synchronisation of growth releases on two levels – individual trees (fig. 3a) and plots (fig. 3b). We can see that disturbances are widely indicated in periods of 1779 - 81, 1797 - 1801, 1807 - 1808, 1813, 1820 – 1826, 1838 – 1840, 1856 – 1857, 1869 – 1880, 1920 – 1925, 1960 – 1961 and 1992 – 1993. Those years could be at least partly explained by evidenced windstorms and bark beetle outbreaks (natural disturbances) that occurred in the wider region - windstorms in 1778, 1801, 1812 – 1813, 1818, 1821 – 1822, windstorms and bark beetles in 1833 – 1840, windstorms in 1853, windstorms and bark beetles in 1868 – 1877, windstorms in 1921 – 1922, 1955 – 1960. The last peak is likely related to the present wave of disturbances, which started in the early 1980s, and would peak decade after the end of the chronology. One-dimensional L-function demonstrated significant ($p < 0.05$) synchronisation (coincidence) between historical windstorm records and peaks on tree-level chronologies. In the first decade after historical records it reached the value of 3.90, which exceeds the simulated upper 95% confidence envelope (3.73). Peaks on plot-level chronologies were not significantly associated to historical records.

Disturbance frequencies and severities are summarized into rotation periods of disturbances of varied severity (fig. 4). This defines the mean interval between disturbances of a given severity on a given place required to disturb an area of a given size. Equally, it defines the mean time required for the whole landscape to be affected by a disturbance of a given severity. The figure tells us that 5% of trees are on average removed every 20 years. Every century there is a disturbance that removes 30% of trees. This effect is spatially inhomogeneous and, therefore, this kind of disturbance occurred on some places every 34 years and on some places every 200 years. High severity disturbances that remove more than 70% of trees occur every 263 years (100 – 500 years). The computed rotation periods become increasingly uncertain beyond the severity class of 70% due to lacking of this disturbance on some plots. On some plots we simply did not reconstructed disturbance of highest severities and therefore we cannot calculate its rotation period.

Cluster analysis of disturbance histories revealed three main types of disturbance histories at the plot level (fig. 5). First group contained 2 plots, second group had 7 plots and third group contained 15 plots. Mean disturbance chronologies for each group (fig. 5b) showed that the severity of disturbances decreases from first to third group (from left to right in fig. 5a). First group experienced high severity disturbances in period 1810 - 1850. On the other hand, in second group severe disturbances occurred in earlier period before 1830. Third group experienced the greatest heterogeneity of disturbance timings and severities, which resulted in broad disturbance chronology with severe disturbances occurring in similar period to whole dataset. Geographical distances did not explain differences in Euclidean distances of disturbance histories (Mantel $r = -0.09$, $p = 0.87$). However on fig. 1 we can see that first group is located in two most northern plots and two southernmost localities consist only of plots classified into group 3. Nevertheless, generally we can say (also based on fig. 2 and 3), that there is no big difference in disturbance histories between localities and that the variability of disturbance histories in larger localities (such as Jezerní, Polom and Plechý) is comparable to the variability in whole mountain range and disturbances are synchronised across the mountain range.

On the other hand, the effect of geographical location on frequency of severe plot-level disturbances was significant (tab. 1). This is related to the observation that most plots in two southernmost (and also easternmost) localities experienced during its establishment more than one severe disturbance. Some differences between localities suggest also its significant effect on maximum severity of disturbances. Altitude and aspect were important predictors of frequency of all disturbances suggesting higher frequency of disturbances in exposed higher altitudes and south-western expositions (tab. 1). Distance of plot from ridge (slope position) was significantly correlated to time since maximum severity disturbance. This interval increases with distance from exposed sites at ridges towards more protected sites farther away from ridges. Significant effect of geological substrate on frequency of severe disturbances is likely related to the differences between localities. Most significant relationships were found for frequency of disturbances; poor relationships existed for disturbance severities.

4. Discussion

4.1 Disturbance history

The disturbance history of mountain Norway spruce forest landscape in Bohemian Forest was highly influenced by severe disturbances (>50% of removed population) that occurred in the history of all plots. Therefore, we confirmed the hypothesis of Müller et al. (2008) that extensive and severe disturbances are typical for this forest type. The regeneration of presently disturbed stands was associated with severe disturbance periods that peaked 133 – 261 years ago. Some stands regenerated likely after one severe disturbance event, but some after few subsequent disturbance events that occurred in relatively short interval. Both dynamics resulted in the replacement of most of the mature trees. These results are partly different from more heterogeneous disturbance histories found in Romanian and Ucrainian Carpathians (Svoboda et al., 2014; Trotsiuk et al., submitted) that showed bigger heterogeneity in disturbance histories including stands affected by low severity disturbances only. However, the results are in accordance with previous studies from Bohemian Forests (Čada and Svoboda, 2011; Svoboda et al., 2012; Čada et al., 2013) and also from wind exposed sites of Tatra Mts. in Slovakia (Zielonka and Malcher, 2009; Zielonka et al., 2010).

Low severity disturbances affected following development of studied stands. Those disturbances occurred frequently but mostly did not stimulated regeneration of new trees. Rotation period of low severity disturbances (10% mortality) was calculated to 29 years. This value is very similar to 29 years period estimated by Fraver et al. (2009) for mixed forest of northern Maine (USA), but lower than 69 years period estimated by Frelich and Lorimer (1991) for hemlock-hardwood forests of Porcupine Mts. in Michigan (USA). Much bigger difference exists in case of severe disturbances (>50% mortality), in which rotation periods were estimated by both Fraver et al. (2009) and Frelich and Lorimer (1991) for more than 1000 years. Our analysis found the rotation period of severe disturbances for 163 years. This value is comparable to rotation period in the area exposed to frequent hurricanes in northeastern USA (Lorimer and White, 2003). One reason for high frequency of severe disturbances in our forest type is likely the influence of specific agent, spruce bark beetle, which likely increase severity of disturbances, particularly after windthrows (Økland and Bjørnstad, 2006; Fraver et al., 2009; Temperli et al., 2013). Second reason could be the location of our study area in high elevation and rather sub-Atlantic conditions, which are affected by more frequent and more intensive windstorms in European perspective (Schelhaas et al., 2003). Landscapes studied by Svoboda et al. (2014) and Trotsiuk et al. (submitted) are located rather out of the sub-Atlantic zone.

Reconstructed disturbances were synchronized across the study area. Most of the disturbances affected big portion of the landscape (indicated on at least half plots). However, the severity of disturbances was spatially heterogeneous. From the perspective of individual locality, this means that one disturbance event could be stand replacing on one plot but low severity on second plot. This is the reason for relatively broad average age structure and disturbance histories at locality and landscape level. The most likely cause of the variability in disturbance severities is the structure and age of the previous stand. This idea is supported by study of Brůna et al. (2013), who found in the same landscape that stand age is the most important predictor of disturbance. The results show that in most cases trees beginning to grow after severe disturbance did no encounter competition from surrounding, undisturbed trees (Oliver, 1980/1981), what suggests its stand replacing effect and extent at least in scale of hectares. There are also cases of neighbouring plots that share similar severe disturbances. If we assume rather homogeneous forest structure between neighbouring plots, it would mean that the patches of severe disturbances could extended to tens of hectares. Our findings are supported by historical forestry maps analysed by Brůna et al. (2013), who showed similar extent of patches affected by disturbance. Similar extent of disturbed patches emerged also from other studies (Zielonka et al., 2010; Panayotov et al., 2011; Svoboda et al., 2012; Svoboda et al., 2014).

Reconstructed disturbances were significantly coincident to historically known windstorms. The disturbances were also synchronised between plots and localities. Those results indicate that primary disturbance agent in our study area was wind and that studied forest was in large extent driven by natural dynamics. Our data support also the occurrence of bark beetle induced mortality in periods of known bark beetle outbreaks, particularly late 19th century (Brůna et al., 2013). The linkage between bark beetle disturbances and previous windthrows is well known (Økland and Bjørnstad, 2006; Temperli et al., 2013) and prevents exact separation of those disturbance agents. We cannot fully exclude anthropogenic impact on forest. It was likely used for cattle grazing and hunting (Macar and Maršík, 2005). Moreover, some selection cutting or harvesting of died trees could be done in the study area. In individual cases, we cannot exclude even more extensive harvesting, which would co-occur with historical windstorm.

In the history of studied forest landscape, there were fundamental changes in disturbance activity. Disturbance chronologies peaked in 1820s at all localities and the severity of disturbances generally decreased to the past and to the present. Twentieth century lacked any severe disturbance in our study area. This could be partly caused by our methodology and stand selection. However, our study plots mostly represent continuous localities without any patches of younger trees, which would be largely avoided. Therefore, other explanation is needed to fully uncover the causes of the change. The decrease of disturbance severities could be caused both by natural variability, and/or by anthropogenic activity. Forest can naturally develop roughly every two centuries into forest structure sensitive to severe disturbances (Turner, 2010). Our knowledge about forest structure before the period of disturbances in early 18th century is limited, which makes the testing of this hypothesis difficult. The intensity and frequency of windstorms or other factors can change in time and, therefore, cause changes in disturbance regime of the landscape (Brázdil et al., 2004; Pederson et al., 2014). Anthropogenic activity could also alter forest dynamics. Forest management in 20th century was focusing on suppression of natural disturbances, particularly bark beetle outbreaks (Zatloukal, 1998). Lack of severe disturbances in 20th century is likely one of the main causes of recent extensive disturbances in the landscape (Lausch et al., 2011; 2013), because most stands developed into ages that are sensitive both to wind and bark beetle disturbance (Seidl et al., 2011). Based on our observation, recent severe disturbance period was at least shorter compared to reconstructed severe disturbance period. Historical period lasted about one century (1780 – 1880); however, recent period lasted three decades (1980 – 2010).

4.2 Effect of site conditions

Site conditions had significant effect on disturbance history. Generally, we found that disturbance frequencies, rather than disturbance severities were related to site conditions. We hypothesise that disturbance severities are dominantly related to stand structure and, therefore, its potential relationships with site conditions are hidden (Brůna et al, 2013). Other explanation could be limitations of our methodology for accurate estimations of disturbance severities. Sample size, climate, injuries and other factors can influence the exact estimation (Lorimer and Frelich, 1989; Fraver and White, 2005). On the other hand, disturbance frequency can be estimated relatively precisely using sufficient sample size. The results further support our statement about the primary role of wind disturbances. Site conditions (altitude, aspect, slope position) that were important for disturbance frequencies are related to exposition of site to wind (Schelhaas et al., 2003; Brázdil et al., 2004). Wind in the region comes mostly from west. Its intensity is, therefore, higher on western expositions and in higher altitudes and decreases with increasing distance from ridges (Schelhaas et al., 2003; Brázdil et al., 2004). It is known that frequency and severity of wind disturbances are related to topography (Frelich, 2002). Our results are one of the first that proved the effect of topography on real disturbance histories. Stands in more protected conditions could grow into higher ages and were affected by less frequent low severity disturbances.

Geographical distances did not strongly explained differences in disturbance histories. This supports the statement about synchronisation of disturbances between localities. Localities (especially the larger ones) recorded comparable range of historical disturbances as recorded whole landscape. Further statistical test, however, indicated some geographical differences in disturbance histories. Cluster analysis suggests the occurrence of first group only on two northernmost plots and two southernmost localities consist only of plots from third group. Stands in two southernmost localities were mostly established after more than one severe disturbance. This partially indicate gradient of increasing disturbance severity from south-east to north-west.

5. Conclusion

High-severity disturbances, defined as the indication of dieback of at least half of tree population in a given period, were identified in the history of all stands. This finding indicates that stands that were severely broken-up recently were established after similar disturbances in the past. The most severe disturbance periods occurred 130 – 230 years ago during the period of 1780 – 1880. The most extensive disturbance occurred around the year 1820 and affected more than half of the study area. The disturbances were synchronized across whole mountain range. Most disturbances were explained by known historical windstorms and bark beetle outbreaks. We conclude that disturbances, including large, high-severity and low-frequency disturbances, contribute to the broad range of variability of central European mountain spruce forests. Sustainable management strategies should therefore incorporate disturbances of various severities and their biological legacies, as many species likely depend on them. In addition, the development trajectory of stands following stand-replacing disturbance, as described here, can be used to predict future development of recently disturbed stands.

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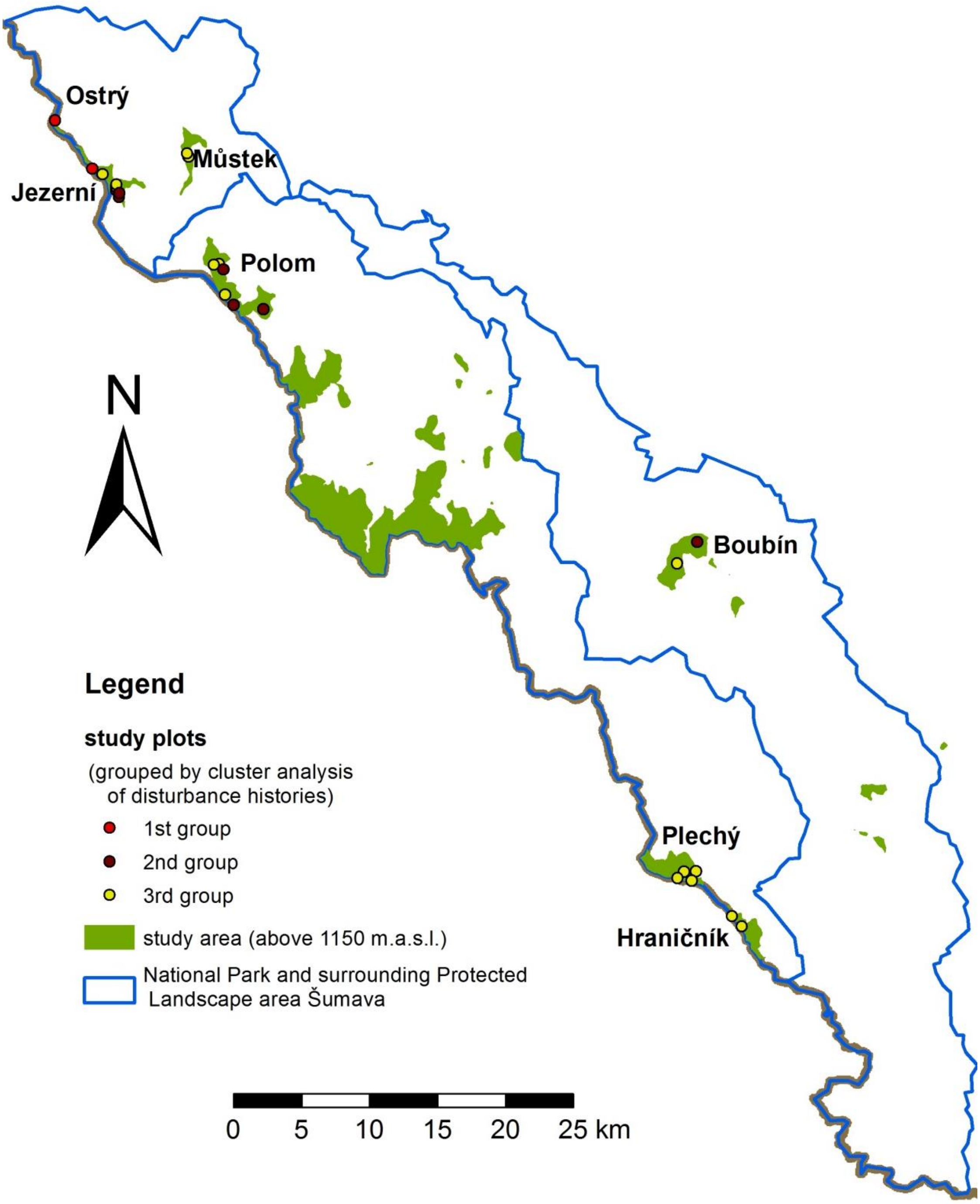

Fig. 1: Location of the study area within the National Park and Protected Landscape Area Šumava in the Czech portion of the Bohemian Forest. The contour of 1150 m. a. s. l. roughly delineates the study area and individual localities. Two central localities of mountain Norway spruce forest could not be used because it was assessed as being younger than 1870. One of those was mostly disturbed in 1990th which prevent extraction of cores due to decay. For more details see methods.

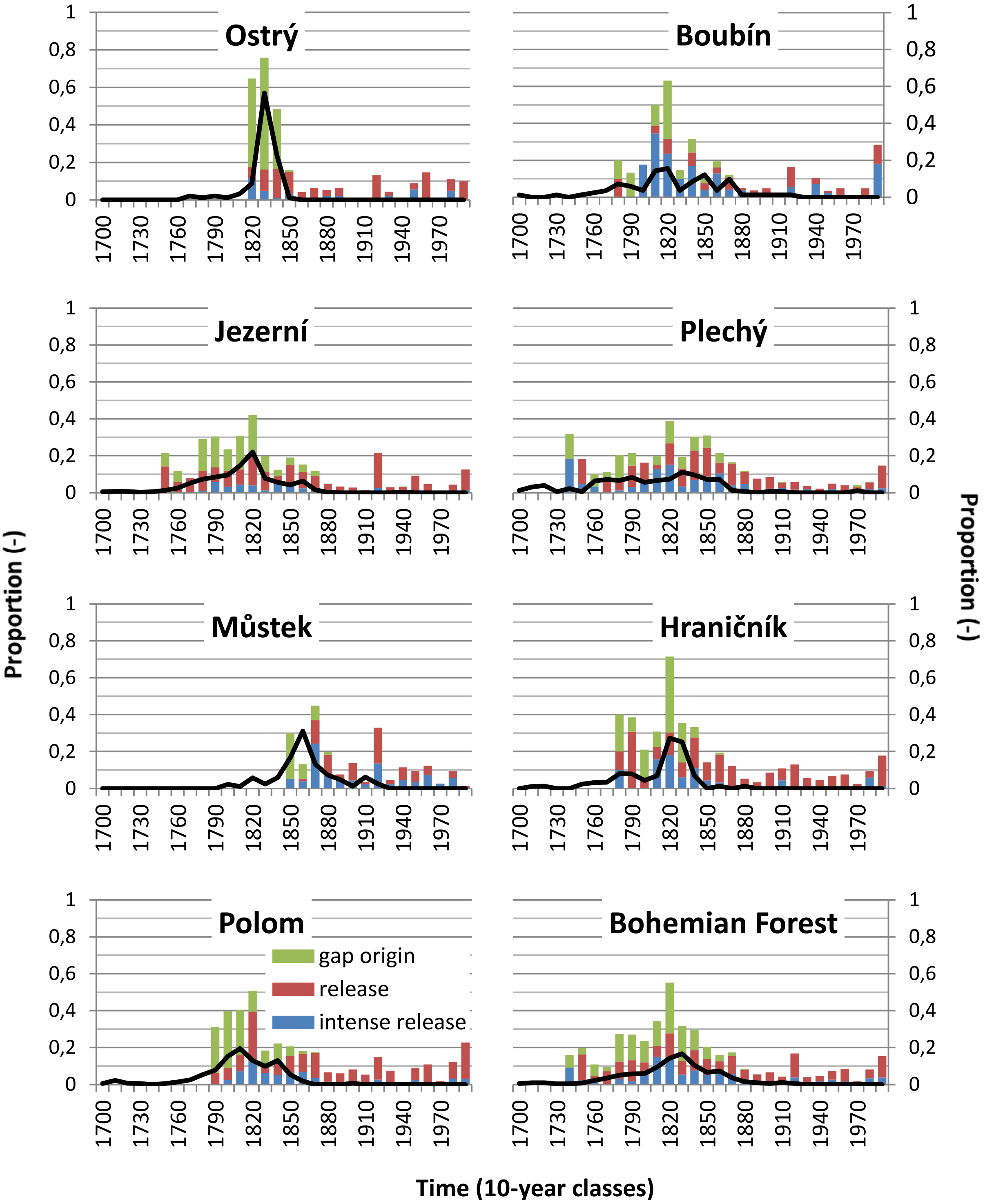

Fig. 2: Average disturbance chronologies and mean age distributions for each locality and for whole study area. The average was calculated from individual plot chronologies. At plot level, events on growth series (intense release, release and gap origin) that are indicative of past disturbances were plotted proportionally to sample depth at the end of each decade. Chronologies were truncated when the sample depth dropped below 10. Peaks above the proportion of 0.1 indicate significant disturbance in that decade. The height of the column indicates the severity of the disturbance (proportion of removed population).

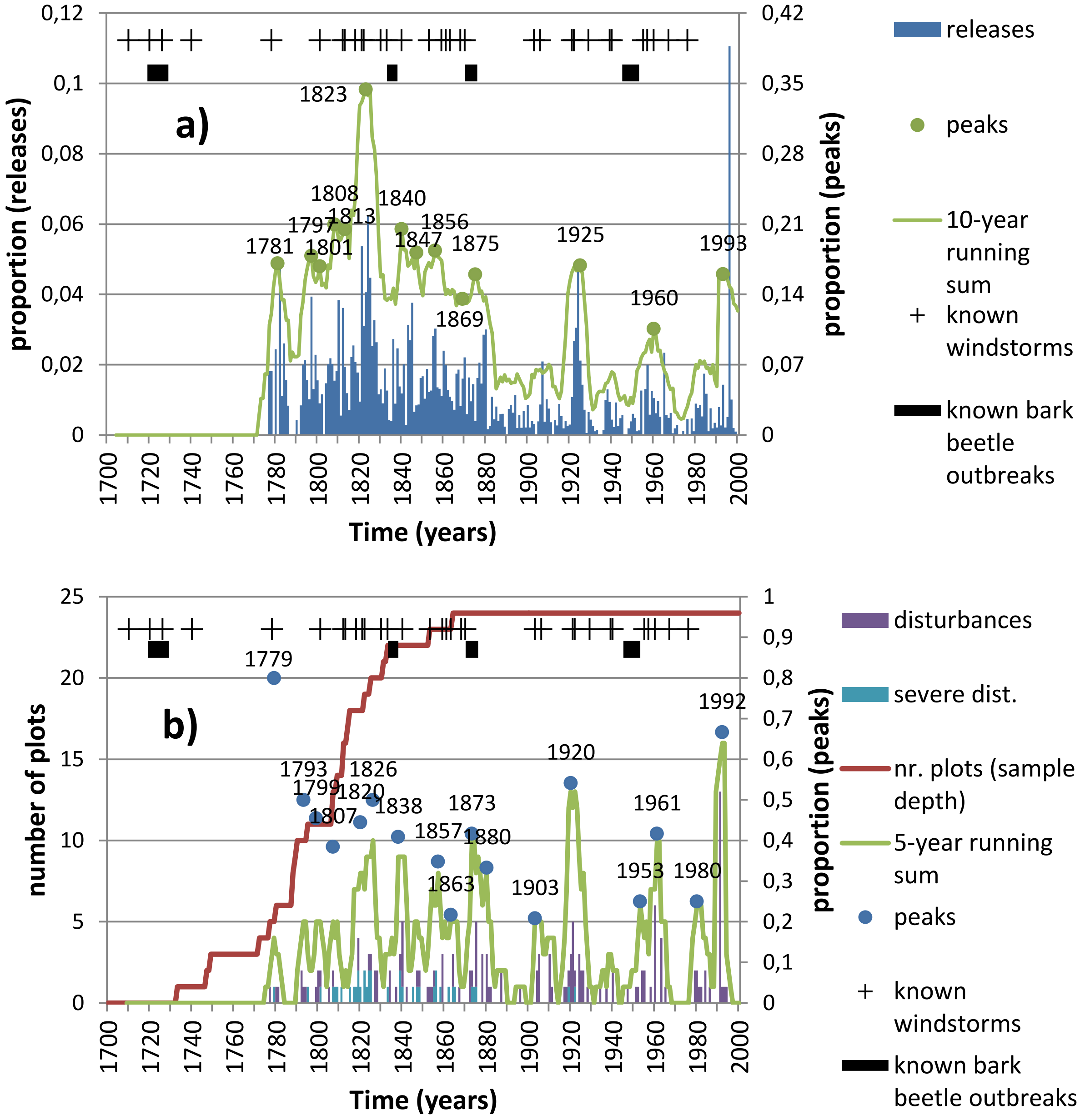

Fig. 3: a) Mean disturbance chronologies (based only on growth releases) in yearly resolution showing the synchronisation of disturbances at the level of individual trees. b) Summarisation of peaks in same disturbance chronologies at the plot level. Peaks in 10-year running sum were plotted in yearly resolution. Peaks higher than 0.5 were defined as severe disturbances and peaks higher than 0.1 as ordinary disturbances. Those were grouped by 5-year running sum and peaks (blue dots) were calculated proportionally to sample depth (number of plots). This shows for example that in the 5-year period around the year 1779 80% of plots (4 out of 5 plots) available in the period were disturbed. Most of the subsequent disturbances are indicated on approximately one half of the study plots.

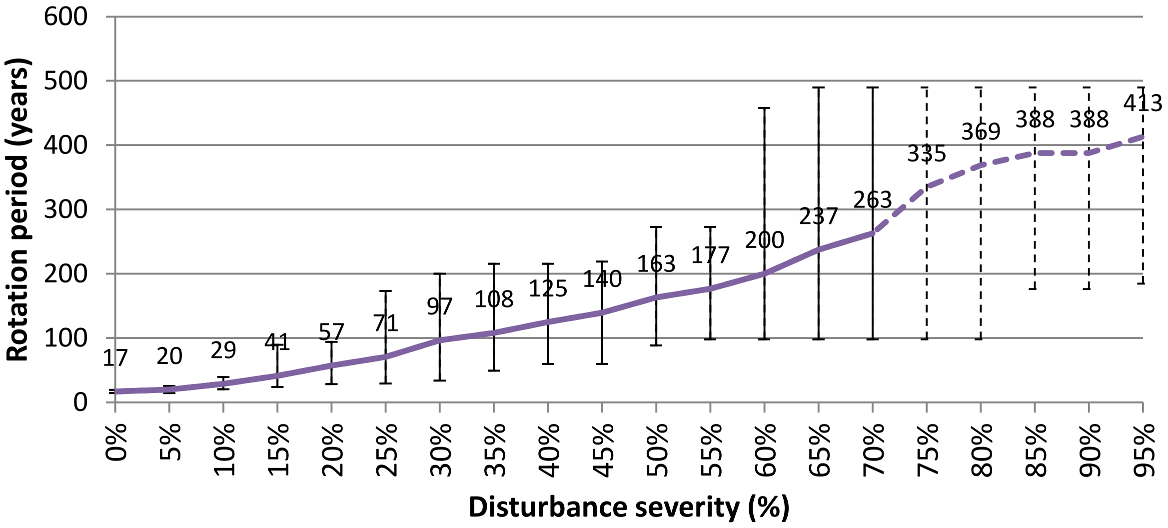

Fig. 4: Rotation period of disturbances of different severity classes (percentage of removed population), which is based on peaks in disturbance chronologies with one year resolution. It is based on frequencies of specific disturbances in the history of plots. The graph becomes increasingly uncertain beyond the severity class of 70% due to lacking of this disturbance types on some plots. The graph simply shows that for example every 100 years there will be a disturbance that remove 25 – 50% of population (average 32%) or that 70% of the population will be removed every 100-500 year (263 years on average).

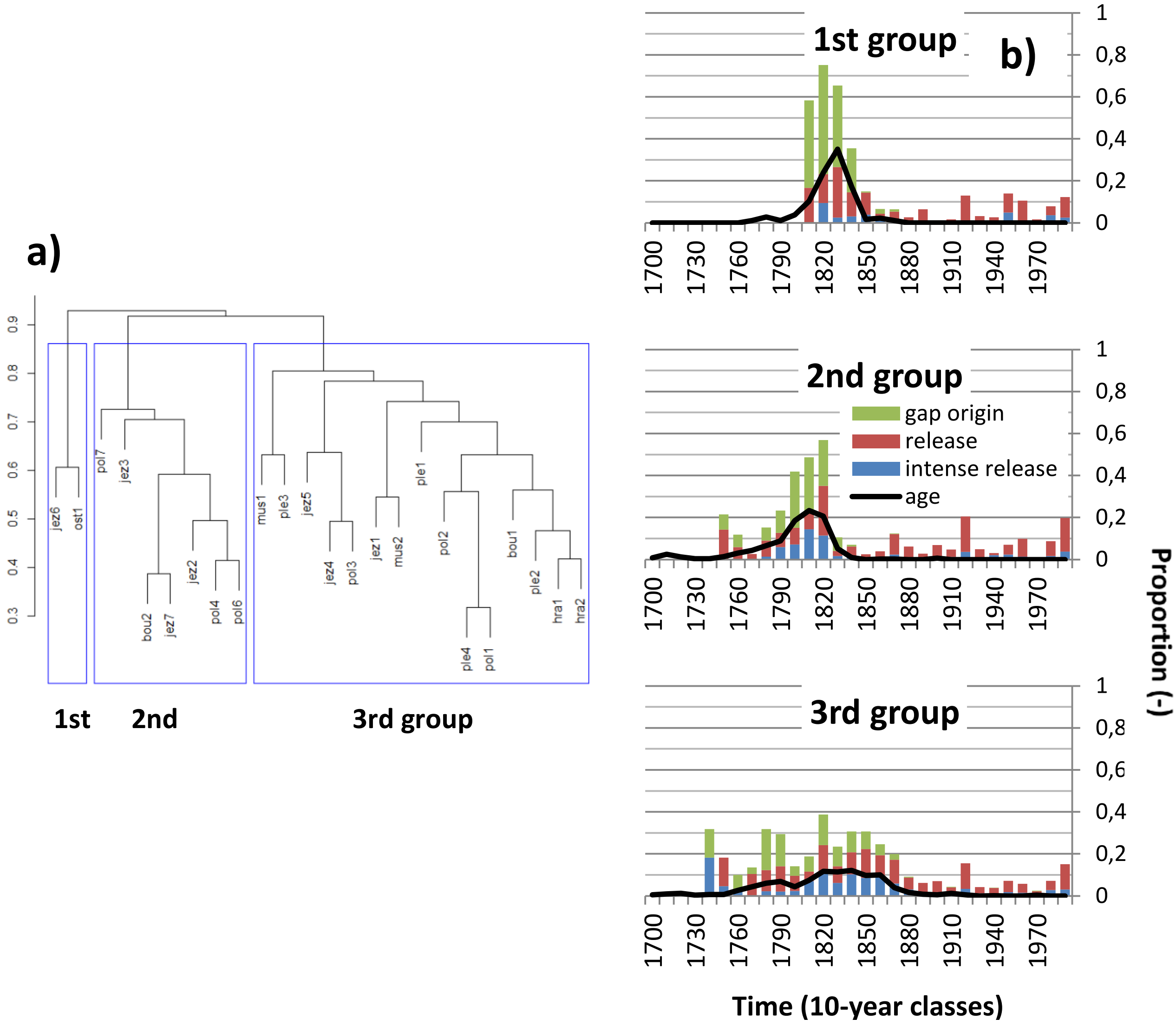

Fig. 5: a) Dendrogram resulting from cluster analysis of decadal scale disturbance chronologies at plot level. This distinguished three groups of plots with different disturbance histories. Three letters in plot names refer to the locality (first three letters of the locality name). Euclidean distances between plots were not significantly related to its geographical distances (Mantel test, -0.09, p = 0.87). b) Average disturbance chronologies (similar to fig. 2) for three obtained groups.

Tab. 1: Spearman nonparametric correlations (r) and Kruskal-Wallis nonparametric ANOVA between characteristics of disturbance regime at plot level and environmental variables. Significant correlations are written in bold and dark ($p < 0.01$) and light ($p < 0.05$) shaded.

	frequency of disturbances	**frequency of disturbances in 20th century**	**frequency of severe disturbances**	**time since maximum severity disturbance**	**average severity**	**maximum severity**
	Spearman correlation (r)					
longitude	-0,31	-0,14	**-0,52**	0,09	0,06	-0,06
latitude	0,16	-0,01	**0,48**	-0,23	-0,19	-0,06
altitude	**0,44**	**0,61**	-0,02	0,06	0,37	-0,13
aspect	-0,40	**-0,44**	-0,04	0,31	-0,07	0,19
slope	0,27	0,23	-0,22	-0,01	0,16	0,09
slope position	-0,15	-0,30	0,06	**0,54**	0,01	0,22
	Kruskal-Wallis ANOVA (H)					
locality	10,40	11,91	9,93	5,72	7,46	**13,07**
vegetation	1,83	0,88	0,37	0,19	4,95	0,05
substrate	1,76	1,42	**9,03**	0,49	1,52	4,26

6. Shrnutí výsledků

6.1 Čada, V., Svoboda, M., 2011. Structure and origin of mountain Norway spruce in the Bohemian Forest. J. For. Sci. 57, 523–535.

V rámci prvního výsledku byly analyzovány tři lokality v CHKO Šumava (Jezerní hora, Můstek a Boubín). Zdejší porosty měly před aktuální disturbancí relativně homogenní strukturu. Tloušťky dosáhly modálního rozdělení s vrcholem ve třídě 45 – 50 cm na lokalitách Můstek a Boubín a 35 – 45 cm na Jezerní hoře. Tendence k levostranné asymetrii rozdělení byla vyšší u věkově heterogennějších porostů. Je známo, že relativně heterogenní tloušťkovou strukturu mají zejména porosty, kde během posledních desetiletí stromy dorůstaly do korunové klenby, což je případ dvouvrstevných porostů, obnovujících se porostů a porostů v raných stádiích sukcese. To zjevně nebyl případ studovaných porostů, kde nejpozději od dekády 1920 žádná obnova nemohla dorůstat do porostní klenby. Zdá se, že to je pravděpodobná příčina visuální homogenity těchto porostů. Podle distribuce tříd rozkladu dřeva bylo usuzováno na nedávnou dynamiku porostů, neboť dynamika mrtvého dřeva následuje dynamiku stromového patra. Malé množství mrtvého dřeva ve vyšších stádiích rozkladu bylo nalezeno v porostech na Můstku a Boubíně, což indikuje to, že k rozpadu porostu došlo poměrně náhle zejména jednorázovým působením vichřice v lednu 2007. Na druhou stranu vyšší zastoupení vyšších stádií rozkladu na Jezerní hoře indikuje to, že k rozpadu zdejšího porostu došlo během delší doby (asi dvaceti let), což kulminovalo vichřicí.

Způsob vzniku porostů ukázal spíše podobný charakter současnému stavu. Hlavní populační vlny byly relativně stejnověké a vznikaly během 2 – 3 dekád. Podíl starších stromů byl různý a závisel zřejmě na charakteru předchozího porostu. Na čtyřech (z celkových šesti) plochách bylo nalezeno pouze několik stromů, které byly v době vzniku porostu starší než deset let, což odpovídá současné zkušenosti. Také v současnosti v podrostu často existovalo pouze relativně malé množství obnovy větší než 0,5 metru a po disturbanci odrůstali zejména malí jedinci, kteří se mohli uchytit těsně před disturbancí, během disturbance, nebo krátce po ní. Vrcholy ve věkové struktuře na studijních plochách se vyskytovaly ve stejné době jako uvolnění z kompetice u starších stromů. K obojímu došlo během relativně krátké doby, což znamená, že porosty vznikaly po silných narušeních, která odstranila většinu předchozího porostu. Podobně jako v současnosti, část ploch pravděpodobně vznikala po několika blízkých událostech, které způsobily, že se předchozí porost rozpadal postupně.

Letokruhová data samostatně neposkytují dostatečné informace pro odhalení faktoru, který způsobil popsaná narušení. Nicméně bylo zjištěno, že narušení byla vysoce (v měřítku let) synchronizovaná mezi plochami a lokalitami na Šumavě, a většina z nich byla vysvětlitelná historicky známými vichřicemi, případně lýkožroutovými gradacemi, což napovídá o vysokém podílu silných přirozených narušení v minulosti zkoumaných porostů. Takováto narušení vedou přirozeně ke vzniku strukturně relativně homogenně vyhlížejících porostů, což ovšem není znakem jejich umělého původu.

6.2 Čada, V., Svoboda, M., Janda, P., 2013. Dendrochronological reconstruction of the disturbance history and past development of the mountain Norway spruce in the Bohemian Forest, central Europe. For. Ecol. Manage. 295, 59–68.

V rámci druhého výsledku byly podrobně analyzovány tři 0,25 ha studijní plochy na lokalitě Jezerní hora. Na všech plochách dominovala jedna populační vlna, která vznikla po silném narušení v minulosti (na dvou plochách s vrcholem v dekádě 1820 a na jedné v dekádě 1860). Během periody silných narušení 82 – 94% existujících stromů indikovalo narušení na svých přírůstových sériích (uvolnění z kompetice, příp. rychlý počáteční přírůst). Průměrný přírůst na všech plochách byl nadprůměrný během období, kdy porosty vznikaly. Období iniciace porostu trvalo na základě intenzity přírůstu 26, 33 a 79 let. Před tímto obdobím byl přírůst stromů podprůměrný s náhlým a razantním zvýšením během narušení a s následným postupným snižováním na průměrnou úroveň. Disturbance v dekádě 1820 na ploše 2 pravděpodobně odstranila až 100% dospělých stromů. Narušení na ploše 1 neodstranila všechny dospělé stromy, ale vývojové trendy byly jinak obdobné, což indikuje podobně otevřené podmínky po narušení. Na ploše 3 existovala před disturbancí početná vyspělá obnova, ale síla narušení byla opět srovnatelná. Na základě věku stromů můžeme rozlišit tři skupiny podle jejich vztahu k narušení: 1) stromy, které dosáhly výšky odběru vzorku více než deset let před narušením a zaznamenaly během narušení uvolnění z kompetice; 2) stromy, které dorostly krátce před či po disturbanci (±10 let) a posléze rostly intenzivně a 3) stromy, které také dorostly krátce před či po disturbanci, ale byly posléze potlačeny, rostly pomalu a první uvolnění zaznamenaly po několika desetiletích během slabšího narušení. Většina stromů na plochách spadala z tohoto pohledu do druhé kategorie. 65% stromů zaznamenalo první událost indikující narušení před dosažením věku 12 let. To potvrzuje hypotézu o tom, že stromy v horských smrčinách mohou obtížně odrůstat v zastínění pod porostem, neboť mají vyšší požadavky na světlo. Obnova lesa je proto vázána na narušení horního stromového patra, vrcholí během disturbance a odrůstá v porostních mezerách.

Následný vývoj porostu po silném narušení byl ovlivňován kompetičními vztahy stromů, a také slabšími narušeními, které se v porostu vyskytovaly. Interval mezi těmito narušeními byl v průměru 35 let. Většina stromů na svých přírůstových chronologiích indikovala 1-3 události narušení. Na základě shlukové analýzy růstových trendů stromů bylo interpretováno pět typů chování smrku po silném narušení (obr. 2). Zásadními faktory pro rozlišení jednotlivých skupin byla intenzita růstu jednak během iniciace porostu a jednak během následujícího vývoje porostu. Nejčastější (zhruba polovina) byla skupina stromů, které rostly intenzivně během iniciace porostu s následným snížením intenzity růstu na průměrnou úroveň. Zhruba čtvrtinu stromů představovala skupina s intenzivním růstem během iniciace porostu a podprůměrným růstem během následujícího vývoje, zřejmě vlivem potlačení. Třetí skupina stromů rostla intenzivně jak během iniciace porostu, tak posléze během následného vývoje, což bylo zřejmě způsobeno uvolněním během slabších narušení. Čtvrtá skupina stromů rostla pomalu během iniciace porostu a začala intenzivně odrůstat až později po uvolnění během slabšího narušení. Pátá skupina stromů rostoucích pomalu jak během iniciace porostu tak během následujícího vývoje představovala pouze 2% jedinců. Tato analýza demonstrovala vysokou plasticitu smrku a toleranci k různé míře zastínění. Smrk je schopný přečkat dlouhé období v nižších patrech korunové klenby a je schopný znovu zintenzivnit růst po uvolnění z kompetice i ve vyšším věku. Věk nebyl korelován s typem růstového trendu stromů po silném narušení, ani s počtem událostí indikujících narušení na přírůstových sériích.

6.3 Čada, V., Bače, R., Svoboda, M., Morrissey, R. C., Janda, P., in prep. Disturbance regime of the mountain Norway spruce forest landscape in the Bohemian Forest, central Europe.

Ve třetí části byl popsán režim narušení horské smrčiny na Šumavě v krajinném měřítku na sedmi lokalitách. Zkoumané porosty horských smrčin byly poměrně stejnověké. V průměru 60 % stromů (38 – 89%) se obnovilo v rozmezí třiceti let. Takto nevyrovnané věkové složení je důsledkem silného narušení, které odstranilo většinu stromů předchozího porostu a dalo vzniknout porostu současnému. To potvrzují i přírůstové série stromů, protože u 70–94 % starších stromů došlo ve stejné době k razantnímu zvýšení přírůstu (uvolnění) a většina nově vzniklých stromů rostla od počátku intenzivně.

Nejzásadnější období, kdy vznikaly porosty na Šumavě, bylo mezi roky 1780 - 1880. Později se vyskytla narušení také v dekádách 1920 a 1940–1960 a samozřejmě také současná vlna disturbancí, která se datuje od 80. let 20. století. Nejrozsáhlejší disturbance se vyskytla kolem roku 1820 a narušila více než polovinu studijní oblasti. Faktorem, který způsobil zmíněné silné disturbance, může být vichřice, gradace lýkožrouta smrkového nebo těžba. Narušení byla synchronizována napříč celým pohořím a mezi vzdálenými lokalitami. Synchronizace mezi uvolněními z kompetice byla prokázána i pro období kratší pěti let. Taková synchronizace nás vede k domněnce, že faktor, po kterém se předchozí porosty plošně rozpadly, byl přírodního původu. Většina rekonstruovaných narušení byla navíc vysvětlitelná známými historickými vichřicemi a gradacemi lýkožrouta smrkového (tab. 1). Vichřice se vyskytly například v letech 1778, 1821-1822, 1853, 1868 a gradace lýkožrouta smrkového v letech 1833 – 1839 a 1870 – 1877.

Na druhou stranu je nepravděpodobné, že by ve stejnou dobu a během poměrně krátkého období pěti let byly lidmi vytěženy porosty v různých vzájemně vzdálených částech Šumavy. Je možné se tedy přiklonit k názoru, že významná část šumavských horských smrčin, vznikala přirozeně po rozpadech předchozích porostů. Vliv lidské činnosti ve studovaném území však zcela vyloučit nelze. Jednak byly porosty zřejmě pod vlivem pastvy, případně lovu. Navíc v porostech mohlo dojít k toulavé těžbě, nebo těžbě přirozeně odumřelých stromů. V jednotlivých případech nelze zcela vyloučit ani rozsáhlejší těžbu, která by se vyskytla synchronizovaně s výskytem vichřice. Nicméně určující roli v historické dynamice velké části horských smrčin na Šumavě zřejmě hrály vichřice (případně s přispěním žíru lýkožrouta smrkového).

Doba od největšího narušení se u studovaných porostů pohybovala v rozmezí 133 – 261 let (v průměru 177 let). Podobně jako v současnosti, také v minulosti docházelo k odumření až 100 % dospělých stromů v porostu. Průměrná síla (severita) nejsilnější disturbance byla 79% odumřelých stromů a v minulosti každé plochy se vyskytovalo narušení, které odstranilo více než 50% stromů. Podle starých lesnických map můžeme odhadovat rozsah takových polomů až na desítky hektarů. Dále se však vyskytovala i slabší narušení, která odstraňovala pouze malou část dospělých stromů. Tato narušení se vyskytla v průměru jednou za 29 let. Zajímavý je také fakt, že ve dvacátém století byl výskyt silných disturbancí ve studované oblasti minimální. To je pravděpodobně jednou z příčin rozsáhlejšího dopadu aktuálně končící vlny narušení, protože většina šumavských smrčin dospěla do fáze, kdy jsou náchylné k rozpadu. Z dostupných dat se totiž jeví, že rozpad lesa proběhl v současnosti rychleji (ca 30 let) oproti minulosti (ca 100 let).

Efekt lokality nebyl příliš výrazný. Jak už bylo zmíněno, narušení byla synchronizována mezi lokalitami. Sousedící plochy nebyly průkazně podobnější v historii narušení oproti plochám vzdálenějším. Na druhou stranu dvě nejjižnější lokality (Plechý, Hraničník) se lišily ve frekvenci silných narušení – porosty většinou vznikaly po více než jedné silné disturbanci. Frekvence všech typů narušení se zvyšovala se zvyšující se nadmořskou výškou, byla vyšší na západních svazích a doba od nejsilnější disturbance na ploše se zvyšovala se vzdáleností od exponovaných hřebenových partií směrem k chráněným partiím v nižších polohách. To potvrzuje význam vichřic v dynamice lesa, neboť všechny tyto faktory mají blízký vztah s exponovaností porostů vůči větru.

7. Závěry

Hodnocení a následně i management horských smrčin na Šumavě se často opíral pouze o vizuální hodnocení. Naše výsledky naznačují, že tímto způsobem nelze věrohodně zjistit, zda se porost vyvíjel v minulosti přirozeně či nikoliv. Podobně jako po těžbě, také po vichřici nebo rozpadu lesa vlivem lýkožrouta dochází k odrůstání jedné, relativně stejnověké nové generace stromů. Během asi 30 let po disturbanci došlo na našich plochách ke vzniku zapojeného porostu bez možnosti další obnovy, a tím ke vzniku relativně homogenního porostu, kde jsou si jednotlivé stromy navzájem podobné svojí tloušťkou, výškou atd.

Bylo zjištěno, že porosty, které se aktuálně rozpadly na velkých plochách, vznikaly po podobných narušeních v období před 133 – 261 lety. Na základě synchronizace rekonstruovaných narušení mezi plochami a lokalitami na Šumavě lze předpokládat, že narušení byla v dominantní míře působena přirozenými faktory. Většina rekonstruovaných narušení byla navíc vysvětlitelná známými historickými vichřicemi, případně gradacemi lýkožrouta smrkového. I když samozřejmě úplně vliv lidské činnosti vyloučit nelze a určitá míra lidského vlivu ve studovaných porostech je pravděpodobná. Jedná se zejména o vliv pastvy, lovu, případně toulavé těžby, či těžby odumřelých stromů. V jednotlivých případech nelze zcela vyloučit ani rozsáhlejší těžbu, která by se vyskytla synchronizovaně s výskytem vichřice. Nicméně určující roli v historické dynamice velké části horských smrčin na Šumavě zřejmě hrály vichřice (případně s přispěním žíru lýkožrouta smrkového).

Síla, rozsah a frekvence narušení je v horských smrčinách na Šumavě zřejmě natolik vysoká, že neumožňuje dosažení fáze klasického starého pralesovitého porostu s rovnovážnou strukturou. Porosty nad 100 – 150 let věku jsou zde natolik náchylné k narušení, že pravděpodobnost jejich dlouhodobého přežití v neporušeném stavu je velice nízká. Nicméně, zdá se, že většina druhů, které v horské smrčině žijí, je takové dynamice lesa přizpůsobena, či je na ní přímo závislá. Disturbance vytvářejí specifické habitaty, které tyto druhy využívají, např. mrtvé dřevo různých forem, narušený půdní drn, přístup světla a tepla. Efektivní management chráněných území, jehož cílem je zajištění habitatu pro tyto druhy, by měl pochopit roli přirozených narušení v horských smrčinách.

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