The role of gap dynamics for the regeneration of the natural spruce forests in the Harz Mountains

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Summary

Studying forest gap dynamics and related effects has a long tradition in ecology. Thus, a vast range of methodological approaches have been developed and applied in all types of forests. As all ecological processes, gap dynamics are also scale-dependent, ranging from impacts on the fitness of individual plants to those on meta-populations on the landscape scale. Gap dynamics in forests are driven by disturbance, in this study defined as any relatively discrete event in time relative to the life span of the studied ecological unit, i.e. an individual tree or a successional community. Disturbance events can therefore act on and across several scales.

Of particular interest for analyzing gap dynamics are (near-) natural forests with no, or only marginal, human impact. Especially in Europe these forests are very rare and the core zone of the Harz National Park at Mt. Brocken, Germany, is a remarkable exception, with native and old *Picea abies* trees. This forest was chosen to investigate gap dynamics at different temporal and spatial scales and to study relationships between regeneration of *P. abies* and gap age and microsite type. In addition, a particular focus was the question of autochthony of Norway spruce in the Harz National Park. The PhD thesis addressed four different scales:

1) On the study area level, I analyzed the characteristics and temporal trends of gap dynamics and their relation to climate by using aerial photographs and climate data from the last 60 years.
2) On the plot level, I determined the effects of gap age and microsite type as well as their interaction effects on the regeneration of *P. abies* by measuring biometric variables and analyzing them with a generalized linear mixed model.
3) On the physiological level, I measured frost hardiness of native and planted morphotypes of *P. abies* by conducting different freezing treatments in a frost chamber and using the electrolyte leakage method.
4) On the molecular level, I assessed the genetic diversity of native and planted spruce stands using seven microsatellite markers and performed a discriminant analysis to distinguish between them.

On the study area level, I found that characteristics describing gap dynamics such as turnover rate, gap formation and gap closure rate were in the range of those reported from other temperate forests. These descriptors of gap dynamics increased over the last decades, coinciding with an increase of mean temperatures at Mt. Brocken. On the plot level, no significant effects of gap age on the density of Norway spruce individuals were encountered. The presence of gaps did increase the heterogeneity of forest structure by creating new microsites such as snags, stumps, and root-plates.

Despite providing such new regeneration sites, spruce individuals growing on these disturbance related microsites did not perform as well with respect to biometric variables (height of trees and number of whorls) than those growing on ordinary, non-gap induced microsites (i.e. forest ground and moss-covered rocks). Finally, no general interaction effect of gap age and microsite type on density of *P. abies* or on biometric variables was encountered as an interaction was only evident in growth rates of *P. abies*. On the physiological level, the native, montane morphotype growing in the core zone of the Harz National Park was more frost resistant than the planted, lowland morphotype growing at the edge of the core zone. However, both morphotypes did not differ in their seasonal course of frost hardiness. Finally, on the molecular level, measures of genetic diversity did not differ between native and planted forest stands. Despite a very low differentiation owing to extensive gene flow between the different provenances, the study succeeded in discriminating between native and planted forest stands using microsatellites. As a result, recruits in gaps could be assigned to one or the other group. The recruits in the gaps of the core zone mostly derived from trees along the gaps' margins and showed a high degree of introgression from planted stands.

In conclusion, the present study displayed an increase of gap dynamics with time, which is probably a direct effect of increasing mean temperatures or an indirect effect of increasing pathogen damage. However, the regeneration studies point to a constancy of this old-growth forest in the long-term run. Despite obvious introgression effects, some spruce recruits in gaps still show a high degree of genetic resemblance to their autochthonous progenitors.

Zusammenfassung

Studien zur Walddynamik und derer Effekte haben eine lange Tradition in der ökologischen Forschung. Dabei wurde eine Vielzahl methodischer Ansätze entwickelt, welche in den verschiedenen Waldtypen angewendet wurden. Wie alle ökologischen Prozesse ist auch die Walddynamik skalenabhängig und reicht dabei von Auswirkungen auf die Fitness von einzelnen Individuen bis hin zu Effekten auf Meta-Populationen. Die Lückendynamik in Wäldern wird vor allem durch Störungen angetrieben. Im Rahmen dieser Studie werden Störungen als ein relativ diskretes Ereignis in einer Zeiteinheit relativ zur Lebensspanne der untersuchten ökologischen Einheit, das heißt beispielsweise eines einzelnen Baumes oder einer Sukzessionsgesellschaft, definiert. Störungsereignisse wirken daher auf verschiedenen Skalenebenen, zusätzlich aber auch über diese Skalenebenen hinweg.

Zur Erforschung der Lückendynamik sind natürliche und naturnahe Wälder, die keinen oder nur geringen menschlichen Einfluss aufweisen, von besonderem Interesse. Vor allem in Europa sind diese Wälder selten, so dass die Kernzone des Harz Nationalparks am Brocken in Deutschland eine bemerkenswerte Ausnahme mit nativen und alten *Picea abies*-Individuen darstellt. Dieser Wald wurde zur Analyse der Walddynamik auf verschiedenen zeitlichen und räumlichen Skalenebenen ausgewählt sowie zur Ermittlung der Beziehung zwischen der Regeneration von *P. abies* und dem Lückenalter sowie der Art des Kleinstandortes (Microsite-Typs). Zudem wurde ein besonderer Schwerpunkt auf die Frage der Autochthonie der Fichten im Harz Nationalpark gelegt. Die Doktorarbeit befasst sich mit vier verschiedenen Skalenebenen:

1) Auf der Ebene des Untersuchungsgebietes habe ich die Eigenschaften und die zeitlichen Trends der Lückendynamik und ihre Beziehung zum Klima analysiert. Die Auswertung erfolgte anhand von Luftbildern und Klimadaten der letzten 60 Jahre.
2) Auf der Ebene von Untersuchungsflächen im Nationalpark habe ich die Effekte des Lückenalters und Microsite-Typs sowie deren Interaktion auf die Regeneration von *P. abies* bestimmt. Hierzu wurden biometrische Daten erhoben, die anschließend mit einem gemischten Model analysiert wurden.
3) Auf der physiologischen Ebene habe ich die Frosthärte von nativen und angepflanzten Morphotypen von *P. abies* bestimmt, indem der Elektrolytverlust nach verschiedenen Frostbehandlungen gemessen wurde.
4) Auf der molekular-genetischen Ebene habe ich die genetische Diversität der nativen und gepflanzten Fichtenbestände abgeschätzt. Die Analyse erfolgte unter Verwendung von sieben

verschiedenen Mikrosatelliten-Markern und einer anschließenden Diskriminanzanalyse zur Unterscheidung zwischen den beiden Gruppen.

Auf der Ebene des Untersuchungsgebietes waren die Eigenschaften zur Beschreibung der Lückendynamik wie beispielsweise Turnover-, Lückenentstehungs- und Lückenschlussrate im Bereich derer von anderen temperaten Wäldern. Diese Indizes der Lückendynamik nahmen mit der Zeit zu, was mit einem Anstieg der mittleren Temperaturen am Brocken einhergeht. Auf der Ebene der Untersuchungsflächen im Nationalpark zeigten sich keine signifikanten Effekte des Lückenalters auf die Dichte der Fichten-Individuen. Das Vorhandensein von Lücken erhöhte die Heterogenität der Waldstruktur durch das Schaffen neuer kleinräumiger Strukturen wie Baumstümpfe, Stubben und Wurzeltellern. Trotz der Bereitstellung solcher neuen Regenerationsorte, zeigten die auf diesen störungsinduzierten Microsites wachsenden Fichten-Individuen im Hinblick auf biometrische Variablen (Höhe der Bäume und Anzahl der Wirtel) eine schlechtere Leistung als solche, die auf herkömmlichen, nicht durch Lückenbildung hervorgerufenen Kleinstandorten (Waldboden, moosbedeckte Felsen) wuchsen. Es wurde kein genereller Interaktionseffekt des Lückenalters und der Art des Microsites auf die *P. abies*-Dichte oder auf biometrische Variablen gefunden, da eine Interaktion nur für die Wachstumsraten von *P. abies* ersichtlich war. Auf der physiologischen Ebene zeigte der native, montane Morphotyp, welcher in der Kernzone des Harz Nationalparks wächst, eine höhere Frostrestistenz als der gepflanzte Tieflagen-Morphotyp, welcher am Rand der Kernzone vorkommt. Dennoch unterschieden sich die beiden Morphotypen nicht in ihrem saisonalen Verlauf der Frosthärte. Auf der molekular-genetischen Ebene unterschieden sich die Maßzahlen der genetischen Diversität nicht zwischen nativen und gepflanzten Waldbeständen. Trotz einer sehr geringen Differenzierung infolge von beträchtlichem Genfluss zwischen den verschiedenen Provenienzen war die Studie bei der Diskriminierung zwischen nativen und gepflanzten Waldbeständen mittels Mikrosatelliten erfolgreich. So konnten junge *P.abies*-Individuen innerhalb der Lücken eindeutig einer der beiden Gruppen zugeordnet werden. Der Aufwuchs in Lücken innerhalb der Kernzone stammte größtenteils von am Lückenrand wachsenden Mutterbäumen ab und zeigte ein hohes Maß an Introgression von gepflanzten Beständen.

Zusammenfassend offenbarte die Studie eine Zunahme der Lückendynamik mit der Zeit, was möglicherweise ein direkter Effekt der Temperaturzunahme sein kann oder ein indirekter Effekt aufgrund der zunehmenden Schädigung durch Pathogene. Trotzdem konnte die Regenerations-Studie die Konstanz dieses Altbestandes auf lange Sicht herausstellen. Obwohl Introgressionseffekte detektiert wurden, zeigen einige Fichten-Nachkommen dennoch einen hohen Grad an genetischer Ähnlichkeit zu ihren autochthonen Vorfahren.

Chapter 1 – Introduction

1.1 General introduction

Research on forest gap dynamics has a long tradition in ecology (Pickett and White, 1985a), comprising a vast variety of forest types ranging from tropical forests (e.g. Denslow, 1980; Kellner and Asner, 2009) over temperate deciduous forests (e.g. Kenderes et al., 2008; Bruelheide and Luginbühl, 2009; Busing et al., 2009) to mixed mesophytic forests (e.g. McCarthy and Bailey, 1996; Busing, 2005), subtropical broadleaved forests (e.g. Barik et al., 1992; Cornelissen et al., 1994) and boreal conifer forests (e.g. Qinghong and Hytteborn, 1991; Drobyshev, 2001; de Römer et al., 2007). Most of these studies focus on single specific aspects of gap dynamics, while more comprehensive studies including different temporal and spatial or hierarchical scales are rare. While analyses of gap formation and gap closure rates as well as turnover rates require data at broad temporal and spatial scales, as obtained for example from evaluation of aerial photographs (Newton, 2007), studies on regeneration of tree species have to employ finer scales. Thus, comprehensive studies have to come from the overall description of forest gap dynamics on the level of the study area to a finer scale, where the effect caused by gap dynamics on plant species can be assessed by measuring biometrical data on target individuals in field. While these data do only describe regeneration patterns of a species, approaches on the physiological and molecular levels are necessary to obtain explanations for species' regeneration success. Mechanisms acting at the physiological and the molecular level are, both, of particular importance for tree species' fitness and regeneration. Most notably, ecotypic variation within tree species can often be found (e.g. *Betula pendula*, Li et al., 2002; *Picea abies*, Geburek et al., 2008), which might have important influences on regeneration success. As discussed by Geburek et al. (2008), it is unlikely, for example for *P. abies* that within the broad range of this tree species only one ecotype will confer highest fitness throughout all environments.

1.1.1 Forest gap dynamics on the study area level

To analyze natural gap dynamics, including rates of gap formation, gap closure and turnover, and its impact on forest tree regeneration, natural or near-natural forests without or negligible anthropogenic influence are required. Although gap closure and regeneration have also been studied in managed forest stands, e.g. by creating artificial gaps (Diaci, 2002), their relevance for natural regeneration of a target tree species can only be adequately addressed in natural forests. Following the definition of Rouvinen and Kouki (2008) natural forests have evolved and reproduced themselves naturally from previously established individuals, with structure and dynamics lacking significant human intervention. Irregular stand patterns, uneven-aged composition and a high proportion of coarse woody debris are typical characteristics of natural forests (White and Pickett, 1985). Only a few remnants of these forests are still existing in Europe; among these are some Scandinavian and Russian boreal forests (McCarthy, 2001; Kuuluvainen et al., 2002) or the old-growth Norway spruce stands in Germany in the core zone of the Harz National Park at Mt. Brocken (Stöcker, 2001).

Gap dynamics are driven by disturbance, which is according to the definition given by White and Pickett (1985) any relatively discrete event in time that disrupts ecosystem, community, or population structure and that changes resources, substrate availability, or the physical environment. The main impacts of disturbances in forests are provided by wind (Ulanova, 2000; Nagel et al., 2006; Busing et al., 2009), insects and pathogens (Bendel et al., 2006; Desprez-Loustau et al., 2006; Raffa et al., 2008), fire (Schumacher and Bugmann, 2006; Shorohova et al., 2009), air pollution and acid rain (Schulze et al., 1989; Patterson and Rundel, 1995), all of them resulting in the creation of gaps. Following Runkle (1982), gaps can be defined as the surface area directly under the canopy opening. The size of gaps can vary from single-tree gaps to several hundred hectares (Spies and Franklin, 1989). Disturbance regimes and therefore gap dynamics can differ largely between forest types. While, for example, in boreal forests in Russia, especially fire is the dominating agent (Shorohova et al., 2009), in evergreen broad-leaved forests in Japan, in particular, typhoons cause large gaps (Miura et al., 2001). Accordingly, the rates of gap closure, as an important component of gap dynamics, depend on the (macro-) climatic conditions and the identity of the dominating tree species, thus, also differs among forest types. For example, Brokaw (1985) described that already two years after creation of treefall gaps, some pioneer tree species reached a height of 10 m to 13.5 m in a tropical forest in Panama, while for subalpine spruce forests in the Carpathian Mountains, Holeksa and Cybulski (2001) found that gap filling was largely retarded as only few individuals reached the height of 10 m after 20 years. As not only the species identity determines the growth rates, and therefore the gap closure rates but also the climatic environment, it can be expected that harsh climatic conditions will lead to a reduced growth of a species. This can be demonstrated by the growth rates of *P. abies* at the high altitudes of Mt. Brocken with its unfavorable climatic conditions (see Chapter 1.3), where only a radial increment of 1.2 mm yr $^{-1}$ over the last decade (own unpublished data) has been found. This increment is low in comparison to the radial growth of 1.8 - 4.8 mm yr $^{-1}$ that has been reported from stands in Southern Finland (Mäkinen and Isomäki, 2004) or a radial growth of up to 3.9 mm yr $^{-1}$ from stands in the Eastern Italian Alps (Rossi et al., 2006). As the forests at Mt. Brocken grow more slowly, lower gap closure rates should be expected compared to other temperate forests.

The necessity to rely on long-term data for analyzing patterns of forest gap dynamics is undeniable, since trees are long-living individuals. There are various methods available to assess forest gap dynamics such as ground surveys with permanent plots (Fraver et al., 2008) or line transects (Runkle, 1981, 1982; Qinghong and Hytteborn, 1991; Newton, 2007), dendrological approaches (McCarthy, 2001; Nagel et al., 2007) or the evaluation of aerial photographs from different points in time that can be used to detect temporal trends in forest gap dynamics (Newton, 2007). These long-term studies offer the opportunity to relate gap formation and gap closure rates to climate as an explanatory variable. Information on the nature of this relationship is particularly important against the background of climate change. According to the IPCC report the frequency and magnitude of weather extremes will increase in the 21st century (Solomon et al., 2007), which might also result in an increase of forest gap dynamics. This can either be expressed in direct effects by windthrow or windbreak (Worrall et al., 2005), but does also imply indirect effects based on an increase of pathogens related to changed climatic conditions (Schlyter et al., 2006).

1.1.2 Effects of gap dynamics on the regeneration of tree species on the plot level

Gap creation promotes the regeneration of individuals since gaps significantly improve the abiotic and biotic conditions at a particular site (White and Jentsch, 2001). Establishment of new seedlings is enhanced in gaps (McCarthy, 2001) and advance regeneration is promoted, i.e. the growth of seedlings and saplings from a seedling bank established prior to gap creation (Yamamoto, 2000; Metslaid et al., 2007; Fraver et al., 2008). These individuals can persist as suppressed juveniles for several years until a gap opens (Oskar syndrome; Silvertown and Doust, 1993). In newly created gaps, an increase in nutrient availability can be found (Prescott, 2002; Beckage and Clark, 2003) Likewise, the microclimate in gaps has changed (Scharenbroch and Bockheim, 2007), as for example the light availability has increased (Poulson and Platt, 1989; Beckage and Clark, 2003). In addition, the spatial heterogeneity (Schaetzl et al., 1989; Beckage and Clark, 2003) based on gap creation is enhanced not only on the level of the study area but also within gaps on the plot level by the creation of new microsites (McCarthy, 2001; Gray and Spies, 1997). These microsites, i.e. logs, snags, stumps and root-plates, are typically invoked by disturbance events as they represent lying or standing dead wood and can be summarized as gap-induced microsites. In contrast, non-gap induced microsites are not related to disturbance events and to dead wood. These microsites, i.e. moss-covered rocks or ordinary forest floor, are permanently available for regeneration. Not only abiotic conditions, but also biotic interactions change after gap creation, as surviving plants are released from the existing competition regime (Szwagrzyk and Szewczyk, 2001; Stan and Daniels, 2010). However, changes in biotic interactions are not universally beneficial. For example, the regeneration of *P. abies* has been observed to be negatively influenced by the inter-specific competition with grasses, in particular with *Calamagrostis villosa* (Reif and Przybilla, 1995). In contrast, enhanced regeneration of *P. abies* on decaying logs has often been pronounced since this is a common phenomenon in spruce forests (e.g. Motta et al., 2006; Zielonka, 2006; Fig. 1.1 A). As these results are typically based on observations of seedlings and saplings, the long-term survival of individuals on this microsite has to be verified to quantify the sustainable contribution of gap-induced microsite for forest regeneration. Furthermore, only little attention has been paid to the relative contribution of alternative regeneration sites such as moss-covered rocks (but see Kupferschmid and Bugmann, 2005). Moss-covered rocks offer the advantage of an elevated position and thus, a head start in terms of light availability in comparison to growing seedlings and saplings in the vicinity is secured, just as a favorable water supply because of moss coverage (Fig. 1.1 B). Contrary to logs or other gap-induced microsites, which have to decay for up to 30 - 60 years in the case of *P. abies* to become appropriate regeneration sites (Zielonka, 2006), moss-covered rocks and the ordinary forest floor can be readily colonized.

Fig. 1.1: *Picea abies* growing on gap-induced and non-gap induced microsite types at Mt. Brocken, Germany. A) Log as a gap-induced microsite. B) Moss-covered rock as a non-gap induced microsite.

To study regeneration on gap- *versus* non-gap induced microsites, the age of the gaps is also of particular importance. On the one hand, the suitability of gap-induced microsites is time-dependent because the dead wood has to decay to a sufficient degree. Thus, an optimum curve of microsite quality can be expected for tree regeneration. On the other hand, it can also be assumed that non-gap induced microsites show a dependency on gap age, because of the decreasing light availability with gap age by lateral growth from surrounding trees or by the growing recruits. Overall, it can be therefore expected that the density of *P. abies* individuals shows a more unimodal relationship when regarded in respect of gap age. Finally, it might well be that there is an interaction between the different optimum curves with regard to microsite quality and the unimodal relationship of tree density, resulting in an interaction effect of microsite type and gap age on spruce regeneration.

1.1.3 Frost hardiness as a key trait for survival on the physiological level

Natural forests are not only important for measuring gap dynamics and regeneration patterns, but they are also rare remnants where old-growth, native individuals, i.e. autochthonous individuals, of a species can be found. Recently, native, autochthonous occurrences of *P. abies* have become the focus of nature conservation efforts because they represent valuable genetic resources from a time before industrial forestry started in the 18th century throughout Central Europe. Norway spruce is especially interesting for forestry as this species shows altitude-dependent differences in morphology, and, thus, *can* be subdivided into a montane and a lowland morphotype (Greger, 1991; see Chapter 1.2). The lowland morphotype of Norway spruce grows faster and produces a higher amount of wood than the montane morphotype (Schütt et al., 2006). Foresty has selected especially for the fastest growing individuals (Hosius et al., 2006), and therefore, has favored the lowland morphotype. In consequence, forest plantations are mainly consisting of the lowland morphotype. Because of the increase in forest management during the last centuries (Hosius et al., 2006), this selected lowland provenance has been planted also at high altitudes adjacent to the montane morphotype. However, the lowland morphotype is, in contrast to the montane morphotype, not adapted to the unfavorable climatic conditions of high altitudes such as strong winds, thick snow cover and severe frosts as discussed by Geburek et al. (2008; see Chapter 1.2).

In particular the resistance against frost is a key trait for the survival of coniferous trees (Holeksa and Cybulski, 2001; Strimbeck et al., 2007), since frost hardiness acts as a limiting factor for productivity and distribution of plants (Sakai and Larcher, 1987; Bannister and Neuner, 2001). Frost hardiness of coniferous trees is affected by several environmental factors like nutrient availability (Jönsson et al., 2001; Jönsson et al., 2004a), drought stress (Beck et al., 2007), photoperiod (Beck et al., 2004), ambient temperature (Beck et al., 2004; Søgaard et al., 2009), altitude and latitude (Skrøppa, 1991; Taulavuori et al., 2004). Besides photoperiod, minimum temperature is the main determinant for hardening and dehardening of coniferous tree species to frost (Sakai and Larcher, 1987; Saxe et al., 2001), which results in distinct seasonal courses in frost hardiness (Repo, 1992; Beck et al., 2004). It has been demonstrated that not only the maximum capacity of frost resistance is decisive for survival of trees, but especially the dehardening in spring is critical as woody plants are usually most susceptible to frost injury around the bud break in spring (Aitken and Hannerz, 2001). Since the dehardening is mainly driven by ambient temperature (Saxe et al., 2001) and comes into effect already after five days with ambient temperatures over +5 °C (Jönsson et al., 2004b), this dehardening phase is especially susceptible against changes in temperature regimes and temperature backlashes. Such changes can be a probable scenario in the context of the forecasted climate change according to the IPCC report (Solomon et al., 2007). The combination of an increase in weather extremes with an increase in mean temperatures (IPCC report, Solomon et al., 2007) might result in an earlier dehardening of trees, which thus contributes to an increase in damage and mortality of individuals by late frosts in spring (Hänninen, 1991; Saxe et al., 2001). With regard to the morphological variation of *P. abies* along altitudinal gradients (Geburek et al., 2008) differences in maximum frost hardiness as well as in hardening and dehardening might be expected. However, studies relating morphological traits to physiological ones, like frost hardiness, are scarce (but see Li et al., 2002; Bresinsky et al., 2008). Nevertheless, it can be assumed that differences in morphology are reflected by differences in physiology.

1.1.4 Genetic diversity and differences of Picea abies morphotypes on the molecular level

During the last centuries the lowland morphotype of *P. abies* has been planted commonly in the neighborhood of native, autochthonous Norway spruce stands also at high altitudes, which bears the risk of genetic erosion through introgression (Hosius et al., 2006). Therefore, it is beyond all questions that actions of forest management have a great impact on the genetic structure and diversity of forest trees. For instance, different cutting modes can affect the genetic variation in a forest stand as shown in the review of Hosius et al. (2006). While schematic thinning in rows showed no effect on genetic variation, the consistent removal of inferior trees, which is a common forestry practice, resulted in a higher heterozygosity of the remaining trees (Hosius et al., 2006). Likewise, the artificial reforestation with individuals from unknown or non-adapted seed material may have drastic effects as this management often leads to a loss of genetic diversity (Rajora et al., 2000; Hosius et al., 2006).

From a nature conservation perspective, the genetic identification of different morphotypes is of high interest because this might also involve the possibility to distinguish between autochthonous and allochthonous individuals. Several attempts have been made to distinguish between these ecotypes. Greger (1991), for example, used allozymes in his study but failed to find a marker for native, autochthonous *P. abies*. Jeandroz et al. (2004) also failed to distinguish between autochthonous and planted *P. abies* individuals using RAPD-analyses. In the last decade, microsatellites have been shown to be an appropriate tool for detecting genetic effects of forest management (Rajora et al., 2000) and introgression (Zalapa et al., 2009). As co-dominant markers, microsatellites allow for assessing heterozygosity, and at the same time, the high number of different available markers primers assures a sufficient resolution in genotyping.

Since the preservation of genetic diversity has become a central task of nature conservation purposes, it is particularly important to conduct genetic studies in natural forest stands. Natural forests are characterized by natural regeneration, which is particularly expressed in the face of gaps (McCarthy, 2001). These gaps are, thus, the obvious places where introgression of allochthonous genes into natural autochthonous stands should be studied. It can be expected that the genetic diversity of recruits in gaps might differ from the neighborhood, even when gaps in natural forest stands are isolated from planted stands by several kilometers. For wind-pollinated trees such as *P. abies,* gene flow can be expected to be of decisive importance for population structure. For Norway spruce, it has been demonstrated that about 50 % of pollen comes from outside the population, even though the stands were not located in the direct vicinity (Xie and Knowles, 1994). For assessing the potential change of genotype composition, not only the occurrence of gaps per se has to be considered, but also the temporal and spatial variation of gap occurrence. Differences in the spatial extent and the age of gaps, which depend on the forest gap dynamics of the landscape scale (i.e. the study area level), might lead to genetically different cohorts of recruits that might undergo different selection regimes. So far, studies that address genetic diversity of recruits in gaps and take gap dynamics into consideration at the same time are still lacking.

1.2 Study species

Picea abies (L.) Karst. belongs to the family of the Pinaceae and is a wind-pollinated, wind-dispersed, evergreen coniferous tree species (Schmidt-Vogt, 1978). Norway spruce individuals can grow up to a height of 30 - 50 m with a dbh (diameter at breast height) of 65 - 150 cm and can reach a maximum age of 250 - 440 years (Schütt et al., 2006).

With regard to climatic requirements, Norway spruce has a wide ecological amplitude. The mean annual temperature optimum within the species' natural distribution range varies between +5 °C and +7.5 °C, although the highest timber production is reached at higher temperatures (Schütt et al., 2006). The optimum precipitation during the vegetation period is above 550 mm. This results in a natural distribution boundary in Southern and Eastern Europe as an effect of drought in summer. The eastern distribution limit ranges from Eastern Scandinavia, Western Russia to the Ural Mountains (Schmidt-Vogt, 1978; Schütt et al., 2006; Fig. 1.2). The western distribution is thought to be caused by an increase of lethal fungi diseases (Schütt et al., 2006), as an effect of warm winters in oceanic climates. Low temperatures and the short vegetation period limit the northern and high-altitude distribution (Schütt et al., 2006). The boundary of the species' range in the North and North-Eastern European Taiga is hard to assess, as there is a huge contact zone of *P. abies* with *P. obovata* (Schütt et al., 2006). Both species are known to hybridize with each other resulting in the *P.* x *fennica* hybrid (Fig. 1.2).

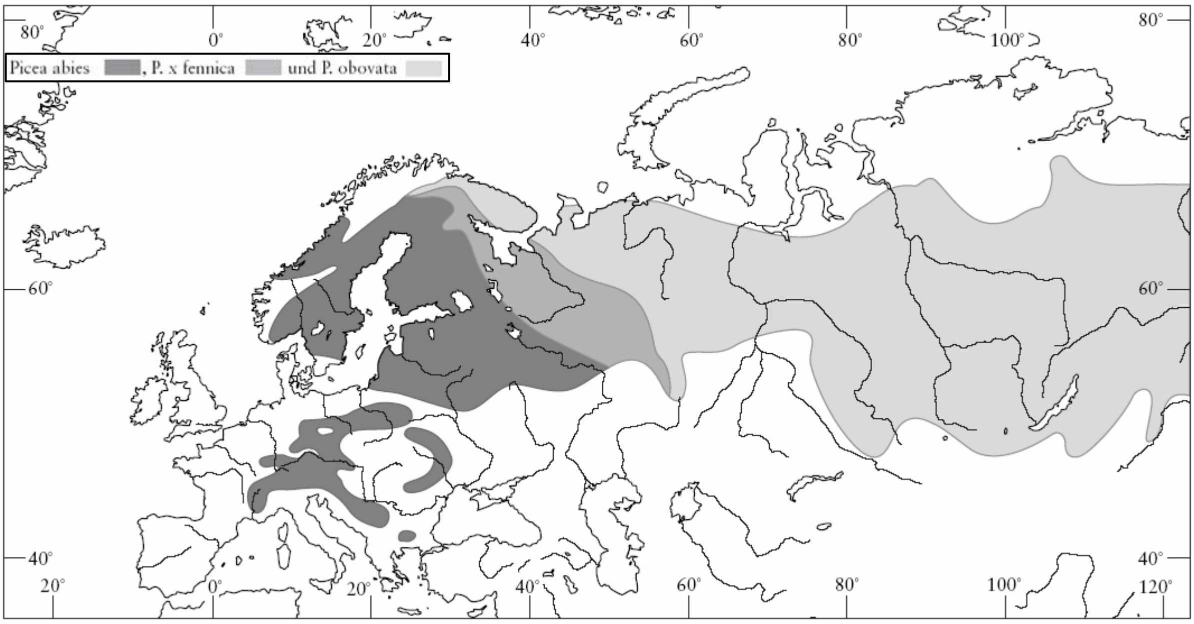

Fig. 1.2: Distribution ranges of *Picea abies* and *P. obovata* as well as its hybrid *P.* x *fennica* (modified according to Schütt et al., 2006).

According to Rubner (1932) the species' range can be subdivided into three different parts: the alpine-south-east European spruce range, the hercynian-carpathian spruce range and the baltic-nordic spruce range. These different sub-ranges are considered to be the result of different migration routes from glacial refugia (Yugoslavia, the Carpathian Mountains, Russia and potentially Italy) during the post-glacial time (Schmidt-Voigt, 1974, 1978). According to Schmidt-Vogt (1987) the Harz Mountains were recolonized from the Carpathians. In Germany, *P. abies* is native to the Alps, the Bavarian Forest, the Black Forest and the Harz Mountains as well as to the Fichtelgebirge, Franconian Forest and the Thuringian Forest (Schmidt-Vogt, 1987). In addition, some native lowland populations are also described for Saxony and Thuringia (Schmidt-Vogt, 1987).

In 1423, *P. abies* was first time used for forestry in Frankfurt/Main (Schütt et al., 2006). Norway spruce is often planted in dense stands and used for forest plantations in areas beyond its natural range, as this species is one of the most common and economically important tree species for timber production in Europe.

P. abies is known for its high variability with regard to morphology resulting in different crown types. According to the second-order branching system the crown types are described as comb type, brush type and plate type (Geburek et al., 2008; Fig. 1.3). Additionally, the length of needles differed between these morphotypes. Needles from the comb type are longer than from the plate type, in total ranging between 10 mm and 25 mm (Schütt et al., 2006). According to Geburek et al. (2008) morphological differences are associated with a "temperature-elevational" gradient. Thus, the comb type mainly occurs in lowlands, while the plate type is the morphotype of the high altitudes (Geburek et al., 2008). The plate type seems to be well-adapted to heavy snow loads and ice breakage because of its cylindrical and slender growth habit (Greger, 1991; Fig. 1.3). Moreover as discussed by Geburek et al. (2008), the slender crown architecture with tightly packed branches maximizes the interception of sunlight and reduces air streams through the crown resulting in a reduction of heat loss.

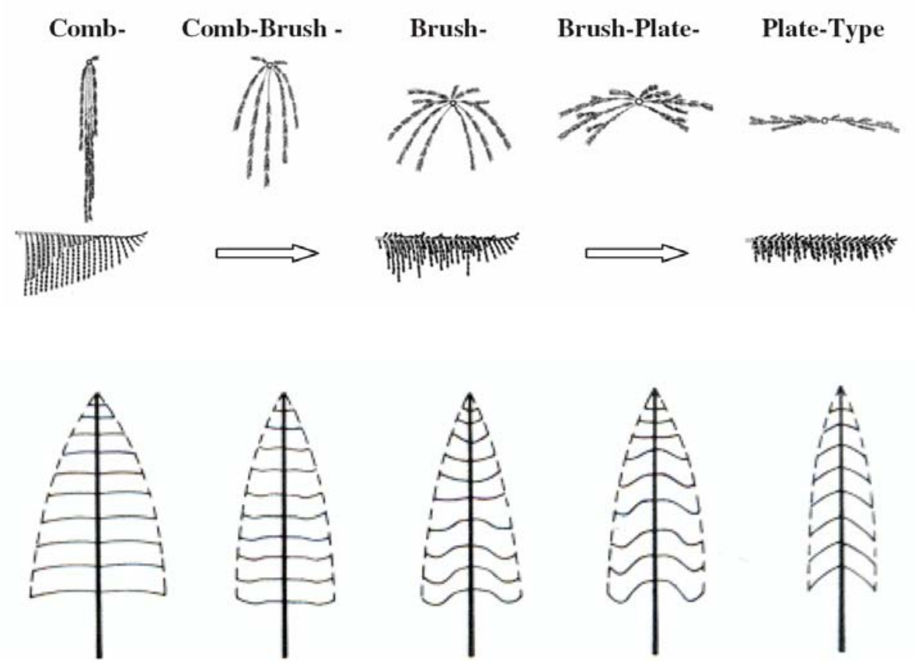

Fig. 1.3: Branching system of the second-order branches and the resulting crown type (modified according to Quack, 2004 and according to Geburek et al., 2008).

Norway spruce is a monoecious tree species and starts to flower at an age of 20 - 40 years but flowering can be delayed to an age of 50 - 70 years in dense stands (Schütt et al., 2006). Flowering starts in April and ends in June (Dierschke, 1995). Reproduction takes mainly place by seeds with a weight of 5 - 8 mg, which are aggregated in cones. There are only a few references of clonal reproduction by adventitious roots (Schütt et al., 2006). *P. abies* is diploid (chromosome number 2n = 24; Oberdorfer, 1983) and self-incompatible (Hagman, 1975). Uncommonly, tri- or tetraploide seedlings can occur (Schütt et al., 2006).

1.3 Study area

The study area is located in the center of Germany on the north-eastern slopes of Mt. Brocken and covers 225.2 ha of a near-natural spruce forest with an altitudinal range of 900 - 1050 m a.s.l. (Fig. 1.4). These near-natural forests of Mt. Brocken belong to the core zone of the Harz National Park and are thus protected areas without any forest management. Mt. Brocken (51°48’02’’N 10°37’02’’E) is with 1142 m a.s.l. the highest elevation of the Harz Mountains (Wegener and Kison, 2002).

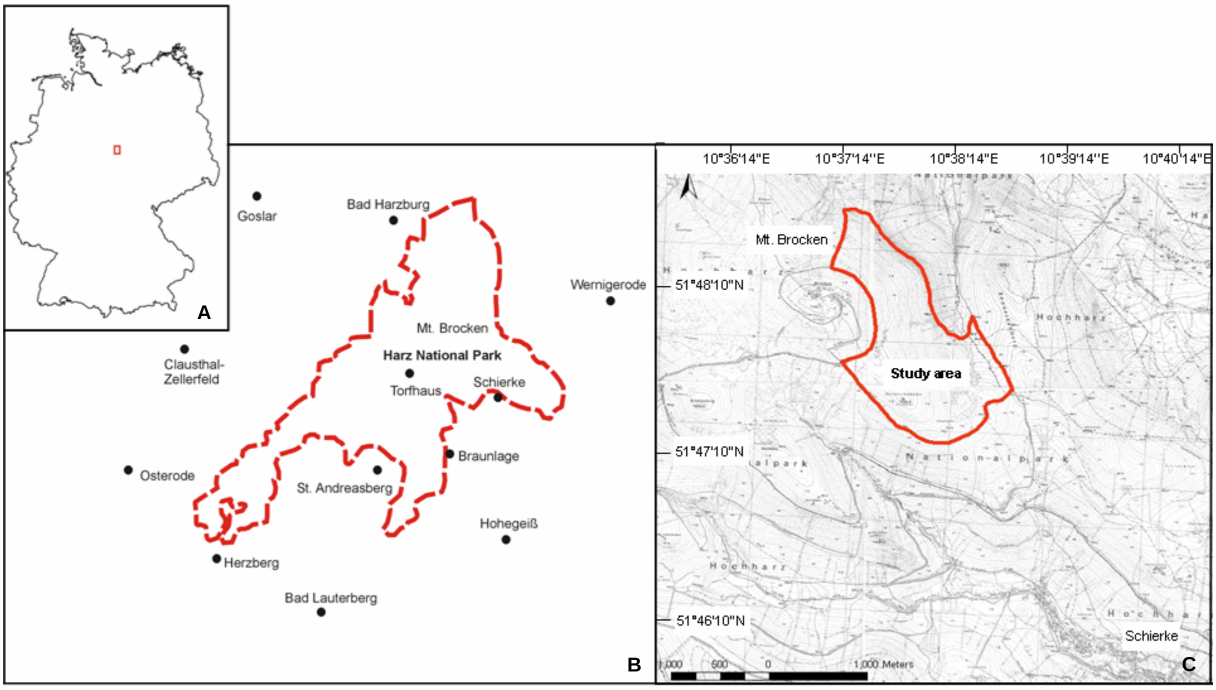

Fig. 1.4: Map of the location of the study area at the core zone of the Harz National Park in Germany. A) Geographic location of the Harz Mountains in Germany (red square). B) The boundary of the Harz National Park (red dashed line). C) The boundary of the study area at Mt. Brocken in the core zone of the Harz National Park (red line).

The Harz Mountains are a complex of different geological ages and substrates and can be described as a fault-block mountain range dissected by numerous deep valleys (Karste et al., 2005). This mountain range is a deeply eroded monocline (Pultscholle) whose basement belongs to the hercynian orogenesis during the Carboniferous (Karste et al., 2005), which was up-lifted again during the late Cretaceous and early Tertiary, resulting in an extreme uplift in the northern edge of the mountain range (Kulke, 1997). Therefore, the Harz Mountains are characterized by a sharp rim at the north where the massif drops abruptly to the northern and north-western foreland (Wegener, 1999a). In contrast, the south-eastern slopes show a soft decline (Wegener, 1999a). The Harz Mountains are part of the Rheno-Hercynian belt of the Central European Variscian orogen and today mainly consist of bedrocks that are rich in silicates and base-poor (Kulke, 1997; Karste et al., 2005). As a result of the granitic bedrock, which is especially found at Mt. Brocken (Karste et al., 2005), soils are poor in nutrients and have low pH values of about 4.0.

The Harz Mountains are the most northern mountain range in Germany and are therefore characterized by harsh climatic conditions (Pflume, 1999). Predominant western winds cause high precipitation values of around 1400 mm yr $^{-1}$ at the windward (western, north-western) side and decreasing rainfall on the leeward (eastern) side with precipitation values of around 600 mm yr $^{-1}$ (Glässer, 1994). As Mt. Brocken is the highest elevation within the Harz Mountains, climatic variables are exceptionally high at the peak of Mt. Brocken (Karste et al., 2005), which is reflected by a mean annual precipitation of 1727 mm yr $^{-1}$ and a mean annual air temperature of only 3.1 °C (1951 - 2005, Deutscher Wetterdienst). In addition, 306 foggy days were counted per year as well as 98 days with a maximum temperature below zero degrees (Wegener and Kison, 2002). Especially the wind shows extreme values, reflected in an annual wind velocity of 5.6 Beaufort (1951 - 2005, Deutscher Wetterdienst) and peaks in wind velocity of 273 km/h (Wegener and Kison, 2002).

The isolated and northern position of the Harz Mountains results in some differences in vegetation compared to other German mountain ranges. The most important one is the altitudinal compression of the vegetation zones (Kison et al., 1994) and a low natural tree line at an altitude of about 1100 m a.s.l. at Mt. Brocken, which is thought to be mainly caused by wind (Wegener, 1999b). In contrast, the tree line in the Alps is not lower than 1700 m a.s.l. (Wegener, 1999b). The vegetation zone from the tree line to the top of Mt. Brocken at 1142 m a.s.l., is considered subalpine, and according to Pflume and Bruelheide (1994) one of the five different vegetation zones that can be defined for the Harz Mountains. Below, from an elevation of 800 to 1100 m a.s.l., the oro-montane zone is located where forests are naturally dominated by *P. abies* (Wegener and Kison, 2002). The near-natural forests found at Mt. Brocken in this zone are comparable to virgin forests that are described for the boreal zone (Stöcker, 1997). The montane vegetation zone is located at an altitudinal range between 500 and 800 m a.s.l. At this zone mixed forest stands consisting of *Fagus sylvatica*, *Acer pseudoplatanus* and *Picea abies* have their natural occurrence (Pflume, 1999). In contrast to natural forests in Thuringia and the Black Forest, there are no *Abies alba* occurrences in this zone, as this species did not reach the Harz Mountains after the last glacial period (Schütt et al., 2006). However, as a result of forest management during the last two centuries, there are many areas where only *P. abies* monocultures can be found in the montane zone. From an elevation of 300 to 500 m a.s.l. the submontane zone is located where beech forests have their main occurrence and which are to some extent running down to the colline zone (100 - 300 m a.s.l.; Pflume, 1999).

In the study area at Mt. Brocken, which is part of the oro-montane vegetation zone, *P. abies* is the main tree species as deciduous tree species like rowan and birch are heavily browsed by deer. The herbaceous layer in the study area is poor in species and dominated by *Calamagrostis villosa*, *Vaccinium myrtillus* and *Avenella flexuosa* (Calamagrostio villosae-Piceetum; Stöcker, 1980). Interspersing bogs and swamps as well as boulder fields render many parts of the study area nearly inaccessible, which in the past has resulted in only sporadically and locally restricted wood removal (Stöcker, 1997; Wegener et al., 2003). As early as in 1937, Mt. Brocken became a part of the nature reserve “Oberharz” (Wegener and Kison, 2002) and in 1990 part of the Harz National Park.

1.4 Structure and objectives of this thesis

In this thesis I mainly focused on the role of gap dynamics for the regeneration of *Picea abies* with a particular emphasis on the question of autochthony of spruce individuals in the natural (oro-) montane spruce forests at Mt. Brocken. More precisely, I investigated the following topics on four different levels:

1) On the study area level, I analyzed the characteristics and temporal trends of gap dynamics, i.e. gap formation and gap closure rate as well as turnover rates and their relation to climate.
2) On the plot level, I determined the effects of gap age and microsite type as well as their interaction effects on the regeneration of *P. abies.*
3) On the physiological level, I tested the frost hardiness of the montane and of the lowland morphotype of *P. abies*.
4) On the molecular level, I assessed the genetic diversity of autochthonous (native) and planted spruce stands. Furthermore, I analyzed their genetic differentiation in order to assign recruits in gaps to one of the both groups.

Chapter 2 focuses on the temporal and spatial aspects of gap dynamics in the natural conifer forest stand at Mt. Brocken, Central Germany. I hypothesized that the level of gap dynamics is lower compared to other temperate forests but have increased in the last decades and that this increase is related to climate change. To have insights in underlying mechanisms of gap formation and gap closure I paid particular attention to the impact of temporal and spatial resolution of the datasets. To test these hypotheses I analyzed aerial photographs of four different points in time of the last 60 years by GIS technique and related gap sizes to climate data.

In Chapter 3, I present a field-approach to investigate the regeneration of seedlings and saplings of Norway spruce on different microsite types in gaps of different ages in undisturbed forest. In this study, I had three main hypotheses, first, that the density of *P. abies* recruits shows a unimodal course as a function of gap age; second, that gap-induced microsites contribute most to tree regeneration; and finally, that the importance of specific microsite types for regeneration of *P. abies* changes with gap age. I focused on five different microsite types in three different classes of gap age compared to undisturbed forest matrix, measured biometrical data of young spruce individuals and light conditions as a key environmental factor that changed as a result of disturbance. According to the hypotheses, I was especially interested in the effect of the interaction of gap age and microsites type on spruce regeneration.

Chapter 4 aims at detecting differences in physiology of different morphotypes of *P. abies*. Therefore, I used individuals of the montane spruce morphotype and from the lowland morphotype to assess the frost hardiness as a key trait for the survival of coniferous tree species. In particular, I hypothesized that montane morphotypes are more resistant to frost damage than lowland morphotypes.

In addition, I expected montane morphotypes to have a lower risk of frost damage by late frosts in spring than lowland morphotypes. To test these hypotheses I investigated the frost hardiness in a monthly interval between October 2006 and April 2007 by using the electrolyte leakage method and related the results to climate variables.

In Chapter 5, I investigate molecular differences between native, autochthonous and planted spruce individuals. I used microsatellite markers and discriminant analyses to answer four main hypotheses. First, I hypothesized that planted individuals show a lower genetic diversity than native individuals of Norway spruce and second, that planted individuals can be distinguished from native, autochthonous individuals by specific microsatellite alleles. Using these specific microsatellite alleles, I hypothesized that recruits in gaps can be assigned to either the native or the planted group. Finally, I assumed that genotype composition of recruits depends on the age of cohorts in gaps, as natural selection will result in changes of genotype composition with time.

In a concluding Chapter 6, I outline the main results and provide an overall discussion of my results to present a general synthesis.

Chapter 2 – Gap dynamics in a near-natural spruce forest at Mt. Brocken, Germany

with Helge Bruelheide

Forest Ecology and Management 259, 624-632

2.1 Abstract

We analyzed indices of gap dynamics, i.e. gap formation and gap closure rates as well as turnover rates, in a montane conifer forest in the temperate zone and asked: 1) Are the characteristics of gap dynamics comparable with those of other temperate forests? 2) Do gap dynamics exhibit temporal trends, and 3) if so, are they related to recent climate change? We also addressed methodological issues concerning the differences observed at differing temporal and spatial scales of the used datasets. Thus, we asked further how the indices of gap dynamics are influenced 4) by differences in the length of observation periods and 5) by differences in gap size categories included in the study?

The study area was located in the near-natural *Picea abies* forests in the core zone of the Harz National Park on the north-eastern slopes of Mt. Brocken, Germany. From this area, aerial photographs from the last 60 yrs (1945, 1991, 2000, 2003) were analyzed by GIS techniques. Total gap area, number of gaps, gap size and area-based turnover rate, rotation time, gap formation and gap closure rate were calculated and correlated with climate variables.

The total gap area varied between 10.9 and 19.0 ha for the study area of 225.2 ha between the different years. Similarly, the median of the gap size was 155.6 m^2 and 87.0 m^2 in 1945 and 2003, respectively. A rotation time of 228 yrs was calculated for the study area. Area-based turnover rates and gap formation rates increased with time, while mean gap size decreased. The most frequently recorded gaps were those in the category < 100 m^2. In particular, small gaps at the level of single trees (≤ 40 m^2) became more frequent in the last decade and showed a higher gap formation rate than larger gaps. Temperature was significantly related to both turnover and gap closure rates.

In conclusion, for the near-natural spruce stands at Mt. Brocken indices of gap dynamics were of a magnitude comparable to those described from other forest types in the temperate zone. However, the indices of gap dynamics increased with time, which coincided with increasing temperatures over the last few decades.

Keywords

Aerial photographs; Disturbance; Gap dynamics; *Picea abies*; Turnover rate.

Chapter 3 – Interaction of gap age and microsite type for the regeneration of *Picea abies*

with Helge Bruelheide

Forest Ecology and Management 259, 1597-1605

3.1 Abstract

To assess the influence of gap age and microsite type within a near-natural montane Norway spruce stand at the Harz National Park in Germany, we tested the following hypotheses: (1) The relationship between *Picea abies* regeneration and gap age is represented by an optimum curve. (2) Within gaps, tree regeneration mainly occurs on gap-induced microsites. (3) The contribution of specific microsites to regeneration changes with gap age.

We randomly established 90 permanent plots stratified into three gap age classes as well as undisturbed forest to assess the density of gap-induced microsites (logs, stumps, root plates) and of microsites not related to disturbance (forest floor, moss-covered rocks) and recorded relative light conditions, spruce density and biometric variables.

We found significant differences in spruce regeneration between microsites as well as between undisturbed and disturbed plots. Sapling density was only related to microsite type, with the highest density being encountered on logs with 2.3 individuals/0.25 m^2, in contrast to moss-covered rocks with 1.8 individuals/0.25 m^2. Logs also ranked, together with root plates, highest in terms of sapling mortality. A larger density of young saplings on gap-induced microsites was compensated for by a higher mortality rate, probably due to self-thinning. In contrast, survival was highest on ordinary microsites, i.e. intact ground. Biometric variables differed significantly between microsites as individuals on ordinary microsites were taller than individuals on gap-induced microsites (94.21 ± 137.09 cm *versus* 39.86 ± 50.45 cm) and had more whorls (12.32 ± 10.55 *versus* 7.73 ± 6.79). Significant interactions between gap age class and microsite type were only evident in growth rates.

In conclusion, although gap-induced microsites enhance spruce establishment, their role in long-term regeneration has been widely overestimated when compared to the relevance of the ordinary microsites, in particular as the latter are permanent and do not depend on disturbances.

Keywords

Advance regeneration; Gap age classes; Microsites; Mortality; Mt. Brocken; Norway spruce.

Chapter 4 – Differences in frost hardiness of two Norway spruce morphotypes growing at Mt. Brocken, Germany

with Helge Bruelheide

Flora 206, in press

4.1 Abstract

Norway spruce (*Picea abies* (L.) Karst.) exhibits strong ecotypic variation along altitudinal gradients in morphological traits, e.g. slenderness of crowns or arrangement of second-order branches. We were interested whether montane and lowland morphotypes differ in a key trait for the survival in cold environments, i.e. frost hardiness, and asked: i) Are montane morphotypes more resistant to frost damage and ii) do they have a lower risk of frost damage by late frosts in spring than lowland morphotypes?

We used the electrolyte leakage-method to measure frost hardiness on a monthly basis from October 2006 - May 2007 in stands of the montane and lowland morphotypes at Mt. Brocken in the Harz Mountains, Germany.

LT_{50} (i.e. the temperature that results in 50 % of maximum electrolyte leakage) was assessed by freezing treatments in a frost chamber and was significantly influenced by morphotype, month and minimum ambient temperatures. LT_{50} was significantly lower in the montane than in the lowland morphotype, with -107 °C and -49 °C, respectively. However, the interactions between morphotype and minimum ambient temperature or month were not significant. Thus, as frost hardiness of the two morphotypes responded to temperature in the same way, both morphotypes can be supposed to be exposed to the same risk of frost damage during hardening in autumn and dehardening in spring.

Keywords

Ambient temperatures; Ecotypes, Electrolyte leakage; Frost injury; LT_{50}; *Picea abies*.

Chapter 5 – Spotting the difference – Using microsatellites for assigning Norway spruce trees and recruits to autochthonous and allochthonous provenances

with Helge Bruelheide

Manuscript, prepared for resubmission after 1. review, American Journal of Botany

5.1 Abstract

As forest management has a great impact on the genetic structure and diversity of *Picea abies*, we analyzed the impact of gene flow from planted spruce stands in the surroundings of old-growth forests with certified autochthonous trees on the genetic structure and diversity of recruits in these old-growth forests. We used microsatellite markers and discriminant analysis to answer the following questions: 1) Do planted Norway spruce stands show a lower genetic diversity than native, autochthonous stands? 2) Can specific alleles be used to distinguish planted, allochthonous individuals from autochthonous ones? 3) To which degree are natural recruits in gaps related to trees in the neighborhood or to planted stands? 4) Does genotype composition of recruits depend on age of cohorts?

The study was carried out in the Harz Mountains, Germany, including autochthonous trees in the core zone of the Harz National Park, recruits in gaps and individuals along the gaps' margins as well as in planted spruce stands in the surroundings of the core zone at a distance of 5 and 10 km.

We found that genetic diversity did not differ between planted and old-growth spruce stands, and only 2 % of molecular variance accounted for this difference. Nevertheless, planted individuals can be clearly discriminated from autochthonous individuals. Although recruits are mostly derived from trees in the surroundings of gaps, they show a high degree of introgression from planted stands. With increasing age, the proportion of autochthonous recruits increased, probably as a result of natural selection against allochthonous recruits.

Keywords

Discriminant analysis; Genetic diversity; Harz Mountains; Natural regeneration; *Picea abies*.

Chapter 6 – Overall discussion

6.1 Main results

The studies of forest gap dynamics on four different levels have been conducted in the core zone of the Harz National Park in Germany and revealed the following main results:

1) On the study area level, the indices of forest gap dynamics were in the range of other temperate forests and increased over the last decades.
2) On the plot level, gaps had a general positive effect on *Picea abies* regeneration, irrespective of gap age. However, gap-induced woody microsites were not characterized by a better growth of individuals compared to non-gap induced microsites or the ordinary forest floor.
3) On the physiological level, differences in morphology of *P. abies* were reflected in differences in maximum frost hardiness but not in differences in the seasonal course of frost hardiness.
4) On the molecular level, in contrast to expectation, planted and native, autochthonous spruce stands did not differ in genetic diversity. Moreover, the autochthonous stands showed introgression from spruce plantations. However, selection pressure in gaps acting on recruits probably results in a stable amount of autochthonous offspring from old-grown progenitors.

A detailed description of the investigated aims and the results found is given in Table 6.1.

Table 6.1: Objectives and main results of this thesis.

Objectives	**Main result**
Study area level: Characteristics and temporal trends of gap dynamics (**Chapter 2**)	
Comparison of gap dynamic indices at Mt. Brocken to those of other temperate forests.	Indices of gap dynamics were in the range of those from other temperate forests.
Assessment of temporal and spatial trends of gap dynamics.	The levels of gap dynamics as expressed for example by turnover rates increased with time, as did the proportion of small gaps.
Analysis of the relationship between gap dynamics with climate change.	Increasing levels of gap dynamics coincided with an increase in mean annual temperature.
Plot level: Effect of gap age and microsite type for the regeneration of Norway spruce (**Chapter 3**)	
Analysis of the relationship between gap age and density of Norway spruce recruits.	Gap age did not have a significant effect on density of spruce recruits.
Assessment of the contribution of gap-induced microsites to the regeneration of *P. abies.*	Saplings grew better on “ordinary” microsites than on gap-induced microsites.
Testing for interactions of gap age and microsite type.	No general interaction effect of gap age and microsite type was found.
Morphological level: Frost hardiness of the montane and of the lowland spruce morphotype (**Chapter 4**)	
Determination of differences in maximum frost hardiness between morphotypes	The montane morphotype was more frost resistant than the lowland morphotype.
Detection of seasonal differences in frost hardiness between both morphotypes.	Both morphotypes showed the same seasonal course in frost hardiness.
Molecular level: Genetic diversity of native spruce stands and genetically assignment of recruits (**Chapter 5**)	
Assessment of genetic diversity of native and planted spruce stands.	Genetic diversity did not differ between native, autochthonous and planted spruce stands.
Discrimination of native and plated spruce individuals.	Microsatellites and discrimination analysis allowed for differentiation between native and planted spruce individuals.
Assignment of recruits in gaps to native and planted spruce individuals.	Recruits were mostly derived from trees in the gaps’ surrounding and showed introgression from planted stands.
Dependency of genotype composition on age of recruit cohorts.	With increasing age of cohorts, the proportion of autochthonous recruits increased slightly.

6.2 Overall discussion

In the overall discussion I pay attention to the most important findings with a particular focus on the role of forest gap dynamics for the regeneration of *P. abies* in the natural spruce forests at Mt. Brocken and on the different scales observed.

6.2.1 The effects of forest gap dynamics on the regeneration of Picea abies ***(Chapter 2)***

The indices of forest gap dynamics measured at Mt. Brocken, i.e. rates of gap formation, gap closure and turnover, were comparable to other temperate forests. This can be illustrated by the turnover rate of 228 yrs at Mt. Brocken, which is perfectly in the range of values reported from Swedish spruce forests (170 - 228 yrs, Liu and Hytteborn, 1991), German beech forests (148 - 247 years, Meyer and Ackermann, 2004) or deciduous forests in Japan (58 - 240 yrs, Nakashizuka et al., 1992). This result was surprising since gap dynamics did not reflect the poor growth conditions: own dendrological measurements showed only low rates of stem increments. However, the turnover rates were comparable to results found by Stöcker (1997, 2001, 2002) in the same area. Stöcker (1997, 2001, 2002) investigated different development stages within the life span of Norway spruce and found that an entire development cycle including regeneration and initial phases, climax, aging and decay phases takes about 250 yrs to 325 ± 25 yrs to be completed.

It might be argued, that the recent increase of values of gap dynamics indices and the shift in gap size towards smaller gaps is caused by preceding land use in the study area, rather than by external drivers. Former land use in the area might comprise turf cutting (Wegener, 2001) and timber removal (Stöcker, 1997). Areas affected by such activities might show increased levels of gap dynamics because tree individuals at used sites share a similar age, and thus, might simultaneously enter a stage of senescence. However, after reviewing the available literature on the study area (e.g. Stöcker, 1997; Wegener, 2001; Wegener et al., 2003) the human impact had probably been rather marginal, because of hampered accessibility in many parts of the study area. An alternative explanation, and the one favored in Chapter 2, is a temperature-driven increase of gap dynamics over the last 60 years. On the one hand, increased temperatures elongate the growing season (Walther et al., 2002; Parmesan, 2006), with the effect of increased gap closure rates. On the other hand, elevated temperatures might lead to drought stress as a direct effect (Schlyter et al., 2006) and to an increase of bark beetles densities (Schlyter et al., 2006; Jönsson et al., 2007) as an indirect effect. Especially the latter one seems to be a decisive factor for gap dynamics as simulation studies revealed a strong increase of damages caused by bark beetles under climate change scenarios (Seidl et al., 2008). Furthermore, a possible result of the elevated temperatures might also be an increase of deciduous tree species at higher altitudes such as *Acer pseudoplatanus* and *Fagus sylvatica*, which have been recently forecasted for the Bavarian Forest, Germany (Müller-Kroehling et al., 2009). However, at the Harz National Park, and in particular in the core zone at Mt. Brocken, deciduous tree species are intensively browsed by deer (personal observations; Hlawatsch and Wegener, 1994), thus, the deciduous tree species are unlikely to become dominant with the current deer densities (Schönborn and Günther, 2010). However, successful management of the high deer densities provided, a consecutive increase of deciduous tree species would most probable lead to changes in the gap dynamic indices. Most notable, on the one hand, the size of single tree gaps would change as for example *Fagus sylvatica* has a higher mean crown projection area (118 m^2; Nagel, 1999) than *Picea abies*. On the other hand, the lateral growth of branches of trees existing at the gaps' margin is an important mechanism for supporting gap closure by beech (Meyer and Ackermann, 2004), which can be, however, neglected for Norway spruce.

To ensure the continuity of a forest ecosystem, the rates of gap formation and gap closure have to be balanced on the long-term run. This is the case for the old-growth spruce forest at Mt. Brocken, were the values of these indices were at the same range for the long-term interval of my analysis, i.e. between 1945 and 2003. It seems that the increased gap formation is counterbalanced by a sufficient gap closure, which might be secured by the presence of readily suitable microsites for regeneration in terms of moss-covered rocks and the ordinary forest ground. By colonization of these microsites, either directly after disturbances or independently of disturbance by advance regeneration a time lag in gap closure processes is unlikely. However, this does not apply to the gap-induced, woody microsites that have to decompose before regeneration can occur (Zielonka, 2006).

*6.2.2 The contribution of gaps and microsites for the regeneration success of Norway spruce **(Chapter 3)***

My study confirmed the positive effect of gaps for the regeneration of *P. abies*, which had been also demonstrated many times before (e.g. Silvertown and Doust, 1993; Kuuluvainen, 1994; McCarthy, 2001; Shorohova et al., 2009). However, against expectation, there was neither an effect of gap age on regeneration success in terms of density of individuals or of biometrical variables, such as number of whorls, nor an interaction between gap age and microsite type. One explanation for this finding might be a continuous establishment of spruce recruits over the full "life-time" of a gap. Establishment was not only confined to the time when woody, gap-induced microsites were sufficiently decomposed for colonization because non-gap induced microsites such as moss-covered rocks were permanently available for regeneration. This phenomenon counterbalances the relatively high mortality of Norway spruce seedlings and saplings, as it has often been observed (e.g. Granhus et al., 2008; Leemans, 1991). The mortality was especially pronounced on gap-induced microsites such as decaying logs, where highest initial seedling densities were found. This high seedling densities will suffer from high intra-specific competition because of shorter individual-to-individual distances (Stöcker and Wegener, 2006), and finally result in higher levels of self-thinning (White, 1981).

The continuous regeneration did not only occur in gaps but also in undisturbed forests, resulting in a high degree of advance regeneration. The establishment of young individuals under the closed canopy is a common phenomenon for *P. abies* (see the review of Metslaid et al., 2007). It is especially pronounced at Mt. Brocken, where the natural forest has a rather “open structure” even under closed canopy (Kirchner et al., 2009). Nevertheless, light intensity differed significantly between closed canopy and gaps. Therefore, the release of these suppressed individuals was pronounced after gap creation. In the category of youngest gaps, advance regeneration comprised about half of the seedlings. Although this is consistent with other studies (Kuuluvainen et al., 1998; Grassi et al., 2004), it does not secure their survival in a long-term perspective as only a low number of adult trees originate from advance regeneration.

Overall, gaps promoted the regeneration of *P. abies*. In contrast to the generally assumed importance of gap-induced microsites for regeneration, non-gap induced, ordinary microsites played a major role for Norway spruce regeneration at Mt. Brocken. This was pronounced in a lower mortality and higher growth rates on non-gap induced microsites.

6.2.3 Frost hardiness as a key trait for survival of Picea abies ***(Chapter 4)***

The continuity of an ecosystem does not only depend on the occurrence of appropriate regeneration sites but also on the survival of the established tree species. With regard to the old-growth spruce forest at the high altitudes of Mt. Brocken, a key trait for survival is the frost hardiness. As expected, the montane (native) morphotype was significantly more frost resistant than its lowland (planted) counterpart. Therefore, the montane morphotype was not only well adapted to harsh climatic conditions at high altitudes with regard to morphology (Greger, 1991; Geburek et al., 2008) but also with regard to physiology. These physiological differences might be determinated by differences in DNA sequences or based on epigenetic effects. Epigenetic effects are changes in gene function which are mitotically and/or meiotically heritable but not associated with changes in DNA sequences (Wu and Morris, 2001). Johnsen et al. (2005) hypothesized in their study on climatic adaptation in *P. abies* progenies that the temperature experienced during the zygotic embryogenesis and seed maturation regulates the “epigenetic memory” in the progenies. These epigenetic effects result in the different expression of genes that may regulate bud phenology and cold acclimation in Norway spruce (Johnsen et al., 2005). It had been demonstrated so far, that the environmental conditions experienced by parent trees during the time of flowering have been shown to exert a major impact on frost hardiness of progenies of *P. abies* (Johnsen et al., 1995, 1996). Johnsen et al. (1995) showed that progenies from the green house seed orchard were more susceptible to frost than their full-sibs from outdoor seed orchards. Thus, the epigenetic effects provide the opportunity for long-living individuals to cope with a changing environment.

The ability to adapt to changing environmental conditions is particularly crucial against the background of climate change with an expected increase in magnitude and frequency of weather extremes (Hundecha and Bárdossy, 2005) as well as a rise in minimum, maximum and mean temperatures (IPPC report, Solomon et al., 2007). In addition, longer, warmer and more numerous intermittent mild spells may occur, as well as temperature backlashes in spring, which might increase the incidence of frost injury (Hänninen et al., 2001). Against the expectation that montane morphotypes have a lower risk of frost damage by late frosts in spring than the lowland morphotype, both morphotypes showed the same seasonal course of frost hardiness including timing and rate of hardening and dehardening during autumn and spring. This leads to the conclusion that both morphotypes respond equally to dehardening temperatures in spring. In consequence, both morphotypes will be equally at risk to temperature backlashes in spring, which are forecasted with ongoing climate change (Walther et al., 2002). Hence, there is no evidence that the differences in frost hardiness will favor any of the two spruce morphotypes at Mt. Brocken under global climate change conditions.

*6.2.4 Genetic differences in Norway spruce and their implication for regeneration **(Chapter 5)***

Against expectation, the natural spruce forest at Mt. Brocken showed no higher genetic diversity than the planted spruce stands in the surrounding. This is mainly explained by a high amount of gene flow in this wind-pollinated tree species, which is in line with previous studies. For instance, the review of Hosius et al. (2006) pointed out that substantial restriction of gene flow is precluded by the rather continuous distribution range of Norway spruce. Consequently, only low levels of population differentiation have been encountered even at large geographical distances (Scotti et al., 2006). Another consequence of high levels of gene flow was the clear indications for introgression, as revealed by the discrimination analysis. Liesebach (1994) has already demonstrated with isozyme-analysis on Norway spruce that discrimination analysis can also be used for molecular analysis. Nevertheless, based on the successful discrimination among native and planted spruce individuals, result of the present study revealed that most recruits clearly differed from autochthonous progenitors.

However, with regard to gap dynamics, recruits in gaps were most closely related to the trees on the gaps' margin. The obvious explanation is a leptokurtic seed shadow with most seeds being dispersed near to the seed donor trees. This is in accordance with findings for an Italian subalpine stand of *P. abies*, where that spatially limited seed dispersal resulted in genetically more or less uniform patches (Scotti et al., 2008). Moreover, recruits in gaps showed slight differences in genetic diversity depending on the age of cohorts as the highest genetic diversity was found in cohorts with individuals younger than ten years. The decrease of genetic diversity points to a selection pressure that, in particular, acts on insufficiently adapted young spruce individuals. Presumably, the genetic variation in the young cohorts will also play a crucial role for adaptation in a changing environment of the forecasted climate change as discussed in the review of Pautasso (2009). This possibility of adaptation is decisive for individuals of long-living species such as trees. The results of the genetic study suggest that the recent recruits in the gaps are already the second or third generation of offspring that have been influenced by introgression from planted spruce stands. This means that also the seed donor trees along the gap margins have already gone through the same processes of introgression and selection. However, despite of introgression a certain number of clearly identifiable autochthonous recruits could be detected in all age classes of cohorts.

6.2.5 General conclusions and outlook

This study contributes to the general understanding of gap dynamics in an important coniferous forest ecosystem. Moreover, several findings of this thesis have been shown to be related to forecasted or already experienced climate change. Furthermore, it has been clearly demonstrated that microsites which are not related to disturbance can secure the regeneration success of Norway spruce. In the long run, the regeneration on these microsites has the potential to counterbalance a further increasing gap formation rate, which can be expected from direct and indirect effects of a temperature increase. The continuous regeneration in gaps will result in a multi-aged recruitment structure. Despite the considerable degree of introgression from planted, lowland spruce stands in the surrounding of the core zone, the montane morphotype with slender crown architecture and tightly packed branches, and as this thesis revealed, a high level of frost hardiness, does still occur in the study area. This might be explained by the fact that there are still individuals that are genetically closely related to the remaining autochthonous individuals or by an effective selection regime.

Nevertheless, the protection of this rare remnant of an old-growth spruce forest is of major priority. The rare autochthonous morphotypes and genotypes have to be protected in order to stop the loss of biodiversity. The preservation of biodiversity and endangered habitats and species is the major goal of the "Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora" of the European Union, which has been adopted in 1992. Moreover, with regard to forest stands the German Government has proclaimed within its "National strategy on biological diversity" (BMU, 2007) the aim to increase the area of near-natural managed forest and to conserve old-growth, natural forest by the year 2020. In this context, national parks will play a major role. The core zones of national parks such as on Mt. Brocken provide the unique opportunity to allow for and secure natural processes without human impact. Natural gap dynamics, for example, can occur or natural selection regimes can act on species. Moreover, the protection of these natural processes and preservation of the genetic identity of the autochthonous spruce genotype of the Harz Mountains does not only display the regional implementation of the "National strategy on biological diversity", but is also a major goal of the Harz National Park (Schönborn and Günther, 2010). Within this scope, the results of the present study increase the knowledge on mechanisms of natural processes in spruce forests and thus, may serve as a valuable contribution to their protection.

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Appendix

Curriculum vitae

Contact information

Name	Sabine Kathke (née Kammermeier)
Address	Felsenstr. 1 B 06114 Halle (Saale)

Personal details

Date of birth	12.10.1979
Place of birth	Regensburg
Nationality	German

Education

04/2005-05/2010	PhD thesis, Martin Luther University Halle Wittenberg Topic: The role of gap dynamics for the regeneration of the natural spruce forests in the Harz Mountains
10/1999-10/2004	Studies of Biology, Georg August University Göttingen Major subject: ecology, minor subjects: microbiology and geology Topic diploma thesis: Unterschiede in der Fundamentalen Nische der vier Waldgrasarten *Brachypodium sylvaticum, Hordelymus europaeus, Bromus ramosus* und *Bromus benekenii* in Bezug auf Licht und Feuchtigkeit
06/1999	Abitur, Jakob Grimm Schule, Rotenburg a. d. Fulda

Work experience

01/2010-present	Project coordinator: Military and nature conservation, Naturstiftung David Erfurt
11/2006-12/2009	Scientific assistant, Martin Luther University Halle Wittenberg
11/2004-08/2005	Research assistant, Martin Luther University Halle Wittenberg
04-07/2004	"Praktikum für die Umwelt", Biosphärenreservat Flusslandschaft Elbe-Brandenburg, Rühstädt
02/2002-07/2003	Research assistant, Georg August University Göttingen

List of publications

Publications in peer review journals

Kathke, S., Bruelheide, H., manuscript (1. review Am. J. Bot.). Spotting the difference – Using microsatellites for assigning Norway spruce trees and recruits to autochthonous and allochthonous provenances.

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Symposia contributions

Kathke, S., Bruelheide, H., 2009. The slender, the tougher – assessment of frost hardiness of high- and low-altitude morphotypes of Norway spruce. Proceedings of the GfÖ 39, 11. Oral presentation.

Kammermeier, S., Bruelheide, H., 2007. “All things change, nothing is extinguished” – gap dynamics of a montane spruce forest. Proceedings of the GfÖ 37, 171. Oral presentation.

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Kammermeier, S., Bruelheide, H., 2007. Slow growth, fast changes: gap dynamics of a montane spruce forest. IAVS Abstracts 50, 14. Oral presentation.

Kammermeier, S., Bruelheide, H., 2006. Gap dynamics in natural spruce forests – a long-term study using aerial photographs. Proceedings of the GfÖ 36, 171. Oral presentation.

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Kammermeier, S., Luginbühl, U., Bruelheide, H., 2005. Correspondence of fundamental and realized niche of four woodland grass species. Proceedings of the GfÖ 35, 337. Poster.

Kammermeier, S., Luginbühl, U., Bruelheide, H., 2005. Experimental testing for fundamental niche in four woodland grass species after windthrow. AVS Abstracts 48, 100. Poster.

Kammermeier, S., Luginbühl, U., Bruelheide, H., 2003. Experimental approach to explain the differential response of four woodland grass species after windthrow. Proceedings of the GfÖ 33, 254. Poster.

Halle, den 20. Mai 2010

Sabine Kathke

Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel "**The role of gap dynamics for the regeneration of the natural spruce forests in the Harz Mountains"** bisher weder der Mathematisch-Naturwissenschaftlich-Technischen Fakultät der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht.

Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle, den 20. Mai 2010

Sabine Kathke