

The importance of gap dynamics for the reproduction of clonal plant species in natural forests in the Harz National Park

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Summary

In near-natural forests that are not managed by forestry, gap dynamics are a natural driver of structural heterogeneity. While most studies have focused on the impact of disturbances brought about by gap dynamics the responses on the canopy species in a wide range of forest types, the effects on species of the herb layer have been largely neglected in the past. This is surprising, considering that herb layer species contribute up to 80% of plant species richness in forests and are known to affect tree species recruitment

In the present PhD thesis, I investigated the response of herb layer species of a near-natural spruce forest on Mt. Brocken, Harz National Park, Germany. Disturbance, mainly driven by wind and bark beetle infestation in this forest, creates canopy gaps and increases the structural heterogeneity of the forest floor. In addition to already existing microsites, such as ordinary forest ground and moss-covered rocks (i.e. non-gap-induced microsites), new microsites such as logs, stumps and root plates (i.e. gap-induced microsites) are created. However, these newly created microsites have to decompose before becoming suitable for settlement of vascular plant species, due to a shortage in water and minerals in freshly fallen trees. Beside higher structural heterogeneity, also the environmental conditions (mainly light availability) are improved in gaps compared to undisturbed forest. Before the background of ongoing climate change, the investigation of gap dynamics is becoming increasingly important, as it is not well-known how increasing temperatures will interact with the provision of new microsites and how uniformly different species will respond.

Most of forest herb layer species display clonal growth, as do the three investigated species of the present PhD thesis (*Trientalis europaea*, *Calamagrostis villosa* and *Vaccinium myrtillus*). The present PhD thesis has two overarching hypotheses. (1) The growth and clone sizes of the target species depend on gap age. More specifically, I tested whether mid-successional gaps were the optimum for clone size and ramet density. In particular, I expected larger and denser clones in gaps than in undisturbed forest. (2) Environmental conditions play a major role for growth of species. While increasing light availability enhances the abundance and the growth of herb layer species, the microsite availability is highest in mid-successional gaps and reduced in later stages of gap

development because of reduced light resources and increased competition. On the contrary, higher temperature and lower precipitation as a result of global climate change will have detrimental effects on the investigated species.

Although, all three investigated species grew better in gaps compared to undisturbed forest. However, an optimum in mid-successional gaps was only detected for *T. europaea* and *V. myrtillus*. All three target species showed a positive relationship to light availability. Additionally, the microsite availability and species establishment on microsites differed between different gap age classes and undisturbed forest. In contrast to young gaps, where species preferred non-gap-induced microsites, this preference changed to gap-induced microsites in older gaps.

Finally, global climate change effects, as tested in a common garden shading experiment at different altitudes, turned out not to be detrimental for all three target species. Quite on the contrary, *C. villosa* seemed to have profited from higher temperature and lower precipitation.

In conclusion, I showed for the investigated species, that gap age is not as important as gap existence. Consequently, higher light availability and higher structural heterogeneity increased the abundance and growth of *T. europaea*, *C. villosa* and *V. myrtillus*. Thus, these species clearly benefited from gap dynamics, and presumably will continue to do so under future climate change.

Zusammenfassung

Die strukturelle Heterogenität wird in naturnahen Wäldern, also Wäldern ohne forstliche Einflüsse des Menschen, hauptsächlich durch Lückendynamik bestimmt.

In der Vergangenheit wurden bereits zahlreiche Studien zur Lückendynamik sowie über die Reaktionen von Baumarten auf Störungen in verschiedensten Waldarten der Welt durchgeführt. Überraschend jedoch ist, dass Krautschichtarten trotz ihrer hohen Artenzahl bisher eher vernachlässigt wurden. Diese tragen bis zu 80% zu der Gesamtdiversität von Wäldern bei und können die Regeneration von Bäumen beeinflussen.

In der vorliegenden Dissertation habe ich die Reaktionen von Krautschichtarten in einem naturnahen Fichtenwald am Brocken im Nationalpark Harz in Deutschland untersucht. Störungen, die im Untersuchungsgebiet hauptsächlich durch Wind oder Borkenkäferbefall hervorgerufen werden, bilden Lücken im Kronendach des Waldes und erhöhen die strukturelle Heterogenität des Waldbodens. In ungestörten Bereichen des Fichtenwaldes am Brocken dienen moosbedeckte Felsen und normaler Waldboden (nicht durch Lücken hervorgerufene Mikrostandorte) der Regeneration von Waldarten. In Lücken jedoch, bereichern neue Mikrostandorte, wie zum Beispiel liegendes Totholz, Baumstümpfe oder Wurzelteller (durch Lücken hervorgerufene Mikrostandorte) den Waldboden. Bevor diese neu gebildeten Standorte allerdings der Regeneration von Krautschichtarten dienen können, müssen die frisch gefallenen Bäume erst verrotten, da sie zu wenig Wasser und Nährstoffe zur Etablierung von Arten enthalten. Neben einer höheren strukturellen Heterogenität sind auch die Umweltbedingungen, insbesondere die Verfügbarkeit von Licht, im Vergleich zu ungestörten Waldbereichen in Lücken verändert. Vor dem Hintergrund des bestehenden Klimawandels ist die Untersuchung von Lückendynamik besonders wichtig, da die Interaktion zwischen steigenden Temperaturen und der Bildung von neuen Mikrostandorten, sowie die Reaktion der einzelnen Arten unter gegebenen Umständen bisher noch nicht verstanden ist.

Wie die meisten Waldarten vermehren sich auch die untersuchten Krautschichtarten (*Trientalis europaea*, *Calamagrostis villosa* und *Vaccinium myrtillus*) in der vorliegenden Arbeit vorwiegend durch klonales Wachstum.

In meiner Dissertation stelle ich zwei übergeordnete Hypothesen auf. (1) Das Wachstum und die Klongrößen der untersuchten Arten hängen vom Lückentalter ab. Im Besonderen habe ich untersucht, ob Lücken mittleren Alters die optimalen Bedingungen bezogen auf Klongröße und Sprossdichte darstellen. Ich erwarte größere und dichtere Klone in Lücken als im ungestörten Wald. (2) Für das Wachstum der Arten sind die Umweltbedingungen entscheidend. Mit höherer Lichtverfügbarkeit wird sowohl die Abundanz als auch das Wachstum der untersuchten Krautschichtarten gefördert. Im Gegensatz dazu ist die Verfügbarkeit von Mikrostandorten für die Regeneration am höchsten in Lücken mittleren Alters, da mit fortwährendem Lückenschluss die Lichtverfügbarkeit wieder abnimmt, während die Konkurrenz zwischen und innerhalb der Arten zunimmt. Steigende Temperaturen und geringere Niederschlagsmengen im Zusammenhang mit Klimawandel haben einen negativen Einfluss auf die untersuchten Arten.

Obwohl alle drei Zielarten besser in Lücken als im ungestörten Wald wuchsen, konnte ein Optimum in Lücken mittleren Alters nur für *T. europaea* und *V. myrtillus* aufgezeigt werden. Alle untersuchten Krautschichtarten zeigten ein besseres Wachstum bei höherer Lichtverfügbarkeit. Des Weiteren waren die Mikrostandortverfügbarkeit und die Etablierung der untersuchten Arten auf den Mikrostandorten in den verschiedenen Lückentalterklassen und ungestörtem Wald unterschiedlich. Im Gegensatz zu jungen Lücken, in denen sich Arten hauptsächlich auf nicht durch Lücken hervorgerufenen Mikrostandorten regenerieren, verschiebt sich diese Präferenz in älteren Lücken eher zu solchen Mikrostandorten, die erst durch Störungen hervorgerufen wurden. Der globale Klimawandel, der in einem Schattierungsexperiment in botanischen Gärten in verschiedenen Höhenlagen simuliert wurde, scheint keinen negativen Einfluss auf die untersuchten Krautschichtarten zu haben. Im Gegenteil, *C. villosa* profitiert wahrscheinlich sogar von höheren Temperaturen und geringerer Niederschlagsmenge.

Zusammenfassend konnte ich für die untersuchten Arten zeigen, dass das Vorhandensein von Lücken wichtiger ist als deren Alter. Demzufolge steigerten auch erhöhte Lichtverfügbarkeit und höhere strukturelle Heterogenität die Abundanz und das Wachstum von *T. europaea*, *C. villosa* und *V. myrtillus*. Da diese Arten klar von der Lückendynamik profitieren, ist anzunehmen, dass sie dies auch mit dem zukünftigen Klimawandel tun werden.

1 Introduction

The herb layer of forests has been often neglected in studies of forest ecology owing to its low contribution to the overall biomass (less than 1%) and to the above-ground net primary productivity (less than 5%, Muller 2003). In contrast, the herb layer accounts for more than 80% of the whole plant species richness of forests (McCarthy 2003, Gilliam 2007). Additionally, after disturbances the understorey species are able to influence the species composition of the tree layer (Gilliam 2007). A dense understorey can suppress the regeneration of tree species by resource competition and allelopathy (Royo & Carson 2006) or by physical inhibition (Connell & Slatyer 1977). For instance, a dense fern layer of *Dennstaedtia punctilobula* was found to constrain the regeneration of two *Betula* species in mixed deciduous forests in central Massachusetts by reducing light availability to 1% of full sunlight (George & Bazzaz 2003).

Usually, the herb layer benefits from disturbance which is defined in the present study as a relatively discrete event, annihilating ecosystem, community or population structure accompanied by changed resources, substrate availability or physical environment according to White & Pickett (1985). The consequences of all types of disturbances in the forest tree layer are canopy gaps. Depending on gap size, three main mechanisms of gap closure can be distinguished. First, the lateral ingrowth of branches of trees on the gap edge is a mechanism that closes only very small gaps and, thus, compensates the mortality of single trees (Runkle 1985). The second way of gap closure is the growth of sapling or individuals present in the herb layer already before gap creation (advance regeneration). The term describes the phenomenon that tree seedlings and saplings were established under canopy prior to gap creation and remain in a suppressed status until gap creation results in changed environmental conditions (e.g. higher light availability, more space, changed competition regime; Metslaid *et al.* 2007). However, this phenomenon also applies for herb species. For instance, *Uvularia perfoliata* produced significantly more clonal offspring in gaps than in undisturbed forest in a deciduous forest in the USA (Wijesinghe & Whigham 1997).

The third mechanism of gap closure is the colonisation of herb layer species by seed input from the surrounding area or by germination from the soil seed bank (Naaf & Wulf 2007). One mechanism of seed input is seed dispersal by endozoochory of large mammals in

forests as for instance the wild boar (*Sus scrofa*). For example, a high amount of *Vaccinium myrtillus* seeds was found in the faeces of *S. scrofa* by Schmidt *et al.* (2004) in forests in Northern Germany.

1.1 Temporal dimensions of gap dynamics

The time required to close gaps is determined by gap size but also by climatic conditions. In addition, the type of forest ecosystem has been shown to influence gap dynamics. For instance, gap closure in temperate coniferous forests is slower than in tropical forests with a mean annual gap closure rate of 0.3% and 0.5%, respectively (Fujita *et al.* 2003, Kathke & Bruelheide 2010a). An index of gap dynamics often used in literature is the turnover rate in years, which is defined as the mean time between two disturbance events (White & Pickett 1985). Similarly to the gap closure rate, temperate coniferous forests exhibit the slowest turnover rates (650 years) in contrast to temperate hardwood and tropical forests with high turnover rate (134 years and 137 years, respectively) reviewed by McCarthy (2001).

Gap dynamics are also fundamentally influenced by the type of disturbance. These types are very manifold, ranging from natural disturbances as fire, storm, pathogens or flooding to human impacts such as clear-cuts or deforestation (Attiwill 1994). It was also demonstrated that gap closure time differs with regard to the type of disturbance (Stewart *et al.* 1991). In addition, the severity within disturbance types might vary, e.g. storms that disturb only small parts of forests and kill only old and frail trees as compared to intense large-area storms that blow down a huge forest stand (Everham & Brokaw 1996). Depending on disturbance type and gap closure time, the time for establishment of herb layer species differs (“windows of opportunity”, Eriksson & Fröborg 1996).

Due to its immense impact on light availability the creation of gaps has a strong direct influence on the herb layer species in the forest (see Chapter 2 and 4). For instance, when a species has been detrimentally affected by a disturbance event a functionally equivalent species might get the chance to establish or expand in abundance or coverage (resilience hypothesis according to Walker *et al.* 1999). Additionally, the creation of gaps increases the spatial heterogeneity and therefore also the species richness (intermediate heterogeneity hypothesis according to Beatty 2003). However, beneficial impact of

heterogeneity shows a peak in species richness, as at extreme levels of heterogeneity physical limitations may exclude species (Beatty 2003).

Finally, also knowing the time since disturbance (i.e. gap age) is necessary for investigating herb layer response to disturbances (De Grandpré *et al.* 2011). Within a newly created gap, especially understorey clonal species have the chance of establishing new genets. As the competition intensity with other species is reduced directly after gap creation (Suding 2001), these new genets have the opportunity to expand laterally. With increasing gap age these newly established genets expand in both directions, inward and outward, and therefore older clones are also denser than younger clones. In the course of time, the outward expansion of clones is limited by gap closure. Additionally, the inward expansion is also restricted by increasing intra-specific competition (Scheepens *et al.* 2007). Only in rare cases it is possible to assess the dimensions of a clone by morphology and it is error-prone for large clones (Oinonen 1967). Therefore, Molecular fingerprinting methods allow determining of clonal diversity and clone sizes exactly (Escaravage *et al.* 1998). However, also with fingerprinting methods sources of bias are somatic mutations (Klekowski 2003) only can be overcome by spatial mapping of genotypes (Chung & Epperson 1999, Ziegenhagen *et al.* 2003, Vonlanthen *et al.* 2010). In the present study, I used the AFLP (amplified fragment length polymorphism) method for spatial mapping of clones of two herb layer species (*Trientalis europaea* and *Calamagrostis villosa*, see Chapter 3).

1.2 Gap dynamics in interaction with environmental factors

The investigation of gaps and their influence on herb layer species cannot be achieved without considering environmental factors. Microclimatic conditions differ significantly between forest gaps and undisturbed forest (Latif & Blackburn 2010). Furthermore, in a coniferous forest, in contrast to a deciduous forest, these differences persist over the whole year. Light availability is the main environmental variable that changes drastically with gap creation and also with gap age (i.e. the time since gap creation, see Fig. 1.1). The understorey of mixed undisturbed forests is characterised by a mean light availability (photosynthetically active radiation) of less than 2% of daylight while gaps provide 37-68% of the full sunlight (Canham *et al.* 1990, Neufeld & Young 2003). As light is a key resource, species have higher growth rates in gaps than in undisturbed forest, which was

shown for instance for *Primula vulgaris* in a deciduous temperate forest in Britain (Valverde & Silvertown 1998). Additionally, the shoot density increases with higher light availability (Sammul *et al.* 2004).

In the present study, I investigated the impact of light availability on three species of the herb layer (*T. europaea*, *C. villosa* and *Vaccinium myrtillus*) under natural conditions (Chapters 2, 3 and 4) as well as under experimental conditions (Chapter 5) in a near-natural spruce forest in the Harz National Park on Mt. Brocken, Germany. Light availability as key environmental factor was addressed in three different ways. First, in Chapters 2 and 4 I studied the coverage of my target species under different light conditions in the field. Similarly, I determined clone sizes using a molecular fingerprinting method and related them to light (Chapter 3). Finally, a common garden experiment was conducted with shading boxes simulated different light availability and growth parameters as for instance, biomass, specific leaf area or response to herbivory (Chapter 5).

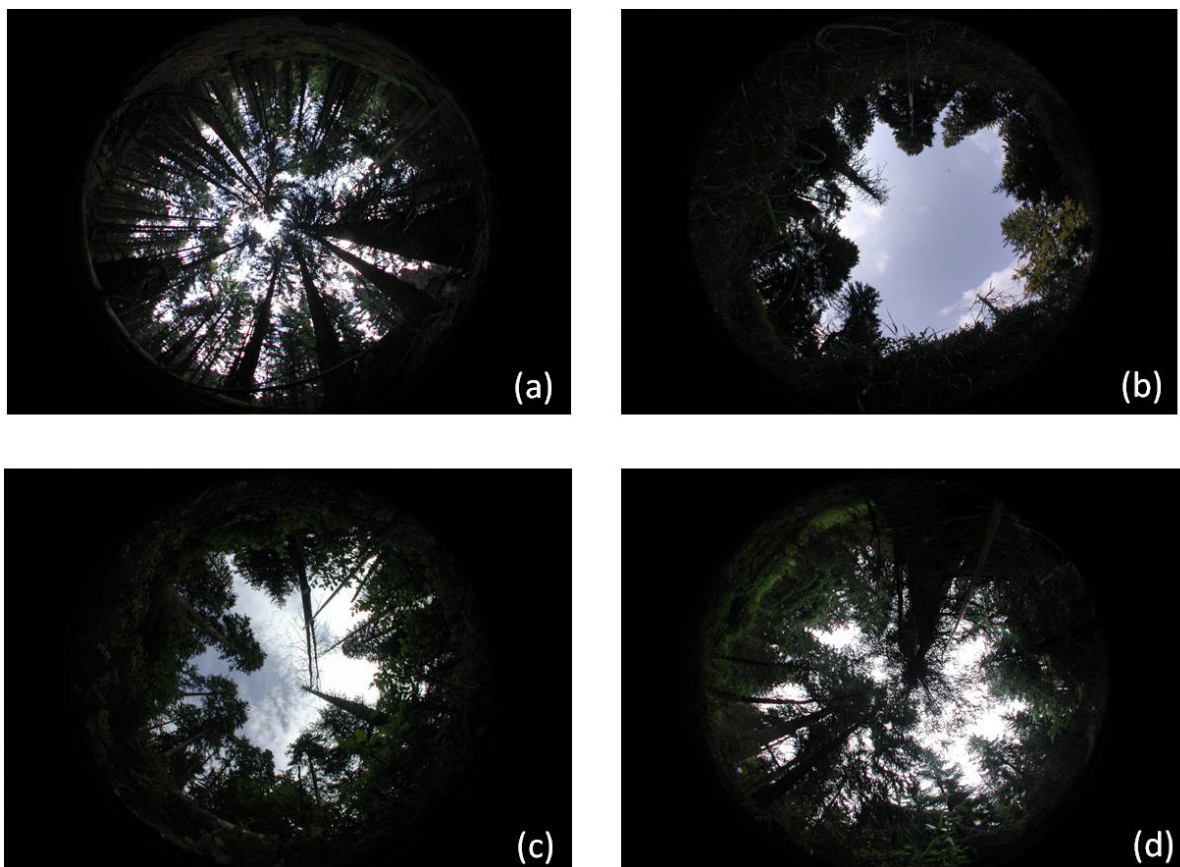


Fig. 1.1 Examples of relative light availability for understory species in (a) undisturbed forest (14.4%), (b) young gaps (< 15 yrs, 46.3%), (c) intermediate aged gaps (15-60 yrs, 30.7%) and (d) old gaps (> 60 yrs, 21.8%) in the near-natural spruce forest on Mt. Brocken.

Besides differences in light availability, gaps and closed forests also differ in other site factors. For example, soil and air temperature tend to be higher in gaps and to fluctuate to a greater extent (Brokaw 1985). Additionally, soil moisture changes with gap creation (Brokaw 1985).

A further aspect of gap creation is the appearance of new structures on the forest ground. With tree death or wind throw additional microsites become available for colonisation by herb layer species. In the montane spruce forests studied here, moss-covered rocks and ordinary forest ground are prevalent under undisturbed canopies (i.e. non-gap-induced microsites, Fig. 1.2) while gap creation results in increased small-scale heterogeneity brought about by microsites like logs, stumps or root plates (i.e. gap-induced microsites, Fig 1.3).



Fig 1.2 Non-gap-induced microsites (a) ordinary forest ground and (b) moss-covered rock in undisturbed forest on Mt. Brocken.



Fig. 1.3 Gap-induced microsites (a) log, (b) stump and (c) root plate in the near-natural forest on Mt. Brocken.

However, due to the lack of water and minerals on recently fallen trees these microsites are not immediately available for species after gap creation (Zielonka & Piątek 2004). On Mt. Brocken, I investigated at what time newly created microsites become suitable sites for establishment of herb layer species (Chapter 4).

1.3 Gap dynamics in the context of global climate change

With ongoing global climate change, gap dynamics might undergo changes and gain even more importance for the entire forest ecosystem (see Chapter 5). It has been demonstrated that temperature on Mt. Brocken rose in the last years, while simultaneously disturbance frequency increased (Kathke & Bruelheide 2010a). With rising temperature and higher evapotranspiration, water availability for species can be assumed to decrease. Furthermore, in accordance with climate change, the summer precipitation

is predicted to decrease and consequently, summer drought will increase in the study area (Meehl *et al.* 2007). The species in our study area are probably well adapted to the cold and wet climate on Mt. Brocken. Therefore, the probability of detrimental effects of climate change on these species can be considered very high, as especially temperature fluctuations are higher in gaps compared to undisturbed forest (Ritter *et al.* 2005). An additional aspect of climate change, in particular of higher temperatures and prolonged vegetation period, is an increasing abundance of herbivores and their effect on plant species (Roy *et al.* 2004).

1.4 Study area

Near-natural coniferous forests, which are characterised by the absence of forest management, mature structural and functional characteristics, are rare in Europe, especially because since millennia Central Europe has been densely settled, cultivated and industrialised (Peterken 1996).

One small remnant of such old-growth spruce forests is located on the north-eastern slope of Mt. Brocken in the Harz Mountains in Germany (Fig. 1.4). Causes of the naturalness are, on the one hand, the very low human impact in former times due to inaccessibility of the area and, on the other hand, the appointment as a nature reserve in 1937 and a National Park in 1990 (Wegener & Kison 2002).



Fig. 1.4 Near-natural forest on Mt. Brocken, Harz Mountains, Germany.

The study area of the present investigation (with an area of 2.25 km²) is located in the Harz National Park on the north-eastern slope of Mt. Brocken (51°48'02"N, 10°37'02"E) in the centre of Germany (Fig 1.5). The Harz Mountains are the northernmost mountain range in Germany with an area of circa 2000 km². One peculiarity of Mt. Brocken (the highest peak of the Harz Mountains) is its exposed location. High wind speeds of 6-7 Beaufort (40-60 km h⁻¹) in winter and 5 Beaufort in summer are usual (Wegener & Kison 2002). In addition to high wind speed, high air humidity is prevalent indicated by 300 foggy days on Mt. Brocken and circa 171 frost days (i.e. daily minimum temperature below 0°C). According to long term weather records, July and August are the only frost free months. Furthermore, there is a low mean annual temperature of 3.1°C and a mean annual precipitation of 1727 mm (Deutscher Wetterdienst). Due to the exposed location the vegetation altitudinal belts are narrower than in other mountain ranges at the same altitude (Hartmann & Schnelle 1970). Whereas the natural timberline in the Alps is at 1800 m a.s.l., the timber line of Mt. Brocken is encountered already at 1100 m a.s.l.; therefore my study area, which is located between the contour lines of 900 to 1050 m

a.s.l., is arranged in the orol altitudinal belt (Pflume & Bruelheide 1994). Due to the exposure and the climate, main disturbance factors occurring at Mt. Brocken are storms or pathogens (personal observation, Kathke & Bruelheide 2010a). In particular, bark beetle (*Ips typographus*) can strongly affect forest development by outbreaks (Veldmann 2000) and, thus, inflict severe detrimental impact. The gap sizes induced by wind, pathogens or natural death of trees on Mt. Brocken range from very small gaps with sizes of only a few square meters to gaps with sizes over 16 000 m². In the present study, I investigated gaps with a minimum size of 100 m² only and therefore neglected gaps caused by single tree mortality (see Chapter 2).

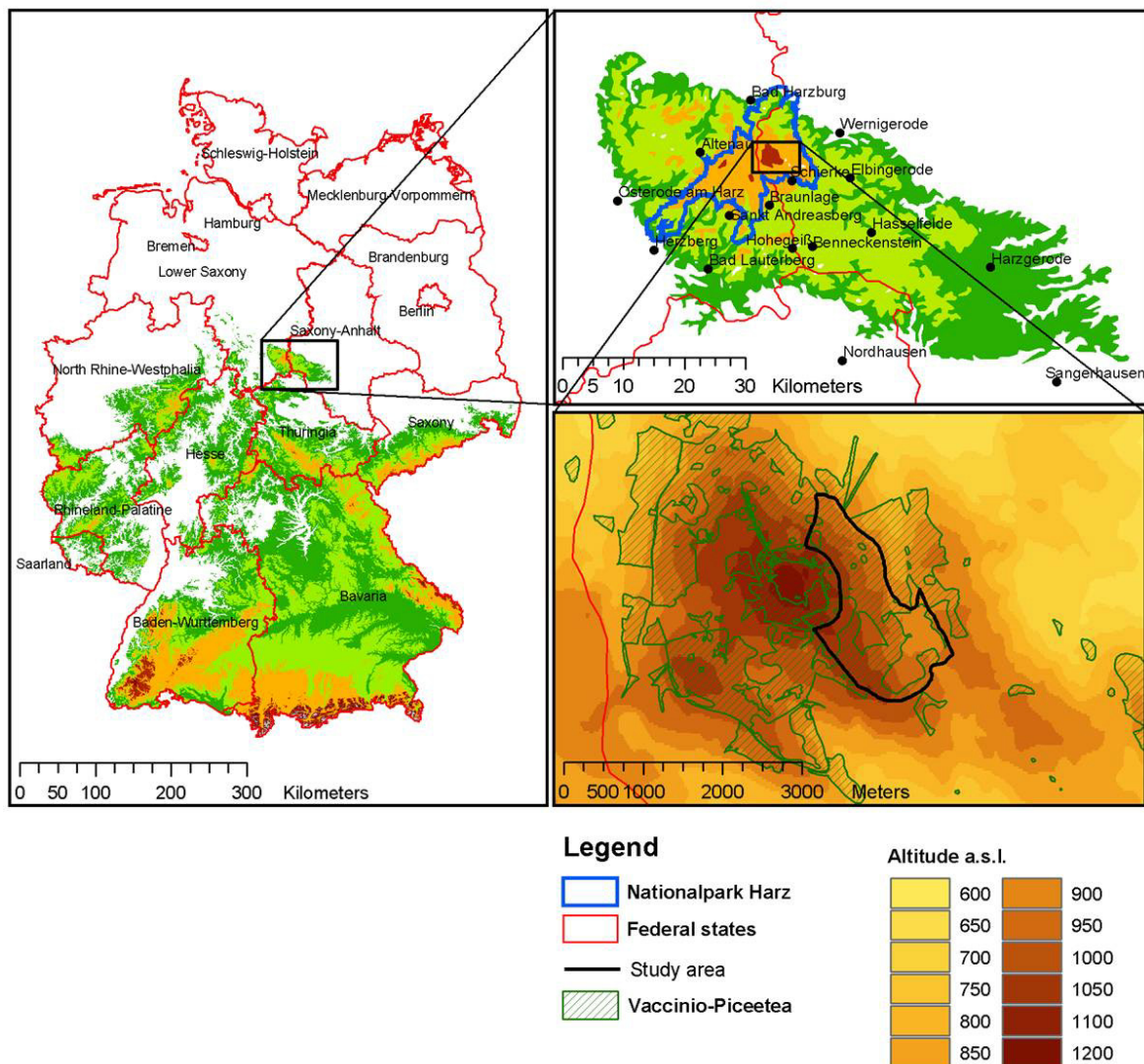


Fig. 1.5 Map of the study area (designed by Erik Welk).

Geologically, Mt. Brocken consists of granite and thus nutrient poor soils with a low soil depth and low soil acidity around of pH 3-4 (Kirchner, unpublished data) are prevalent in the study area. In consequence of the nutrient-poor acidic soils, species diversity in this spruce forest is low with only one dominating tree species (*Picea abies*). Similarly, the herb layer is characterised by low species numbers, reproducing mostly, as usual in forests, vegetatively (Klimeš *et al.* 1997). Two grass species (*Deschampsia flexuosa* and *C. villosa*) occur with high dominance, several herb species (mainly *Galium saxatile*, *T. europaea* and *Oxalis acetosella*), a few fern species (e.g. *Dryopteris carthusiana*) as well as some dwarf shrubs (e.g. *V. myrtillus*, for a species list see Chapter 4) can be found.

Consequently, the prevalent association is the *Calamagrostio villosae-Piceetum* (R. Tx. 1937) Hartm. ex Schlüt. 1966 (Karste *et al.* 2006). The climatic conditions on Mt. Brocken and the surface morphology promote formation of fens (Damm 1994, Wegener & Kison 2002). In flat places, swamp forest communities such as the *Bazzanio-Piceetum* Br.-Bl. et Siss. 1939 in Br.-Bl. et al. 1939 and fen communities such as the *Sphagno-Eriophoretum angustifoliae* (Hueck 1925) R. Tx. 1958 em. Succ. 1974 nom. inv. are frequent (Karste *et al.* 2006). In contrast to the *Calamagrostio villosae-Piceetum*, these plant communities are more diverse, with species such as *V. vitis-idaea*, *V. uliginosum*, *Eriophorum angustifolium*, *E. vaginatum*, *Sphagnum spp.* and *Carex spp.* (Wegener & Kison 2002).

1.5 Study species

I investigated three species with different life forms occurring in the herb layer of the near-natural spruce forest on Mt. Brocken (herb: *Trientalis europaea* L., grass: *Calamagrostis villosa* (Chaix.) J. F. Gmel., dwarf shrub: *Vaccinium myrtillus* L.).

Formerly assigned to the Primulaceae, recent studies have grouped *T. europaea* into the Myrsinaceae, also a “primoluid” family in the Ericales s.l. (Källersjö *et al.* 2000, Morozowska *et al.* 2011). However, in the following chapters I used the nomenclature of species according to Rothmaler (2005) and classified *T. europaea* as Primulaceae. The genus *Trientalis* consists of two species. The congeneric species of *T. europaea* is *T. borealis*, distributed in North America, whereas *T. europaea* is distributed in northern Europe and southwards in mountains to Corsica. *Trientalis europaea* is a small perennial herb with a height of 10 to 15 cm, white heptamerous flowers and black seeds, held together by a white thin membrane as a “ball”, which outlast several months until

separation (Matthews & Roger 1941, cited in Taylor *et al.* 2002). Germination of *T. europaea* seeds was found to be very low in the nature (Hiirsalmi 1969, Chapter 2), hence the preferred reproduction type is vegetative propagation by stolons. A peculiarity of *T. europaea* is the pseudoannual life form described by Krumbiegel (2001). Ramets of this species die after one growing season but prior to that create understorey overwintering tubers. Therefore, the stolons which connect several ramets are ephemeral (Taylor *et al.* 2002). In the following growing season, these tubers produce single stems with four to eight leaves and one to two flowers.

The second target species was the Poaceae *C. villosa*. The genus *Calamagrostis* consists of 266 species worldwide, with most species being distributed in South America (100 species) and only 15 species in Europe (Clayton *et al.* 2006). *Calamagrostis villosa* is mainly distributed in montane mountain ranges of Central and Southeast Europe (Meusel *et al.* 1965, Koppisch 1994) and due to its dominance, *C. villosa* is associated with only a few other species in their habitats (Fiala 2000). In the hercynian section of the distribution range, *C. villosa* is closely linked to the natural occurrence of *Picea abies* (Fiedler & Höhne 1987) and prefers moist, acid and nutrient poor soils (Koppisch 1994). *Calamagrostis villosa* is a rhizomatous, perennial species with summer-green leaves, forming a dense lawn with two types of rhizomes, those with and those without internodes (Schretzenmayr 1970, cited in Fiedler & Höhne 1987). Especially the rhizome type without internodes and with many buds forms dense mats in the soil. The unbranched culms of *C. villosa* attain a length of 50 to 150 cm (Clayton *et al.* 2006) and many of them are sterile. The flowering time of *C. villosa* is in July and August (Klotz *et al.* 2002), though flowering in the shadow is rare (Schretzenmayr 1970, cited in Fiedler & Höhne 1987). Therefore, the reproduction occurs mainly vegetatively by rhizomes.

Finally, the third target species was *Vaccinium myrtillus* (Ericaceae). The genus *Vaccinium* includes around 400 species worldwide and some of them are native on all continents except Antarctica and Australia (Luby *et al.* 1991, cited in Ballington 2001). *Vaccinium myrtillus* is a deciduous, rhizomatous dwarf shrub with a height of 10 to 60 cm and angular (young) to terete (old) shoots. The species prefers acidic soils in woodlands, heaths and bogs (Ritchie 1956, Flower-Ellis 1971). The broad range of ecological tolerance (e.g. on temperature and light availability) was shown by Timoshok (2000) in Western Siberia and might explain its wide distribution range. *Vaccinium myrtillus* reproduces in

accordance to the other two target species mainly vegetatively by rhizomes (Albert *et al.* 2003), whereas seedlings are rare in nature (Ritchie 1956). Flowering occurs in spring and early summer and flowers are both insect- and self-pollinated. The berries of *V. myrtillus* are dark blue, fleshy and contain on average 18 seeds per berry (Ritchie 1956) and are dispersed by birds or mammals (Honkavaara *et al.* 2007).

1.6 Thesis objectives and outline of the study

The present study deals with the response of herb layer species (i.e. *T. europaea*, *C. villosa* and *V. myrtillus*) in a near-natural spruce forest to gaps created mainly by wind and insect infestation. I investigated this response in different ways. At first, I observed responses under natural conditions directly in the study area. Then, I investigated the species with molecular genetic tools to find differences between individuals from undisturbed and disturbed forest stands. Finally, one aim was to study the possible response to gap dynamics in the future against the background of global climate change.

Therefore, two overarching hypotheses were tested in the present PhD thesis:

1. The growth and clone sizes of the target species depend on gap age. More specifically, I tested whether mid-successional gaps were the optimum for clone size and ramet density. In particular, I expected larger and denser clones in gaps than in undisturbed forest due to reduced competition (Fig. 1.6).

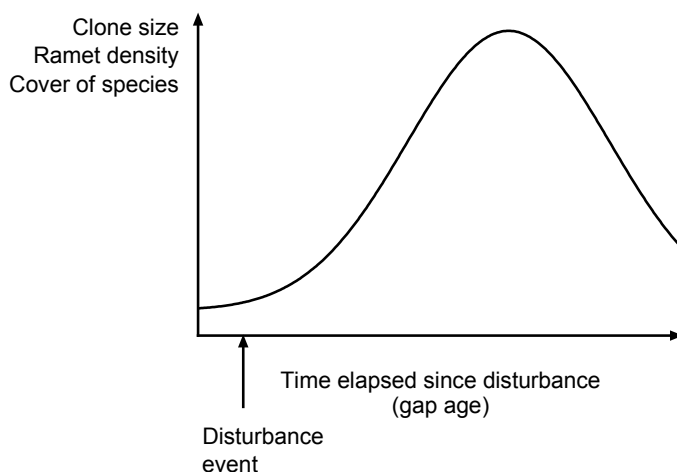


Fig. 1.6 The relationship between time (i.e. gap age) and species growth variables.

2. Environmental conditions play a major role for growth of species. While increasing light availability enhances the abundance and the growth of herb layer species, the microsite availability is highest in mid-successional gaps. On the contrary, higher temperature and lower precipitation as a result of global climate change will have detrimental effects on the investigated species (Fig. 1.7).

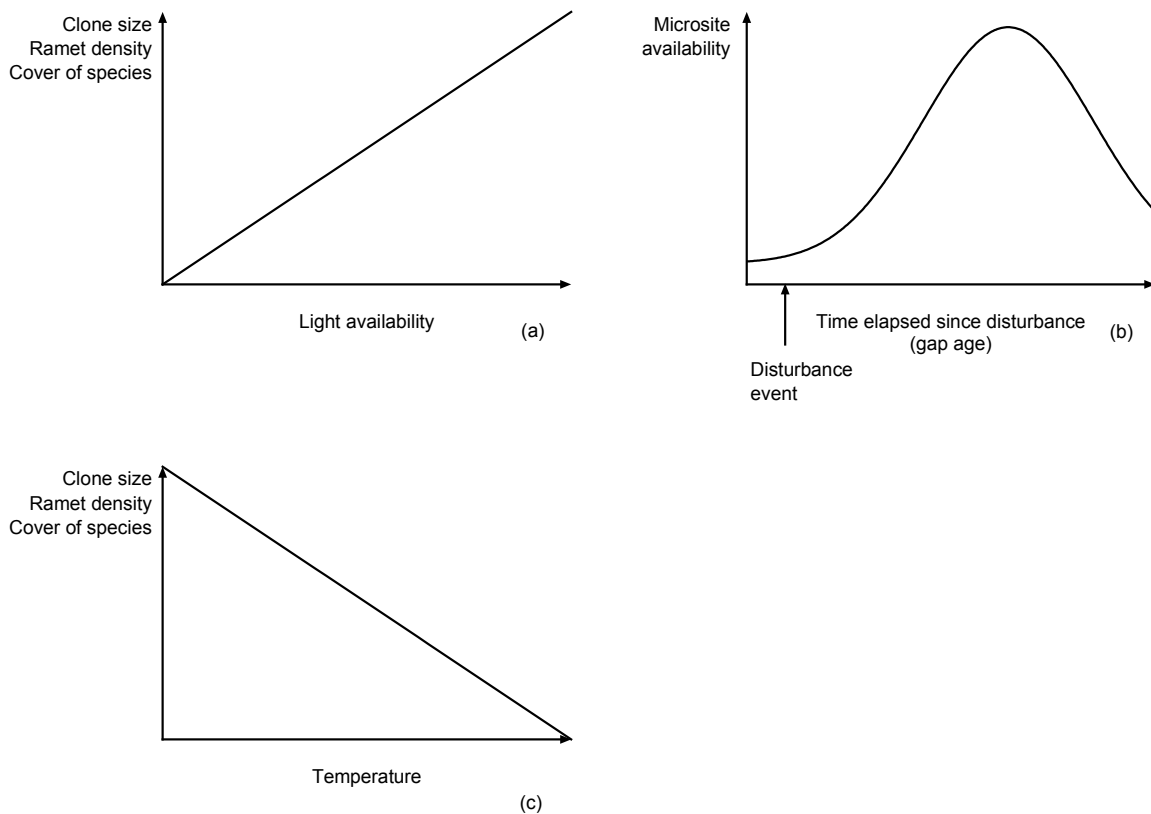


Fig. 1.7 The relationship between (a) light availability, (b) microsite availability in course of time and (c) temperature and species growth variables.

To answer these two overarching hypotheses of my PhD thesis, I employed different approaches in the different chapters of this study.

In Chapter 2, the focus was on the target species *T. europaea* and the investigation of the effect of gap size and gap age on this species. In particular, I tested for a positive relationship between gap size and the performance of populations and individuals. Similarly, the impact of gap age as well as of light availability as covariables was related to variables describing population and individual characteristics of *T. europaea*.

The genetic structure of *T. europaea* and *C. villosa* was investigated in Chapter 3. A unimodal relationship was expected between gap age and clone size and a linear one between light availability and clone sizes. Furthermore, I tested whether fast growing species achieved larger clone sizes and reached maximum clone sizes in earlier successional stages than slow growing species (for instance dwarf shrubs). An additional question asked was whether higher ramet densities were encountered in larger clones.

In the following Chapter (Chapter 4), I studied the effect of microsites and their availability on the target species (*T. europaea*, *C. villosa* and *V. myrtillus*). Especially, I wanted to know if species prefer microsites induced by gap creation (gap-induced microsites) or microsites that are also available in undisturbed forest (non-gap-induced microsites). More specifically, a preference of species was expected for non-gap-induced microsites in young gaps, due to the inaccessibility of gap-induced microsites. Finally, I assessed the negative influence of strong competitors on the study species.

In Chapter 5, I conducted a common garden transplantation experiment from Mt. Brocken (1142 m a.s.l.) to Halle (93 m a.s.l.) to predict the response of herb layer species to gap dynamics in the future. I hypothesized disadvantages for montane species at lower altitudes. However, grass species and herb species are predicted to profit from higher temperature, whereas dwarf shrubs will have a disadvantage owing to reduced phenotypic plasticity. Furthermore, I tested for an antagonistic relationship between higher light availability and temperature at low altitudes.

Finally, in Chapter 6 I summarize the main results and provide an overall discussion as well as a conclusion of the PhD thesis.

Chapter 2 - The response of the pseudoannual species *Trientalis europaea* L. to forest gap dynamics in a near-natural spruce forest

With Sabine Kammermeier and Helge Bruelheide

Forest Ecology and Management **257**, 1070-1077

2.1 Abstract

The objective of this study was to test relationships between gap size, gap age and performance of the pseudoannual forest herb layer species *Trientalis europaea*. We also tested for a potential covariation of performance variables with light as the putative driving factor of gap size and gap age effects. The study took place in the core zone of the Harz National Park in a near-natural spruce forest at Mt. Brocken, Germany. We established 70 randomly distributed plots of three different gap age classes (< 15 years, > 15 and < 60 years, > 60 years) and undisturbed forest stands. We recorded growth variables of *Trientalis* (e. g. height of ramets, number of flowers and fruits per ramet and number of daughter tubers per ramet) and measured PPFD (photosynthetic photon flux density). Gap sizes were assessed with GPS, ranged from 131 m² to 16 400 m² and were independent from gap age. Population density of *Trientalis europaea* was neither affected by gap size nor by gap age. However, gap age had an effect on the fitness of *Trientalis* ramets. In gaps, the species produced a higher number of flowers and fruits. In general, the average proportion of flowering and fruiting was very low, with 13% and 4%, respectively. In contrast, light intensity had a significant positive effect on ramet density, while the number of daughter tubers differed between 0.8 and 0.5 tubers per individual under lowest light and full light intensity, respectively. The general conclusion is that gap size had no effects on the performance of *Trientalis europaea*, while gap age had both direct effects and indirect effects mediated by light.

Keywords: disturbance, forest herb layer, gap age, gap size, PPFD

Chapter 3 - Is the degree of clonality of forest herbs dependent on gap age? Using fingerprinting approaches to assess optimum successional stages for montane forest herbs.

With Helge Bruelheide

Ecology and Evolution, doi: 10.1002/ece3.23

3.1 Abstract

Using molecular fingerprinting (amplified fragment length polymorphism (AFLP) method) we explored the potential of small-scale population analysis for understanding colonisation patterns of herb layer species in forests after canopy disturbance. We investigated three common forest understorey species with different life forms (*Trientalis europaea*, *Calamagrostis villosa* and *Vaccinium myrtillus*) in the Harz Mountains in Germany in three different gap age classes and undisturbed forest. For two of them (*T. europaea* and *C. villosa*), we analysed clone sizes and clonal structure. We hypothesized that clone sizes depend on age since gap formation and are affected by light availability. Mean patch sizes of *V. myrtillus*, *T. europaea* and *Calamagrostis villosa* formed were 3.7 m², 27.9 m² and 40.6 m², respectively. *Trientalis europaea* and *C. villosa* patches consisted mostly of more than one genet. Largest clone sizes of *T. europaea* were encountered in gaps of intermediate successional age (15-60 years, averaged minimum estimation of clone sizes: 6.56 m²) whereas clone size of *C. villosa* was found to be independent from gap age and had a mean minimum clone size of 0.49 m². In both species, clone size was positively related to light availability. Additionally, there was a positive relationship between clone size and ramet density for *T. europaea* and *C. villosa*. Genetic variation was higher within populations of *T. europaea* and *C. villosa* than among populations. *T. europaea* was the only species with a clear genetic isolation by distance, pointing at equilibrium between gene flow and genetic drift.

In conclusion, we showed that forest canopy gap dynamics clearly affect the small-scale structure of populations of understorey plants. Species with high lateral growth rates,

such as *T. europaea* offer the possibility to serve as "ecological clock" for dating ecological processes.

Keywords: AFLP, *Calamagrostis villosa*, clone sizes, gap dynamics, *Trientalis europaea*, *Vaccinium myrtillus*

Chapter 4 - The interaction of gap age and microsite for herb layer species in a near-natural spruce forest

With Sabine Kathke & Helge Bruelheide

Journal of Vegetation Science **22**, 85-95

4.1 Abstract

Question: To what degree does the regeneration of understorey forest species depend on gaps of different age and on gap-induced and non-gap-induced microsites? Do the species preferences for a specific microsite change with the developmental stage of the gap? How do different species in the understorey interact over time?

Location: Near-natural spruce forest on Mt. Brocken in the Harz National Park, Germany.

Methods: We established 90 study plots, stratified according to different gap age classes and undisturbed forest, and including subplots with three different gap-induced types of microsites (logs, stumps and root plates) and two non-gap-induced microsites (moss-covered rocks and ordinary forest ground).

Results: Significant interactions of species were encountered with gap age as well as with microsite type, light availability and competition. While shoot densities of *Vaccinium myrtillus* were highest at intermediate gap age, *Calamagrostis villosa* and *Trientalis europaea* showed highest densities in the oldest gaps. The species preferred different microsites but had higher densities on non-gap-induced microsites and their preferences changed over time. Unexpectedly, species shoot densities were not always negatively affected by the densities of competing species.

Conclusion: The results confirmed the importance of gaps for regeneration of forest herb layer species, but pointed to a much higher importance of microsites that were not induced by gaps compared to gap-induced microsites. Niche differentiation between different herb layer species can be conceived as species-specific preferences for microsite types that change with gap age, as a result of light conditions, degree of decay of logs and root plates and presence of competitors.

Keywords: *Calamagrostis villosa*, habitat heterogeneity, Mt. Brocken, *Picea abies* forests, relative light availability, *Trientalis europaea*, understorey vegetation, *Vaccinium myrtillus*

Nomenclature: Rothmaler (2005)

Abbreviations: PPFD = photosynthetic photon flux density

Chapter 5 - Global climate change – only bad news for boreal forest herb layer species?

With Helge Bruelheide

submitted for publication in *Climatic Change*

5.1 Abstract

Global warming presents a threat to plant species distributed at montane or alpine altitudes if the topography does not allow upward shifts in distribution ranges. Nevertheless, the species might also benefit from increasing temperatures and their secondary effects, such as a changed disturbance regime in montane forests with the consequence of higher light availability. We addressed these interactions in a common garden experiment in Central Germany at different altitudes, representing cold and moist versus warm and dry conditions. We investigated three montane species with different life forms, including a herb (*Trientalis europaea*), a grass (*Calamagrostis villosa*) and a dwarf shrub (*Vaccinium myrtillus*) under three shading treatments (3%, 28% and 86% of full sunlight). We hypothesized that montane species are at disadvantage in the lowland, with the dwarf shrub suffering more than the grass. Furthermore, we hypothesized an antagonistic interaction of increased temperature and increased light conditions. While *T. europaea* and *V. myrtillus* showed only slightly responses to low altitude conditions, *C. villosa* displayed a nearly fifteen fold increase in biomass production, despite higher observed herbivory levels in the lowland. We failed to show an antagonistic effect of increased temperature and increased light availability, as all study species suffered from deep shade conditions and grew best under full light conditions at both sites. In conclusion, both improved temperature and light conditions might be principally beneficial for the investigated boreal species, in particular for the grass species *C. villosa*.

Keywords: *Calamagrostis villosa*, common garden experiment, gap dynamics, phenotypic plasticity, *Trientalis europaea*, *Vaccinium myrtillus*

6 Synthesis

6.1 Main results

In the following, I summarize the main results presented in the preceding chapters of this PhD thesis.

In Chapter 2, the focus was put on the response of *T. europaea* to gap dynamics. Contrary to my hypothesis, gap size did not affect the density of this herb layer species. In addition, gap age was irrelevant for growth and reproduction of *T. europaea*. However, the existence of gaps generally favoured the density and reproduction of the target species. This pattern was explained with increased light availability in gaps compared to undisturbed forest. I showed that higher light availability enhances the cover of *T. europaea*.

According to the assumption given in Chapter 3, I demonstrated a unimodal relationship between gap age and clone size for *T. europaea*. Although, clone size of *C. villosa* did not follow this relationship, patch sizes were also distributed unimodally. Similarly, the relationship between clone size and light availability was significant for *T. europaea*, while the same trend of larger clones with higher light availability was also shown for *C. villosa*. Furthermore, *T. europaea* as the species with the highest mobility also achieved the largest clone sizes. Finally, increased ramet density was demonstrated in larger clones for both target species (*T. europaea* and *C. villosa*).

The effect of microsites on all target species (*T. europaea*, *C. villosa* and *V. myrtillus*) was investigated in Chapter 4. I answered the question of different preferences of the species for gap-induced or non-gap-induced microsites. In general, densities of the target species were highest on non-gap-induced microsites. However, this preference changed in the course of gap closure. Whereas the species preferred non-gap-induced microsites in young gaps, they later colonised gap-induced microsites. Additionally, I confirmed the hypothesis that the density of a strong competitor decreases the density of other species. *Vaccinium myrtillus* as a strong competitor suppressed the other two species. In contrast, *T. europaea* had a positive influence on *C. villosa* and vice versa.

Chapter 5 dealt with the possible effect of climate change and the response of the three target species. Against my expectation, all target species showed rather a positive than a

negative response to higher temperatures and lower precipitation at low altitudes. However, especially *C. villosa* and *T. europaea* suffered from higher herbivory at lower altitudes. The altered environmental conditions induced by the common garden experiment conducted, enhanced the performance of *C. villosa* most but I failed to show a positive response for *T. europaea* and a negative one of *V. myrtillus* as expected. Furthermore, no antagonistic relationship was encountered between higher light availability and temperature at low altitudes, as the highest biomass production of *C. villosa* was on unshaded plots at low altitudes and not as expected on half-shaded plots that provided a higher humidity.

6.2 Discussion

The present PhD thesis offers predictions for almost the entire herb layer plant community of this forest, since owing to low species richness of this spruce forest on Mt. Brocken, all dominant components of the herb layer could be investigated. In this unmanaged near-natural forest, I could cover a variety of different life and clonal growth forms (*T. europaea*: herb, guerrilla strategist; *C. villosa*: grass, guerrilla strategist and *V. myrtillus*: dwarf shrub, phalanx strategist). As the investigation approaches were so manifold, general conclusions could be made about the competitive ability under natural conditions. The response of different life forms to disturbances, gap creation, gap closure and about clonal growth depending on gap age and accordingly light availability could be demonstrated. Finally, also the possible response of the target species on future environmental conditions against the background of global climate change could be predicted by the present thesis.

In accordance to the first overarching hypothesis (Fig. 1.6), an increased density and better growth (e.g. higher coverage of target species, higher biomass production and higher reproduction rates) of the target species was shown in gaps compared to undisturbed forest. However, this pattern is not explicable without the environmental context, with a particular role of light availability as a key resource. In coniferous forests, light availability is intimately connected with canopy gaps, as in contrast to deciduous forests, the differences in light availability between gaps and undisturbed forest are present during the whole year. For instance, in a deciduous forest in Illinois, USA, the light irradiance was much higher in March ($822 \mu\text{mol m}^{-2} \text{s}^{-1}$) as in May ($189 \mu\text{mol m}^{-2} \text{s}^{-1}$) after

canopy development (Myers & Anderson 2003). Nonetheless, gap existence was more important than gap age in most cases for all target species, a pattern was also shown by Abe *et al.* (1995) for a temperate, deciduous forest. One explanation for lacking significant differences between gap age classes could be the openness of the investigated forest of the present study. In consequence of a high structural heterogeneity, also in undisturbed forest stands, the tree layer was not as dense as in managed spruce forests. The present study showed a significant positive relationship of light availability with ramet densities as well as with other growth variables (i.e. biomass) for all of the target species. Therefore, this part of the second overarching hypothesis (Fig. 1.7a) can be confirmed, too. Similar to *T. europaea*, the forest understorey clonal herb *Primula sieboldii* severs all connections to other ramets and acquires resources self-contained (Washitani *et al.* 2005). In an investigation on *P. sieboldii*, Noda *et al.* (2004) showed a four fold higher biomass production under highest light availability and sufficient water supply. With a higher light availability in open sites (72% light penetration) compared to deciduous forest sites (4% light penetration), Sammuli *et al.* (2004) described also an increased ramet density of the herb layer species in Estonia (4400 ramets per m² in open sites compared to 630 ramets in forest sites). These results match the finding of a higher average ramet density of the three target species in gaps compared to undisturbed forest (265 ramets and 155 ramets per m², respectively).

Additionally, the expectation of largest clone sizes and highest ramet densities in mid-successional gaps (Fig. 1.7b) could be confirmed for *T. europaea* (Chapter 3) and *V. myrtillus* (Chapter 4) and a trend for this pattern was shown also for *C. villosa* (Chapter 3). This unimodal pattern of density and growth variables (i.e. clone size) can be explained by an increased resource availability and lower competition intensity in gaps. For instance, in a coniferous forest in South Carolina (USA) the nutrient availability strongly increased after disturbance and later returned to the undisturbed level (Guo *et al.* 2004). After a lag-phase in young gaps, the species tended to expand the existing patches or establish new patches via seed input (survivors and gap coloniser, *sensu* Hughes & Fahey 1991). This lag-phase was demonstrated for instance by Moola & Vasseur (2009) for *Gaultheria procumbens*, an evergreen sub-shrub of the Ericaceae and a growth habit similar to *Vaccinium myrtillus*, in a mixed forest in North America. *Gaultheria procumbens* did not show significantly higher stem density two years after clear-cutting compared to late-

successional forest but ramet density (per m²) increased even five fold compared to undisturbed forest eight years after clear-cutting (Moola & Vasseur 2009). In the course of time when gaps close slowly, space becomes limited and competition between or within species increases and maximum patch sizes or height of individuals are attained. The effect of interspecific competition was clearly demonstrated as a negative effect of *V. myrtillus* on the two other target species in the present thesis (Chapter 4). The high competitive ability of this species is not reflected in high relative growth rates or productivity but is explained by allelopathy (Mallik & Pellissier 2000). This was also confirmed by Souto *et al.* (2000) who investigated the mycorrhizal fungi of *P. abies* and *V. myrtillus*. Whereas *Hebeloma crustuliniforme* (symbiont of *P. abies*) was inhibited by soil phenolics, *Hymenoscyphus ericae* (symbiont of *Vaccinium myrtillus*) was promoted. Soil phenolics are an additional source of carbon for *H. ericae*, consequently this species outcompetes other mycorrhizal fungi, thus explaining the dominance of *V. myrtillus* (Souto *et al.* 2000). In contrast, facilitation as another form of species interaction might have an important role especially in communities with harsh environmental conditions (Brooker & Callaghan 1998). For instance, Treberg & Turkington (2010) showed a positive effect of neighbouring plants in a nutrient poor mixedwood forest in Canada. Also in the present study, I detected those facilitation effects between *T. europaea* and *C. villosa*. However, besides interspecific interaction also intraspecific competition is not to be neglected. Intraspecific competition has been shown *Alliaria petiolata*, where plants of low-density populations were larger and more fecund than individuals of high-density stands (Rebek & O'Neil 2006). Furthermore, the age of patches plays a decisive role, as the growth of the deciduous dwarf shrub *Vaccinium uliginosum* slightly decreased with age in a study of Shevtsova *et al.* (1995) in Northern Finland. Additionally, Pitelka (1984) discussed the “-3/2 power law” of Yoda *et al.* (1963, cited in Pitelka 1984). Pitelka (1984) distinguished two responses of clonal plants to high ramet densities. One strategy is to stop patch growth and maintaining mean density and ramet weight, whereas the other option is a continuous increase in density increase with the consequence of a decrease in ramet weight. In the present study, I demonstrated that the target species followed the first strategy as after reaching the maximum density, the ramet density rather decreased than increased.

Because of the low species richness on Mt. Brocken, the results allow conclusions on the whole herb layer. Gilliam (2007) stated that the “resident” herb layer (i.e. vascular species that are 1 m less in height) has high competitive ability, and thus, a high impact on the “transient” herb layer (i.e. seedlings of trees and shrubs, which occur in the herb layer only temporarily). In consequence, herb layer species are able to influence the composition of the regenerating forest (Gilliam 2007). In accordance, the highest germination rates of the dominating tree species in my study area (*Picea abies*), were found on decaying logs (Kathke & Bruelheide 2010b) and not on ordinary forest ground with highest densities of herb layer species (mean density of target species was 91.1 ramets per m² and 27.6 ramets per m² for ordinary forest ground and logs, respectively, Chapter 4).

Environmental factors other than light availability have to be mentioned as well, e. g. soil moisture and temperature. In gaps, soils showed higher maximum temperatures and lower minimum temperatures compared to undisturbed forest (Collins *et al.* 1985).

With gap creation by tree fall, microsites such as logs, stumps or root plates increase the structural heterogeneity, substrate quality, resource availability and the vegetation structure of the forest (Kuuluvainen & Juntunen 1998). However, these microsites have to decompose before suitable for species’ settlement, with the wood of *Picea abies* being relatively soft and, thus, decomposing faster compared to other tree species (Zielonka & Piątek 2004). Nonetheless, wood decomposition rate of spruce depends on climatic conditions and varies from 50-70 years in Southern Scandinavia (Hytteborn & Packham 1987) to 200 years in Swedish Lapland (Hofgaard 1993). In the investigation of Hofgaard (1993), logs were first settled by *Vaccinium* species 70 years after tree death. However, as the decomposition rate varies strongly between several forests, time since tree death is not an optimal proxy to predict times of species establishment. A better proxy is the decomposition scale of Zielonka & Piątek (2004), where wood decay is classified into eight stages, from freshly fallen (stage 1) to completely rotten logs (stage 8). In decomposition stage 2 the bark is partially intact and the surface bends under the pressure of a knife, whereas in decomposition stage 6 the bark is no longer present and only the core of the log is still solid. In contrast, I recognized the first establishment of *V. myrtilus* at decay stage 2 and of the other herb layer species at decay stage 3-4 at Mt. Brocken.

As I showed in Chapter 4, *V. myrtillus* is a strong competitor and had a negative effect on the two other target species and this species had the highest probability of presence on decayed log. Additionally, *V. myrtillus* is able to establish first on decayed logs (decay stage 2), instead of the other two investigated species (establishment of *T. europaea* and *C. villosa* firstly on decay grade 3 and 4, respectively). Nonetheless, *V. myrtillus* preferred moss covered rocks and not decayed logs. Additionally, only a few other species are able to compete with the investigated dominant herb layer species, mainly spruce seedlings. Kathke & Bruelheide (2010b) observed most of the seedlings of *P. abies* on decayed logs at Mt. Brocken. However, all investigated species preferred other microsites than decayed logs (*C. villosa* mostly present on ordinary forest ground, whereas *V. myrtillus* achieved highest densities on moss covered rocks and in old gaps on root plates). Therefore, the competition between species might be reduced by different resource use, taking colonised sites as a general type of resource. Even in old gaps enough regeneration sites for the target species seem to be available. The same observation was made by Kathke & Bruelheide (2010b) who also found no relationship between gap age and spruce regeneration at Mt. Brocken.

Finally, the assumption of detrimental effects driven by climate change, i.e. elevated temperature and lower precipitation (Fig. 1.7c), has to be rejected for all target species. In contrast, *C. villosa* benefited from higher temperatures and had a nearly fifteen fold increase in biomass production. This result is in the line with the study of Fiala (2000) of *C. villosa* at an altitudinal gradient (625 m to 1250 m a.s.l.) in the Carpathians. Fiala (2000) observed a negative relationship between altitude and growth rate for *C. villosa*. The other two target species of the present study showed only moderate but also positive responses. However, with elevated temperature also herbivory, mainly brought about by slugs, increased, resulting in decrease in performance of *C. villosa* and *T. europaea*. In contrast, *V. myrtillus* was not affected by higher herbivory as this target species is protected by two defence mechanisms against slug herbivory. First, slugs prefer plants with soft leaves more than those with hard leaves (Dirzo 1980). The second defence mechanism is the accumulation of phenolics in *V. myrtillus* as a defensive compound (Keller *et al.* 1999, Mallik & Pellissier 2000). Higher temperature can induce very manifold changes on herbivores as for instance, life cycle duration, voltinism, population density, size, genetic composition and the extent of host plant exploitation (Bale *et al.* 2002).

Müller *et al.* (2009) investigated the species richness and abundance of molluscs in the Bavarian Forest National Park in Germany, and predicted higher species richness and abundance with higher temperature in the course of climate change. The reasons for a higher future species richness are a shift from low altitude species to higher altitudes and the invasion of new species (Müller *et al.* 2009). Beside higher temperature also the precipitation regime will change and for the study area a decrease in precipitation has been predicted (Meehl *et al.* 2007). Under drought conditions, the amount of decaying leaf material increases and therefore, also species feeding on dead material will increase (Sternberg *et al.* 1999, Sternberg 2000).

Against the background of climate change the target species seems to be not threatened as long as the near-natural spruce forest on Mt. Brocken continues to exist. In the course of global climate change, *Fagus sylvatica* which is distributed in the Harz Mountains up to 800 m a.s.l. (Pflume 1999), is expected to expand the distribution range upwards. With replacement of spruce by *F. sylvatica*, not only site conditions will change as the forests are going to be darker, also other herb layer species will colonise and might outcompete the resident herb layer species at Mt. Brocken. However, based on recent recruitment observations on spruce, Kathke (2010) saw no evidence of threat of spruce forest displacement at high altitudes of Mt. Brocken in the near future. Although *F. sylvatica* is a strong competitor, the species requires a January mean temperature above -3°C , less than 141 frost days (daily minimum temperature below 0°C) and is sensitive against late frosts (Bolte *et al.* 2007). On Mt. Brocken, according to long term weather records (1951-1980), the mean January temperature is about -4.5°C and the number of frost days is 171 (Wegener & Kison 2002). Additionally, the strong browsing pressure by deer, which presently is present in high densities in the study area (Hlawatsch & Wegener 1994), will probably counteract the establishment of deciduous trees.

In conclusion, in my PhD thesis I could demonstrate that for the herb layer species investigated the existence of gaps is more important than gap age. Additionally, all three target species prefer vegetative reproduction in contrast to generative reproduction. As was demonstrated by Kathke & Bruelheide (2010a), the frequency of disturbance events increased in the last years and they will be frequent also in the future. With higher disturbance frequency, light availability will increase as will spatial heterogeneity of the forest floor. Consequently, more regeneration “safe-sites” for the herb layer species will

be created. In summary, this could mean that the herb layer species of Mt. Brocken might be positively affected from global climate change in the short run.

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Appendix

Curriculum vitae

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Date of birth: 13.01.1982
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Work experience

Present – 04/2011 Scientific assistant, Martin Luther University Halle Wittenberg
12/2010 – 10/2010 Scientific assistant, Martin Luther University Halle Wittenberg
07/2010 – 05/2007 Scientific assistant, Martin Luther University Halle Wittenberg
02/2004 – 11/2003 Occupational training, Institut für Bioanalytik, Umwelttoxikologie und Biotechnologie, Halle-Lettin
08/2001 – 09/2000 Gap year taken to work as a volunteer in environmental projects, “Ziegenalm“, Sophienhof (Harz)

Education

Present – 05/2007 PhD thesis, Martin Luther University Halle Wittenberg
Topic: The importance of gap dynamics for the reproduction of clonal plant species in natural forests in the Harz National Park.
04/2007 – 10/2001 Studies of Biology, Martin Luther University Halle Wittenberg
Major subject: geobotany
Minor subjects: microbiology, nature conservation and soil science
Diploma thesis: Die vegetative und generative Vermehrung der pseudoannuellen Art *Trientalis europaea* L. in Kronenlücken

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 08/2000 Abitur, Staatliches Gymnasium „Wilhelm von Humboldt“,
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List of publications

Publications in peer review journals

- Patsias, K & Bruelheide, H (2011) Is the degree of clonality of forest herbs dependent on gap age? Using fingerprinting approaches to assess optimum successional stages for montane forest herbs. *Ecology and Evolution*, doi: 10.1002/ece3.23.
- Patsias, K & Bruelheide, H (under review) Global climate change – only bad news for boreal forest herb layer species? *Climatic Change*.
- Kirchner, K, Kathke, S & Bruelheide H (2011) The interaction of gap age and microsites for herb layer species in a near-natural spruce forest. *Journal of Vegetation Science* **22**, 85-95.
- Kirchner, K, Kammermeier, S & Bruelheide, H (2009) The response of the pseudoannual species *Trientalis europaea* L. to forest gap dynamics in a near-natural spruce forest. *Forest Ecology and Management* **257**, 1070-1077.

Symposia contributions

- Patsias, K & Bruelheide H (2011) Assessing optimal successional stages for montane forest herbs with AFLP markers, *Proceedings of the GfÖ 41*, **52**, Oral presentation.
- Kirchner, K & Bruelheide, H (2010) Global climate change - Only bad news for boreal forest herb layer species? *Proceedings of the GfÖ 40*, **184**, Oral presentation.
- Kirchner, K, Kammermeier, S & Bruelheide, H (2007) The response of *Trientalis europaea* L. to spruce forest gap dynamics. *Proceedings of the GfÖ 37*, **377**, Oral presentation.
- Kirchner, K, Kammermeier, S & Bruelheide, H (2006) *Trientalis europaea* - investigation of the life cycle of a pseudoannual plant. *Plant Population Biology – Abstracts*, **73**, Poster.

Halle (Saale), 13.10.2011

Kathrin Patsias

Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel **“The importance of gap dynamics for the reproduction of clonal plant species in natural forests in the Harz National Park“** 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 (Saale), 13.10.2011

Kathrin Patsias