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FACTORS INFLUENCING TREE REGENERATION AFTER WINDTHROW IN SWISS FORESTS

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“By three methods we may learn wisdom:

First, by reflection, which is noblest;

Second, by imitation, which is easiest;

And third by experience, which is the bitterest.”

(Confucius)

Photo was taken by Hansheinrich Bachofen.

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Summary

Severe wind damage is one of the most important disturbance agents in European forest ecosystems. In a biodiversity context, wind disturbance is viewed as an enrichment, because increased light availability and modified microclimatic conditions promote plant diversity in the years following the disturbance. However, severe damage to mountain forests transiently reduces the protective effect of forests against natural hazards like avalanches or rockfall, and generally leads to economic loss. The frequency of wind disturbance, most often in the frame of European winter storms, has increased in the recent years, and thereby the damaged forest area. The natural regeneration ability of windthrown forests and the factors explaining the variability of regeneration are, therefore, of considerable interest (*Chapter I*).

The quantity of lying and standing deadwood is changed strongly by windthrow and after subsequent salvage logging. It is an important component of forest ecosystems, since many deadwood-associated species depend on the presence of deadwood. Also for tree regeneration success, deadwood can be crucial. Yet, little is known about deadwood quantity and quality after windthrow in Central Europe and how much deadwood is left after salvage logging (*Chapter II*).

Another factor clearly changing after windthrow is the cover of ground vegetation. Due to increased light availability, fast growing species can rapidly form dense vegetation cover that significantly suppresses tree regeneration. One example of such a species is bracken (*Pteridium aquilinum* L.). It is assumed that bracken suppresses tree regeneration especially through the release of phytotoxic compounds (allelopathy). Regeneration failure of beech (*Fagus sylvatica* L.)

and sycamore (*Acer pseudoplatanus* L.) in dense bracken stands has not been investigated for allelopathy yet, although beech forests are frequent in Europe (*Chapter III*).

Chapter I. Natural tree regeneration was recorded in 2010 and 2011 in 90 windthrow gaps (each ≥ 3 ha) in Switzerland. The forest gaps were caused by two severe storms in 1990 (Vivian) and 1999 (Lothar). Soil pH, vegetation cover, post-storm treatment (‘salvage-logging’ or ‘no timber harvesting’) and elevation were the four most important predictors explaining the variability of sapling density. Although general trends could be detected, the heterogeneity among forest gaps was large. In contrast to conventional wisdom on forest succession after disturbance, late-successional tree species dominated in a majority of gaps 10 to 20 years after wind disturbance regarding sapling density.

Chapter II. Deadwood amount and quality were investigated on the same gap sample as the natural tree regeneration in *Chapter I*. A special focus was on the post-storm treatments ‘salvage-logging’ or ‘no timber harvesting’. The study revealed surprisingly high deadwood volumes (74.6 m^3 ha^{-1}) in salvage-logged forest gaps. This value distinctly exceeds the proposed minimum deadwood volumes for forest stands in a conservation context. Additionally, a wide variety of decay stages and diameter classes (10 to ≥ 70 cm) was found in both salvage-logged and unharvested gaps, suggesting considerable habitat diversity for deadwood-associated species irrespective of the treatment. Since it takes a few decades until deadwood turns into a suitable seedbed, the storm- induced deadwood pieces that were up to a maximum of 20 years old did not provide an appropriate substrate for tree establishment yet.

Chapter III. To test causes of regeneration failure in dense bracken stands, germinating seeds of beech and sycamore were exposed to bracken leachates in a greenhouse experiment. Moreover, seedlings exposed to bracken leachates in the greenhouse experiment were compared with seedlings grown in shadow or with bracken rhizomes in a common garden experiment. Except for a significantly but only slightly reduced germination rate of beech in the bracken treatment, no other allelopathic influences of bracken were found in either experiment. In contrast, strong evidence for light competition was detected as probably one of the most important factors causing regeneration failure of beech and sycamore in dense bracken stands during the first vegetation period.

Overall, the two studies based on the data inventory of the 90 forest gaps (*Chapter I* and *II*) revealed general driving forces of natural tree regeneration, as well as the insight that current logging practices in Switzerland leave enough and diverse deadwood ensuring habitat diversity for deadwood-associated species. Moreover, in contrast to the assumption that bracken causes tree regeneration failure through the release of phytotoxic compounds, the third chapter showed that mainly light competition led to lower growth performance in beech and sycamore.

Zusammenfassung

Windwurf ist eine der wichtigsten Störungen in den Waldökosystemen Europas. In den Jahren nach der Störung führen erhöhte Lichtverfügbarkeit sowie veränderte mikroklimatische Bedingungen zu einer erhöhten Pflanzenvielfalt, weshalb Windschäden für die Natur als Bereicherung angesehen werden können. In den Bergen hingegen ist die Schutzwirkung der Wälder gegen Lawinen oder Steinschlag durch Sturmschäden oft stark oder zumindest vorübergehend beeinträchtigt. Zudem verursachen grosse Schäden wirtschaftliche Verluste. Die Zahl der Winterstürme in Europa hat in den letzten Jahren zugenommen und somit auch das Ausmass an Schäden in den Wäldern. Die natürliche Regenerationsfähigkeit von geschädigten Wäldern sowie die Faktoren, die die Verjüngungsvariabilität der Bäume erklären, sind daher von grossem Interesse (*Kapitel I*).

Sowohl Sturmschäden wie auch nachfolgende Räumungsaktivitäten verändern das Totholzvolumen in Wäldern deutlich. Totholz ist eine wichtige Komponente in Waldökosystemen, da das Vorkommen und Überleben vieler Arten vom Totholz abhängig ist. Ferner kann Totholz in einigen Wäldern für eine erfolgreiche Baumverjüngung entscheidend sein. Bisher ist wenig über die Totholzmenge und –qualität nach Windwurf in Mitteleuropa bekannt, wie auch darüber, wie viel Totholz tatsächlich nach anschliessenden Räumungsaktivitäten noch vorhanden ist (*Kapitel II*).

Ein weiterer Faktor, der sich nach Windwurf oft ändert, ist der Deckungsgrad der Bodenvegetation. Schnellwüchsige Pflanzen können durch die erhöhte Lichtverfügbarkeit nach Sturmschäden rasch dichte Vegetationsteppiche bilden,

welche die Baumverjüngung beeinträchtigen. Ein Beispiel für eine solche Pflanzenart ist der Adlerfarn (*Pteridium aquilinum* L.). Es wird angenommen, dass der Adlerfarn vor allem durch die Freisetzung phytotoxischer Stoffe (Allelopathie) das Wachstum von Bäumen hemmt. Der Ausfall von natürlich verjüngten Buchen (*Fagus sylvatica* L.) und Bergahorn (*Acer pseudoplatanus* L.) in dichten Adlerfarnbeständen wurde bisher noch nicht bezüglich einer allelopathischen Wirkung des Adlerfarns untersucht, obwohl Buchenwälder in Europa stark verbreitet sind (*Kapitel III*).

Kapitel I. In den Jahren 2010 und 2011 wurde die natürliche Baumverjüngung von 90 Windwurfflächen (jede Fläche $\geq$ 3 ha) in der Schweiz erfasst. Die untersuchten Windwurfflächen wurden durch die zwei schweren Stürme Vivian (1990) und Lothar (1999) verursacht. Der Boden pH, die Bodenvegetationsbedeckung, die Behandlung nach dem Sturmschaden („Räumung des Totholzes“ oder „keine Räumung des Totholzes“) und die Höhe über Meer stellten sich als die vier wichtigsten erklärenden Faktoren für die Variabilität der Baumdichten auf den Windwurfflächen heraus. Obwohl wir Tendenzen der Naturverjüngung sichtbar machen konnten, war die Heterogenität zwischen den einzelnen Windwurfflächen sehr hoch. Wenn man die Baumdichten betrachtet, dominierten im Gegensatz zu traditionellen Sukzessionstheorien in den jungen sich entwickelnden Wäldern 10 oder 20 Jahre nach dem Windwurf Nicht-Pionierbaumarten.

Kaptiel II. Das Totholzvolumen sowie die Totholzqualität wurden in derselben Stichprobe untersucht wie die Baumverjüngung in *Kapitel I*. Ein spezieller Fokus lag auf dem Vergleich zwischen geräumten und belassenen Flächen. Geräumte Flächen zeigten ein erstaunlich hohes Totholzvolumen von 74.6 m^3 ha^{-1}. Dieser Wert übertrifft deutlich das vorgeschlagene Mindest-Totholzvolumen in Wäldern im Zusammenhang mit einer nachhaltigen Erhaltung der Artenvielfalt. Zudem wurde eine hohe Variabilität an Abbaustufen sowie Durchmesserklassen des Totholzes ermittelt, was eine hohe Variabilität an Habitaten für totholzassoziierte Arten vermuten lässt. Da es einige Jahrzehnte dauert, bis Totholz zu einem geeigneten Keimungssubstrat wird, war das erfasste Totholz, welches höchstens 20 Jahre alt war, noch nicht geeignet für die Baumverjüngung.

Kapitel III. In diesem Kapitel untersuchten wir die Auswirkungen von Adlerfarn auf Buche und Bergahorn. Um Ursachen für die Ausfälle der Naturverjüngung in dichten Adlerfarnbeständen zu finden, wurden Samen und Keimlinge von Buche und Bergahorn in einem Gewächshausexperiment phytotoxischen Stoffen des Adlerfarns ausgesetzt. Die Wachstumsleistung der Bäumchen, die den phytotoxischen Stoffen des Adlerfarns ausgesetzt waren, wurde mit der von Bäumchen verglichen, die in einem Gartenexperiment unter Schatten oder im Kontakt mit Adlerfarnrhizomen wuchsen. Ausser einer signifikanten, jedoch nur geringen Reduktion der Keimungsrate bei Buchen wurden keine weiteren allelopathischen Effekte des Adlerfarns gefunden. Hingegen stellte sich die Lichtkonkurrenz als einer der wahrscheinlich wichtigsten Faktoren heraus, der den Ausfall von Buche und Bergahorn in dichten Adlerfarnbeständen während der ersten Vegetationsperiode verursacht.

Die Studien zu den 90 Windwurfflächen in *Kapitel I* und *II* zeigen wichtige Einflussfaktoren für die Naturverjüngung auf, und dass die gegenwärtige Bewirtschaftung von Windwurfflächen in der Schweiz eine ausreichende Menge an diversem Totholz hinterlässt, was eine grosse Zahl an vielfältigen Habitaten für totholzassoziierte Arten gewährleistet. Im Gegensatz zu der Annahme, dass Adlerfarn vor allem durch das Freisetzen von phytotoxischen Stoffen die natürliche Verjüngung hemmt, stellt sich in *Kapitel III* vielmehr die Konkurrenz um das Licht als treibender Faktor heraus.

General Introduction

Background

Disturbance in forest ecosystems

Natural disturbances occur over a large range of temporal and spatial scales and affect many ecological systems (Pickett and White 1985). It is generally accepted that they are a key process shaping the structure and function of forest ecosystems (cf. Attiwill 1994). Due to recurring disturbances and the ensuing successional processes, a wide range of various habitats at different scales are becoming available and their maintenance at the landscape level is thus ensured, which is crucial for forest biodiversity (cf. Kuuluvainen 2002). Disturbances at small and large scales often prevent forests from attaining a "climax" state (Attiwill 1994; Kuuluvainen 1994). At small scales, primarily autogenic disturbances such as the death of single trees or tree groups through competition, insect infestation or senescence keep forests in a constant state of change. At large scales, allogenic disturbances are prevailing such as storms or fires, although large-scale attacks by insects or pathogens are important as well (Kuuluvainen 1994). Different parts of the globe are characterized by different prevailing large-scale disturbance agents. For Central Europe, windthrow and insect attacks are most important (cf. Schelhaas et al. 2003). Thus, the focus of this thesis is on forests that have been severely damaged by wind in Switzerland, and on the environmental predictors influencing the subsequent regeneration process.

Wind disturbance

Wind disturbances play an important role in the dynamics of forest ecosystems throughout the world (e.g. Lawton and Putz 1988; Peterson 2000; Ulanova 2000; Wohlgemuth et al. 2002). In European forest ecosystems, severe storms are one of the most important disturbance agents. Between 1950 and 2000, an annual average of 18.7 million m^3 of timber was damaged by storms, with a high interannual variability (Schelhaas et al. 2003). The frequency of wind disturbances, which are occurring most often in the context of European winter storms, has even increased in Europe in recent years, and thereby the size of the damaged forest area (Schelhaas et al. 2003; Usbeck et al. 2010).

In Switzerland, the two most severe storms during the last 100 years (Usbeck et al. 2010) occurred in 1990 ('Vivian') and 1999 ('Lothar'), producing 5 million m^3 (*Schüepp* et al. 1994) and 13 million m^3 (BUWAL and WSL 2001) of damaged timber, respectively. At these times, five million m^3 of timber corresponded roughly to the amount of annually harvested timber in Switzerland (BUWAL and WSL 2001). The total area of severely damaged forests, i.e. where nearly all trees were windthrown, amounted to 4900 ha after Vivian and 10 600 ha after Lothar (Fig. 1), which together amounted to 1.2 % of the total forest area of Switzerland (Cioldi et al. 2010).

The severity of storm damage in forest stands depends on abiotic factors such as topography and soil characteristics. Also biotic factors such as species composition of the forest, tree height, stand and age structure are crucial. Likewise, also the intensity of the prevailing storm is essential, in particular maximum wind gust speed (Attiwill 1994; Romme et al. 1998; Usbeck et al. 2010). Therefore, the impact of storms on forest stands varies greatly, from scattered windthrown trees

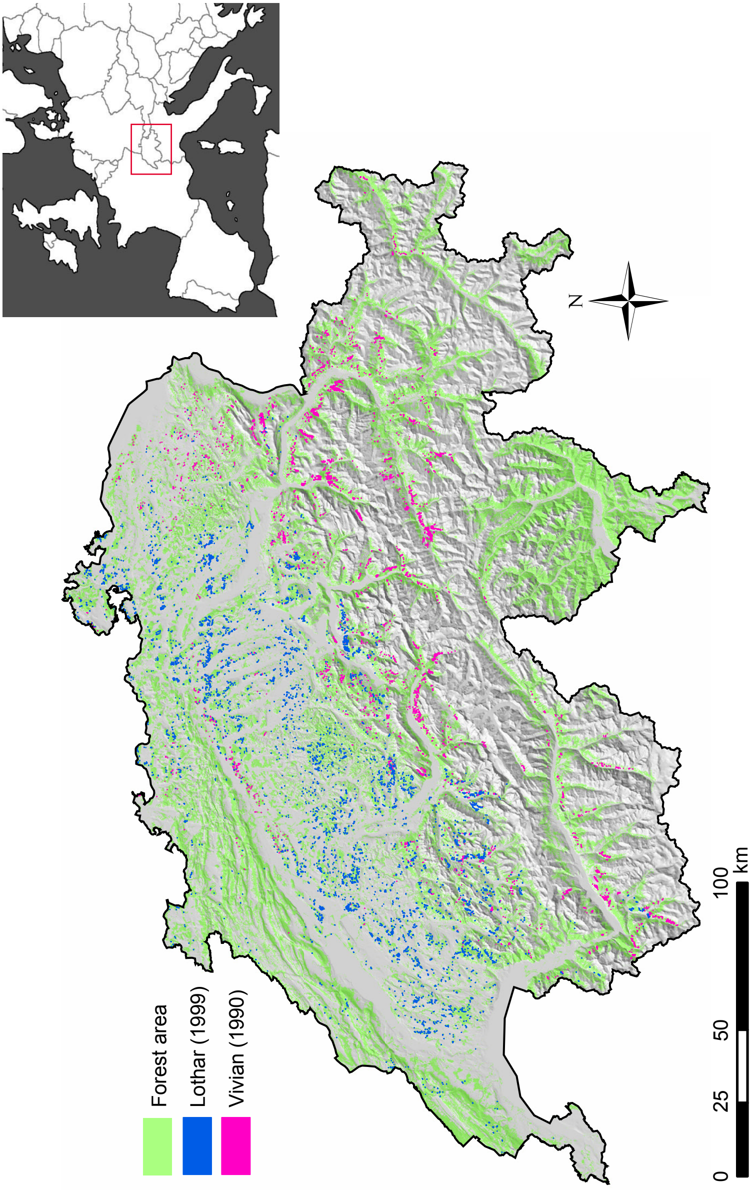

Fig. 1 Wind disturbed forest areas in Switzerland where nearly all trees were windthrown. Source of map: BFS GEOSTADT/Bundesamt für Landestopographie (Federal Office of Topography), © BAFU, 3003 Bern

across small canopy gaps to large openings (review by Attiwill 1994; Schindler et al. 2009; Hanewinkel et al. 2010).

In large windthrows and large canopy gaps, the availability of resources such as light, water or nutrients transiently increases and microclimatic conditions are modified strongly (Peterson et al. 1990; Galhidy et al. 2006). Some of the emerging microsites are associated with uprooted trees, such as mounds and pits. Light availability, soil moisture and temperature differ strongly among these microsites (Peterson et al. 1990). Compared to the pre-windthrow situation, the disturbance creates a high number of different habitats. Additionally, wind disturbances produce varying amounts of lying vs. standing deadwood, which is an important component of the ecosystem (Harmon et al. 1986). Since numerous organisms such as birds (Bütler et al. 2004; Lain et al. 2008), saproxylic beetles (Sippola et al. 2002; Sahlin and Ranius 2009) and fungi (Nordén et al. 2004) depend on the presence of deadwood and contribute strongly to biodiversity, decaying wood has been proposed as a surrogate for overall species richness (Juutinen et al. 2006). Moreover, deadwood as a substrate is known to be crucial for tree regeneration in moist coniferous forests, as found in many studies e.g. in North America (e.g. McKee et al. 1982; Harmon and Franklin 1989), Switzerland (Imbeck and Ott 1987) and the Czech Republic (Svoboda et al. 2010). In short, the increase in resource availability and the modified microclimatic conditions promote biodiversity in the years following after a wind disturbance (Degen et al. 2005; von Oheimb et al. 2007).

However, severe wind damage to mountain forests transiently increases the risk of avalanches or rockfall (Schönenberger 2002) and therefore has a negative connotation. In Switzerland, for example, 43% of all forests are defined as protection forests (Duc et al. 2010). The natural regeneration ability of windthrown forests and the factors to explain the spatial and temporal variability of tree regeneration are, therefore, of considerable scientific and practical interest. More generally, catastrophic windthrow produces enormous economic loss.

Tree regeneration after wind disturbance

When the storm ‘Vivian’ damaged forests mainly in the Swiss Alps, little was known about natural tree regeneration on large windthrow areas, and there were no related studies for the Alps (Schönenberger et al. 1992). Due to the damage caused by 'Vivian' in many protection forests, several studies were begun to investigate tree regeneration dynamics (summarized in Schönenberger et al. 2002). They all focused, however, on the detailed study of four windthrow areas; this is why generalisations of these findings are strongly limited. The next catastrophic winter storm was 'Lothar', affecting forests across Central Europe (Mayer et al. 2005). In Switzerland, the forests damaged by 'Lothar' are predominantly located at lower elevations, i.e. on the Central Plateau. Also after 'Lothar', studies were conducted focussing on the recolonisation by plants and animals in 16 case studies (Brang 2005, Koch and Brang 2005). The two main findings after these two storms were that mountain forests regenerate slowly compared to lowland forests regarding stem density (Wohlgemuth et al. 2002), and that salvage-logged windthrow areas have generally a higher number of naturally regenerated trees than unharvested ones (Schönenberger 2002). These results of higher regeneration densities in lower elevated and salvage-logged windthrow areas are in line with other studies. Elevation is known to be negatively correlated with seedling and sapling densities (e.g. Peterson and Pickett 1990; van Mantgem et al. 2006), and Ilisson et al. (2007) found higher regeneration densities on salvage-logged than unharvested windthrow areas. Furthermore, several studies on post-windthrow tree regeneration found additional factors that are important for shaping successional processes after such events. For example, investigations in small to intermediate windthrow gaps in France five years after Lothar showed that tree regeneration densities were higher at gap edges than in gap centers and that soil pH influenced the probability of presence of hornbeam (*Carpinus betulus* L.), ash (*Fraxinus excelsior* L.), field maple (*Acer campestre* L.), and sycamore (*Acer pseudoplatanus* L.; Van Couwenberghe et al. 2010). Similarly, a case study in Germany revealed that soil pH is an important predictor of sapling density and species composition after windthrow (Kompa and Schmidt 2006). A study on seed dispersal showed that in large clearings, seed availability of *Picea rubens* and *P. engelmanii* decreased drastically within 100 m of the forest edge (Greene and Johnson 1996). Due to increased light availability on the forest floor after anthropogenic (e.g. clear-cuts) or natural (e.g. wind damage) disturbances, herbaceous plants such as bracken (*Pteridium aquilinum* L.) spread rapidly, which often hinders tree regeneration (Koop and Hilgen 1987; Royo and Carson 2006). Another factor affecting tree regeneration is herbivory. Seedlings growing on treefall mounds created after windthrow were, for example, browsed less and seedlings established next to mounds were taller (Long et al. 1998; Krueger and Peterson 2006). In other words, microsites created by wind disturbance can serve as refugia from herbivory. Furthermore, on a larger scale browse consumption may be reduced and thereby sapling density increased if woody debris after wind disturbances (Peterson and Pickett 1995; Moser et al. 2008) or fires (de Chantal and Granström 2007) is not removed. Since food availability is often assumed to be similar in undisturbed forests as well as in salvage-logged or unharvested forests after disturbance (Moser et al. 2008), the presence of woody debris appears decisive for limiting browsing by large herbivores. Even though the factors influencing natural tree regeneration after wind disturbance in forests are well known now, their relative importance varies strongly between forest types, and generalizations remain difficult. Quite often, the limited generalization originates from the small number of sites considered in earlier studies, which constrains the range of environmental variability that they covered. Therefore, in this thesis I will investigate tree regeneration 20 and 10 years after the two severe wind disturbances 'Vivian' and 'Lothar' in Switzerland (Central Europe), respectively, using a sample of 90 windthrow areas along a broad environmental gradient.

Below, I review in detail two effects of windthrow that are decisive for tree regeneration: i) the amount of deadwood, and ii) the density of bracken (*Pteridium aquilinum* L. Kuhn), which may rapidly advance to dense stands in disturbed forests as light availability increases (Koop and Hilgen 1987).

i) Deadwood quantity and quality after wind disturbance

Deadwood is a key resource for maintaining forest diversity, since it provides a wide variety of microhabitats (Juutinen et al. 2006). In an advanced stage of decay, deadwood is a suitable substrate for tree regeneration (Zielonka 2006), especially in moist coniferous forests (McKee et al. 1982; Imbeck and Ott 1987). Logging activities after windthrow drastically reduce deadwood volume, and although deadwood is an important component for forest ecosystems, its quantity and quality on windthrow areas with subsequent logging activities in Central Europe have not been assessed yet.

In Switzerland, only rough estimates of post-windthrow deadwood abundance and quality are available. Those obtained from large-scale forest inventory data ranged from 45 to 90 m^3 ha^{-1} on sample plots totally or partially damaged by storms (most often with logging activities following the disturbance; Cioldi et al. 2010). Unfortunately, there are no other studies investigating deadwood volumes after windthrow in Central Europe, which is why a comparison is not possible. However, in a study in Sweden, deadwood amounted to 42.3 m^3 ha^{-1} on traditional (control) clear-cuts and 26.0 m^3 ha^{-1} on clear-cuts after additional harvesting of all fuels (Eräjää et al. 2010). These volumes were much greater than expected, and imply that windthrow areas in Switzerland that are either salvage-logged or left without intervention may have a large deadwood potential. Therefore, I will analyze deadwood data gathered from the same sample of windthrow areas as used for the tree regeneration investigation. In addition, I will also focus on the importance of deadwood as a substrate for tree establishment.

ii) Bracken (*Pteridium aquilinum* L.) interference with tree seedlings

Dense ground vegetation layers, often resulting from the spread of fast growing species after disturbances, mainly interfer with tree regeneration by competition, especially for light. One example of such a species is bracken (review by Royo and Carson 2006). It is an aggressive weed competing for light (Tolhurst and Turvey 1992; Gaudio et al. 2011), water and nutrients (Evans et al. 1990; Smith and Lockwood 1990). In addition to its effectiveness in this regard, several studies suggest a high allelopathic potential (Cooper-Driver 1976; Dolling et al. 1994). Various studies found significantly reduced germination rates and/or lower early growth of several plant species due to phytotoxic compounds released by bracken (Gliessman and Muller 1972; Gliessman and Muller 1978; Ferguson and Boyd 1988; Dolling 1996). However, to date no investigations have addressed the possible phytotoxic influence of bracken on beech (*Fagus sylvatica* L.) and sycamore (*Acer pseudoplatanus* L.), although these two species are widespread in Europe (Huntley et al. 1989, Keller et al. 1998). Thus, regeneration failure of beech and sycamore in dense bracken stands cannot be assessed, as an important piece of information is lacking. This knowledge would be important to better understand by which mechanisms bracken interferes with tree seedling development, which would permit the development of management recommendations that counter bracken-mediated tree regeneration failure after forest disturbance.

Objectives and research questions

The main aims of this thesis are (i) to elucidate the main factors that determine post-storm tree regeneration and (ii) to develop general rules explaining tree regeneration failure or success after severe wind disturbance. Specifically, I addressed three subjects:

(i) the identification of environmental variables that cause a high or low natural tree regeneration density (*Chapter I*);

(ii) the deadwood potential of wind-disturbed areas with respect to the treatments 'salvage logging' vs. 'no intervention' (i.e., the windthrown and broken trees were not removed), with an emphasis on deadwood as a potentially suitable substrate for tree regeneration 10 or 20 years after a storm (*Chapter II*);

(iii) the detailed investigation of the factor ‘bracken’ that may significantly prevent tree regeneration after windthrow, and the pathways of bracken interference with regeneration (*Chapter III*).

With this thesis, I expect to contribute to the improvement of management decisions after windthrow by providing knowledge on the natural regeneration ability of disturbed forests, and by showing the deadwood potential of both salvage-logged and unharvested windthrow areas.

In the three main chapters of my thesis, the following research questions are addressed:

I) Post-storm tree regeneration after wind disturbance

> How dense are stands in gaps 10 and 20 years after a severe wind disturbance, and how diverse are these stands in terms of tree species?
>
> Which are the most important environmental factors determining tree regeneration after wind disturbance?
>
> How important are the post-storm treatments (‘salvage logging’ vs. ‘no intervention’) and the time elapsed since the disturbance (10 vs. 20 years) for the developing natural tree regeneration?

II) Deadwood quantity and quality after wind disturbance

> How much deadwood is left on unharvested and on salvage-logged windthrow areas?
>
> Do salvage-logged windthrow areas provide the same diversity of deadwood habitats as unharvested ones?
>
> Is deadwood an important factor for the success of tree regeneration in windthrow areas?

III) Bracken interference with tree seedlings

Is light competition or the release of phytotoxic compounds (allelopathy) more important for tree regeneration failure in dense bracken stands?

References

Attiwill PM (1994) The disturbance of forest ecosystems – the ecological basis for conservative management. Forest Ecol Manag 63: 247-300.

Brang P (2005) Räumliche Verteilung der Naturverjüngung auf grossen Lothar-Sturmflächen. Schweiz Z Forstwes 12: 467-476.

Bütler R, Angelstam P, Ekelund P, Schlaepfer R (2004) Dead wood threshold values for the three-toed woodpecker presence in boreal and sub-Alpine forest. Biol Conserv 119: 305-318.

BUWAL, WSL (2001) Lothar. Der Orkan 1999. Ereignisanalyse. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft, Birmensdorf. Bundesamt für Umwelt, Wald und Landschaft, BUWAL, Bern.

Cioldi F, Baltensweiler A, Brändli U-B, Duc P, Ginzler C, Bonardi AH, Thürig E, Ulmer U (2010) Waldressourcen. In: Brändli U-B (ed) Schweizerisches Landesforstinventar Ergebnisse der dritten Erhebung 2004-2006. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft WSL, Birmensdorf. Bundesamt für Umwelt BAFU, Bern, pp. 31-114.

Cooper-Driver G (1976) Chemotaxonomy and phytochemical ecology of bracken. Botanical Journal of the Linnean Society 73: 35-46.

de Chantal M, Granström A (2007) Aggregations of dead wood after wildfire act as browsing refugia for seedlings of *Populus tremula* and *Salix caprea*. Forest Ecol Manag 250: 3-8.

Degen T, Devillez F, Jacquemart AL (2005) Gaps promote plant diversity in beech forests (*Luzulo-Fagetum*), North Vosges, France. Ann For Sci 62: 429-440.

Dolling A, Zackrisson O, Nilsson MC (1994) Seasonal variation in phytotoxicity of bracken (*Pteridium aquilinum* L. Kuhn). Journal of Chemical Ecology 20: 3163-3172.

Dolling AHU (1996) Interference of bracken (*Pteridium aquilinum* L Kuhn) with Scots pine (*Pinus sylvestris* L) and Norway spruce (*Picea abies* L Karst) seedling establishment. Forest Ecol Manag 88: 227-235.

Duc P, Abegg M, Brändli UB (2010) Schutzwald. In: Brändli U-B (ed) Schweizerisches Landesforstinventar Ergebnisse der dritten Erhebung 2004-2006. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft WSL, Birmensdorf. Bundesamt für Umwelt BAFU, Bern, pp. 231-251.

Eräjää S, Halme P, Kotiaho JS, Markkanen A, Toivanen T (2010) The Volume and Composition of Dead Wood on Traditional and Forest Fuel Harvested Clear-Cuts. Silva Fenn 44: 203-211.

Evans GR, Nordmeyer AH, Kelland CM (1990) Biomass and nutrient pools of bracken growing under radiata pine, Nelson, New Zealand. In: Thomson JA, Smith RT (eds) Bracken Biology and Management. Australian Institute of Agricultural Science, Sydney.

Ferguson DE, Boyd R, J. (1988) Bracken fern inhibition of conifer regeneration in northern Idaho. Res Pap INT-388 Ogden, UT: US Department of Agriculture, Forest Service, Intermountain Research Station: 11.

Galhidy L, Mihok B, Hagyo A, Rajkai K, Standovar T (2006) Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a Hungarian beech forest. Plant Ecol 183: 133-145.

Gaudio N, Balandier P, Philippe G, Dumas Y, Jean F, Ginisty C (2011) Light-mediated influence of three understorey species (*Calluna vulgaris*, *Pteridium aquilinum*, *Molinia caerulea*) on the growth of *Pinus sylvestris* seedlings. Eur J For Res 130: 77-89.

Gliessman SR, Muller CH (1972) The phytotoxic potential of bracken, *Pteridium aquilinum*. Madrono 21: 299-304.

Gliessman SR, Muller CH (1978) The allelopathic mechanisms of dominance in bracken (*Pteridium aquilinum*) in southern California. J Chem Ecol 4: 337-362.

Greene DF, Johnson EA (1996) Wind dispersal of seeds from a forest into a clearing. Ecology 77: 595-609.

Hanewinkel M, Peltola H, Soares P, Gonzalez-Olabarria JR (2010) Recent approaches to model the risk of storm and fire to European forests and their integration into simulation and decision support tools. For Syst 19: 30-47.

Harmon ME, Franklin JF (1989) Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. Ecology 70: 48-59.

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. Adv Ecol Res 15: 133-302.

Huntley B, Bartlein PJ, Prentice IC (1989) Climatic control of the distribution and abundance of beech (*Fagus* L.) in Europe and North America. J Biogeogr 16: 551-560.

Ilisson T, Koster K, Vodde F, Jogiste K (2007) Regeneration development 4-5 years after a storm in Norway spruce dominated forests, Estonia. Forest Ecol Manag 250: 17-24.

Imbeck H, Ott E (1987) Verjüngungsökologische Untersuchungen in einem hochstaudenreichen subalpinen Fichtenwald, mit spezieller Berücksichtigung der Schneeablagerung und der Lawinenbildung. Eidgenösschische Forschungsanstalt für Wald, Schnee und Landschaft WSL, Birmensdorf.

Juutinen A, Monkkonen M, Sippola AL (2006) Cost-efficiency of decaying wood as a surrogate for overall species richness in boreal forests. Conserv Biol 20: 74-84.

Keller W, Wohlgemuth T, Kuhn N, Schütz M, Wildi O (1998) Waldgesellschaften der Schweiz auf floristischer Grundlage. Mitt. Eidgenöss. Forsch.anst. Wald Schnee und Landsch.

Koch R, Brang P (2005) Extensive Verjüngungsverfahren nach Lothar. Schlussbericht zuhanden der Forstdirektion de BUWAL. Eidg. Forschungsanstalt WSL, Birmensdorf, pp. 90.

Kompa T, Schmidt W (2006) Zur Verjüngungssituation in südniedersächsischen Buchen-Windwurfgebieten nach einem lokalen Orkan von 1997. Forstarchiv 77: 3-19.

Koop H, Hilgen P (1987) Forest dynamics and regeneration mosaic shifts in unexploited beech (*Fagus sylvatica*) stands at Fontainebleau (France). Forest Ecol Manag 20: 135-150.

Krueger LM, Peterson CJ (2006) Effects of white-tailed deer on *Tsuga canadensis* regeneration: Evidence of microsites as refugia from browsing. Am Midl Nat 156: 353-362.

Kuuluvainen T (1994) Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland - a review. Ann Zool Fenn 31: 35-51.

Kuuluvainen T (2002) Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. Silva Fenn 36: 97-125.

Lain EJ, Haney A, Burris JM, Burton J (2008) Response of vegetation and birds to severe wind disturbance and salvage logging in a southern boreal forest. Forest Ecol Manag 256: 863-871.

Lawton RO, Putz FE (1988) Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. Ecology 69: 764-777.

Long ZT, Carson WP, Peterson CJ (1998) Can disturbance create refugia from herbivores: an example with hemlock regeneration on treefall mounds. J Torrey Bot Soc 125: 165-168.

Mayer P, Brang P, Dobbertin M, Hallenbarter D, Renaud JP, Walthert L, Zimmermann S (2005) Forest storm damage is more frequent on acidic soils. Ann For Sci 62: 303-311.

McKee A, LaRoi G, Franklin JF (1982) Structure, composition and reproductive behavior of terrace forests, south Fork Hoh River, Olympic National Park. In: Starkey EE, Franklin JF, Matthews JW (eds) Ecological research in national parks of the Pacific Northwest. Oregon State University, Forest Research Laboratory, Corvallis, Oregon, USA, pp. 22-29.

Moser B, Schütz M, Hindenlang KE (2008) Resource selection by roe deer: Are windthrow gaps attractive feeding places? Forest Ecol Manag 255: 1179-1185.

Nordén B, Ryberg M, Götmark F, Olausson B (2004) Relative importance of coarse and fine woody debris for the diversity of wood-inhabiting fungi in temperate broadleaf forests. Biol Conserv 117: 1-10.

Peterson CJ (2000) Damage and recovery of tree species after two different tornadoes in the same old growth forest: a comparison of infrequent wind disturbances. Forest Ecol Manag 135: 237-252.

Peterson CJ, Carson WP, McCarthy BC, Pickett STA (1990) Microsite variation and soil dynamics within newly created treefall pits and mounds. Oikos 58: 39-46.

Peterson CJ, Pickett STA (1990) Microsite and elevational influences on early forest regeneration after catastrophic windthrow. J Veg Sci 1: 657-662.

Peterson CJ, Pickett STA (1995) Forest reorganization - A case-study in an old-growth forest catastrophic blowdown. Ecology 76: 763-774.

Pickett STA, White PS (1985) The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, FL.

Romme WH, Everham EH, Frelich LE, Moritz MA, Sparks RE (1998) Are large, infrequent disturbances qualitatively different from small, frequent disturbances? Ecosystems 1: 524-534.

Royo AA, Carson WP (2006) On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Can J For Res-Rev Can Rech For 36: 1345-1362.

Sahlin E, Ranius T (2009) Habitat availability in forests and clearcuts for saproxylic beetles associated with aspen. Biodivers Conserv 18: 621-638.

Schelhaas MJ, Nabuurs GJ, Schuck A (2003) Natural disturbances in the European forests in the 19th and 20th centuries. Glob Change Biol 9: 1620-1633.

Schindler D, Grebhan K, Albrecht A, Schönborn J (2009) Modelling the wind damage probability in forests in Southwestern Germany for the 1999 winter storm 'Lothar'. Int J of Biometerol 53: 543-554.

Schönenberger W (2002) Post windthrow stand regeneration in Swiss mountain forests: the first ten years after the 1990 storm Vivian. For Snow Landsc Res 77: 61-80.

Schönenberger W, Fischer A, Innes JL (Eds.), 2002. Vivian's Legacy in Switzerland - impact of windthrow on forest dynamics. Swiss Federal Research Institute WSL Birmensdorf. Paul Haupt Verlag, Berne, Stuttgart, Vienna.

Schönenberger W, Kasper H, Lässig R (1992) Forschungsprojekte zur Wiederbewaldung von Sturmschadenflächen. Schweiz Z Forstwes 143: 829-847.

Schüepp M, Schiesser HH, Huntrieser H, Scherrer HU, Schmidtke H (1994) The winterstorm Vivian of 27 February 1990 - about the meteorological development, wind forces and damage situation in the forests of Switzerland. Theor Appl Climatol 49: 183-200.

Sippola AL, Siitonen J, Punttila P (2002) Beetle diversity in timberline forests: a comparison between old-growth and regeneration areas in Finnish Lapland. Ann Zool Fenn 39: 69-86.

Smith RT, Lockwood JG (1990) Bracken invasion and bracken replacement: guidelines for the prediction of hydrological changes. In: Thomson JA, Smith RT (eds) Bracken Biology and Management. Australian Institute of Agricultural Science, Sydney.

Svoboda M, Fraver S, Janda P, Bace R, Zenáhlíková J (2010) Natural development and regeneration of a Central European montane spruce forest. Forest Ecol Manag 260: 707-714.

Tolhurst KG, Turvey ND (1992) Effects of bracken (*Pteridium esculentum* (Forst. f.) Cockayne) on eucalypt regeneration in west-central Victoria. Forest Ecol Manag 54: 45-67.

Ulanova NG (2000) The effects of windthrow on forests at different spatial scales: a review. Forest Ecol Manag 135: 155-167.

Usbeck T, Wohlgemuth T, Dobbertin M, Pfister C, Bürgi A, Rebetez M (2010) Increasing storm damage to forests in Switzerland from 1858 to 2007. Agric For Meteorol 150: 47-55.

Van Couwenberghe R, Collet C, Lacombe E, Pierrat JC, Gegout JC (2010) Gap partitioning among temperate tree species across a regional soil gradient in windstorm-disturbed forests. Forest Ecol Manag 260: 146-154.

van Mantgem PJ, Stephenson NL, Keeley JE (2006) Forest reproduction along a climatic gradient in the Sierra Nevada, California. Forest Ecol Manag 225: 391-399.

von Oheimb G, Friedel A, Bertsch A, Hardtle W (2007) The effects of windthrow on plant species richness in a Central European beech forest. Plant Ecol 191: 47-65.

Wohlgemuth T, Kull P, Wüthrich H (2002) Disturbance of microsites and early tree regeneration after windthrow in Swiss mountain forests due to the winter storm Vivian 1990. For Snow Landsc Res 77: 17-47.

Zielonka T (2006) When does dead wood turn into a substrate for spruce replacement? J Veg Sci 17: 739-746.

Chapter I

Soil pH and ground vegetation are major predictors of tree regeneration in large forest gaps 10 and 20 years after windthrow in Central Europe

Submitted as:

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Summary

Aim: Wind disturbance is the main natural driver of forest stand dynamics in Central and Northern Europe. Regeneration of trees following windthrow has usually been studied at small spatial extents or with small sample sizes only. On the basis of a large sample of windthrow gaps, we aimed to quantify natural tree regeneration after wind disturbance, and to identify factors influencing tree regeneration dynamics.

Location: 90 windthrown forests (each ≥ 3 ha) caused by two catastrophic wind events in 1990 and 1999 in an ecologically diverse region extending over 20 000 km^2 on the Central Plateau and in the Alps of Switzerland, Central Europe.

Methods: Regeneration status was assessed on six circular sample plots per windthrow gap in 2010/2011. We recorded soil pH, organic layer, post-windthrow treatment, elevation, aspect, slope, browsing damage, presence of predominant vegetation cover at the plot (n=540) and windthrow gap level (n=90). We compared regeneration density and composition in gaps with and without salvage logging and elucidated the most important environmental factors influencing tree regeneration after wind disturbance using generalized linear models (GLM) and linear mixed effects models.

Results: Ten and 20 years after wind disturbance, late-successional tree species such as beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) H. Karst.) frequently dominated, independent of the post-storm treatment. In both GLM (gap level) and linear mixed effects models (plot level) analyses, soil pH was the most important predictor of sapling density, followed by ground vegetation. At the gap level, the variation explained was moderate ($D^2 = 0.41$) if all gaps of both storm events were pooled in the analysis. Higher explanatory power resulted at subsample levels (D^2 up to 0.73), i.e. if focusing on one storm event only or on specific forest types.

Conclusion: As a rule of thumb, stem density is higher on neutral or slightly alkaline soils and lower if ground vegetation is dense. Late-successional tree species dominate by number in a majority of gaps 10 to 20 years after wind disturbance in terms of sapling density, contrary to conventional wisdom on forest succession after disturbance.

Keywords

Blowdown, salvage logging, regeneration dynamics, forest composition, wind disturbance, environmental predictors, succession

1. Introduction

Wind disturbance is one of the most important factors influencing forest stand dynamics (Lawton and Putz 1988; Peterson 2000; Ulanova 2000). The severity of wind impacts on forests depends on many factors, including the intensity of wind gusts, the duration of strong winds and current forest structure (Romme et al. 1998). These wind-related factors affect forest stands differently, resulting from scattered individual tree mortality across patterns of small canopy gaps to large openings (cf. Attiwill 1994). Depending on the size of a canopy gap, the availability of resources such as light, water or nutrients may considerably increase. Microclimatic conditions are modified (Peterson et al. 1990; Galhidy et al. 2006) and plant diversity is promoted in the first few years after windthrow (Degen et al. 2005; von Oheimb et al. 2007). Severe wind disturbance to mountain forests temporarily reduces the protective effect of forests against natural hazards such as avalanches or rockfall (Schönenberger 2002), and generally leads to economic loss. Therefore, post-disturbance treatments usually aim at a quick restocking, often through artificial regeneration using late-successional species. In this context, knowledge not only on the speed of natural regeneration is of considerable scientific and practical interest, but also on the factors driving tree regeneration including its variability.

Among the various aspects of natural regeneration after windthrow, the following are of particular interest from a management perspective: stem density, height growth rate, species composition and spatial distribution of the regenerated saplings. Windthrown trees may be replaced by tree individuals of the same species, which has been described as “direct re-growth”, in particular after fire (Romme et al. 2011). In contrast, according to the classical succession theory in temperate forests, tree species composition after disturbance starts by characteristic pioneer communities composed of early-successional tree species and would subsequently be replaced by late-successional species (e.g. Clements 1936; Scherzinger 1996; Kimmins 2004). Recent studies, however, have described a disturbance-mediated acceleration of succession, with stands of pioneer species being replaced mainly by late-successional species, if wind disturbance gained importance due to fire suppression (Allen et al. 2012; Holzmueller et al. 2012).

In 1990 and 1999 two severe winter storms caused large forest damage in Central Europe. In particular, many protection forests in the Swiss Alps were affected by the storm Vivian in 1990 (5 million m^3; Schüepp et al. 1994), which led to several studies on early tree regeneration dynamics in some affected areas (Schönenberger 2002; Wohlgemuth et al. 2002). Since these studies focused on a very small number of windthrow areas, the findings could not be generalised for forests of a larger region. Winter storm Lothar hit Central Europe in 1999 (Mayer et al. 2005) and caused damage of 180 million m^3 of wood (Schelhaas et al. 2003). In Switzerland, it resulted in twice as much damaged timber (13 million m^3; BUWAL and WSL 2001) than the storm Vivian. In contrast to Vivian, Lothar damaged forests mainly at lower elevations, especially on the Central Plateau (Fig. 1). Research after Lothar focussed on the recolonisation by plants and animals and to date has not been published internationally (Appendix A). The case studies conducted in Switzerland after Vivian (n=4 windthrow areas) and Lothar (n=16 windthrow areas) suggest that windthrown mountain forests regenerate slowly in comparison to lowland forests (Wohlgemuth et al. 2008a), and that salvage-logged windthrow areas have a higher density of natural regeneration than unharvested ones (Schönenberger 2002). A study on small-to-intermediate windthrow gaps in the Lorraine region (France) five years after

Lothar showed that tree regeneration densities were higher at gap edges than in gap centres and that soil pH influenced the probability of the occurrence of particular tree species (Van Couwenberghe et al. 2010).

In the present study, we therefore aimed to investigate tree regeneration over a wide range of environmental conditions by selecting 90 windthrow areas located on the Central Plateau and in the Swiss Alps. We considered only stands with total damage (all trees windthrown in a gap) 20 and 10 years after the two severe storm events Vivian (1990) and Lothar (1999). Specifically, our study aimed (i) to detect differences in tree species composition in post-windthrow regeneration between the two post-storm treatments "salvage-logged" (SL treatment in this paper) and "no intervention" (windthrown trees were not removed; NI treatment in this paper), and (ii) to identify the most important environmental factors influencing tree regeneration after wind disturbance, with a particular focus on the post-storm treatments (SL vs. NI) and the different time periods since the disturbance events.

2. Material and methods

2.1 Gap sample

The studied windthrow gaps in Switzerland, subsequently called 'gap sample', were caused by the winter storms Vivian, 1990, and Lothar, 1999 (Fig. 1 and Table 1). Gaps were selected from a database of geospatial information for windthrow patches all over Switzerland, derived from visual interpretations of post-disturbance aerial photographs (Vivian: Federal Office for the Environment FOEN; Lothar: Engineering Consultants H. U. Scherrer). The selection was made according to six criteria: 1) gaps with total damage, 2) gap ≥3 ha, 3) forest type in the gap belongs to one of the four most widespread forest types in Switzerland, i.e. beech, silver fir-beech (‘fir-beech’ in this paper), silver fir-Norway spruce (‘fir-spruce’ in this paper), or Norway spruce forest (Wohlgemuth et al. 2008b), 4) the treatments SL and NI are evenly represented in the gap sample (information on salvage-logging activities was derived from interviews with local foresters), 5) post-disturbance regeneration in gaps is exclusively natural, and 6) gaps represent all regions in Switzerland that were affected by severe windthrow damage. The selection resulted in 90 gaps located in the Jura Mountains, the Central Plateau and the Alps, with wide ranges in elevation (350–1800 m a.s.l.), aspect and slope (0–52°). The forest types of the gaps were categorised as 24% beech, 16% fir-beech, 23% fir-spruce, and 37% spruce forests. Field work was conducted on the 24 Vivian and 66 Lothar gaps between December 2009 and January 2011.

2.2 Data collection

In each gap, six circular sample plots 20 or 50 m^2 in size were defined. Plot sizes of 20 m^2 were used for gaps below 1200 m a.s.l., and sizes of 50 m^2 for those above 1200 m a.s.l. to take into account the higher regeneration densities expected at lower elevations (Wohlgemuth et al. 2008a), so as to optimise time-consuming data collection.

The circular plots were defined at each gap along the two axes of an ideal ellipse fitted to the windthrow area, at distances of 20, 40, and 80 m away from the forest edge to take into account the variation of regeneration with distance from the edge (Fig. 2). If a gap was large enough, one of the two transect lines paralleled the contour line and the second one was placed perpendicular to and upslope of the first one. If the gap had an unsuitable shape and the distance rule could

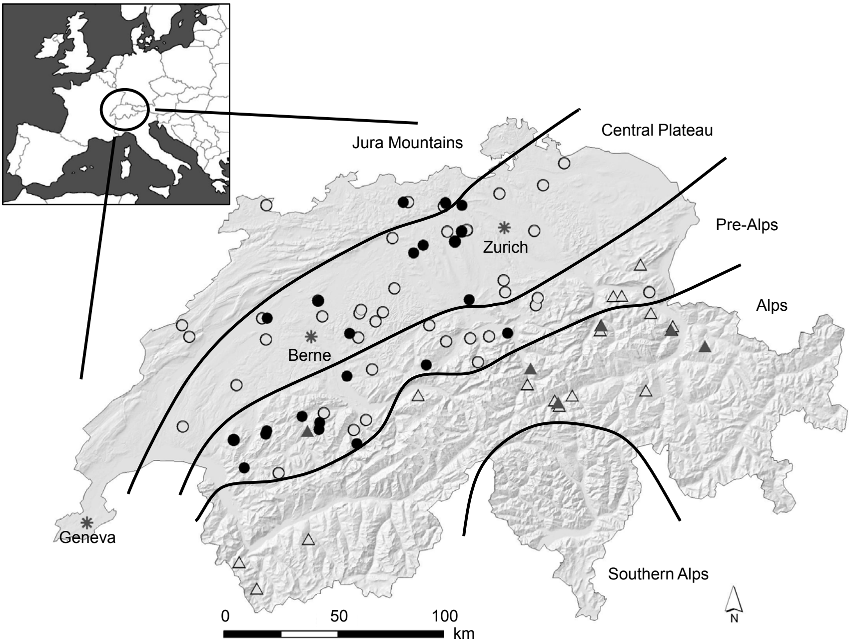


Fig. 1 Location of windthrow gaps in Switzerland. Vivian (1990): Δ = salvage-logged, ▲ = no intervention. Lothar (1999): ○ = salvage-logged, ● = no intervention. Source of map: BFS GEOSTADT/Bundesamt für Landestopografie (Federal Office of Topography) and Swiss Federal Institute of Forest, Snow and Landscape Research WSL .

Table 1 Number of gaps per strom event, treatment, average elevation (± SE), and region.

Region	Vivian				Lothar			
	SL	NI	ELE [m a.s.l.]		SL	NI	ELE [m a.s.l.]	
Jura Mountains	0	0	-	-	5	3	695	±114
Central Plateau	0	0	-	-	24	9	627	±31
Pre-Alps	3	1	1338	±100	14	11	1233	±42
Alps	15	5	1447	±52	0	0	-	-
Total	18	6	1429	±46	43	23	860	±44

therefore not be applied, the two transect lines were slightly shifted. However, the right angle between the two transect lines was always maintained. Transects were rotated clockwise (90°, 180° or 270°) around the centre point if obstacles such as rocks made a proper data assessment impossible.

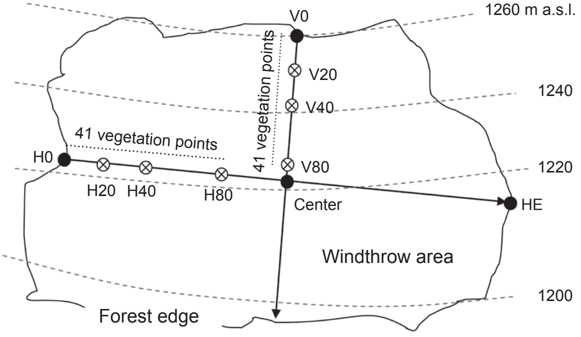


Fig. 2 Sampling design in gaps: Six circular plots were selected in each gap at growing distances from two forest edges of 20 m (H20, V20), 40 m (H40, V40), and 80 m (H80, V80), following the axes of an ellipse fitted to the windthrow patches. Points along the foest edge are indicated by H0, V0, and HE.

On the circular sample plots, all saplings ≥ 20 cm tall were measured as long as the stem base of each tree was growing inside the plot. For each sapling, we recorded the following characteristics: species identity, height, diameter at breast height (DBH at 1.3 m height), age type (pre- or post-storm origin), substrate type (forest soil or deadwood), and damage type (only main shoot browsed, main and lateral shoots browsed, presence of fraying damage, or other damage). Deadwood quantity was recorded according to the method described by Priewasser et al. (2012). We took soil samples from both organic and mineral horizons at the centre of each circular plot (2x6x90=1080 samples), dried them in an oven for 48 hours at 60°C, and afterwards milled and sieved the soil (2 mm mesh width). We measured pH in a 0.01 M CaCl2 solution, yielding a total of 2160 pH measurements, i.e. two measurements were made per soil sample.

Along the two transect lines in each gap, we defined the vegetation cover every two meters from points H0 to H80, and from V0 to V80 (Fig. 2), resulting in 82 vegetation records per gap. We assigned the vegetation from the vertical projection of the topmost plant, and classified it as tree, bracken (*Pteridium aquilinum* (L.) Kuhn), other ferns, raspberry (*Rubus idaeus* L.), bramble (*Rubus fruticosus* L.), blueberry (*Vaccinium myrtillus* L.), grasses, rushes (*Juncus* spec.), sedges (*Carex* spec.), herbs, tall herbs (if present, they were classified as *Adenostyles* or *Petasites* type), or no vegetation (bare soil). Frequencies of vegetation types served for transformation into percentages per gap (n=82) or per circle plot (n=10). For circle plots, the ten preceding vegetation points of a circle plot were used to calculate the percentages of the vegetation types (Fig. 2).

2.3 Variables for the statistical analysis

We used three dependent variables to characterize the regeneration: 1) density of woody plants ≥ 20 cm per windthrow gap, reg_{lig} (standardized to n ha^{-1}), which reflects the status quo 10 years after the storm Lothar and 20 years after the storm Vivian; 2) density of tree saplings per windthrow gap, reg_{tr} (n ha^{-1}), and 3) density of tree saplings per circle plot (n ha^{-1}). The following explanatory variables were derived from environmental factors: *ELE* = elevation (m a.s.l.), *EXP* = aspect (N,S,E,W, no EXP), *SLO* = slope (in degrees), pH_{M} = mineral soil pH, pH_{O} = organic soil pH, *TRT* = treatment (SL or NI), VEG_{fb} = vegetation cover of all ferns and berry species (bramble, raspberry, blueberry (*Vaccinium myrtillus* L.)), VEG_{bb} = vegetation cover of bracken and bramble, LA_{o} = thickness of organic layer (cm), *BR* = browsing damage, *DIS* = Distance to forest edge (used in the plot level analysis only) and *YRS* = time since disturbance (10 or 20 years; Table 2). Since a large number of plots lacked any saplings, we used the variable *BR* at the gap level only.

As we were mainly interested in regeneration established after wind disturbance, we distinguished between pre- and post-storm regeneration. For this, we estimated sapling age by counting the whorls on conifers or the tree rings from a stem of a tree outside the circle plot. Alternatively, we counted the tree rings from the oldest branch of a tree inside the circle plot.

Table 2 Explanatory variables (at the gap level).

Variables	Description	Range	
		Vivian	Lothar
ELE	elevation (m a.s.l.)	890-1800	370-1590
BR	browsing damage (% browsed saplings)	0-65	0-60
DIS	distance from the forest edge (m)	20, 40, 80	20, 40, 80
EXP	aspect (categorial)	N, E, S, W, no	N, E, S, W, no
LA_O	layer organic material (cm)	1-9	2-11
pH_M	pH mineral soil	3.0-6.6	3.1-7.2
pH_O	pH organic soil	3.2-6.4	2.9-6.7
SLO	slope (°)	25-52	0-45
TRT	treatment (categorial)	SL, NI	SL, NI
VEG_{bb}	vegetation cover (% bracken and bramble)	0-28	0-59
VEG_{fb}	vegetation cover (% ferns and berries)	0-44	0-66
YRS	years since disturbance	20	10

2.4 Data analysis

Unless otherwise noted, we used only the data from post-storm regeneration. The statistical computing system R (version 2.11.1, R Development Core Team 2011) served for all analyses.

2.4.1 Gap level analysis (n=89)

Regeneration data of the six plots per gap were pooled and standardized to counts per hectare. We excluded one Lothar gap that lacked any post-storm regeneration (thus, n=89). We used a mixed ANOVA design to analyse sapling density, tree height and different vegetation cover proportions with respect to gap subsamples differing in storm event and post-windthrow treatments (SL or NI). We entered treatment as between-gap factor and in some analyses tree species or vegetation cover as within-gap factor. We used t-tests or Wilcoxon rank sum tests to detect differences in tree species diversity (Shannon Index, Evenness) and browsing (variable *BR*) regarding SL and NI gaps. Prior to all ANOVA analyses, we transformed the response variables using the square root or the logarithm (log plus the smallest unit) to meet the assumptions of normality and/or homogeneity of variance.

As a classification system of pioneer vs. late-successional species, we used the definition by Brzeziecki and Kienast (1994). Accordingly, pioneer species consist of ruderals, stress-tolerant ruderals, competitive ruderals and competitive stress-tolerant ruderals: *Populus alba* L., *Populus nigra* L., *Populus tremula* L., *Betula pendula* Roth, *Betula pubescens* Ehrh., *Salix* spec., *Alnus incana* (L.) Moench, *Alnus glutinosa* (L.) Gaertn., *Acer campestre* L., *Acer pseudoplatanus* L., *Fraxinus excelsior* L., *Larix decidua* Mill., *Pinus sylvestris* L., *Sorbus aucuparia*

L., *Sorbus aria* (L.) Crantz, *Prunus avium* L., *Prunus padus* L. Competitive stress tolerators and competitors were classified as late-successional species: *Fagus sylvatica* L., *Abies alba* Mill., *Quercus* spec., *Picea abies* L., *Ulmus* spec., *Tilia* spec., *Acer platanoides* L., *Carpinus betulus* L.

To evaluate the influence of the explanatory variables on post-storm regeneration, we employed Generalised Linear Models (GLM). Because of overdispersion, i.e. the variance of the dependent variable being larger than its mean, we applied a negative binomial GLM (glm.nb; package MASS). If two or more explanatory variables were inter-correlated (Pearson, $r > 0.55$), we only considered the variable with superior explanatory power for modelling. Variables were permutated (Table 2) according to set numbers, and GLM models were run using all variable sets. We ranked the results according to the Akaike Information Criterion (AIC) as a measure for the goodness of fit (Venables and Ripley 1999) and considered further only those models with all explanatory variables being significant.

2.4.2 Plot level analysis (n=540)

For the plot level analysis we used the data from all circular sample plots. Although regeneration after the storm was absent on many plots (reg_{lig} = 12% and reg_{tr} = 16%), we did not exclude any of the plots from the analysis. For analyses, we log-transformed the data in the same way as described for the gap sample and standardized stem densities to n ha^{-1}. We used linear mixed effects models (lmer; package lme4) to take into account the random gap effect and to test the fixed effects of the explanatory variables. The gap served as a random effect and the following explanatory variables as fixed effects: *ELE*, *SLO*, *EXP*, *TRT*, LA_o, *DIS*, *pH*, *VEG* and *YRS*. If two or more explanatory variables were inter-correlated

(Pearson, r > 0.55), we considered only the variable with superior explanatory power for modelling. For each model term, p-values were calculated by the function pvals.fnc (package languageR). We defined the best model according to the same procedure as described for the gap sample.

3. Results

3.1 Gap level (n=89)

3.1.1 Regeneration densities

Gaps from Vivian and Lothar storm events had an average elevation of 1430 m and 860 m a.s.l., respectively (Table 1). In the Vivian gaps, 11% of the saplings were assessed as advance regeneration (435 ± 134 tree saplings ha^{-1}, mean ± SE; Fig. 3). In contrast, in the (younger) Lothar gaps, this amounted to 29% or nearly three times more than in Vivian gaps (2856 ± 860 ha^{-1}). The density of the saplings established after wind disturbance was twice as high in the Lothar than in the Vivian gaps (ANOVA for all woody species: $F_{1,87} = 4.87$, $P = 0.030$; for all tree species: $F_{1,87} = 4.44$, $P = 0.038$; Fig. 3). Regeneration densities in NI gaps were generally smaller than in SL gaps (Fig. 4), but the differences were not significant (ANOVA for Vivian: all woody species $F_{1,22} = 1.79$, $P = 0.20$, only tree species: $F_{1,22} = 2.75$, $P = 0.11$ and for Lothar: all woody species $F_{1,63} = 1.61$, $P = 0.21$, only tree species $F_{1,63} = 1.65$, $P = 0.20$).

Regeneration densities in the SL Lothar gaps were highest in beech forests with 9936 ± 2910 (mean ± SE) tree saplings ha^{-1}. In the other three forest types, tree sapling density amounted to 6419 ± 2104 ha^{-1} in fir-spruce, 6262 ± 1945 in spruce and 6258 ± 1375 in fir-beech forests. The tree sapling density in the NI

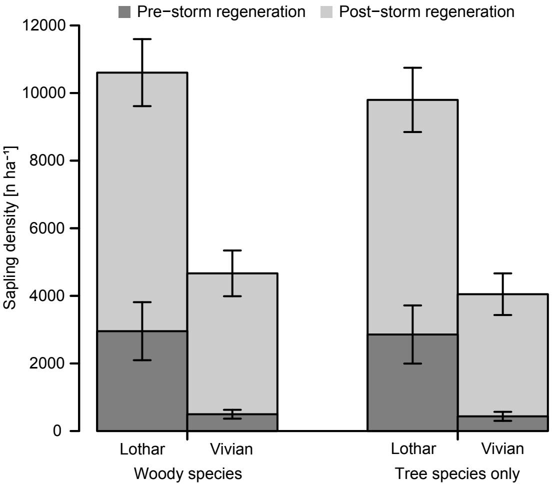


Fig. 3 Regeneration densities in 2010 in the Vivian (20-year-old) and Lothar (10-year-old) gaps, ordered according to the established saplings before or after the wind disturbance (tree individuals ≥ 20 cm high).

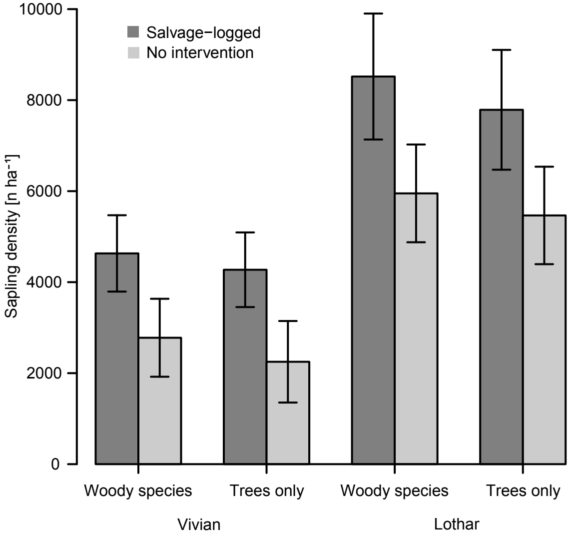


Fig. 4 Regeneration densities in 2010 originated from post-storm establishment, in the Vivian (20-year-old) and Lothar (10-year-old) gaps, ordered according to treatments salvage-logged or no intervention (tree individuals ≥ 20 cm high).

Lothar gaps was again highest in beech forests (7333 ± 2355 ha^{-1}). For the other forest types, tree sapling densities amounted to 6336 ± 2799 (fir-spruce forests), 4372 ± 1947 (fir-beech forests) and 3460 ± 1396 ha^{-1} (spruce forests). The tree sapling density in the SL Vivian gaps was 4098 ± 742 ha^{-1}. In the NI Vivian gaps, densities were smallest (2161 ± 898 ha^{-1}; Appendix B).

3.1.2 Species composition

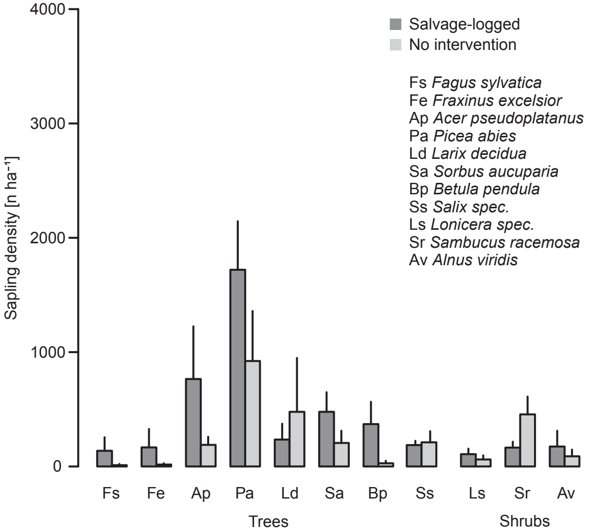
All woody species with at least 100 individuals per hectare in either SL or NI gaps were compared (for data on all woody species, see Appendix B). Results are presented i) for all Vivian gaps pooled, as a distinction between the main forest types was not possible due to the low sample size, and ii) for the Lothar gaps according to forest type, as the four forest types can be distinguished reasonably well.

i) Vivian gaps (n=24)

The Vivian gaps consisted of fir-spruce and spruce forests only. The most abundant tree species in the SL Vivian gaps (n=24) were spruce (37% of all saplings), followed by sycamore (*Acer pseudoplatanus* L.), rowan (*Sorbus aucuparia* L.), birch (*Betula pendula* Roth), larch (*Larix decidua* Mill.), willow (*Salix* spec.), ash (*Fraxinus excelsior* L.) and beech (Fig. 5). In NI Vivian gaps spruce was also the most frequent species (33%), but typically the frequency of the other species varied widely, and many species grew in low densities. The exceptions were the pioneers red elder (*Sambucus racemosa* L.) and larch, which were more prominent in NI than SL gaps. Sapling densities did not differ between treatments

(ANOVA: $F_{1,22} = 0.29$, $P = 0.60$), but they did between species (ANOVA: $F_{10,220} = 13.07$, $P < 0.001$). Moreover, sapling densities per woody species did not differ significantly between SL and NI Vivian gaps (ANOVA for the interaction between woody species and treatment: $F_{10,220} = 0.95$, $P = 0.49$).

Fig. 5 Regeneration densities in 2010 (originated from post-storm establishment) of individual tree species in the 20-year-old Vivian gaps (tree individuals ≥ 20 cm).



ii) Lothar gaps

Beech forests (n=22)

The most frequent tree species regenerated after disturbance was beech with nearly half of all saplings in SL gaps (5181 ± 2529 ha^{-1}) and as many as 75% (5683 ± 2107 ha^{-1}) in NI gaps (Fig. 6a). In SL gaps, another 11 woody species with at least 100 saplings per hectare were found, whereas in NI gaps only seven additional woody species were present (Fig. 6a). Interestingly, aspen (*Populus tremula* L.), hornbeam (*Carpinus betulus* L.) and red elder were absent in NI gaps. Ash was the second most frequent species in SL gaps, but it was almost entirely absent in NI gaps. Similar to the results in the Vivian gaps, regeneration density did not differ between treatments (ANOVA: $F_{1,20} = 0.79$, $P = 0.38$). Sapling densities of woody species differed significantly (ANOVA: $F_{11,220} = 8.05$, $P < 0.001$), but there were no significant differences between the SL and NI gaps regarding the individual woody species (ANOVA for the interaction between tree species and treatment: $F_{11,220} = 1.28$, $P = 0.23$).

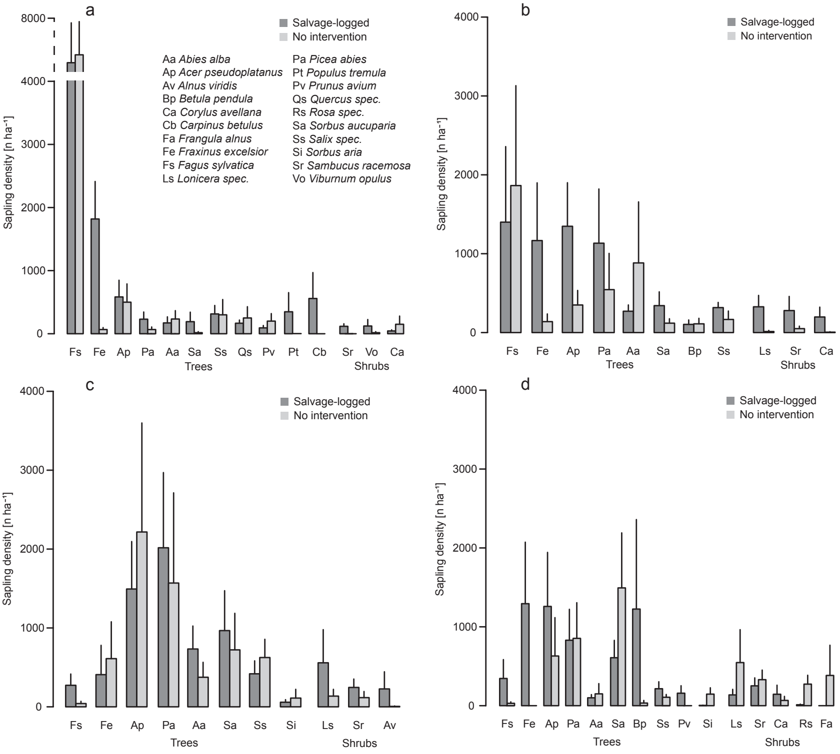


Fig. 6 Regeneration densities in 2010 (originated from post-storm establishment) of individual tree species in 10-year-old Lothar gaps (tree individuals ≥ 20 cm high): a = beech forests, b = fir-beech forests, c = fir-spruce forests, d = spruce-forests.

Fir-beech forests (n=14)

In SL gaps, beech, sycamore, ash and spruce dominated and had similar sapling densities (Fig. 6b). These four tree species together accounted for 71% of total sapling density. In NI gaps beech was clearly the most abundant tree species, amounting to 41%. Fir is a potential late-successional tree in these forests and had only an inferior position in SL gaps, whereas it was the second most abundant species in NI gaps. The densities of the most abundant woody species were significantly higher in SL than in NI gaps (ANOVA: $F_{1,12} = 7.91$, $P = 0.016$). Differences between the selected species were highly significant (ANOVA: $F_{10,120} = 3.18$, $P = 0.001$), but there was no significant interaction between woody species and treatment (ANOVA: $F_{10,120} = 0.64$, $P = 0.78$).

Fir-spruce forests (n=14)

Spruce was the most dominant tree species (27%) in SL gaps, followed by sycamore and rowan (Fig. 6c). The same three species were also most abundant in NI gaps, but sycamore was the most frequent species, accounting for about one third of total sapling density. Densities did not differ between treatments (ANOVA: $F_{1,12} = 0.24$, $P = 0.64$), but between species (ANOVA: $F_{10,120} = 6.51$, $P < 0.001$), and the differences in the sapling densities of the individual woody species did not differ significantly between SL and NI gaps (ANOVA for the interaction between tree species and treatment: $F_{10,120} = 0.85$, $P = 0.58$).

Spruce forests (n=15)

The deciduous species ash, sycamore and birch dominated in gaps of SL spruce forests, whereas spruce made up only 12% of all saplings (Fig. 6d). Similarly, rowan was most abundant with a proportion of about 30% in NI gaps, while spruce was only second with a proportion of 16%. Sapling densities did not differ significantly between treatments (ANOVA: $F_{1,13} = 0.07$, $P = 0.79$), but they did between species (ANOVA: $F_{14,182} = 4.47$, $P < 0.001$). There were no significant differences between the SL and NI gaps regarding the individual woody species (ANOVA for the interaction between tree species and treatment: $F_{14,182} = 1.34$, $P = 0.19$).

3.1.3 Tree species diversity after disturbance

The number of tree species differed slightly, but never significantly between the gaps with different post-storm treatments (NI vs. SL; Table 3). Shannon diversity in NI Vivian gaps was significantly higher than in SL Vivian gaps. In contrast, the SL Lothar gaps (beech and fir-beech forests) tended to be more diverse than the corresponding NI gaps. However, tree species diversity in the NI Lothar spruce and fir-spruce forest gaps was also higher than in the corresponding SL gaps. Nevertheless, these differences were not significant. In most cases, the tree species were more evenly distributed (evenness value closer to 1) in NI than in SL gaps, except for gaps in NI Lothar beech forests, where beech dominated strongly. However, evenness did not differ significantly at any data level.

Table 3 Diversity measures of all tree species based on sapling densities and average numbers of tree species per gap. Differences in tree diversity between no intervention (NI) and salvage-logged (SL) gaps were analysed with a Wilcoxon rank sum test (significant values in bold).

Sample	# tree species	p-value	Shannon-index	p-value	Evenness	p-value
Vivian and Lothar						
All forests (n=89)						
NI	5.5	0.413	1.192	0.501	0.723	0.144
SL	6.0		1.132		0.659	
Vivian						
All forests (n=24)						
NI	5.7	0.257	1.337	**0.014**	0.776	0.061
SL	5.0		0.952		0.620	
Lothar						
Beech forests (n=22)						
NI	5.0	0.278	0.721	0.078	0.476	0.210
SL	6.6		1.133		0.635	
Silver fir-beech forests (n=14)						
NI	5.7	0.185	1.236	0.552	0.779	0.484
SL	7.1		1.371		0.702	
Silver fir-Norway spruce forests (n=15)						
NI	6.0	0.773	1.340	0.534	0.757	0.487
SL	5.8		1.223		0.706	
Norway spruce forests (n=15)						
NI	4.8	0.389	1.257	0.686	0.799	0.215
SL	5.9		1.194		0.697	

3.1.4 Sapling height

Trees were slightly but not significantly taller in Vivian gaps (151 ± 23 cm; mean ± SE) than in Lothar gaps (138 ± 14 cm; ANOVA: $F_{1,87} = 0.96$, $P = 0.33$). Pioneer tree species were significantly taller (Vivian SL: 208 ± 30 cm, Vivian NI: 220 ± 22 cm; Lothar SL: 169 ± 14 cm, Lothar NI: 192 ± 38) than late-successional tree species (Vivian SL: 98 ± 10 cm, Vivian NI: 71 ± 7 cm; Lothar SL: 96 ± 11 cm, Lothar NI: 108 ± 17 cm) in the SL and NI Vivian and Lothar gaps (ANOVA for

Vivian NI gaps $F_{1,5} = 72.89$, $P < 0.001$and SL gaps $F_{1,17} = 10.11$, $P = 0.005$, for Lothar NI gaps $F_{1,21} = 5.75$, $P =0.026$ and SL gaps $F_{1,42} = 26.96$, $P < 0.001$; Fig. 7). In 24 gaps (25.8 %), however, average tree height of late-successional species was higher than or equal to the height of the pioneers.

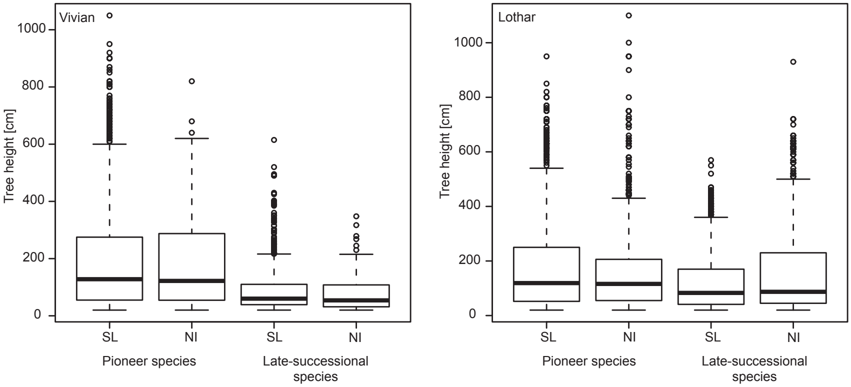


Fig. 7 Average tree height in 2010 of pioneer or late-successional tree species, ordered according to storm event and treatment (tree individuals ≥ 20 cm).

3.1.5 Browsing damage

The considerable, although not significant differences in sapling density of woody species between treatments (Fig. 4) could be explained best by the variable *BR* (% browsed trees) as an interaction term. The average proportion of browsed trees in the Vivian gaps was significantly smaller in the NI than in the SL treatment (t-test, p=0.053), and the result for the Lothar gaps was similar (Wilcoxon rank sum test, p = 0.009), i.e. browsing was less frequent in NI than in SL gaps. However, *BR* was important in the GLM analyses of the Vivian but not of the Lothar gaps.

3.1.6 Vegetation cover

The vegetation cover ‘tree’ was the most frequent type, followed by ‘berry species’ (bramble, raspberry, blueberry), no vegetation, ferns, grasses, tall herbs and the rarely found rushes/sedges/herbs. The proportion of vegetation types varied considerably in both the Vivian and Lothar gaps (ANOVA for Vivian: $F_{6,132} = 13.4$, $P < 0.001$; for Lothar: $F_{6,384} = 138.2$, $P < 0.001$). Surprisingly, SL and NI gaps did not differ regarding the cover of individual vegetation types (ANOVA for Vivian: $F_{1,22} = 0.20$, $P = 0.66$; for Lothar: $F_{1,64} = 0.17$, $P = 0.68$).

3.1.7 Predictors of sapling densities

The most important variables explaining sapling densities throughout all GLM models were soil pH and the dominant vegetation cover (percentage of points covered with fern and berry species; Table 4). The best model for the whole data set (n=89 gaps) included the significant variables soil pH, vegetation cover, treatment (SL or NI) and elevation, and explained 41% of the variation (deviance D^2) in sapling density. In Vivian gaps the variables treatment, soil pH, elevation and browsed trees were most important, and in Lothar gaps the variables treatment, soil pH and vegetation cover. Models for Lothar subsets, i.e. regarding the forest types beech, fir-beech, fir-spruce and spruce forests resulted in a higher D^2 (up to 73% in beech and spruce forests; cf. Table 5).

Soil pH was related to sapling densities in all cases in a positive manner. In contrast, high vegetation cover was negatively correlated with regeneration: fewer saplings were found where a high percentage of fern and berry species were present. In SL gaps, sapling density was generally higher than in NI gaps.

Elevation was related negatively to tree regeneration density in all gaps, except in the Lothar fir-spruce and spruce forests (Fig. 8).

Table 4 Results of the regression analyses at the gap level, ordered according to storm disturbance. Variables with no postponed sign are highly significant ($p < 0.01$), variables with postponed "*" are weakly significant ($p < 0.05$), and variables with postponed "°" are significant on a 10% level ($p < 0.10$; reg_{lig} = all lignified species, reg_{tr} = only tree species).

Vivian & Lothar: N=89				**Vivian: N=24**			**Lothar: N=65**		
Response var.									
#	**Explanatory var.**	**D^2**	**AIC**	**Explanatory var.**	**D^2**	**AIC**	**Explanatory var.**	**D^2**	**AIC**
reg_{lig}									
1	ELE	0.08	1740	EXP°	0.10	446	pH_O	0.25	1276
	pH_O	0.20	1727				VEG_{fb}	0.34	1267
	VEG_{fb}	0.24	1722						
2	ELE* VEG_{fb}	0.28	1718	pH_M° TRT*	0.18	446	pH_O VEG_{fb}	0.40	1262
	pH_O VEG_{fb}	0.30	1716	ELE* pH_M*	0.20	445			
	ELE pH_O	0.32	1713						
3	BR° pH_O ELE	0.34	1712	TRT° ELE* pH_M*	0.29	444	TRT° pH_O VEG_{fb}	0.42	1262
	TRT* pH_O ELE	0.35	1710						
	VEG_{fb} pH_O ELE	0.37	1707						
4	BR* TRT pH_O ELE	0.40	1706	BR* TRT ELE pH_M	0.45	440			
	TRT* VEG_{fb} pH_O ELE	0.41	1704						
reg_{tr}									
1	ELE	0.09	1723	TRT°	0.10	441	BR°	0.04	1283
	pH_O	0.15	1717				pH_O	0.19	1270
	VEG_{fb}	0.21	1709				VEG_{fb}	0.31	1259
2	pH_O* VEG_{fb}	0.25	1706	ELE° pH_M°	0.16	442	pH_O* VEG_{fb}	0.34	1257
	ELE VEG_{fb}	0.26	1705	pH_M° TRT*	0.22	440			
	ELE pH_O	0.27	1703						
3	BR° pH_O ELE	0.30	1702	ELE° TRT* pH_M	0.29	439			
	TRT* pH_O ELE	0.31	1701						
	VEG_{fb} pH_O ELE	0.32	1698						
4	BR* TRT pH_O ELE	0.34	1697	BR* TRT ELE pH_M	0.41	437			
	TRT* VEG_{fb} pH_O ELE	0.35	1696						

Table 5 Results of the regression analyses at the gap level in the Lothar subset, subdivided according to forest type (Lothar$_B$ = beech, Lothar$_{FB}$ = fir-beech, Lothar$_{FS}$ = fir-spruce, and Lothar$_S$ = spruce forest). Variables with no postponed sign are highly significant ($p < 0.01$), variables with postponed "*" are weakly significant ($p < 0.05$), and variables with postponed "°" are significant on a 10% level ($p < 0.10$; reg$_{lig}$ = all lignified species, reg$_{tr}$ = only tree species).

Lothar$_B$: N=22				**Lothar$_{FB}$: N=14**			**Lothar$_{FS}$: N=14**			**Lothar$_S$: N=15**		
Response var.												
#	**Explan. var.**	**D^2**	**AIC**	**Explan. var.**	**D^2**	**AIC**	**Explan. var.**	**D^2**	**AIC**	**Explan. var.**	**D^2**	**AIC**
reg$_{lig}$												
1	pH$_O$	0.40	442				VEG$_{fb}$*	0.21	279	VEG$_{fb}$*	0.46	287
	VEG$_{bb}$	0.66	428				pH$_M$	0.64	267			
2	pH$_O$* VEG$_{bb}$	0.73	426	TRT* ELE*	0.32	272				TRT* VEG$_{fb}$*	0.57	285
3				pH$_O$° TRT* ELE	0.43	271				ELE° TRT* VEG$_{fb}$	0.64	284
reg$_{tr}$												
1	pH$_O$	0.35	442				VEG$_{fb}$*	0.19	276	VEG$_{fb}$*	0.38	285
	VEG$_{bb}$	0.68	425				pH$_M$	0.56	267			
2	pH$_O$° VEG$_{bb}$	0.71	424	TRT* ELE*	0.29	271				ELE° VEG$_{fb}$	0.46	285
										TRT* VEG$_{fb}$	0.60	280
3										ELE TRT VEG$_{fb}$	0.73	276

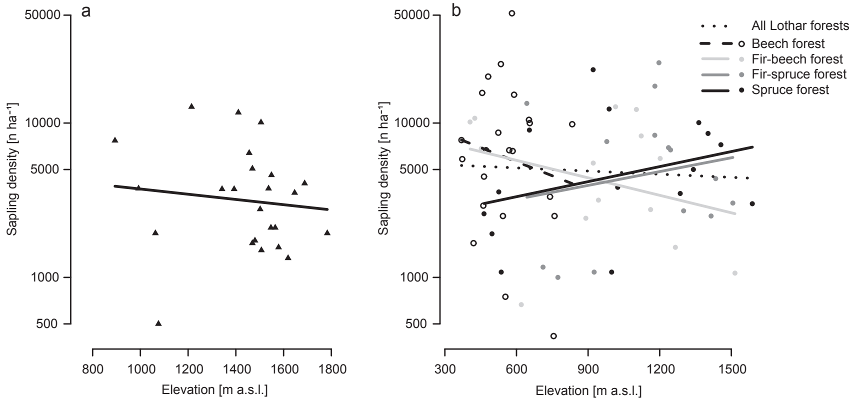


Fig. 8 Regeneration densities in 2010 (originated from post-storm establishment) vs. elevation for the 20-year-old Vivian gaps (a), and for forest subsets of the 10-year-old Lothar gaps (b; tree individuals ≥ 20 cm high). Regression lines: Vivian: $r^2 = 0.013$, $p = 0.60$; Lothar: $r^2 = 0.003$, $p = 0.66$; beech forests: $r^2 = 0.025$, $p = 0.48$; fir-beech forests: $r^2 = 0.097$, $p = 0.28$; fir-spruce forests: $r^2 = 0.034$, $p = 0.53$; spruce forests: $r^2 = 0.112$, $p = 0.22$.

3.2 Plot level (n=540)

3.2.1 Sapling density vs. distance from the forest edge

In the Lothar fir-beech forest gaps, sapling density was positively correlated with distance from the forest edge (*DIS*; ANOVA: $F_{1,82} = 4.70$, $P = 0.033$). Similarly, this distance effect was also present in the Lothar beech forest gaps on a 10% level (ANOVA: $F_{1,130} = 3.59$, $P = 0.060$). In contrast, distance from the forest edge had no significant influence on sapling density in all other subsets (both Vivian and Lothar gaps).

3.2.2 Predictors of sapling densities at the plot level

As with the GLM analyses of the gap sample, the results of the linear mixed effects models analyses at the plot level showed similar influences of the predictor variables on sapling densities, which were higher on plots with high soil pH, low vegetation cover, and salvage-logging (Table 6). Sapling densities were higher at distances closer to the forest edge in the Lothar beech forest gaps, the Lothar fir-beech forest gaps and in the entire Lothar data set. Compared to the models for the gap level, regeneration was weakly but significantly influenced by the additional variable aspect (*EXP*). Plots with a westerly aspect generally had higher sapling densities. There was no difference between the south- vs. north-facing plots. Regarding the entire data set (n=540), the variable *YRS* (time since disturbance) was weakly but significantly related to tree regeneration: densities in the 20-year old Vivian gaps were significantly smaller than in the 10-year old Lothar gaps.

Table 6 Results of the linear mixed effects model analyses: AIC values for null models, for models with the highest number of significant variables and for models with fewer variables included and lower AIC values compared to the preceding model, p-values were calculated with the R-function pvals.fnc.Variables with no postponed sign are highly significant ($p < 0.01$), variables with postponed "*" are weakly significant ($p < 0.05$), and variables with postponed "°" are significant on a 10% level ($p < 0.10$). The dependent variable is at any data level the density of tree saplings (reg$_{tr}$ = only tree species). Lothar$_{B}$ = beech, Lothar$_{FB}$ = fir-beech, Lothar$_{FS}$ = fir-spruce, and Lothar$_{S}$ = spruce forest.

Samples Null model	Model with the highest number of sign. vars		Lower AIC models with continual remove of 1 var	
AIC		AIC		AIC
Lothar & Vivian: N=90x6				
992	VEG$_{fb}$ pH$_{M}$* YRS* TRT° EXP°	978	VEG$_{fb}$ pH$_{M}$* YRS* TRT°	974
			VEG$_{fb}$ pH$_{M}$* YRS°	973
			VEG$_{fb}$ pH$_{M}$* TRT°	973
			VEG$_{fb}$ pH$_{M}$*	971
			VEG$_{fb}$ YRS°	969
			VEG$_{fb}$	967
Vivian: N=24x6				
226	VEG$_{fb}$ TRT*	232	VEG$_{fb}$	231
			TRT*	226
Lothar: N=66x6				
651	VEG$_{fb}$ pH$_{M}$ EXP* DIS*	644	VEG$_{fb}$ pH$_{M}$ DIS*	643
			VEG$_{fb}$ pH$_{M}$ EXP*	634
			VEG$_{fb}$ pH$_{M}$	633
Lothar$_{B}$: N=22x6				
233	VEG$_{bb}$ pH$_{M}$ EXP* DIS°	239	VEG$_{bb}$ pH$_{M}$ DIS°	236
			VEG$_{bb}$ pH$_{M}$ EXP*	230
			VEG$_{bb}$ pH$_{M}$	226
Lothar$_{FB}$: N=14x6				
141	VEG$_{fb}$ DIS*	152	DIS*	148
			VEG$_{fb}$	144
Lothar$_{FS}$: N=15x6				
125	pH$_{M}$* EXP°	130	EXP°	128
			pH$_{M}$*	128
Lothar$_{S}$: N=15x6				
132	VEG$_{fb}$ ELE*	150	VEG$_{fb}$	138

4. Discussion

Tree sapling densities differed widely in the windthrow gaps in Switzerland that we studied, ranging from 0 to > 50 000 ha^{-1}. Such large variation is in fact similar to that found in other studies on post-disturbance regeneration worldwide. For example, stem densities four years after a storm event in Germany and Slovakia varied from 1500 to 52 000 ha^{-1} (Kompa and Schmidt 2006; Jonásová et al. 2010). The number of tree individuals six to ten years after windthrow in Canada, the USA, Russia and Germany varied between 4800 and 20 200 ha^{-1} (Cooper-Ellis et al. 1999; Močalov and Lässig 2002; Kreyling et al. 2008; Fischer and Fischer 2012). Similar numbers were reported from 12 to 20 years old wind-disturbed areas in the USA and Germany, with densities ranging from 995 to more than 50 000 ha^{-1} (Arévalo et al. 2000; Zhao et al. 2006; Palik and Kastendick 2009; Fischer and Fischer 2012).

In addition to our confirmation of the widely demonstrated heterogeneity of post-windthrow regeneration, we identified several predictor variables that deserve an individual interpretation before being considered synoptically.

Treatment (salvage-logged vs. no intervention)

There are basically two options for forest management after windthrow: to salvage the lying timber (SL), or to leave it in place (NI). Sapling densities tended to be higher in SL than NI gaps, which is in line with findings from other studies (Schönenberger 2002; Ilisson et al. 2007). On the one hand, salvage harvesting involves perturbating the soil, and although it reduces the abundance of advance regeneration, it offers excellent germination substrate transiently free of competition early after the disturbance (Connell 1978; Davis et al. 2000). On the other hand, deadwood is known to be crucial for tree regeneration at higher elevations in moist spruce forests, as found in many studies in America (e.g. McKee et al. 1982; Harmon and Franklin 1989), in Swiss mountain forests (Imbeck and Ott 1987), and in the Bohemian forest in the Czech Republic (Svoboda et al. 2010). Ten year old decaying wood is, however, not yet an appropriate seedbed. Its significance as a substrate increases with age (cf. Zielonka 2006; Priewasser et al. 2012). Accordingly, deadwood has no significant (positive) effect on regeneration in the first 10 to 20 years after a disturbance.

It is often assumed that salvage logging changes species composition for several decades by allowing pioneer species to prevail (Močalov and Lässig 2002; Schönenberger 2002), and that the variety of microsites is greater in SL than NI gaps (Peterson and Leach 2008). These two factors would imply a transiently higher tree species richness in SL gaps. Peterson and Leach (2008) found, however, that both sapling density and richness did not significantly differ between SL and NI windthrow areas, but they did between microsites. Regarding sapling density in our study, pioneer species were equally frequent in both SL and NI gaps, with mainly late-successional species such as beech and spruce being dominant in gaps after both storm events, except in Lothar spruce forests. Our findings correspond to those of Lang et al. (2009), who found that a SL and NI gap shared the same dominant tree species. In our study, sapling densities of individual woody species in SL and NI gaps were not significantly different due to the high variability of sapling densities among windthrow gaps. In the younger Lothar gaps, tree species diversity (Shannon) did not significantly differ between NI and SL treatment. Such a difference was only found in 20-year-old Vivian gaps, with higher diversity in NI gaps, which is in line with Ilisson et al. (2007). Our results cannot confirm the hypothesis that post-windthrow SL favors pioneer species more than NI areas, but they support the phenomenon of direct re-growth (Romme et al. 2011), i.e. the late-successional tree species forming the pre-storm stands rapidly gain dominance under post-disturbance conditions in both SL and NI gaps.

Nonetheless, pioneer tree species were significantly taller than late-successional tree species. In other words, while late-successional tree species are more abundant than pioneer species 20 years after Vivian and 10 years after Lothar, they are still lagging behind the pioneer species in growth performance, regardless of the treatment.

Elevation and time since disturbance

Since the elevation of the gap samples correlated to some extent with time since disturbance, these variables have to be discussed together. Generally, after a period when stem densities continuously increase following a storm event, self-thinning starts (review by Lugo 2008). Elevation is known to correlate negatively with seedling and sapling densities (e.g. Peterson and Pickett 1990; van Mantgem et al. 2006). Accordingly, wind-disturbed forests in the Swiss lowlands were found to have higher sapling densities than those at higher elevations (Wohlgemuth et al. 2008a).

In contrast to the literature, elevation is difficult to interpret as a predictor of sapling densities in our study as its influence was different with respect to storm events and forest types (Figs. 8a, 8b). The fact that sapling densities in 20-year-old Vivian gaps were significantly lower than in the 10-year-old Lothar gaps can, however, largely be explained by elevation: gaps of the Vivian event were, on average, 570 m higher than those of the Lothar event. As a confirmation, average tree height in Vivian and Lothar gaps did not differ, in spite of the different times that had passed since the wind disturbance. A low regeneration speed at higher elevations was also reported by Schönenberger (2002) who found sapling densities between 543 and 2315 ha^{-1} ten years after a storm event at elevations of 1100 and 1500 m a.s.l. Based on our study, we assume that regeneration in many of the Vivian gaps has not reached the thinning phase yet. In short, elevation is an important factor, but its influence on sapling density and growth rate is less clear than expected. The surprisingly weak influence of elevation on the regeneration densities in our study presumably relates to the disproportionately high number of soils with higher pH at higher elevations. Since soil pH is positively correlated with sapling density (see below), soil pH compensated for the influence of elevation.

Soil pH

Soil pH was among the top three factors that positively influenced sapling density in the windthrow gaps. Apart from gaps in Lothar spruce forests, soil pH was a good predictor of tree density in all other sample sets, with low densities on acidic substrate and high densities on alkaline substrates. Other studies have also identified soil pH as a positive predictor of species density, e.g. Gough et al. (2000) in Alaskan arctic tundra or Peet et al. (2003) in the Southern Blue Ridge Mountains. Soil pH may positively influence species diversity (e.g. Gough et al. 2000; Van Couwenberghe et al. 2010). High species richness on alkaline soils has been explained as arising from evolutionary history (Pärtel 2002), especially in temperate zones. Pärtel (2002) and Ewald (2003) found that the species pool is larger in calcareous habitats than on acidic soils in Central Europe. The latter author explained this fact with ecological drift imposed by a historical ‘bottleneck’, i.e. the extinction of more acidophilous than calciphilous species due to less acidic soils in times when refugial areas were scarce. A majority of the plant species in Central Europe have, therefore, adapted to calcareous soils and consequently may germinate and/or grow better on calcareous than on acidic soils (Rorison 1960).

Vegetation cover

Anthropogenic (e.g. clear-cuts) or natural (e.g. wind damage) disturbances generally lead to increased light availability on the forest floor, which promotes the rapid spread of herbaceous plants, often at the expense of tree regeneration (see the review of Royo and Carson 2006). Therefore, we expected that the relationship between specific vegetation cover and sapling density would be negative. Our results confirmed such an influence for bracken and other ferns, as well as for berry species (*Rubus* spec. and *Vaccinium myrtillus* L.). In most of the examined forest types (except Lothar fir-spruce forests), vegetation cover in gaps was as important as soil pH for explaining the variation in sapling densities. Several studies support our findings, such as a field experiment in the silver fir-Norway spruce forests in Germany, where dense *Rubus fruticosus* stands distinctly reduced the establishment of silver fir and Norway spruce (Schreiner 2000). Similarly, thickets of blackberry (*Rubus discolor*) had a negative effect on the growth of oak seedlings in a Californian savanna (Williams et al. 2006). In beech forests in France, for example, bracken (*Pteridium aquilinum*) is significantly hindering tree regeneration after wind disturbance (Koop and Hilgen 1987). In long-term simulations (25 years) for unsalvaged *Picea abies* snag stands in Switzerland, raspberries (*Rubus idaeus*) in the montane zone were slowly replaced by Norway spruce, whereas in the subalpine zone ferns and *Calamagrostis villosa* dominated for several decades and made it impossible for trees to regenerate (Kupferschmid and Bugmann 2005).

Distance from the forest edge

Several studies have shown that tree density and species composition within large windthrow areas vary from the forest edge to the centre (Greene and Johnson 1996; Greene et al. 1999; White and Jentsch 2001). In particular, tree density close to the edge of an intact forest is supposed to be higher than at the centre of large forest gaps (White and Jentsch 2001). We adapted this view in our design of circular sample plots to test this hypothesis. Our results confirm the results from the literature in Lothar beech and fir-beech forest gaps by a weak, but significant, negative correlation in the plot-level analysis. In contrast, no such trend was found in the range of 80 m edge distance in coniferous forests after the storm Lothar and in the Vivian subset. We surmise that the strength of the correlation between distance to forest edge and stem density is influenced by the specific seed weight of the tree species, and therefore we propose that this relationship is valid for beech-dominated forests but not for forests dominated by conifers. It is likely that with respect to coniferous forests, distances were too small to detect any correlations between stem density and distance to forest edge. For the conifers *Picea rubens* and *P. engelmannii*, seed numbers were found to decrease drastically within 100 m of the forest edge (Greene and Johnson 1996).

Browsing damage

Our findings of less browsing damage (*BR*) in NI than in SL gaps in both the Vivian and Lothar forests confirms the hypothesis that *BR* is lower in terrain with obstacles. Browsing had statistically more influence on sapling density in windthrow gaps with generally scarce regeneration (Vivian), whereas no such significance was found in Lothar gaps having generally higher sapling densities. Many studies of browsing in disturbed forests support our findings and frequently highlight treefall mounds created after windthrow as suitable regeneration refugia (Long et al. 1998; Krueger and Peterson 2006). In addition, browse consumption on a larger scale seems to be reduced if woody debris is not removed after windthrow (Peterson and Pickett 1995; Moser et al. 2008), fires (de Chantal and Granström 2007) or disease (Relva et al. 2009). Since food availability is often assumed to be similar in undisturbed forests as well as in salvage-logged or unharvested forests after disturbance (Moser et al. 2008), the presence of woody debris appears decisive for limiting browsing by large herbivores. A few studies, however, contradict these findings, e.g. in a windthrow case study in Pennsylvania (Krueger and Peterson 2009) and in an experiment in eastern France (Pellerin et al. 2010).

Accordance with succession theories

Twenty years after Vivian and 10 years after Lothar, early-successional tree species have lower densities than late-successional tree species, but pioneers grew faster, and thus have developed larger crowns than the late-successional tree species. Therefore, young forests in the studied windthrow gaps appear generally as communities of pioneer species following disturbance, which visually confirms the succession theory by Clements (1936) and has been recently reported in forest succession studies (see also Kimmins 2004; Pickett et al. 2009). Our data demonstrate the simultaneous establishment of early- and late-successional species, and even a dominance of the latter in terms of sapling density. Such a simultaneous establishment of various tree species after severe disturbance is in line with the ‘Initial Floristic Composition’ hypothesis by Egler (1954), which is that from the beginning all plant species (from weeds, grasses and shrubs to trees) are present, but due to different growth rates individual functional groups appear to dominate in particular succession stages. In the context of post-windthrow regeneration this hypothesis has been rarely reported (Hibbs 1983; Liu and Hytteborn 1991; Ishizuka et al. 1998). In a surprisingly large number of gaps (25%), however, late-successional species have even advanced to equal or larger height than the pioneer species, which is why the regeneration process in our study resembles, to a considerable extent, the phenomenon of direct re-growth, a phenomenon that seems consistent in forests severely disturbed by fire (Romme et al. 2011).

5. Conclusion

Based on our large gap sample of windthrow gaps, we were able to identify general rules underlying tree regeneration after wind disturbance in the four most widespread forest types in Switzerland: regeneration densities in gaps 10 and 20 years after a storm event are particularly high in gaps with a high soil pH, a low cover of competing species, at low elevation and in salvage-logged gaps. Increasing distance from the forest edge (up to 80 m) reduces regeneration density in forests dominated by beech (heavy seeds), but not in silver fir-Norway spruce and Norway spruce forests. Browsing damage is presumably a factor reducing sapling density in gaps with salvage-logging. Although distinct patterns are visible overall, the succession of individual windthrow gaps can deviate greatly from the general trends. This confirms the reported heterogeneity of regeneration among wind disturbed areas.

Overall, our study shows a numerical prevalence of late-successional tree species in both treatments (SL and NI; except for the Lothar spruce forests) and thus challenges the Clementsian succession theory after disturbance, suggesting pathways that start with pioneer trees followed by late-successional species eventually gaining dominance. Even though tree regeneration 10 or 20 years after disturbance is visually dominated by pioneer species in a majority of the assessed gaps, it is already on its way to transform to stands dominated by pre-disturbance species. In face of the regeneration patterns found, we conclude that regeneration stages numerically dominated by pioneer trees are rare, and a mixture of early and late-successional species appears as ‘normality’ 10 to 20 years after disturbance in temperate forests in Central Europe.

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References

Allen MS, Thapa V, Arévalo JR, Palmer MW (2012) Windstorm damage and forest recovery: accelerated succession, stand structure, and spatial pattern over 25 years in two Minnesota forests. Plant Ecol 213: 1833-1842.

Arévalo JR, DeCoster JK, McAlister SD, Palmer MW (2000) Changes in two Minnesota forests during 14 years following catastrophic windthrow. J Veg Sci 11: 833-840.

Attiwill PM (1994) The disturbance of forest ecosystems - the ecological basis for conservative management. Forest Ecol Manag 63: 247-300.

Brzeziecki B, Kienast F (1994) Classifying the life-history strategies of trees on the basis of the Grimian model. Forest Ecol Manag 69: 167-187.

BUWAL, WSL (2001) Lothar. Der Orkan 1999. Ereignisanalyse. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft, Birmensdorf. Bundesamt für Umwelt, Wald und Landschaft, BUWAL, Bern.

Clements FE (1936) Nature and structure of the climax. J Ecol 24: 252-284.

Connell JH (1978) Diversity in tropical rain forests and coral reefs - high diversity of trees and corals is maintained only in a non-equilibrium state. Science 199: 1302-1310.

Cooper-Ellis S, Foster DR, Carlton G, Lezberg A (1999) Forest response to catastrophic wind: Results from an experimental hurricane. Ecology 80: 2683-2696.

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88: 528-534.

de Chantal M, Granström A (2007) Aggregations of dead wood after wildfire act as browsing refugia for seedlings of *Populus tremula* and *Salix caprea*. Forest Ecol Manag 250: 3-8.

Degen T, Devillez F, Jacquemart AL (2005) Gaps promote plant diversity in beech forests (*Luzulo-Fagetum*), North Vosges, France. Ann For Sci 62: 429-440.

Egler FE (1954) Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4: 412-417.

Ewald J (2003) The calcareous riddle: Why are there so many calciphilous species in the Central European flora? Folia Geobot 38: 357-366.

Fischer A, Fischer HS (2012) Individual-based analysis of tree establishment and forest stand development within 25 years after windthrow. Eur J For Res 131: 493-501.

Galhidy L, Mihok B, Hagyo A, Rajkai K, Standovar T (2006) Effects of gap size and associated changes in light and soil moisture on the understorey vegetation of a Hungarian beech forest. Plant Ecol 183: 133-145.

Gough L, Shaver GR, Carroll J, Royer DL, Laundre JA (2000) Vascular plant species richness in Alaskan arctic tundra: the importance of soil pH. J Ecol 88: 54-66.

Greene DF, Johnson EA (1996) Wind dispersal of seeds from a forest into a clearing. Ecology 77: 595-609.

Greene DF, Zasada JC, Sirois L, Kneeshaw D, Morin H, Charron I, Simard MJ (1999) A review of the regeneration dynamics of North American boreal forest tree species. Can J For Res-Rev Can Rech For 29: 824-839.

Harmon ME, Franklin JF (1989) Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. Ecology 70: 48-59.

Hibbs DE (1983) Forty years of forest succession in Central New England. Ecology 64: 1394-1401.

Holzmueller EJ, Gibson DJ, Suchecki PF (2012) Accelerated succession following an intense wind storm in an oak-dominated forest. Forest Ecol Manag 279: 141-146.

Ilisson T, Koster K, Vodde F, Jogiste K (2007) Regeneration development 4-5 years after a storm in Norway spruce dominated forests, Estonia. Forest Ecol Manag 250: 17-24.

Imbeck H, Ott E (1987) Verjüngungsökologische Untersuchungen in einem hochstaudenreichen subalpinen Fichtenwald, mit spezieller Berücksichtigung der Schneeablagerung und der Lawinenbildung. Eidgenösschische Forschungsanstalt für Wald, Schnee und Landschaft WSL, Birmensdorf.

Ishizuka M, Toyooka H, Osawa A, Kushima H, Kanazawa Y, Sato A (1998) Secondary succession following catastrophic windthrow in a boreal forest in Hokkaido, Japan: The timing of tree establishment. Journal of Sustainable Forestry 6: 367-388.

Jonásová M, Vávrová E, Cudlín P (2010) Western Carpathian mountain spruce forest after a windthrow: Natural regeneration in cleared and uncleared areas. Forest Ecol Manag 259: 1127-1134.

Kimmins JP (2004) Forest Ecology: a foundation for sustainable forest management and environmental ethics in forestry, 3rd Edition. Prentice Hall, NJ, USA.

Kompa T, Schmidt W (2006) Zur Verjüngungssituation in südniedersächsischen Buchen-Windwurfgebieten nach einem lokalen Orkan von 1997. Forstarchiv 77: 3-19.

Koop H, Hilgen P (1987) Forest dynamics and regeneration mosaic shifts in unexploited beech (*Fagus sylvatica*) stands at Fontainebleau (France). Forest Ecol Manag 20: 135-150.

Kreyling J, Schmiedinger A, Macdonald E, Beierkuhnlein C (2008) Potentials of natural tree regeneration after clearcutting in subalpine forests. West J Appl For 23: 46-52.

Krueger LM, Peterson CJ (2006) Effects of white-tailed deer on *Tsuga canadensis* regeneration: Evidence of microsites as refugia from browsing. Am Midl Nat 156: 353-362.

Krueger LM, Peterson CJ (2009) Effects of woody debris and ferns on herb-layer vegetation and deer herbivory in a Pennsylvania forest blowdown. Ecoscience 16: 461-469.

Kupferschmid AD, Bugmann H (2005) Predicting decay and ground vegetation development in *Picea abies* snag stands. Plant Ecol 179: 247-268.

Lang KD, Schulte LA, Guntenspergen GR (2009) Windthrow and salvage logging in an old-growth hemlock-northern hardwoods forest. Forest Ecol Manag 259: 56-64.

Lawton RO, Putz FE (1988) Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. Ecology 69: 764-777.

Liu QH, Hytteborn H (1991) Gap structure, disturbance and regeneration in a primeval *Picea abies* forest. J Veg Sci 2: 391-402.

Long ZT, Carson WP, Peterson CJ (1998) Can disturbance create refugia from herbivores: an example with hemlock regeneration on treefall mounds. J Torrey Bot Soc 125: 165-168.

Lugo AE (2008) Visible and invisible effects of hurricanes on forest ecosystems: an international review. Austral Ecol 33: 368-398.

Mayer P, Brang P, Dobbertin M, Hallenbarter D, Renaud JP, Walthert L, Zimmermann S (2005) Forest storm damage is more frequent on acidic soils. Ann For Sci 62: 303-311.

McKee A, LaRoi G, Franklin JF (1982) Structure, composition and reproductive behavior of terrace forests, south Fork Hoh River, Olympic National Park. In: Starkey EE, Franklin JF, Matthews JW (eds) Ecological research in national parks of the Pacific Northwest. Oregon State University, Forest Research Laboratory, Corvallis, Oregon, USA, pp. 22-29.

Močalov SA, Lässig R (2002) Development of two boreal forests after large-scale windthrow in the Central Urals. For Snow Landsc Res 77: 171-186.

Moser B, Schütz M, Hindenlang KE (2008) Resource selection by roe deer: Are windthrow gaps attractive feeding places? Forest Ecol Manag 255: 1179-1185.

Palik B, Kastendick D (2009) Woody plant regeneration after blowdown, salvage logging, and prescribed fire in a northern Minnesota forest. Forest Ecol Manag 258: 1323-1330.

Pärtel M (2002) Local plant diversity patterns and evolutionary history at the regional scale. Ecology 83: 2361-2366.

Peet RK, Fridley JD, Gramling JM (2003) Variation in species richness and species pool size across a pH gradient in forests of the southern blue ridge mountains. Folia Geobot 38: 391-401.

Pellerin M, Saïd S, Richard E, Hamann JL, Dubois-Coli C, Hum P (2010) Impact of deer on temperate forest vegetation and woody debris as protection of forest regeneration against browsing. Forest Ecol Manag 260: 429-437.

Peterson CJ (2000) Damage and recovery of tree species after two different tornadoes in the same old growth forest: a comparison of infrequent wind disturbances. Forest Ecol Manag 135: 237-252.

Peterson CJ, Carson WP, McCarthy BC, Pickett STA (1990) Microsite variation and soil dynamics within newly created treefall pits and mounds. Oikos 58: 39-46.

Peterson CJ, Leach AD (2008) Salvage logging after windthrow alters microsite diversity, abundance and environment, but not vegetation. Forestry 81: 361-376.

Peterson CJ, Pickett STA (1990) Microsite and elevational influences on early forest regeneration after catastrophic windthrow. J Veg Sci 1: 657-662.

Peterson CJ, Pickett STA (1995) Forest reorganization - A case-study in an old-growth forest catastrophic blowdown. Ecology 76: 763-774.

Pickett STA, Cadenasso ML, Meiners SJ (2009) Ever since Clements: from succession to vegetation dynamics and understanding to intervention. Appl Veg Sci 12: 9-21.

Priewasser K, Brang P, Bachofen H, Bugmann H, Wohlgemuth T (2012) Impacts of salvage-logging on the status of deadwood after windthrow in Swiss forests. Eur J For Res.

R Development Core Team (2011) R: a language and environment for statistical computing. In. R Foundation for Statistical Computing, Vienna.

Relva MA, Westerholm CL, Kitzberger T (2009) Effects of introduced ungulates on forest understory communities in northern Patagonia are modified by timing and severity of stand mortality. Plant Ecol 201: 11-22.

Romme WH, Boyce MS, Gresswell R, Merrill EH, Minshall GW, Whitlock C, Turner MG (2011) Twenty Years After the 1988 Yellowstone Fires: Lessons About Disturbance and Ecosystems. Ecosystems 14: 1196-1215.

Romme WH, Everham EH, Frelich LE, Moritz MA, Sparks RE (1998) Are large, infrequent disturbances qualitatively different from small, frequent disturbances? Ecosystems 1: 524-534.

Rorison IH (1960) Some experimental aspects of the calcicole-calcifuge problem. I. The effects of competiton and mineral nutrition upon seedling growth in the field. J Ecol 48: 585-599.

Royo AA, Carson WP (2006) On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Can J For Res-Rev Can Rech For 36: 1345-1362.

Schelhaas MJ, Nabuurs GJ, Schuck A (2003) Natural disturbances in the European forests in the 19th and 20th centuries. Glob Change Biol 9: 1620-1633.

Scherzinger W (1996) Naturschutz im Wald: Qualitätsziele einer dynamischen Waldentwicklung. Ulmer, Stuttgart.

Schönenberger W (2002) Post windthrow stand regeneration in Swiss mountain forests: the first ten years after the 1990 storm Vivian. For Snow Landsc Res 77: 61-80.

Schreiner M (2000) Vorkommen und Ausbreitung von Brombeeren sowie ihre Bedeutung für die Naturverjüngung von Tannen-Fichten-Wäldern - dargestellt am Beispiel der Region „Oberer Neckar“. Ph.D. thesis, University of Freiburg im Breisgau, Germany.

Schüepp M, Schiesser HH, Huntrieser H, Scherrer HU, Schmidtke H (1994) The winterstorm Vivian of 27 February 1990 - about the meteorological development, wind forces and damage situation in the forests of Switzerland. Theor Appl Climatol 49: 183-200.

Svoboda M, Fraver S, Janda P, Bace R, Zenáhlíková J (2010) Natural development and regeneration of a Central European montane spruce forest. Forest Ecol Manag 260: 707-714.

Ulanova NG (2000) The effects of windthrow on forests at different spatial scales: a review. Forest Ecol Manag 135: 155-167.

Van Couwenberghe R, Collet C, Lacombe E, Pierrat JC, Gegout JC (2010) Gap partitioning among temperate tree species across a regional soil gradient in windstorm-disturbed forests. Forest Ecol Manag 260: 146-154.

van Mantgem PJ, Stephenson NL, Keeley JE (2006) Forest reproduction along a climatic gradient in the Sierra Nevada, California. Forest Ecol Manag 225: 391-399.

Venables WN, Ripley BD (1999) Modern applied statistics with S-Plus. Springer-Verlag, New York.

von Oheimb G, Friedel A, Bertsch A, Hardtle W (2007) The effects of windthrow on plant species richness in a Central European beech forest. Plant Ecol 191: 47-65.

White PS, Jentsch A (2001) The search for generality in studies of disturbance and ecosystem dynamics. In: Esser K, Lüttge U, Kadereit JW, Beyschlag W (eds) Progress in Botany. Springer, Berlin, Heidelberg, New York, pp. 399-450.

Williams K, Westrick LJ, Williams BJ (2006) Effects of blackberry (*Rubus discolor*) invasion on oak population dynamics in a California savanna. Forest Ecol Manag 228: 187-196.

Wohlgemuth T, Conedera M, Kupferschmid A, Moser B, Usbeck T, Brang P, Dobbertin M (2008a) Effekte des Klimawandels auf Windwurf, Waldbrand und Walddynamik im Schweizer Wald. Schweiz Z Forstwes 159: 326-334.

Wohlgemuth T, Kull P, Wüthrich H (2002) Disturbance of microsites and early tree regeneration after windthrow in Swiss mountain forests due to the winter storm Vivian 1990. For Snow Landsc Res 77: 17-47.

Wohlgemuth T, Moser B, Brändli UB, Kull P, Schütz M (2008b) Diversity of forest plant species at the community and landscape scales in Switzerland. Plant Biosyst 142: 604-613.

Zhao DH, Allen B, Sharitz RR (2006) Twelve year response of old-growth southeastern bottomland hardwood forests to disturbance from Hurricane Hugo. Can J For Res-Rev Can Rech For 36: 3136-3147.

Zielonka T (2006) When does dead wood turn into a substrate for spruce replacement? J Veg Sci 17: 739-746.

Appendix A

Results of the case studies in Switzerland after Lothar were not internationally published, but are found in the following publications:

Angst et al. 2004: Waldentwicklung nach Windwurf in tieferen Lagen der Schweiz 2000-2003, Schlussbericht zuhanden der Forstdirektion des BUWAL. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft, Birmensdorf, 95 S.

Koch and Brang 2005: Extensive Verjüngungsverfahren nach Lothar. Schlussbericht zuhanden der Forstdirektion des BUWAL. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft, Birmensdorf, 90 S.

Appendix B (next three pages)

Frequencies of tree and shrub species originated from post-storm establishment (tree individuals ≥ 20 cm high) in the different Vivian and Lothar gaps.

		Vivian				Lothar			
		Fir-spruce and spruce forest				All forest types			
		SL		NI		SL		NI	
		n ha^{-1}	±SE	n ha^{-1}	±SE	n ha^{-1}	±SE	n ha^{-1}	±SE
	All woody species	4'631	839	2'778	857	8'561	1'381	5'951	1'074
	Only tree species	4'098	742	2'161	898	7'786	1'314	5'373	1'086
trees	*Abies alba* Mill.	7	6	22	16	278	74	430	216
	Acer campestre L.	0	0	0	0	6	4	0	0
	Acer platanoides L.	0	0	0	0	35	28	0	0
	Acer pseudoplatanus L.	765	461	189	70	1'067	240	957	411
	Alnus incana (L.) Moench	2	2	17	17	4	4	0	0
	Berberis vulgaris L.	0	0	0	0	0	0	2	2
	Betula pendula Roth	370	195	28	22	337	265	46	22
	Carpinus betulus L.	0	0	0	0	221	165	11	11
	Fagus sylvatica L.	137	118	11	11	2'440	1'056	1'818	731
	Fraxinus excelsior L.	167	161	17	11	1'313	333	220	133
	Juglans regia L.	0	0	0	0	6	3	0	0
	Larix decidua Mill.	235	139	478	471	14	8	0	0
	Picea abies (L.) H. Karst.	1'720	424	922	437	870	250	786	349
	Pinus mugo Turra	0	0	11	11	0	0	0	0
	Pinus strobus L.	0	0	0	0	0	0	4	4
	Pinus sylvestris L.	2	2	0	0	16	7	15	15
	Populus tremula L.	19	9	50	34	159	121	0	0
	Prunus avium L.	0	0	0	0	76	28	45	31
	Prunus padus L.	0	0	0	0	21	21	0	0
	Pseudotsuga menziesii (Mirb.) Franco	0	0	0	0	0	0	4	4
	Quercus spec.	0	0	0	0	122	34	76	45
	Salix spec.	187	37	211	98	311	65	308	94
	Sorbus aria (L.) *Crantz*	0	0	0	0	19	10	64	36
	Sorbus aucuparia L.	478	172	206	107	460	129	572	225
	Taxus baccata L.	0	0	0	0	4	4	0	0
	Tilia spec.	0	0	0	0	6	3	15	12
	Ulmus spec.	9	9	0	0	1	1	0	0
shrubs	*Alnus viridis*(Chaix) DC.	174	138	89	58	42	41	5	4
	Buddleja	0	0	0	0	2	2	0	0
	Cornus sanguinea L.	0	0	0	0	41	24	0	0
	Corylus avellana L.	39	19	11	7	91	36	60	32
	Crataegus laevigata L.	0	0	0	0	8	5	0	0
	Daphne mezereum L.	0	0	0	0	2	2	0	0
	Euonymus europaeus L.	0	0	0	0	33	27	0	0
	Frangula alnus Mill.	0	0	0	0	2	2	87	87
	Ilex aquifolia L.	0	0	0	0	4	4	0	0
	Juniperus communis L.	0	0	0	0	0	0	2	2
	Laburnum anagyroides Medik.	0	0	0	0	0	0	11	11
	Lonicera spec.	107	48	61	36	226	86	165	101
	Prunus spinosa L.	0	0	0	0	0	0	4	4
	Rhamnus spec.	0	0	0	0	0	0	18	18
	Ribes	0	0	0	0	2	2	7	5
	Rose spec.	48	29	0	0	22	11	68	34
	Sambucus nigra L.	0	0	0	0	47	20	19	13
	Sambucus racemosa L.	165	52	456	156	203	47	120	42
	Viburnum lantana L.	0	0	0	0	1	1	0	0
	Viburnum opulus L.	0	0	0	0	52	41	11	8

		Lothar							
		Beech forest				Fir-beech forest			
		SL		NI		SL		NI	
		n ha^{-1}	±SE	n ha^{-1}	±SE	n ha^{-1}	±SE	n ha^{-1}	±SE
	All woody species	10'564	3'019	7'583	2'267	7'133	1'345	4'494	1'909
	Only tree species	9'936	2'910	7'333	2'355	6'258	1'375	4'372	1'947
trees	*Abies alba* Mill.	172	97	233	133	271	80	883	774
	Acer campestre L.	15	11	0	0	0	0	0	0
	Acer platanoides L.	74	68	0	0	0	0	0	0
	Acer pseudoplatanus L.	583	265	500	290	1'348	552	350	185
	Alnus incana (L.) Moench	0	0	0	0	21	21	0	0
	Berberis vulgaris L.	0	0	0	0	0	0	0	0
	Betula pendula Roth	78	37	17	17	104	56	111	70
	Carpinus betulus L.	559	411	0	0	0	0	42	42
	Fagus sylvatica L.	5'181	2'529	5'683	2'107	1'400	958	1'864	1'267
	Fraxinus excelsior L.	1'819	594	67	31	1'167	732	139	98
	Juglans regia L.	10	7	0	0	0	0	0	0
	Larix decidua Mill.	10	10	0	0	31	31	0	0
	Picea abies (L.) H. Karst.	230	114	67	41	1133	687	544	460
	Pinus mugo Turra	0	0	0	0	0	0	0	0
	Pinus strobus L.	0	0	0	0	0	0	14	14
	Pinus sylvestris L.	25	16	0	0	0	0	56	56
	Populus tremula L.	348	304	0	0	42	31	0	0
	Prunus avium L.	93	38	200	200	0	0	0	0
	Prunus padus L.	54	54	0	0	0	0	0	0
	Pseudotsuga menziesii (Mirb.) Franco	0	0	0	0	0	0	14	14
	Quercus spec.	167	51	250	179	21	21	56	56
	Salix spec.	314	135	300	242	317	66	167	107
	Sorbus aria (L.) *Crantz*	0	0	0	0	42	42	0	0
	Sorbus aucuparia L.	191	151	17	17	342	175	119	56
	Taxus baccata L.	10	10	0	0	0	0	0	0
	Tilia spec.	5	5	0	0	10	10	14	14
	Ulmus spec.	0	0	0	0	10	10	0	0
shrubs	*Alnus viridis*(Chaix) DC.	0	0	0	0	0	0	14	14
	Buddleja	5	5	0	0	0	0	0	0
	Cornus sanguinea L.	50	36	0	0	0	0	0	0
	Corylus avellana L.	45	18	150	130	198	125	6	6
	Crataegus laevigata L.	20	13	0	0	0	0	0	0
	Daphne mezereum L.	0	0	0	0	0	0	0	0
	Euonymus europaeus L.	83	69	0	0	0	0	0	0
	Frangula alnus Mill.	5	5	0	0	0	0	0	0
	Ilex aquifolia L.	10	10	0	0	0	0	0	0
	Juniperus communis L.	0	0	0	0	0	0	0	0
	Laburnum anagyroides Medik.	0	0	0	0	0	0	0	0
	Lonicera spec.	74	38	0	0	327	145	14	14
	Prunus spinosa L.	0	0	17	17	0	0	0	0
	Rhamnus spec.	0	0	0	0	0	0	0	0
	Ribes	0	0	17	17	8	8	0	0
	Rose spec.	0	0	0	0	42	27	11	11
	Sambucus nigra L.	98	49	50	50	21	14	28	28
	Sambucus racemosa L.	118	40	0	0	279	180	50	32
	Viburnum lantana L.	0	0	0	0	0	0	0	0
	Viburnum opulus L.	123	103	17	17	0	0	0	0

		Lothar							
		Fir-spruce forest				Spruce forest			
		SL		NI		SL		NI	
		n ha^{-1}	±SE	n ha^{-1}	±SE	n ha^{-1}	±SE	n ha^{-1}	±SE
	All woody species	7'583	2'624	6'678	2'810	6'898	2'043	5'193	1'607
	Only tree species	6'419	2'104	6'336	2'799	6'262	1'945	3'460	1'396
trees	*Abies alba* Mill.	733	291	375	190	100	41	150	130
	Acer campestre L.	0	0	0	0	0	0	0	0
	Acer platanoides L.	0	0	0	0	25	25	0	0
	Acer pseudoplatanus L.	1494	602	2217	1382	1'258	685	630	487
	Alnus incana (L.) Moench	0	0	0	0	0	0	0	0
	Berberis vulgaris L.	0	0	6	6	0	0	0	0
	Betula pendula Roth	8	8	17	11	1'225	1'135	33	33
	Carpinus betulus L.	0	0	0	0	0	0	0	0
	Fagus sylvatica L.	273	143	42	28	345	240	30	19
	Fraxinus excelsior L.	408	372	611	467	1'293	780	0	0
	Juglans regia L.	0	0	0	0	8	8	0	0
	Larix decidua Mill.	0	0	0	0	17	17	0	0
	Picea abies (L.) H. Karst.	2017	953	1569	1144	830	392	853	453
	Pinus mugo Turra	0	0	0	0	0	0	0	0
	Pinus strobus L.	0	0	0	0	0	0	0	0
	Pinus sylvestris L.	0	0	0	0	25	18	0	0
	Populus tremula L.	21	21	0	0	42	42	0	0
	Prunus avium L.	0	0	0	0	158	95	0	0
	Prunus padus L.	0	0	0	0	0	0	0	0
	Pseudotsuga menziesii (Mirb.) Franco	0	0	0	0	0	0	0	0
	Quercus spec.	21	14	0	0	100	52	17	17
	Salix spec.	419	165	625	232	215	89	107	36
	Sorbus aria (L.) *Crantz*	58	33	111	111	3	3	147	81
	Sorbus aucuparia L.	967	506	722	464	608	220	1'493	698
	Taxus baccata L.	0	0	0	0	0	0	0	0
	Tilia spec.	0	0	42	42	8	8	0	0
	Ulmus spec.	0	0	0	0	0	0	0	0
shrubs	*Alnus viridis*(Chaix) DC.	227	218	6	6	0	0	0	0
	Buddleja	0	0	0	0	0	0	0	0
	Cornus sanguinea L.	0	0	0	0	92	83	0	0
	Corylus avellana L.	15	11	33	27	145	115	67	52
	Crataegus laevigata L.	0	0	0	0	0	0	0	0
	Daphne mezereum L.	10	10	0	0	0	0	0	0
	Euonymus europaeus L.	0	0	0	0	0	0	0	0
	Frangula alnus Mill.	0	0	0	0	0	0	383	383
	Ilex aquifolia L.	0	0	0	0	0	0	0	0
	Juniperus communis L.	0	0	0	0	0	0	7	7
	Laburnum anagyroides Medik.	0	0	39	39	0	0	0	0
	Lonicera spec.	558	420	136	86	137	71	547	417
	Prunus spinosa L.	0	0	0	0	0	0	0	0
	Rhamnus spec.	0	0	0	0	0	0	80	80
	Ribes	0	0	0	0	0	0	13	13
	Rose spec.	62	52	11	11	12	9	273	113
	Sambucus nigra L.	21	21	0	0	0	0	0	0
	Sambucus racemosa L.	246	107	117	78	252	101	330	122
	Viburnum lantana L.	4	4	0	0	0	0	0	0
	Viburnum opulus L.	21	21	0	0	0	0	33	33

Chapter II

Impacts of salvage-logging on the status of deadwood after windthrow in Swiss forests

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Abstract

Downed and standing deadwood (DW) is a key resource for maintaining forest biodiversity. Although extreme events such as windthrow and fires produce large quantities of DW, this substrate is often drastically reduced by logging activities. To elucidate the respecting consequences of salvage-logging, we assessed both quantity and quality of storm-derived DW (storms Vivian 1990 and Lothar 1999) in Swiss forests using a sample of 90 windthrow sites with ≥3 ha complete windthrow and at elevations ranging from 350 to 1800 m a.s.l. The majority had been salvage-logged (SL) a few years after the windthrow. On each site we recorded DW amount and quality on six circular sample plots 20 or 50 m^2 in size. DW volume on SL sites was surprisingly high, with 76.4 m^3 ha^{-1} on average 20 years after Vivian and 73.8 m^3 ha^{-1} 10 years after Lothar. In comparison, DW volumes on unsalvaged sites, i.e. with no post-windthrow intervention (NI), amounted to 270 m^3 ha^{-1}. A wide variety of wood decay stages and diameter classes (10 to ≥ 70 cm) was found on both NI and SL sites, suggesting considerable habitat diversity for DW-associated species irrespective of the treatment. The considerable amounts of DW left after salvage-logging distinctly exceed the minimum DW volumes in forest stands proposed by Müller and Bütler (2010) in a conservation context, which demonstrates the importance of wind disturbance for biodiversity. Further studies should quantify DW of individual tree species, since habitat requirements are species-specific.

Keywords: Coarse woody debris, decay stage, diameter classes, wind disturbance

1. Introduction

Deadwood (DW) in the form of standing dead trees (snags), logs (downed deadwood), stumps, and buried wood is a natural component of forest ecosystems (Harmon et al. 1986). Decaying wood provides a wide variety of micro-habitats and has therefore been proposed as a surrogate for overall species richness (Juutinen et al. 2006), especially in boreal forests (Lassauce et al. 2011). Because species requirements for DW quantity and quality vary considerably (Berg et al. 1994; Schiegg 2001), the availability of downed and standing DW in different stages of decomposition is crucial for species composition and richness (Harmon et al. 1986; Bader et al. 1995). Moreover, DW provides a favourable substrate for tree regeneration (Zielonka 2006b; Baier et al. 2007; Svoboda et al. 2010), particularly in moist mountain forests where luxuriantly growing tall herb communities often impede tree regeneration on open ground (Imbeck and Ott 1987; Wohlgemuth et al. 2002b).

Given the multiple functions of DW, lack of DW may have disadvantageous effects on soil fertility, forest biodiversity and forest regeneration. For biodiversity, threshold values for DW of 20 m^3 ha^{-1} have been suggested for European temperate deciduous forests (Kappes et al. 2009), and 33 m^3 ha^{-1} for subalpine Norway spruce (*Picea abies* L.) forests (Bütler and Schlaepfer 2004). In a careful review of DW thresholds in European forests, Müller and Bütler (2010) proposed similar minimum values, namely 20–30 m^3 ha^{-1} for boreal coniferous forests, 30–50 m^3 ha^{-1} for lowland oak-beech forests and 20–30 m^3 ha^{-1} for mixed montane forests.

DW abundance has been investigated in different types of natural and managed forests, as well as on disturbed sites like clear-cuts and burnt sites (Pedlar et al.

2002; Gibb et al. 2005; Eräjää et al. 2010). While many studies have quantified the DW amount and quality on burnt sites, and related the results to species richness (e.g. Little et al. 1994; Turner et al. 1997; Tinker and Knight 2000), few have addressed the relationship between DW in windthrow gaps and biodiversity (Bouget and Duelli 2004; Lain et al. 2008). To our knowledge, DW quantity and quality on windthrow areas and clear-cuts in Central Europe have not been assessed, even though there is growing awareness of the contribution of natural disturbances (Schelhaas et al. 2003) to the naturalness of forests (Wohlgemuth et al. 2002a).

In the frame of European winter storms, the two most severe events in Switzerland during the last 100 years (Usbeck et al. 2010), namely Vivian (February 1990) and Lothar (December 1999), blew down about 5 million m^3 (Schüepp et al. 1994) and 13 million m^3 (BUWAL and WSL 2001) of timber, respectively. On most of these windthrow areas, the windthrown or broken timber was salvage-logged (‘SL’ treatment in this paper), whereas only a few windthrow patches were left unsalvaged with no intervention (i.e. windthrown trees were not removed; ‘NI’ treatment in this paper). In Switzerland, only rough estimates of post-windthrow DW abundance and quality are available. Those obtained from large-scale forest inventory data ranged from 45 to 90 m^3 ha^{-1} DW on sample plots either totally or partially damaged by storms (Cioldi et al. 2010). DW in a study in Sweden amounted to 42.3 m^3 ha^{-1} on traditional (control) clear-cuts and 26.0 m^3 ha^{-1} on clear-cuts after additional harvesting of all fuels (Eräjää et al. 2010). These volumes were much greater than expected, and imply that windthrow areas in Switzerland that are either salvage-logged or left with no intervention may still have a large DW potential. In addition, even though the general importance of

DW for regeneration success in various forests is well known, it has rarely been quantified in Central Europe.

This study therefore aims to: (i) quantify DW in windthrow areas with total damage caused by the storms Vivian (1990) or Lothar (1999); (ii) analyse salvage-logging impacts on DW amounts, DW composition (log, stump, and snag volumes), size classes, and decay stages; (iii) assess how decay rates vary with elevation (350 to 1800 m a.s.l.) 10 years after windthrow; and (iv) quantify DW as a substrate for tree regeneration after windthrow.

2. Material and methods

2.1 Sample sites

We used a sample of 90 windthrow areas in Switzerland, in the following called ‘sample sites’, caused by either the winter storm Vivian, 1990, or Lothar, 1999 (Fig. 1 and Table 1). The sample sites were selected from a database of geospatial information for windthrow patches all over Switzerland, derived from visual interpretations of post-disturbance aerial photographs (Vivian: Federal Office for the Environment FOEN; Lothar: Engineering Consultants H. U. Scherrer) according to two criteria: 1) forest area with full damage and 2) windthrow patch greater than 3 ha. Another criterion was that 3) the type of forest on the site should be one of the four most widespread forest types in Switzerland, i.e. beech (*Fagus sylvatica* L.), silver fir- (*Abies alba* Mill.) beech, silver fir-Norway spruce, or Norway spruce forest (Wohlgemuth et al. 2008b). Moreover, 4) both SL and NI sites were aimed at being represented evenly. Information about salvage-logging activities was derived from interviews with local foresters. Furthermore, we preferred 5) sample sites with exclusively natural regeneration.

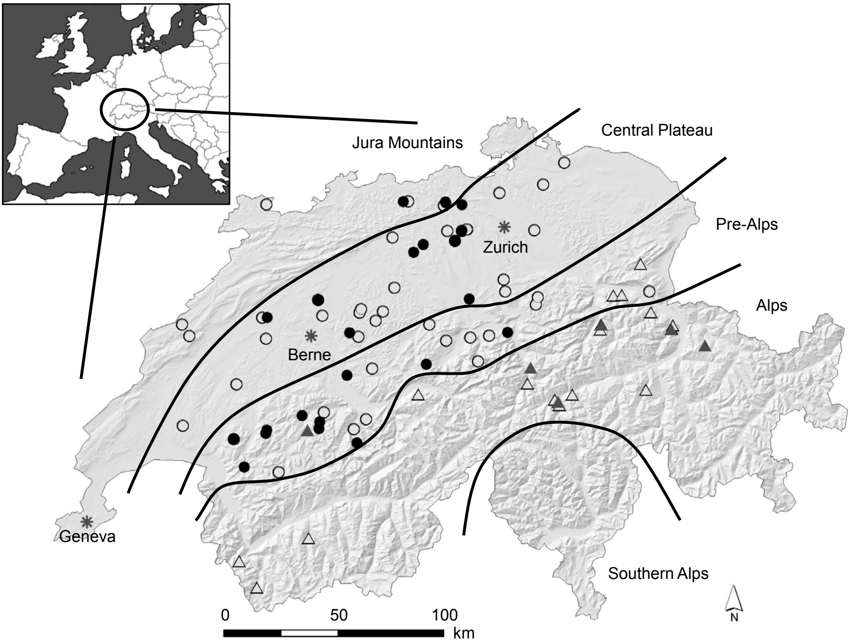

Fig. 1 Windthrow sample sites in Switzerland: Vivian (1990): *empty triangles* = salvage-logged, *solid triangles* = no intervention. Lothar (1999): *empty dots* = salvage-logged, *solid dots* = no intervention. Source of map: BFS GEOSTADT/Bundesamt für Landestopographie (Federal Office of Topography) and Swiss Federal Institute for Forest Snow and Landscape Research WSL.

Table 1 Number of sample sites per storm event, treatment and region.

Region	Vivian		Lothar	
	Salvage-logged	No intervention	Salvage-logged	No intervention
Jura Mountains	0	0	5	3
Central Plateau	0	0	22	9
Pre-Alps	3	1	16	11
Alps	15	5	0	0
Total	18	6	43	23

The initial number of sample sites was high, but applying these five selection criteria reduced the number considerably. Finally, 6) the sample sites were also selected to geographically represent the spatial distribution of windthrow damage in Switzerland from the Jura Mountains to the Alps. This also ensured that the range of elevation (350–1800 m a.s.l.), aspect and slope (0–52°) was wide. As a result of this selection procedure, 90 sites were left for the data collection, and the final sample consisted of 60%pure coniferous forest, 24% deciduous forest, and 16% mixed coniferous-deciduous forest.

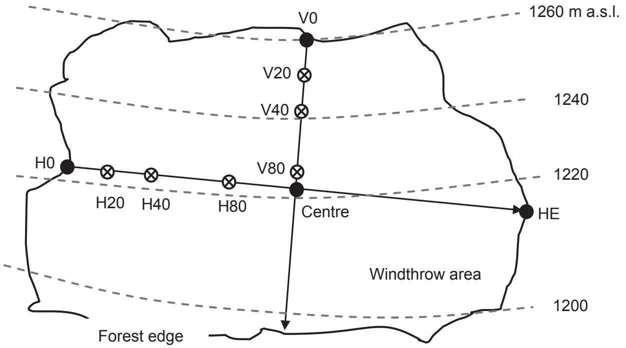

Fig. 2 Sampling design for each windthrow area: Six circular plots were selected on each sample site at the following distances away from two forest edges following the axes of an ellipse fitted to the windthrow patches: 20 m (H20, V20), 40 m (H40, V40), and 80 m (H80, V80), where H0, V0, and HE are points along the edge of the forest.

2.2 Data collection

Field work was conducted on 24 Vivian and 66 Lothar sample sites between December 2009 and January 2011. We distinguished between DW as logs (downed DW), stumps (standing DW with height ≤1.3 m), and snags (standing DW with height >1.3 m). On each sample site, six circular sample plots 20 or

50 m^2 in size were defined. Plot sizes of 20 m^2 were used for sample sites below 1200 m a.s.l., and of 50 m^2 for sites above 1200 m a.s.l. to account for presumed higher regeneration densities at lower elevations (Wohlgemuth et al. 2008a) and to optimise time-consuming data collection.

On each sample site, the six circular sample plots were defined along the two axes of an ideal ellipse fitting the windthrow area at distances of 20, 40, and 80 m from the forest edge (Fig. 2). If a sample site was large enough, one of the two transect lines was placed parallel to the contour line and the second perpendicular to and upslope of the first one. If the sample site shape was unsuitable for applying the distance rule, the two transect lines were slightly shifted. However, the right angle between the two transect lines was always maintained. Transects were rotated clockwise (90°, 180° or 270°) around the centre point if obstacles such as rocks made proper data assessment impossible.

On each circular sample plot, all DW pieces with a minimum small-end diameter of 10 cm and a minimum length of 10 cm were measured. Diameters at both ends and the length or height of each DW piece were recorded. The parts of DW lying outside of the circular line and buried DW were not measured. For each DW piece, decay was evaluated according to Zielonka's (2006a) eight-stage scale, which considers the shape of DW, the average depth of knife penetration, the presence of branches, and the presence of bark (Table 2). Averaged small- and large-end diameters served for the classification into seven diameter classes (I = 10–19 cm, II = 20–29 cm, …, VII ≥ 70 cm). Since identifying the species of DW pieces by visual examination was often ambiguous given the great variety of forests visited, DW species were not recorded. Prior to the storms Vivian and Lothar, the amount of DW in Swiss forests was generally small. The second Swiss National Inventory (1993 to 1995; Brassel and Brändli 1999) recorded

Table 2 Eight-degree scale of deadwood decomposition stage (Zielonka 2006a).

Decay stage	Shape	Average depth of knife penetration	Branches	Bark
D1	Round, smooth	0-1 mm; hard wood	All branches present	Intact
D2	Round, smooth	1–5 mm	Branches over 20 mm present	Partially intact
D3	Round, crevices several mm deep	5-10 mm	Over 30 mm thick present	Remains on upper side of log
D4	Round, crevices approx. 5 mm deep	10–40 mm	Only base part present	Usually lacking
D5	Round, crevices approx. 10 mm deep	40–60 mm	Only thickest base parts present	Mostly lacking
D6	Slightly flattened, several cm thick, pieces tear off easily	Solid only in central part of log	Only thickest base parts present	Completely lacking
D7	Distinctly flattened, whole log covered with furrows several cm deep	Throughout	Completely lacking	Completely lacking
D8	Flattened, covered with vegetation	Throughout	Completely lacking	Completely lacking

averages of 6.5 m^3 DW ha^{-1} in the Jura Mountains, 4.0 in the Central Plateau and 14.5 in the Northern Pre-Alps. We assume that these DW amounts can be applied not only to the Lothar forests, but also to the situation in forests before Vivian (1990) as the inventory was conducted soon after Vivian. Accordingly, we assumed that most of the DW found in the windthrow sites resulted from the two storms.

In the circular sample plots, saplings taller than 19 cm that had established after the windthrow were assessed on both DW and forest soil. To distinguish between pre- and post-storm regeneration, we estimated sapling age by counting the whorls on conifers or the tree rings from a stem of a tree outside the circle plot. Alternatively, the tree rings from the oldest branch of a tree inside the circle plot were counted.

2.3 Data analysis

One circular sample plot from one salvage-logged Lothar sample site had to be excluded from all analyses because of one huge standing dead tree that was responsible for the 'NI' aspect of the sample plot in spite of the sample site having been cleared.

The volumes of all DW pieces were calculated with the formula of a truncated circular cone:

$$V = \tfrac{1}{3}\pi h(r_1^2 + r_1 r_2 + r_2^2)$$

where h is height or length, r_1 the small-end radius and r_2 the large-end radius of the DW piece. To calculate the amount of DW per sample site, measurements of the six circular sample plots were pooled and scaled up to standard values (m^3

ha^{-1}). Volume, diameter classes and decay stages of DW were related to treatments (SL vs. NI), windthrow event (20-year-old Vivian and 10-year-old Lothar sites), and elevation. Analyses were performed using a mixed ANOVA design with one between-site factor (treatment), and in some analyses with one within-site factor (type of DW or decay stage). Post-hoc pairwise Tukey HSD tests were used to calculate the p-values. Prior to all analyses, response variables were square-root transformed (unless otherwise noted) to meet the assumptions of normality and/or homogeneity of variance. All analyses were performed using the statistical computing system R, version 2.11.1 (R Development Core Team 2011).

3. Results

3.1 Deadwood volume and structure

Standing and lying DW covered altogether between 0.05 and 21.0% of the surface on the 90 sample sites. Volumes of DW varied from 1 to 650 m^3 ha^{-1} (Fig. 3), with almost four times more DW on no intervention (NI) sites (average of 270.0 m^3 ha^{-1}) than on salvage-logged (SL) sites (74.6 m^3 ha^{-1}). In detail, DW volumes on SL Vivian and SL Lothar sites were similar: 76.4 ± 11.6 (mean ± SE) and 73.8 ± 18.1 m^3 ha^{-1}, respectively (Table 3). The differences in DW volumes between NI Vivian and NI Lothar sample sites were also small: 284.7 and 266.1 m^3 ha^{-1}, respectively (Table 3). Differences between NI and SL sites were, in contrast, highly significant (ANOVA for Vivian: $F_{1, 22} = 39.81$, $P < 0.001$; for Lothar: $F_{1, 64} = 96.8$, $P < 0.001$).

On both SL and NI sites, DW consisted predominantly of logs (Fig. 4). The total log volumes on NI sites were five times higher than on SL sites (ANOVA for Vivian: $F_{1, 22} = 21.88$, $P < 0.001$; for Lothar: $F_{1, 64} = 41.06$, $P < 0.001$; Table

3). Stump volumes were higher on SL than on NI sites, but the difference was significant for Lothar sites only. On both NI Vivian and Lothar sites, snag volumes were higher than on SL sites, but for both storm types, the differences were not significant (Table 3). The composition of DW (log, stump, and snag volumes) on SL Vivian and Lothar sites, as well as on NI Vivian and Lothar sites, was similar (Fig. 4), with no significant differences (ANOVA for the interaction between storm and type of DW (log, stump, and snag volumes): for SL sites: $F_{1, 59} = 0.72$, $P = 0.399$; for NI sites: $F_{1, 27} = 0.42$, $P = 0.522$).

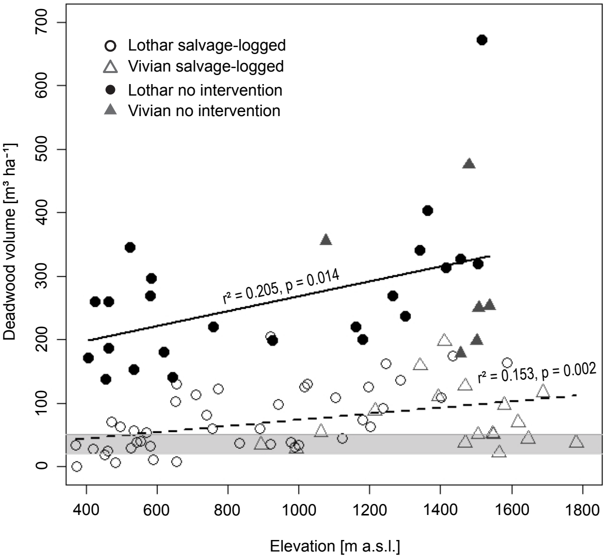

Fig. 3 Deadwood volume and elevation per sample site according to storm event and treatment (salvage-logged, no intervention). *Solid line* = all sample sites without intervention, *dashed line* = all salvage-logged sample sites, *grey stripe* = target deadwood volume range for the three main European forests (lowland oak-beech forests, mixed-montane forests, and boreal coniferuous forests).

Table 3 Deadwood volume ($m^3\ ha^{-1}$) in 2010 resulting from the winter storms Vivian (1990) and Lothar (1999) (mean ± SE).

	Vivian			Lothar		
	Salvage-logged	No intervention	p	Salvage-logged	No intervention	p
Type of DW						
Snags	8.0 ± *2.6*	21.3 ± *13.7*	0.890	8.0 ± *2.9*	26.1 ± *11.1*	0.199
Stumps	16.6 ± *2.9*	9.2 ± *6.1*	0.852	19.8 ± *2.5*	4.0 ± *1.3*	**0.018**
Logs	51.8 ± *11.1*	254.2 ± *51.3*	**< 0.001**	46.0 ± *7.1*	236.0 ± *18.0*	**< 0.001**
Decay stages						
D2	1.1 ± *1.0*	14.4 ± *12.2*	0.927	5.2 ± *2.2*	20.7 ± *6.9*	0.264
D3	6.1 ± *2.4*	10.1 ± *3.6*	0.999	16.3 ± *3.5*	107.2 ± *20.3*	**< 0.001**
D4	13.4 ± *5.3*	51.9 ± *16.7*	**0.022**	23.5 ± *4.3*	85.4 ± *9.8*	**< 0.001**
D5	14.8 ± *2.6*	70.8 ± *21.4*	**0.001**	12.7 ± *3.0*	37.9 ± *10.4*	0.121
D6	13.5 ± *3.1*	64.2 ± *28.5*	**0.006**	6.1 ± *1.7*	11.0 ± *2.7*	0.994
D7	25.3 ± *4.4*	68.6 ± *17.7*	0.096	7.3 ± *1.4*	3.8 ± *1.3*	0.999
D8	2.2 ± *1.3*	4.7 ± *2.7*	1.000	2.7 ± *1.6*	0.2 ± *0.1*	1.000
Diameter classes						
I (10-19 cm)	2.8 ± *1.0*	18.5 ± *9.5*	0.804	6.0 ± *0.9*	29.1 ± *3.8*	**< 0.001**
II (20-29 cm)	7.9 ± *1.3*	90.7 ± *22.0*	**< 0.001**	8.8 ± *1.5*	79.0 ± *10.1*	**< 0.001**
III (30-39 cm)	18.1 ± *5.0*	86.3 ± *11.7*	**< 0.001**	11.6 ± *2.5*	93.1 ± *10.6*	**< 0.001**
IV (40-49 cm)	18.1 ± *3.6*	49.2 ± *34.1*	0.977	16.4 ± *3.2*	33.5 ± *7.4*	0.699
V (50-59 cm)	14.0 ± *3.1*	31.4 ± *14.7*	0.999	11.8 ± *2.8*	23.3 ± *8.5*	0.996
VI (60-69 cm)	9.2 ± *3.1*	6.3 ± *4.5*	0.999	8.5 ± *2.5*	4.4 ± *2.0*	0.998
VII (> 70 cm)	6.4 ± *2.3*	2.3 ± *2.3*	0.999	10.8 ± *3.0*	3.8 ± *3.8*	0.713
Total	76.4 ± *11.6*	284.7 ± *45.5*	**< 0.001**	73.8 ± *18.1*	266.1 ± *9.1*	**< 0.001**

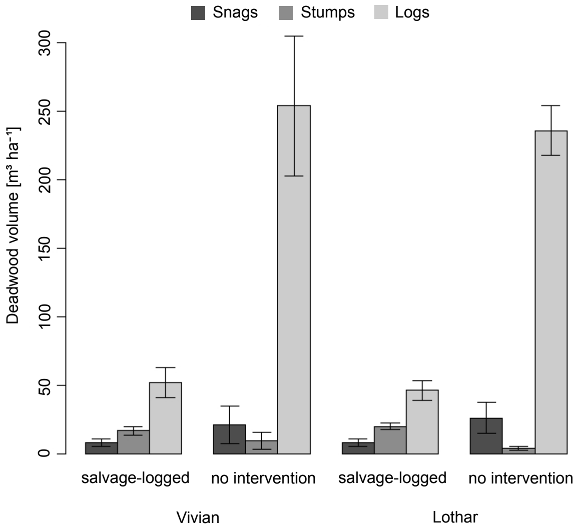

Fig. 4 Snag, stump, and log volumes on salvage-logged and no intervention Vivian (1990) and Lothar (1999) sample sites.

3.2 Decay stages and size class distribution on Vivian sample sites

The majority of DW on both SL and NI 20-year-old Vivian sites was in decay stages D4–D7 (Fig.5). These decay stages (D4–D7) accounted for 90% of the total DW volume on NI sites and for 88% on SL sample sites. No DW in decay stage D1 was found. The proportion of slightly decayed DW (D2 and D3) was 9% on both SL and NI sites, whereas that of highly decayed DW (D8) was 1% on NI and 3% on SL sites. DW volumes were greater on NI than on SL sample sites for all decay classes, but the differences were only significant for the decay stages D4, D5, and D6 (ANOVA: $F_{1, 22} = 43.02$, $P < 0.001$; Table 3).

On NI sites, 97% of the total DW volume consisted of diameter classes I–V. In contrast, on SL sites, the contribution to these classes was smaller with only 80% of the total DW volume (Table 3), where DW volume followed approximately a normal distribution. Volumes of DW differed significantly between NI and SL sites in diameter classes II and III only (ANOVA: $F_{1, 22} = 21.48$, $P < 0.001$; Table 3).

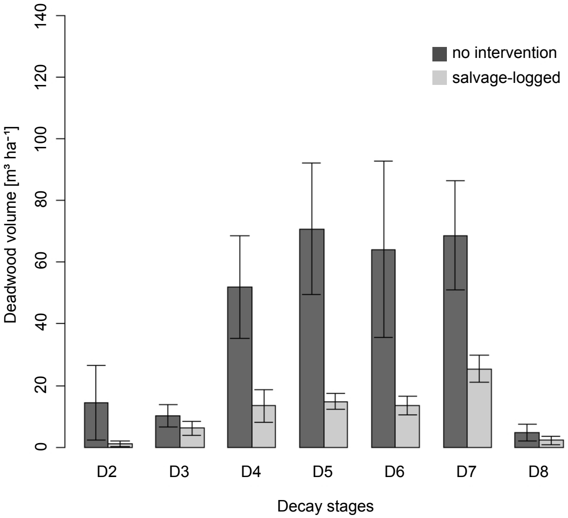

Fig. 5 Deadwood volume per decay stage on Vivian (1990) sample sites. For abbreviations, see Table 2.

3.3 Decay stages and size class distribution on Lothar sample sites

Ten years after the windthrow disturbance, the majority of DW on Lothar sites was in the decay stages D3–D5 (Fig. 6), with 87% on NI and 73% on SL sites. As on Vivian sites, no DW in decay stage D1 was found. Early decay stages (D2) were only present in 7% of the volume of all DW pieces (both NI and SL sites), and advanced decay stages (D6–D8) had a proportion of 6% on NI sites and 20% on SL sites. DW volumes were greater on NI than SL sites in decay stages D1–D6, and smaller in decay stages D7 and D8. Only DW volumes from decay stages D3 and D4 differed significantly between SL and NI sample sites (ANOVA: $F_{1, 64} = 78.91$, $P < 0.001$; Table 3).

NI sites had the same proportion (97%) of total DW volume in diameter classes I–V as NI Vivian sites, but the proportion on SL Lothar sites (74%) was 6% smaller than on SL Vivian sites (80%). On SL Lothar sites the volume in the seven diameter classes followed, as on SL Vivian sites, approximately a normal distribution. DW volumes in diameter classes I–V were greater on NI than on SL sites, and smaller in diameter classes VI and VII. Only in the three smallest diameter classes (I–III) was DW volume significantly higher on NI than on SL sites (ANOVA: $F_{1, 64} = 51.03$, $P < 0.001$; Table 3).

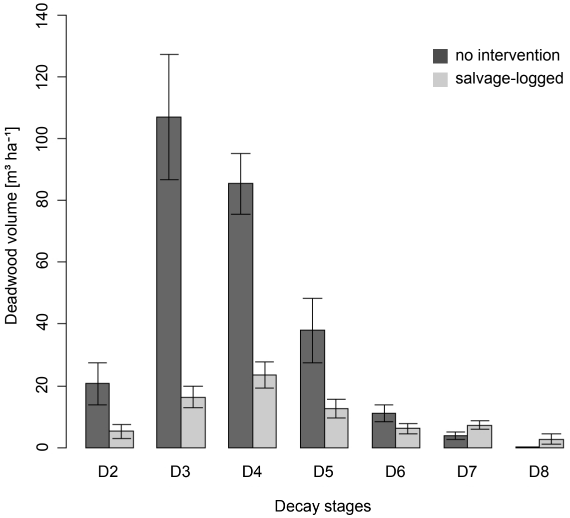

Fig. 6 Deadwood volume per decay stage on Lothar (1999) sample sites. For abbreviations, see Table 2.

3.4 Decay rates on Lothar sites along an extended elevational gradient

We expected the decomposition rate to be a function of temperature, i.e. decay to decrease with increasing elevation. To test this effect, we selected NI Lothar sample sites (n=23) with a large range of DW pieces in different decay stages (three decay classes: D2–D3, D4–D5, D6–D8). Volumes from 13 sites below and 10 sites above 1000 m a.s.l. were compared. DW volumes above 1000 m a.s.l. were significantly higher than those below (ANOVA: $F_{1,\ 21} = 7.39$, $P = 0.013$). Decay stage distributions also clearly differed (ANOVA: $F_{2,\ 42} = 29.04$, $P < 0.001$), and the interaction of decay and elevation showed significant differences (ANOVA: $F_{2,\ 42} = 7.65$, $P = 0.001$). Above 1000 m a.s.l., the average volume of slightly decayed DW (D2 and D3) was significantly higher than below 1000 m a.s.l. (Tukey's HSD: $P < 0.001$; Fig. 7). In contrast, volumes of moderately decayed DW (D4 and D5) were smaller on sites above 1000 m than on sites below 1000 m a.s.l., although volumes did not differ significantly (Tukey's HSD: $P = 0.895$). DW volumes in advanced decay stages (D6–D8) were similar below and above 1000 m a.s.l. The highest volumes of moderately decayed DW occurred below 1000 m a.s.l., in contrast to slightly decayed DW, which was most prominent above 1000 m a.s.l. (significant at the 10% level; Tukey's HSD: $P = 0.062$ and $P = 0.060$, respectively; Fig. 7).

3.5 Tree regeneration on deadwood

On the 20-year-old Vivian sample sites (n=24), a total of 81 saplings ≥20 cm were found on DW substrate. In contrast, 62 saplings were found on the 10-year-old Lothar sample sites (n=66). On 83% (n=20) of all Vivian sites, saplings were present on DW, but regeneration on this substrate was restricted to only 32%

(n=21) of the younger Lothar sites. Since saplings on DW were absent on the majority of the Lothar sites (n=45), only Vivian sites were considered for further analysis.

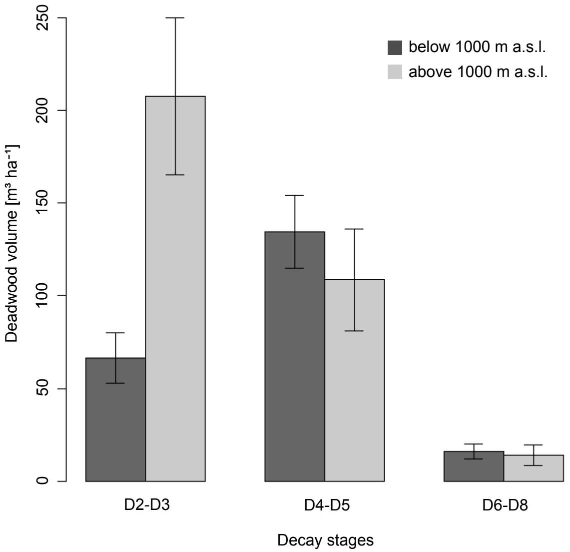

Fig. 7 Volumes of deadwood per elevation zone and of slightly decayed (D2-D3), moderately decayed (D4-D5), and well-decayed deadwood (D6-D8) on no intervention Lothar (1999) sample sites.

For each Vivian site, sapling numbers were transformed to densities per square meter of substrate, distinguishing ‘deadwood’ and ‘forest soil’. Sapling density did not vary significantly between deadwood (0.50 ± 0.15 m^{-2}) and forest soil (0.42 ± 0.07 m^{-2}; ANOVA: $F_{1, 23} = 0.47$, $P = 0.496$). However, the 81 saplings found on deadwood are very few compared to 2920 saplings counted on forest soil. Two-thirds (66.7%) of all saplings found on deadwood were Norway spruce, 8.6% European larch (*Larix decidua* Mill.), 7.4% rowan (*Sorbus aucuparia* L.), and 17.3% individuals belonging to other tree species. On forest soil, the proportions were 35.6% Norway spruce, 15.3% sycamore (*Acer pseudoplatanus* L.), 9.9% rowan, 7.1% European larch, 5.8% red elder (*Sambucus racemosa* L.), and 26.3% other woody species. Average sapling height on deadwood was 63.8 ± 12.6 cm, which is clearly and significantly smaller than on forest soil, where saplings grew to 143.7 ± 8.2 cm (no square root-transformation, ANOVA: $F_{1, 23} = 29.91$, $P < 0.001$).

4. Discussion

Our study revealed surprisingly high DW volumes (74.6 m^3 ha^{-1}) on salvage-logged windthrow areas in Switzerland. Since buried DW was not measured, total DW volumes are likely to be even larger. A comparison with DW amounts from other windthrow areas worldwide is not possible due to the lack of comparable studies. However, our measured values exceed post-clearcut DW volumes in Canada and Scandinavia by factors as high as 2.3 (Sturtevant et al. 1997; Eräjää et al. 2010) and 5.5 (Gibb et al. 2005). These distinct differences may have several explanations. One reason may be that the growing stock in boreal forests today (MCPFE 2007) is small, with averages of 98 m^3 ha^{-1} in Finland, 111 m^3 ha^{-1} in Sweden or 201 m^3 ha^{-1} in Estonia. In comparison, growing stocks in Swiss forests (dimensions from the pole stage upward, i.e. DBH >12 cm) amount to 374 m^3 ha^{-1} (Cioldi et al. 2010). Another explanation of the big differences may be that calculations of DW volumes are strongly affected by the measurement method used, and comparisons of DW volumes calculated by different researchers must thus be treated with caution (Eräjää et al. 2010). Adapting the criteria in Gibb et al. (2005) to our sample sites, the estimates of DW volumes for SL windthrow areas diminish to 50.2 m^3 ha^{-1} (Vivian) and to 49.9 m^3 ha^{-1} (Lothar). The resulting amounts are, nevertheless, still clearly higher than those measured by Gibb et al. (2005). Importantly, the DW volumes found in SL windthrow areas are twice as large as the target DW ranges proposed by Müller and Bütler (2010) in a biodiversity conservation context.

The average DW volume on unsalvaged sites, i.e. with no post-windthrow intervention (NI), was surprisingly low (270.0 m^3 ha^{-1}) compared to the growing stock in Swiss forests, which, on average, ranges from 327 m^3 ha^{-1} in the Alps to 475 m^3 ha^{-1} in the Pre-Alps (Cioldi et al. 2010). We assume that, among the 29 NI sites found, stands with a low growing stock were overrepresented because windthrown stands with a high growing stock had mostly been harvested, i.e. a presumed reason for no intervention was actually a low growing stock.

On all sites, logs accounted for the great majority of DW, although the log volume on SL sites was much smaller than on NI sites. The volume of stumps and snags was similar on SL and NI sites, but on NI Lothar sites stump volume was smaller than on SL Lothar sites, probably due to the fact that harvesting leaves stumps. Not only was the DW variation similar on SL and NI sites, but so too was the diameter class distribution of DW volumes. On all NI windthrow sites, DW volumes in diameter classes <50 cm dominated. We presume that those windthrow areas stocked with small diameter trees were more likely to have had no intervention than the ones stocked with thicker trees, as can be seen in Fig. 3, where only six of the 29 NI sites had DW volumes exceeding the level of average growing stock for forests in the Alps, i.e. 327 m^3 ha^{-1} (Cioldi et al. 2010). In Switzerland, however, two thirds of the total volume of living trees is comprised of trees with a DBH between 12 and 51 cm.[1] On both SL Vivian and

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[1] http://www.lfi.ch/resultate.php?zigrNr=21&befundNr=1029&invNr=350&auswNr=434&p=crit&indNr=102&frmFnc=Resultate+anzeigen&itNr=15237, 08.11.2011

SL Lothar sites, the highest DW volumes were found in diameter classes III–V (30–59 cm), while clear-cuts in Canada and Scandinavia had the highest DW volumes or number of DW pieces in diameter classes <20 cm (Pedlar et al. 2002; Gibb et al. 2005; Moroni and Ryan 2010). The range of DW diameter classes in our study was large irrespective of the post-windthrow management.

The decay stages of DW depend on the time since tree death (Zielonka 2006a), which in our study directly translates into the time since disturbance. Since we only assessed windthrow areas with total damage, we found no recent DW (D1) on Vivian and Lothar sites, i.e. no new DW had accumulated since the storms. Not surprisingly, DW on 20-year-old Vivian sites (1990) was in a more advanced stage of decay than DW on 10-year-old Lothar sites (1999). Pre-storm DW volumes were assumed to be in decay stages D8 on the Vivian and D7/D8 on the Lothar sample sites, and were generally small (Fig. 5 and 6). In contrast to untouched old-growth forests (Sippola et al. 1998; Zielonka 2006a), the simultaneous presence of all decay stages is merely a transient phenomenon in a post-windthrow area with total damage. In such areas it is likely that locally there will be a lack of less decayed DW, but a supply of highly decayed DW in the medium and long term until new disturbances produce new DW. In the long term, the composition of DW in areas with total windthrow damage will develop differently from that in untouched old-growth forests with a small-scale disturbance regime, where repeated but episodic disturbances eventually result in the co-occurrence of all DW decay stages (Spies et al. 1988; Mountford 2002; Christensen et al. 2005).

Regarding DW structure (DW type, diameter class and decay stage), SL windthrow areas are not less diverse than NI windthrow areas. Hence, they provide as many habitats for different DW-associated species requiring particular DW structures as

NI areas. Since many DW dwellers depend not only on particular DW structures (Berg et al. 1994; Bader et al. 1995; Schiegg 2001), but also on particular DW tree species (Jonsell et al. 2004; Lohmus et al. 2010), further studies should focus on the tree species composition of DW and the specific decay time involved with respect to disturbance regimes.

In the 10-year-old Lothar sites, volumes of slightly decayed DW peaked above 1000 m a.s.l., and volumes of moderately decayed DW below 1000 m a.s.l. This suggests slower decay rates with increasing elevation, which is in line with Kueppers et al.'s (2004) finding that the turnover time of lodgepole pine DW on cool sites was twice that on a site where air temperature was 2.5–3 °C higher. Mackensen et al. (2003) also found that the mean annual temperature strongly correlated with the DW decay rate. However, DW decay rates also depend on other factors, such as how long the wood has been in contact with the ground (Zielonka 2006a) or the tree species. The windthrow sites we sampled at higher elevations had, on average, higher DW volumes than sites at lower elevations (Fig. 3). This is partly due to the fact that harvesting at higher elevations is less cost-efficient because slopes are generally steeper and less accessible than in the lowlands.

After 30 years, DW turns into an appropriate seedbed, but the first seedlings may already establish during the second decade after tree death (Zielonka 2006b). Since our assessment was only 20 years after Vivian and only tree individuals taller than 19 cm were measured, we suspect that part of the DW-borne regeneration established on DW pieces older than 20 years. However, the sapling density of 0.5 m^{-2} on DW substrate was roughly similar to that found on forest soil, where the great majority of regenerating trees had already grown taller than the saplings on DW. Deadwood as substrate may be crucial for regeneration in moist spruce forests, as found by Imbeck and Ott (1987) in Swiss mountain forests and Svoboda et al. (2010) in the Bohemian forest, Czech Republic. Given the presence of advanced decayed DW on Vivian windthrow sites, this substrate seems to have been as important for tree recruitment as forest soil. Further, the availability of DW is also important for the heterogeneous establishment of tree seedlings during the succession process, since it provides a delayed seedbed for tree regeneration (Zielonka 2006b), and consequently leads to a more complex and uneven-aged forest in the long term (Donato et al. 2012).

Our findings indicate that wind disturbances are important for DW accumulation, independent of the post-storm management, and that current practices of salvage-logging on windthrow areas are likely to leave enough DW to ensure a wide diversity of habitats for DW dwellers. While we are confident that our results are highly representative for the climatically and edaphically diverse forests of Switzerland, we are cautious regarding their implications for other regions and larger scales. We found, however, similar DW conditions in the windthrow areas produced by the two winter storms Vivian (1990) and Lothar (1999). Specifically, the total DW amount, the DW volume variation across the three DW types (logs, stumps, and snags) and the diameter class distribution were similar on Vivian and Lothar sites even though the two storms happened at different times and affected different regions (Usbeck et al. 2010). Questions still remain about whether the wide range of logging practices in Switzerland (especially the variations between lowland and mountain forestry) are similar to logging practices in other countries in Central Europe. Further studies with more detailed information about DW tree species are needed to determine whether forests in other countries affected by windthrow also exhibit the same post-disturbance deadwood patterns, which would enable generalizations for forests in Central and Western Europe, where European winter storms are most frequent.

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References

Bader P, Jansson S, Jonsson BG (1995) Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. Biol Conserv 72: 355-362.

Baier R, Meyer J, Göttlein A (2007) Regeneration niches of Norway spruce (*Picea abies* [L.] Karst.) saplings in small canopy gaps in mixed mountain forests of the Bavarian Limestone Alps. Eur J For Res 126: 11-22.

Berg A, Ehnström B, Gustafsson L, Hallingbäck T, Jonsell M, Weslien J (1994) Threatened plant, animal, and fungus species in Swedish forests - distribution and habitat associations. Conserv Biol 8: 718-731.

Bouget C, Duelli P (2004) The effects of windthrow on forest insect communities: a literature review. Biol Conserv 118: 281-299.

Brassel P, Brändli UB (1999) Schweizerisches Landesforstinventar: Ergebnisse der Zweitaufnahme 1993 - 1995. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft, WSL, Birmensdorf. Bundesamt für Umwelt, Wald und Landschaft, BUWAL, Bern.

Bütler R, Schlaepfer R (2004) Wie viel Totholz braucht der Wald? Schweiz Z Forstwes 150: 31-37.

BUWAL, WSL (2001) Lothar. Der Orkan 1999. Ereignisanalyse. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft, Birmensdorf. Bundesamt für Umwelt, Wald und Landschaft, BUWAL, Bern.

Christensen M, Hahn K, Mountford EP, Ódor P, Standovár T, Rozenbergar D, Diaci J, Wijdeven S, Meyer P, Winter S, Vrska T (2005) Dead wood in European beech (*Fagus sylvatica*) forest reserves. Forest Ecol Manag 210: 267-282.

Cioldi F, Baltensweiler A, Brändli U-B, Duc P, Ginzler C, Bonardi AH, Thürig E, Ulmer U (2010) Waldressourcen. In: Brändli U-B (ed) Schweizerisches Landesforstinventar Ergebnisse der dritten Erhebung 2004-2006. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft WSL, Birmensdorf. Bundesamt für Umwelt BAFU, Bern, pp. 31-114.

Donato DC, Campbell JL, Franklin JF (2012) Multiple successional pathways and precocity in forest development: can some forests be born complex? J Veg Sci 23: 576-584.

Eräjää S, Halme P, Kotiaho JS, Markkanen A, Toivanen T (2010) The Volume and Composition of Dead Wood on Traditional and Forest Fuel Harvested Clear-Cuts. Silva Fenn 44: 203-211.

Gibb H, Ball JP, Johansson T, Atlegrim O, Hjältén J, Danell K (2005) Effects of management on coarse woody debris volume and composition in boreal forests in northern Sweden. Scand J Forest Res 20: 213-222.

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. Adv Ecol Res 15: 133-302.

Imbeck H, Ott E (1987) Verjüngungsökologische Untersuchungen ein einem hochstaudenreichen subalpinen Fichtenwald, mit spezieller Berücksichtigung der Schneeablagerung und der Lawinenbildung. Eidgenösschische Forschungsanstalt für Wald, Schnee und Landschaft WSL, Birmensdorf.

Jonsell M, Nitterus K, Stighall K (2004) Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. Biol Conserv 118: 163-173.

Juutinen A, Monkkonen M, Sippola AL (2006) Cost-efficiency of decaying wood as a surrogate for overall species richness in boreal forests. Conserv Biol 20: 74-84.

Kappes H, Jabin M, Kulfan J, Zach P, Topp W (2009) Spatial patterns of litter-dwelling taxa in relation to the amounts of coarse woody debris in European temperate deciduous forests. Forest Ecol Manag 257: 1255-1260.

Kueppers LM, Southon J, Baer P, Harte J (2004) Dead wood biomass and turnover time, measured by radiocarbon, along a subalpine elevation gradient. Oecologia 141: 641-651.

Lain EJ, Haney A, Burris JM, Burton J (2008) Response of vegetation and birds to severe wind disturbance and salvage logging in a southern boreal forest. Forest Ecol Manag 256: 863-871.

Lassauce A, Paillet Y, Jactel H, Bouget C (2011) Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecol Indic 11: 1027-1039.

Little RL, Peterson DL, Conquest LL (1994) Regeneration of sub-alpine fir (*Abies lasiocarpa*) following fire-effects of climate and other factors. Can J For Res-Rev Can Rech For 24: 934-944.

Lohmus A, Kinks M, Soon M (2010) The Importance of Dead-Wood Supply for Woodpeckers in Estonia. Baltic For 16: 76-86.

Mackensen J, Bauhus J, Webber E (2003) Decomposition rates of coarse woody debris - A review with particular emphasis on Australian tree species. Aust J Bot 51: 27-37.

MCPFE (2007) State of Europe's forests 2007. The MCPFE report on sustainable forest management in Europe. In: MCPFE, UNECO, FAO (Eds.), Warsaw, p. 263.

Moroni MT, Ryan DAJ (2010) Deadwood abundance in recently harvested and old Nova Scotia hardwood forests. Forestry 83: 219-227.

Mountford EP (2002) Fallen dead wood levels in the near-natural beech forest at La Tillaie reserve, Fontainebleau, France. Forestry 75: 203-208.

Müller J, Bütler R (2010) A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. Eur J For Res 129: 981-992.

Pedlar JH, Pearce JL, Venier LA, McKenney DW (2002) Coarse woody debris in relation to disturbance and forest type in boreal Canada. Forest Ecol Manag 158: 189-194.

R Development Core Team (2011) R: a language and environment for statistical computing. In. R Foundation for Statistical Computing, Vienna.

Schelhaas MJ, Nabuurs GJ, Schuck A (2003) Natural disturbances in the European forests in the 19th and 20th centuries. Glob Change Biol 9: 1620-1633.

Schiegg K (2001) Saproxylic insect diversity of beech: limbs are richer than trunks. Forest Ecol Manag 149: 295-304.

Schüepp M, Schiesser HH, Huntrieser H, Scherrer HU, Schmidtke H (1994) The winterstorm Vivian of 27 February 1990 - about the meteorological development, wind forces and damage situation in the forests of Switzerland. Theor Appl Climatol 49: 183-200.

Sippola AL, Siitonen J, Kallio R (1998) Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish Lapland. Scand J Forest Res 13: 204-214.

Spies TA, Franklin JF, Thomas TB (1988) Coarse woody debris in douglas-fir forests of western Oregon and Washington. Ecology 69: 1689-1702.

Sturtevant BR, Bissonette JA, Long JN, Roberts DW (1997) Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecol Appl 7: 702-712.

Svoboda M, Fraver S, Janda P, Bace R, Zenáhlíková J (2010) Natural development and regeneration of a Central European montane spruce forest. Forest Ecol Manag 260: 707-714.

Tinker DB, Knight DH (2000) Coarse woody debris following fire and logging in Wyoming lodgepole pine forests. Ecosystems 3: 472-483.

Turner MG, Romme WH, Gardner RH, Hargrove WW (1997) Effects of fire size and pattern on early succession in Yellowstone National Park. Ecol Monogr 67: 411-433.

Usbeck T, Wohlgemuth T, Dobbertin M, Pfister C, Bürgi A, Rebetez M (2010) Increasing storm damage to forests in Switzerland from 1858 to 2007. Agric For Meteorol 150: 47-55.

Wohlgemuth T, Bürgi M, Scheidegger C, Schütz M (2002a) Dominance reduction of species through disturbance - a proposed management principle for central European forests. Forest Ecol Manag 166: 1-15.

Wohlgemuth T, Conedera M, Kupferschmid A, Moser B, Usbeck T, Brang P, Dobbertin M (2008a) Effekte des Klimawandels auf Windwurf, Waldbrand und Walddynamik im Schweizer Wald. Schweiz Z Forstwes 159: 326-334.

Wohlgemuth T, Kull P, Wüthrich H (2002b) Disturbance of microsites and early tree regeneration after windthrow in Swiss mountain forests due to the winter storm Vivivan 1990. For Snow Landsc Res 77: 17-47.

Wohlgemuth T, Moser B, Brändli UB, Kull P, Schütz M (2008b) Diversity of forest plant species at the community and landscape scales in Switzerland. Plant Biosyst 142: 604-613.

Zielonka T (2006a) Quantity and decay stages of coarse woody debris in old-growth subalpine spruce forests of the western Carpathians, Poland. Can J For Res-Rev Can Rech For 36: 2614-2622.

Zielonka T (2006b) When does dead wood turn into a substrate for spruce replacement? J Veg Sci 17: 739-746.

Chapter III

Resource competition not allelopathy drives interference of bracken with beech and sycamore during germination and early growth

Submitted as:

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Abstract

After disturbances in forests, fast growing species that develop a dense ground vegetation layer can suppress tree regeneration through competition or allelopathy. One example of such a species is bracken (*Pteridium aquilinum* L.). Besides its effectiveness in competing for resources such as light, moisture and nutrients, bracken is known to release phytotoxic compounds that have been suggested to hinder the establishment of other species. Although beech (*Fagus sylvatica* L.) forests are an important plant community in Europe, beech regeneration failure in dense bracken stands after disturbances has not yet been studied for allelopathy. We exposed germinating seeds of beech and sycamore (*Acer pseudoplatanus* L.) to bracken leachates in a greenhouse experiment, and compared germination rate and growth performance of seedlings exposed to bracken leachates with seedlings grown in shadow or with bracken rhizomes in a common garden experiment. Germination rate of beech was reduced by about 7% in the presence of bracken leachates. Surprisingly, all other results did not show any conclusive evidence of an allelopathic influence of neither bracken leachates nor bracken rhizomes on the early growth of beech and sycamore. We conclude that light competition is one of the key reasons causing establishment failure of beech and sycamore seedlings in wind-disturbed beech forests whose ground vegetation is dominated by bracken. Yet, studies under field conditions are required to confirm our findings.

Keywords

Pteridium aquilinum L. Kuhn, *Fagus sylvatica* L., *Acer pseudoplatanus* L., beech forest, tree regeneration, Switzerland

1. Introduction

Bracken (*Pterdidium aquilinum* (L.) Kuhn) is one of the most widely distributed plant species in the world (Harper 1977), ranging from boreal forests in America to Sub-Saharan regions in Africa. Bracken dominates a variety of vegetation types from coniferous and deciduous woodlands to cool-temperate grasslands and pastures (review in Marrs and Watt 2006). The abundance of bracken is tied to the availability of light: in closed-canopy forests, bracken occurs in gaps only (Marrs and Watt 2006), but it may become a pestilent weed in disturbed forests such as in burnt or windthrow areas, or in clearcuts (Long and Fenton 1938). In such habitats, bracken often forms dense stands that can suppress tree establishment for decades (Koop and Hilgen 1987; Royo and Carson 2006). It has been suggested that the frequency of wind disturbances in Europe will increase with climatic change, and hence the extent of the damaged area (Schelhaas et al. 2003; Usbeck et al. 2010), thus possibly increasing bracken abundance at the landscape scale. To assess the consequences for forest regeneration and to develop appropriate adaptive management measures, it is important to improve our understanding on the processes underlying the interference between bracken presence and tree seedling establishment.

Due to its pestilent nature, the ecology of bracken has been studied for a long time (Jefries 1917; Ghorbani et al. 2006; Marrs and Watt 2006). The rapid accumulation of a dense and deep litter layer may act as a mechanical barrier for seeds to reach the forest soil (Ghorbani et al. 2006), and the smothering effect of dead fronds can cause increased mortality of tree seedlings (Dolling 1996). Bracken is also known to be an efficient competitor for resources, especially for light (Tolhurst and Turvey 1992; Gaudio et al. 2011). In addition, its extensive rhizome system is effective in capturing water and nutrients (Evans et al. 1990;

Smith and Lockwood 1990), and is able to store large amounts of resources that are protected from frost or fire (Marrs and Watt 2006; Royo and Carson 2006). Moreover, bracken is almost completely avoided by large herbivores (Marrs and Watt 2006). Since bracken produces a variety of secondary plant compounds that are toxic and act as defenses against pathogens and predators (Cooper-Driver 1990; Storey 1991), several authors have suggested that bracken also has an allelopathic potential (e.g. Cooper-Driver 1976; Dolling et al. 1994; Table 1).

Although unambiguous proof of allelopathic compounds is still lacking, leachates from dead bracken fronds have been found to reduce the germination rate (Gliessman and Muller 1978) as well as the root growth of several herb and grass species (Gliessman and Muller 1972). Similar bioassays, however, showed no inhibitory effect of bracken extracts in Scots pine (*Pinus sylvestris* L.; Den Ouden 1995). By contrast, Dolling (1996) found lower numbers of germinated Scots pine on bracken litter than on mineral soil, and Ferguson and Boyd (1988) found high mortality rates of germinated Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and grand fir (*Abies grandis* (Douglas ex D.Don) Lindl.) in soils where bracken had been removed before the experiment. Interference of bracken rhizomes alone with tree seedlings and understory vegetation is less investigated. Gliessman and Muller (1978) suggested that the influence of the rhizomes is negligible for several herb species due to different rhizome/rooting depths. Wang et al. (2011) found, however, an inhibitory effect of rhizome extracts on seed germination and radical elongation in many vegetables, albeit the negative effect of frond leachates was much stronger. Thus, evidence from investigations of the allelopathic effects of bracken on other plant species are contradicting (Table 1). This may partly be attributable to the fact that species differ in their susceptibility to the chemicals released by bracken. Most evidence of allelopathic interference by bracken was found in bioassays, but these do not reflect natural concentrations of potentially toxic compounds and neglect the abiotic (physical and chemical) and biotic (microbial) factors mitigating allelochemical activity in the soil (Inderjit 2001). By contrast, field experiments have not been able to discriminate between allelopathy and other interferences such as competition yet (Weidenhamer 1994).

The aim of the present study was to disentangle potential phytotoxic effects of bracken's secondary plant compounds from the effects of light competition during germination and early establishment of beech (*Fagus sylvatica* L.) and sycamore (*Acer pseudoplatanus* L.) seedlings. Beech forests are widespread in Central Europe (Packham et al. 2012) and are also affected by the increased wind disturbance frequency in Europe in the last years (Schelhaas et al. 2003; Usbeck et al. 2010), but so far, interference between bracken and seedling establishment has not been studied in these forests. In an experiment in a greenhouse, we tested if seeds stratified with bracken and subsequently watered with bracken leachates show reduced germination rates, and compared the abiotic effects of a bracken litter layer (reduced light availability) with those of bracken litter leachates on the early growth of beech and sycamore (2 and 6 months after sowing). Another experiment in a common garden aimed at unraveling the effects of bracken rhizomes vs. light competition by bracken fronds on seedling growth. We examined if light competition is more important than allelopathic effects of the bracken rhizomes for the growth of 5 months-old seedlings.

In contrast to previous studies, we investigated not only the allelopathic potential of bracken litter leachates and rhizomes, but also took into account competition between bracken and tree seedlings for light. The result of this study will help to better understand at what stage and by which mechanisms bracken interferes with tree recruitment. This is important to develop management options to counter bracken-mediated failure of tree regeneration after forest disturbance.

Table 1 Overview of results obtained from studies in temperate climates investigating the phytotoxic effects of bracken on other plant species. Results are divided according to the test media in which the seeds or seedlings were exposed to bracken material, the components of the bracken that were used to test for allelopathy, and the life stages of the target plant (GR = Germination rate, RG = Radicle growth, SG = Seedling growth). Negative effects are indicated by * ($p < 0.05$), ** ($p < 0.01$), - (significance unknown), -- (significance unknown, reduction ≥ 20%). 'n.s.' indicates no difference between bracken treatment and control.

	Seeds in petri dishes						Seeds in soil substrate				Seeds in forest soil/soil substrate with bracken			Ref.
	Green frond leachates			Dead frond/litter leachates			Green frond leachates		Dead frond/ litter leachates		Dead fronds/litter			
	GR	RG	SG	GR	RG	SG	GR	RG	GR	RG	GR	RG	SG	
Conifers														
Picea abies (L.) Karst													n.s.	4
Pinus banksiana Lamb.	n.s.													8
Pinus sylvestris L.											-			3
P. sylvestris	n.s.	n.s.		n.s.	n.s.								n.s.	4
P. sylvestris	**										**			5
Pseudotsuga menziesii (Mirb.) Franco				n.s.							-		n.s.	6
P. menziesii			n.s.			--								7
Broadleaved trees														
Betula pendula Roth				n.s.	n.s.									4
Populus tremula L.	**	**		n.s.										5
Others														
Ceratocapnos claviculata (L.) Lidén				*	n.s.									4
Rubus parviflorus Nutt.				-							-		-	6
Rubus spectabilis Pursh.				-							-		n.s.	6
Avena fatua L.				**	**				-	-		*	-	1/2
Bromus mollis L.				n.s.	n.s.							**		2
Bromus rigidus Roth		n.s.			**				n.s.	-				1
B. rigidus		n.s.		n.s.	*							n.s.		2
Bromus tectorum L.			--			--								7
Clarkia purpurea (Curtis) A. Nelson & J.F. Macbr.				**	n.s.									2
Festuca megalura Nutt.				**	**									2
Festuca rubra L. agg.							n.s.	n.s.	n.s.	n.s.	n.s.	n.s.		9
Hordeum vulgare L.			--			--						n.s.		7
Hypochoeris glabra L.				**	**							**		2
Lolium festuca L.							n.s.	n.s.	n.s.	n.s.	n.s.	n.s.		9
Trifolium repens L.							n.s.	n.s.	n.s.	n.s.	n.s.	n.s.		9

Ref: 1 = Gliessman & Muller (1972), 2 = Gliessman & Muller (1978), 3 = Dolling (1996), 4 = Den Ouden (2000), 5 = Dolling et al. (1994), 6 = (Stewart 1975), 7 = (Del Moral and Cates 1971), 8 = (Brown 1967), 9 = (Martin and Sparke 1982)

2. Material and Methods

Beech forest is the predominant forest type between 350 and 1200 m a.s.l. in Switzerland (Wohlgemuth et al. 2008) and throughout large parts of Central Europe (Huntley et al. 1989). Sycamore is a frequent species in beech forests (Keller et al. 1998), but is less shade tolerant than beech (Petritan et al. 2007). Experiments were conducted in the Central Plateau of Switzerland (Birmensdorf, 47°22'N 8°27'E, located at 520 m a.s.l.).

2.1 Greenhouse experiment

The greenhouse experiment was designed to test effects of bracken leachates on seed germination rate and subsequent growth of beech and sycamore seedlings two and six months after sowing. To initiate the germination process, seeds were first stratified for 70 days in a wet mixture of 50% turf and 50% sand (4 liter each). The germination rate of beech and sycamore seeds in bracken litter was examined by adding dried bracken litter (243 g) to half of the sand/turf mixture. This corresponded to the amount of bracken found on 0.25 m^2 in a windthrow area near Habsburg (Switzerland), which was locally dominated to nearly 100% by bracken. In February 2010, the stratified seeds were sown into containers (20 x 15 x 5 cm^3) filled with a mixed substrate (42% bark humus, 42% turf, 12% wood fiber and 4% clay; soil pH 5.5 – 6.2) and supplemented with a fertilizer (0.625 g N, 0.625g P, and 1.25 g 'FLORANID permanent' per liter substrate). Each container was split into two halves, one containing 50 beech seeds, the other 50 sycamore seeds, both from the same stratification treatment.

The experiment included two stages. During the germination stage, the seeds stratified with bracken were watered twice a week with bracken leachates (2 dl per container; see below), while the seeds stratified without bracken were watered with the same amount of tap water. Seeds were not covered with soil, so that germination of individual seeds could be recorded daily. As soon as the radical was visible, germination was declared successful. After 3 weeks, the germination stage was considered to be terminated, and factorial combinations of the factors bracken leachate (watering with tap water vs. bracken leachates), and litter layer (straw layer vs. bracken layer) were applied to individual containers in addition to the stratification treatment (Table 2). Each factor combination (stratification x bracken leachates x litter layer) was replicated 8 times (control 6 times), which resulted in 60 containers containing a total of 3000 beech and 3000 sycamore seeds. The containers were arranged in a fully randomized design and rotated regularly to minimize influences of the variability within the greenhouse environment, such as different times of exposure to sunlight.

Table 2 Levels of the factors *litter layer* and *bracken leachate*s and their implementation in the greenhouse experiment. Bracken cover corresponded to an equivalent of 970 g dead bracken litter per m^2 as measured in a windthrow area near Habsburg, Switzerland. The same amount of straw was used for the layer treatment without bracken. Bracken leachates were obtained by drizzling water through a layer of dried bracken litter of the same density.

	Bracken leachates	
Litter layer	No	Yes
No	No cover Watered with tap water (Control)	No cover Watered with bracken leachates
Yes	Straw cover Layer 7–8 cm thick Watered with tap water	Bracken cover Layer 7–8 cm thick Watered with bracken leachates

Containers were watered continuously with a sprinkler system to prevent desiccation. The system was manually adjusted so that the soil substrate was moist but never water saturated. The bracken leachate treatment included watering with tap water or with bracken leachates, respectively. At the beginning, 3 dl of liquid were added twice a week to each container in addition to the automatic watering. After one and a half months the sprinkler system was turned off and the seedlings were watered twice a week (three times during periods with temperatures > 25°C) with 6 dl of tap water or bracken leachates. Bracken leachates were produced by sprinkling water over nets filled with dried bracken equivalent to the density of bracken litter found in the field. The water containing the water-soluble compounds of bracken (bracken leachates) was collected underneath the nets. The factor litter layer was designed to simulate abiotic effects of bracken (reduced light availability) and was implemented by covering the seeds with a layer of either dried bracken or straw. The amount of straw/bracken was equivalent to the dry weight of bracken litter found on an area of 20 cm x 15 cm (container size; 970 g bracken m^{-2}) in the field, and was between 7 and 8 cm thick in the treatment.

Due to the large number of germinated sycamores, these seedlings were thinned at the beginning of March 2010. We randomly chose 20 sycamore seedlings per container and removed the remaining seedlings. Two months after sowing, we randomly harvested 5 beech and 5 sycamore seedlings per container. Shoot and root biomass of each seedling was measured after drying in an oven for 48 hours at 60 °C. Subsequently, we randomly chose 5 containers per treatment and transplanted 5 random seedlings per species and container in larger containers (27 x 35 x 23 cm^3). The treatments per container remained the same. A fungicide (Thiran, Leu & Gygax AG) and an insecticide (Pirimor, Syngenta Agro. AG) were applied once to protect seedlings from mildew and pests. All seedlings were harvested six months after sowing. The plant material was dried, and root and shoot biomass of each seedling was measured.

2.2 Common garden experiment

The common garden experiment was designed to investigate the influence of bracken rhizomes and light competition on the early growth of beech and sycamore during one vegetation period. The experiment included factorial combinations of the factors bracken rhizomes and shading (Fig. 1), which were applied to individual seedbeds (110 x 145 x 60 cm^3). The growth of seedlings in the presence of bracken rhizomes was tested by adding an equivalent of the amount of bracken rhizomes that was found on a windthrow area (cf. greenhouse experiment) on 110 cm x 145 cm to half of the seedbeds. The influence of light was tested by removing the bracken fronds that developed from these rhizomes (i.e., to remove light competition) or by artificial shading of the seedbeds without bracken rhizomes. Each factorial combination was replicated 5 times, thus resulting in 20 seedbeds. The seedbeds were arranged randomly in the common garden of the WSL research institute at Birmensdorf, Switzerland.

Seeds were sown on 29th March 2011 into the same substrate as in the greenhouse experiment. Each seedbed was split into two halves, one containing 100 beech seeds, the other 100 sycamore seeds. Seeds were sown in pairs on a grid of 7 x 10 cm. If both seeds of the pair germinated, we randomly cut one of them after the cotyledons had emerged.

The shading in the treatment ‘no rhizomes with artificial shading’ (Fig. 1b) was changed from a light shading (50% sunlight) at the beginning to a denser shading

(25% sunlight) as the vegetation period progressed. The level of shading was chosen on the basis of light measurements in the bracken treatment (Fig. 1d). The seedbeds were watered regularly according to weather conditions so that the top ten centimeters of the soil substrate never dried out. As in the greenhouse experiment, we sprayed once against pest animals.

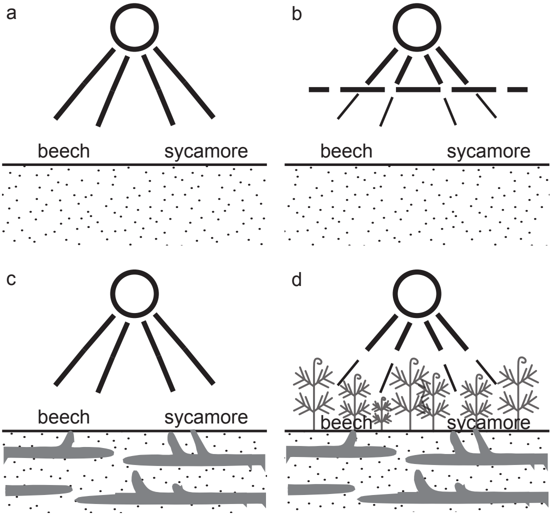

Fig. 1 Factorial combinations of the factors *bracken rhizomes* and *shading* and their implementation in the common garden experiment: a) No bracken rhizomes, full sunlight; b) no bracken rhizomes, artificial shading; c) bracken rhizomes in the substrate, full sunlight (bracken shoots were regularly cut at the soil surface); d) bracken rhizomes in the substrate, shading by bracken fronds that developed from the rhizomes.

Five months after sowing, 10 sycamore seedlings per seedbed were randomly selected and harvested. In six seedbeds, only a few beech seedlings had established, thus we randomly selected 15 seedlings per seedbed where possible. Thus, a total of 200 sycamore and 220 beech seedlings were harvested. After drying in an oven for 48 hours at 60 °C, shoot and root biomass of each seedling was measured.

2.3 Data analysis

The layout of both experiments was a block design with three factors in the greenhouse experiment (stratification, bracken leachate and litter layer) and two factors in the common garden experiment (bracken rhizomes and light competition). Effects of these factors on seedling biomass were analyzed using a three-way ANOVA with the containers as blocks in the greenhouse experiment, and a two-way ANOVA with the seedbeds as blocks in the common garden experiment. A one-way ANOVA was used to analyze the effect of the factor stratification on germination rate. Post-hoc pairwise Tukey HSD tests were used to calculate statistical differences between treatments using univariate GLM procedure of spss Statistics (Release 17.0.0, SPSS Inc., 2008, Chicago, IL, USA). To meet the assumptions of normality and homogeneity of variance, data were square-root transformed prior to all analyses. In the common garden experiment, six of the 20 seedbeds contained very low numbers of beech seedlings at the time of harvest, so that the sample size per block was not balanced. Excluding these seedbeds from the analyses did not affect ANOVA results, thus we show the results including all seedbeds. Since the three-way interaction was not significant for any analysis, we performed the analyses without including this interaction.

3. Results

3.1 Germination

Germination of seeds stratified with bracken and subsequently watered with bracken leachates was reduced in beech (ANOVA of 60 containers: $F_{1,58} = 8.03$, $P = 0.006$) but not in sycamore ($F_{1,58} = 2.05$, $P = 0.16$). On average 54.8% (27.4 ± 0.9 out of 50; mean ± SE) beech seeds germinated under control conditions compared to 48.0% (24.0 ± 0.8) that were treated with bracken leachates. In sycamore, similar numbers of seeds germinated in both treatments: 78.6% (39.3 ± 0.6) in the control, and 76.2% (38.1 ± 0.6) in the bracken treatment.

3.2 Bracken litter leachates vs. litter layer

Two months after sowing, root biomass of sycamore seedlings was reduced by 41.1% in the presence of a layer. Root biomass was smaller irrespective of whether the layer consisted of bracken or straw (Table 3 and Fig. 2). Consequently, root to total biomass ratios were on average 36.9% larger in the treatments without a layer. Six months after sowing, the effect of the litter layer on shoot and root biomass reverted, and they became smaller in treatments without a layer (reduction of 42.3% and 54.1%, respectively). Root to total biomass ratio remained lower (21.3%) in the layer treatments. Bracken leachates had a positive effect on sycamore biomass in the presence of a litter layer after 2 months of seedling growth, but this effect was no longer visible after 6 months. Similar to sycamore, 2 months after sowing root to total biomass ratios of beech seedlings were on average reduced by 15.1% in treatments with a layer. Six months after sowing, the layer effect disappeared. However, beech biomass allocation showed no clear pattern, neither for the treatments with a layer nor for the presence of bracken leachates (Table 3 and Fig. 3). In both species, early growth was unaffected by the stratification treatment.

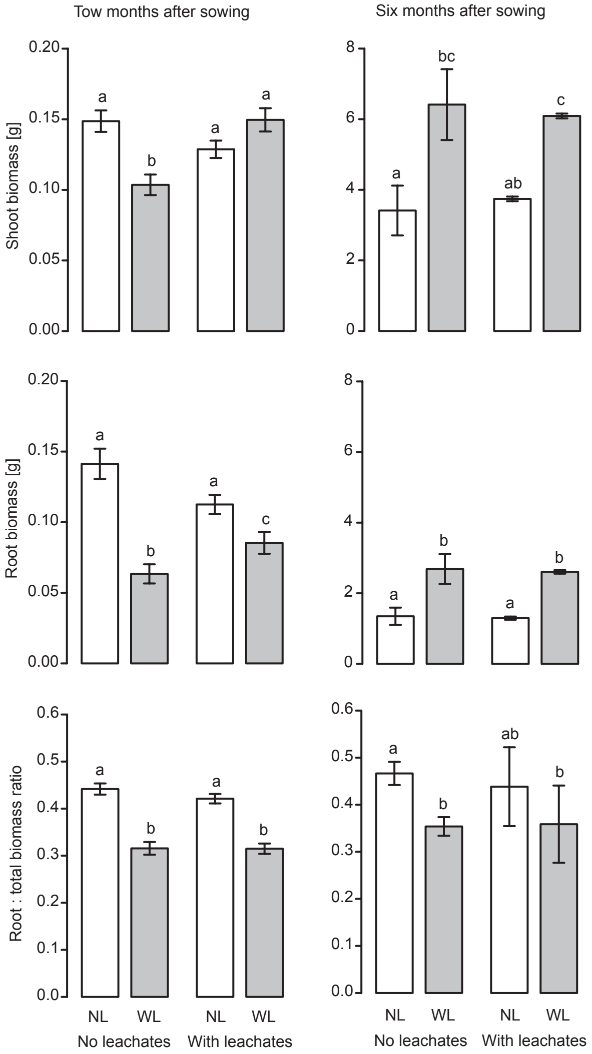

Fig. 2 Shoot and root biomass, and root to total biomass ratio (mean ± SE) of sycamore seedlings 2 and 6 months after sowing. Seedlings were grown under factorial combinations of the factors *bracken leachates* and *litter layer* (NL: no layer, white bars; WL: with layer, grey bars). Identical letters above two bars indicate no statistical difference (ANOVA followed by Tukey's HSD tests). Note that scales differ between graphs.

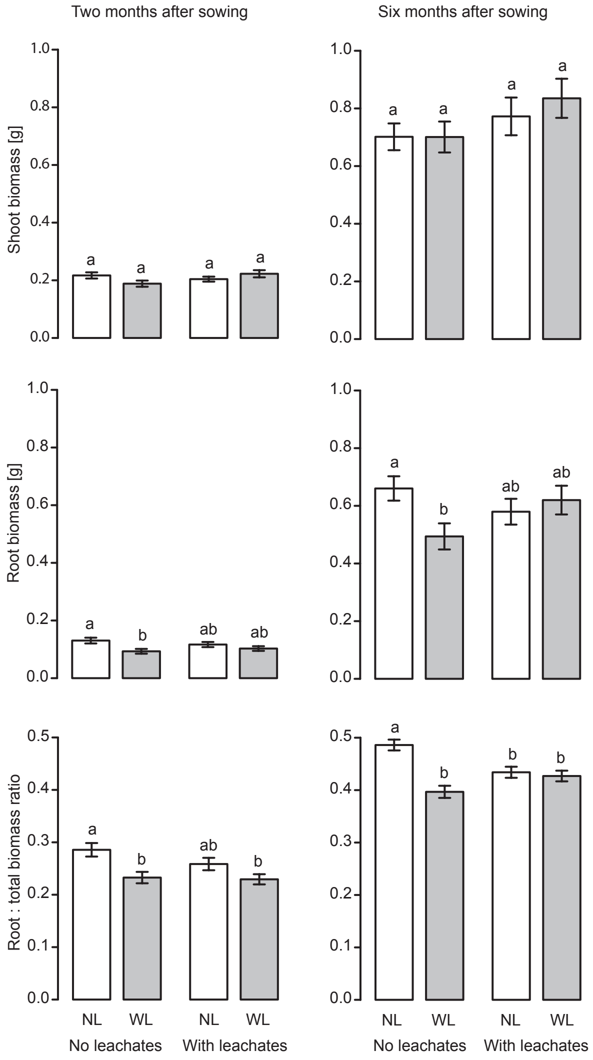

Fig. 3 Shoot and root biomass, and root to total biomass ratio (mean ± SE) of beech seedlings 2 and 6 months after sowing. Seedlings were grown under factorial combinations of the factors *bracken leachates* and *litter layer* (NL: no layer, white bars; WL: with layer, grey bars). Identical letters above two bars indicate no statistical difference (ANOVA followed by Tukey's HSD tests).

Table 3 ANOVA results for the effects of *stratification* (no bracken vs. with bracken), *litter layer* (straw vs. bracken) and *bracken leachates* (tap water vs. bracken leachates) on seedling biomass and root to total biomass ratio of beech and sycamore seedlings 2 and 6 months after sowing in the greenhouse experiment. Significant values are displayed in bold font.

		Shoot biomass		Root biomass		Root to total biomass ratio	
	df	F	P	F	P	F	P
2 months							
Beech							
Stratification	1	0.25	0.618	1.34	0.253	2.08	0.155
Layer	1	1.21	0.276	7.83	**0.007**	7.50	**0.008**
Leachates	1	1.03	0.315	0.04	0.840	1.11	0.297
Stratification x layer	1	2.21	0.143	0.76	0.388	0.05	0.823
Stratification x leachates	1	0.17	0.686	0.05	0.824	0.03	0.875
Layer x leachates	1	5.44	**0.024**	1.80	0.186	0.82	0.369
Residuals	292						
Sycamore							
Stratification	1	0.00	0.960	0.15	0.698	0.27	0.603
Layer	1	6.95	**0.011**	47.68	**<0.001**	72.67	**<0.001**
Leachates	1	5.16	**0.027**	0.09	0.769	0.30	0.587
Stratification x layer	1	0.46	0.500	0.08	0.773	0.03	0.870
Stratification x leachates	1	0.06	0.810	0.61	0.437	0.65	0.423
Layer x leachates	1	26.41	**<0.001**	9.95	**0.003**	0.64	0.426
Residuals	292						
6 months							
Beech							
Stratification	1	4.60	**0.040**	1.37	0.251	1.90	0.178
Layer	1	0.12	0.735	3.79	0.060	12.67	**0.001**
Leachates	1	2.51	0.123	0.50	0.485	0.47	0.497
Stratification x layer	1	0.24	0.629	0.02	0.888	0.80	0.379
Stratification x leachates	1	0.90	0.350	5.12	**0.031**	4.16	0.050
Layer x leachates	1	0.43	0.515	7.42	**0.010**	9.26	**0.005**
Residuals	191						
Sycamore							
Stratification	1	2.74	0.108	2.32	0.138	2.63	0.115
Layer	1	32.22	**<0.001**	48.20	**<0.001**	20.25	**<0.001**
Leachates	1	0.25	0.622	0.14	0.713	0.29	0.594
Stratification x layer	1	0.00	0.959	0.04	0.837	0.04	0.853
Stratification x leachates	1	1.08	0.307	0.87	0.359	0.00	0.974
Layer x leachates	1	0.03	0.871	0.74	0.396	0.78	0.385
Residuals	190						

3.3 Bracken rhizomes vs. light competition

Beech and sycamore seedlings produced more biomass in full light than under shade (Table 4 and Fig. 4); in the absence of bracken rhizomes, shoot and root biomass in beech seedlings was increased by 54.1% and 49.0%, respectively. In sycamore seedlings, only shoot biomass was larger (increase by 176.9%). In the treatments with bracken rhizomes, shoot and root biomass in beech and sycamore seedlings was consistently larger in full light. For beech, shoot biomass increased by 152.5% and root biomass by 132.2%; for sycamore the increase was much larger with 763.3% and 517.2%, respectively. The presence of bracken rhizomes reduced the root to total biomass ratio of both beech and sycamore seedlings. In sycamore, however, the proportion of root biomass depended primarily on light conditions: seedlings produced up to 30% more root biomass under shade than in full light, independent of the presence of bracken rhizomes.

Table 4 ANOVA results for the effects of *bracken rhizomes* (no rhizomes vs. rhizomes) and *light competitio*n (no shading vs. shading) on seedling biomass and root to total biomass ratio of beech and sycamore seedlings 5 months after sowing in the garden experiment. Significant values are displayed in bold font.

		Shoot biomass		Root biomass		Root to total biomass ratio	
	df	F	P	F	P	F	P
Beech							
Rhizome	1	0.91	0.346	0.68	0.416	9.60	**0.004**
Light	1	7.67	**0.009**	9.13	**0.005**	2.09	0.158
Rhizome x light	1	0.25	0.621	0.44	0.513	1.99	0.168
Residuals	215						
Sycamore							
Rhizome	1	24.38	**<0.001**	28.17	**<0.001**	5.05	**0.039**
Light	1	52.21	**<0.001**	86.26	**<0.001**	9.86	**0.006**
Rhizome x light	1	16.20	**0.001**	36.95	**<0.001**	0.26	0.615
Residuals	195						

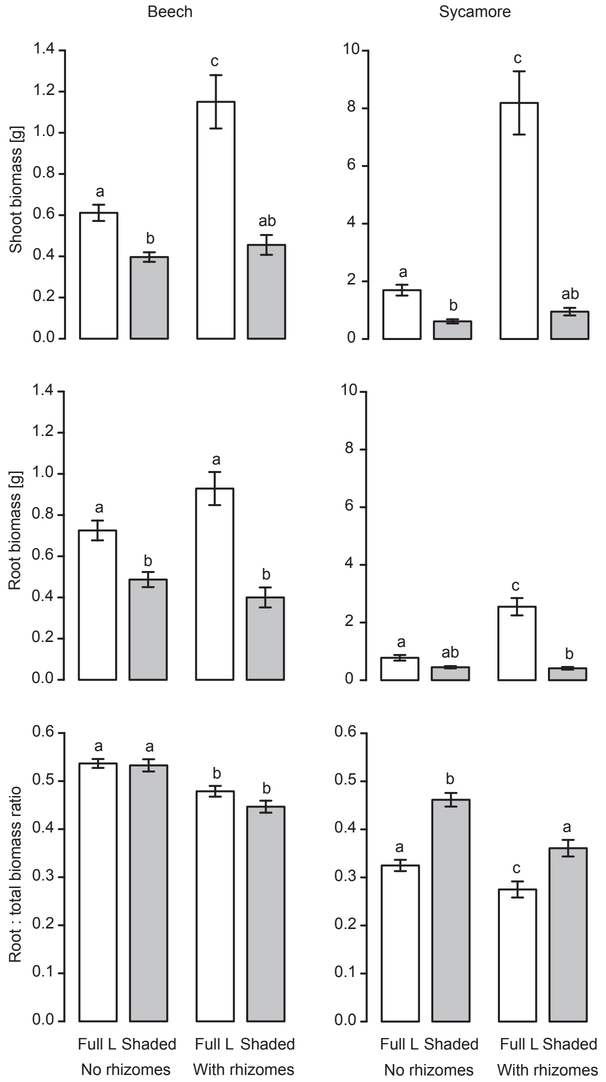

Fig. 4 Shoot and root biomass, and root to total biomass ratio (mean ± SE) of beech and sycamore seedlings 5 months after sowing. Seedlings were grown under factorial combinations of the factors *bracken rhizomes* and *shading* (Full L: full light, white bars; shading: grey bars). Identical letters above two bars indicate no statistical difference (ANOVA followed by Tukey's HSD tests). Note that scales differ between graphs.

4. Discussion

Dense ground vegetation layers, often resulting from the spread of fast growing species after disturbances, mainly interfere with tree regeneration by aboveground competition especially for light (review by Royo and Carson 2006). Many species such as bramble (*Rubus fruticosus* agg.; Schreiner 2000), grasses (Kupferschmid and Bugmann 2005) or ferns (Hill and Silander 2001; Gaudio et al. 2011) are known to form dense mats and consequently reduce light availability for emerging trees. For dense bracken stands, it has been suggested that allelopathy also plays a major role for the failure of tree regeneration (e.g. Gliessman and Muller 1978; Dolling et al. 1994). Our results, however, show only an inferior effect of allelopathy on the germination and early growth in beech and sycamore.

Germination ability

Effects of bracken on seed germination varies between species and plant parts involved in the experiments (Table 1), indicating both differences in the susceptibility of species to the phytotoxic compounds released by bracken as well as differences with respect to experimental methods. Our results confirm the heterogeneity of the results in that beech and sycamore seem not to be equally susceptible to bracken during germination. Although statistically significant, the reduction in germination rate of beech seeds in the presence of bracken leachates is smaller than the year-to-year variability in the germination rate of beech seeds collected in the same region (5-year average 39.4 ± 7.6%; mean ± SE; A. Burkart, unpubl. data). Consequently, the measured negative effect of bracken on beech germination may be ecologically negligible. We suggest that other factors such as seed quality or environmental conditions (e.g. moisture) are likely to be more important for beech germination success.

It is not surprising that we found only minor effects of bracken on seed germination ability since it has never been shown explicitly that allelopathy affects the germination process of a species (Fenner and Thompson 2005). Both beech and sycamore seeds undergo a period of dormancy before germination, during which the seeds are protected by the seat coat and are not susceptible to chemical compounds (Webb and Wareing 1972; Thomas et al. 1973). Similar results have been found in *Pinaceae*, where allelopathic extracts of lichen and raspberry did not affect germination but inhibited initial root growth of black spruce (*Picea mariana* (Mill.) Britt.; Arsenault 1978) and red pine (*Pinus resinosa* Ait.; Norby and Kozlowski 1980), respectively.

Influence of litter layer and bracken leachates on seedling growth

Bracken leachates showed no negative effect on either beech or sycamore seedling growth, but sycamore seedlings were affected by the layer treatment (Table 3). Two months after sowing, sycamore seedlings were smaller in the treatments with a layer. After six months, the effect of the litter layer reverted and seedlings had accumulated more biomass in the layer treatments. Beech seedlings did not show such a shift. Since sycamore is less shade-tolerant than beech (Petritan et al. 2007) the lower light availability in the litter layer treatment very likely limited its growth during the first two months, when seedlings were still shorter than the layer. We suggest that once the seedlings had penetrated the layer they benefit from a moister microclimate as a result of reduced evaporation in the presence of a bracken/straw layer. This is corroborated by the proportionally higher root growth in the non-layer treatments, which indicates a resource limitation in that treatment (van Hees 1997). This pattern was apparent already two months after sowing, and was also found in beech seedlings (Fig. 3). In both species, the presence of bracken during stratification had no effect on seedling growth neither two nor six months after sowing.

Experimental simulation of allelopathy is challenging because it is difficult to mimic the concentration of phytotoxic compounds effectively encountered by a species. Since we neglected the long-term accumulation of allelochemicals by using a soil substrate that had not previously been vegetated by bracken, the amount of allelochemicals in forest soils might exceed the levels in our experiment. As shown by Ferguson and Boyd (1988), soil earlier dominated by bracken reduced germination rate in alder (*Alnus sinuate* (Regel.) Rydb.) and huckleberry (*Vaccinium globulare* Rydb.) but not in four conifer species (*Abies lasiocarpa* (Hooker) Nuttall, *A. grandis*, *Picea engelmannii* Parry ex Engelm., and *Pseudotsuga menziesii*). On the other hand, Inderjit (2001) suggested that the soil may weaken the phytotoxic effect of the chemicals to the target plant due to diluting effects. Nevertheless, our results are similar to those of many other studies, which did also not find allelopathic effects of bracken leachates on other plant species (Table 1); even bioassays that probably feature much higher concentrations compared to natural conditions did not consistently yield allelopathic effects.

Similar to germination, differences in the susceptibility to allelopathy have been reported frequently between species or functional groups such as grasses (Gliessman and Muller 1972), conifers (Dolling et al. 1994; Den Ouden 1995) and broadleaved trees (Dolling et al. 1994). Scots pine seedlings grown in a bracken stand, for example, showed high mortality, suggesting high phytotoxicity, whereas Norway spruce (*Picea abies*) seedlings remained unaffected (Dolling 1996). It is hard to disentangle to what degree these differences are due to true differences between species vs. different methods used in testing for allelopathy. Based on our data, we propose that beech and sycamore are not susceptible to phytotoxic compounds released from dead bracken fronds, at least not during the first vegetation period.

Influence of bracken rhizomes vs. light competition on seedling growth

The allelopathic influence of bracken rhizomes has hardly been studied and there are, to our knowledge, no investigations testing the influence of the bracken rhizomes on beech and sycamore. Contrary to our expectations, light was the main factor influencing biomass allocation in both beech and sycamore (Fig. 4). In the absence of shading, shoot biomass was even higher in the bracken rhizome treatment (definition see Fig. 1) than in the control. We surmise that the large biomass production of both species in the bracken rhizome treatment without shading was caused by a fertilization effect due to inoculation: when we collected the bracken rhizomes, a small amount of forest soil was transferred to our seedbeds. Probably, we also brought in some favorable microorganisms and mycorrhizal fungi. With higher light availability, tree species generally grow better (van Hees 1997; Petritan et al. 2007) and consequently require more nutrients, which were likely made available by the microorganisms that we inoculated inadvertently.

In short, bracken rhizomes did not negatively affect growth of either beech or sycamore seedlings. The main factor driving early growth of these species was light availability. This is in line with Gaudio et al. (2011) who found lower biomass in Scots pine seedlings due to competition for light beneath bracken.

Generally, we cannot confirm a potential allelopathic effect of dead bracken frond leachates on beech and sycamore. We only found weak evidence for the existence of phytotoxic compounds, i.e. a slightly but ecologically negligible reduction in the germination rate of beech. By contrast, we provide strong evidence for light competition as the primary factor causing regeneration failure of beech and sycamore in wind disturbed forest areas with dense bracken cover. Additional factors hindering tree seedling establishment in bracken stands have been reported by several authors. Thick layers of accumulated bracken litter can act as a mechanical barrier, making it impossible for seedling roots to reach the mineral soil after germination (Ghorbani et al. 2006). Furthermore, bracken is very efficient in capturing nutrients and water (Evans et al. 1990; Smith and Lockwood 1990), and may thus outcompete tree seedlings at a very early stage. High mortality rates of tree seedlings through the smothering effect of dying bracken fronds may also be important (Dolling 1996; Humphrey and Swaine 1997). Lastly, in contrast to trees and shrubs, bracken is hardly affected by herbivory (Marrs and Watt 2006). Together, these factors are much more likely to explain tree regeneration failure under bracken cover than allelopathic effects.

References

Arsenault P (1978) Effets allélopathiques causés par les lichens fucticuleux terricoles sur *Picea mariana*. MS, thesis, Université Laval, Québec (Canada).

Brown RT (1967) Influence of naturally occurring compounds on germination and growth of jack pine. Ecology 48: 542-&.

Cooper-Driver GA (1976) Chemotaxonomy and phytochemical ecology of bracken. Bot J Linn Soc 73: 35-46.

Cooper-Driver GA (1990) Defense strategies in bracken, *Pteridium aquilinum* (L.) Kuhn. Ann Mo Bot Gard 77: 281-286.

Del Moral R, Cates RG (1971) Allelopathic potential of dominant vegetation of Western Washington. Ecology 52: 1030-&.

Den Ouden J (1995) Allelopathy in bracken in the Netherlands. In: Smith RT, Taylor JA (eds) Bracken: An Environmental Issue Contributions to an international conference, July 1994, University of Wales, Aberystwyth, pp. 43-46.

Den Ouden J (2000) The role of bracken (*Pteridium aquilinum*) in forest dynamics. Ph.D. thesis, Department of Environmental Science, Wageningen.

Dolling AHU (1996) Interference of bracken (*Pteridium aquilinum* L Kuhn) with Scots pine (*Pinus sylvestris* L) and Norway spruce (*Picea abies* L Karst) seedling establishment. Forest Ecol Manag 88: 227-235.

Dolling AHU, Zackrisson O, Nilsson MC (1994) Seasonal variation in phytotoxicity of bracken (*Pteridium aquilinum* L. Kuhn). J Chem Ecol 20: 3163-3172.

Evans GR, Nordmeyer AH, Kelland CM (1990) Biomass and nutrient pools of bracken growing under radiata pine, Nelson, New Zealand. In: Thomson JA, Smith RT (eds) Bracken Biology and Management. Australian Institute of Agricultural Science, Sydney.

Fenner M, Thompson K (2005) The ecology of seeds. Cambridge University Press, Cambridge.

Ferguson DE, Boyd R, J. (1988) Bracken fern inhibition of conifer regeneration in northern Idaho. Res Pap INT-388 Ogden, UT: US Department of Agriculture, Forest Service, Intermountain Research Station: 11.

Gaudio N, Balandier P, Philippe G, Dumas Y, Jean F, Ginisty C (2011) Light-mediated influence of three understorey species (*Calluna vulgaris*, *Pteridium aquilinum*, *Molinia caerulea*) on the growth of *Pinus sylvestris* seedlings. Eur J For Res 130: 77-89.

Ghorbani J, Le Duc MG, McAllister HA, Pakeman RJ, Marrs RH (2006) Effects of the litter layer of *Pteridium aquilinum* on seed banks under experimental restoration. Appl Veg Sci 9: 127-136.

Gliessman SR, Muller CH (1972) The phytotoxic potential of bracken, *Pteridium aquilinum*. Madrono 21: 299-304.

Gliessman SR, Muller CH (1978) The allelopathic mechanisms of dominance in bracken (*Pteridium aquilinum*) in southern California. J Chem Ecol 4: 337-362.

Harper JL (1977) Population Biology of Plants. Academic Press, London.

Hill JD, Silander JA (2001) Distribution and dynamics of two ferns: *Dennstaedtia punctilobula* (Dennstaedtiaceae) and *Thelypteris noveboracensis* (Thelypteridaceae) in a Northeast mixed hardwoods-hemlock forest. Am J Bot 88: 894-902.

Humphrey JW, Swaine MD (1997) Factors affecting the natural regeneration of *Quercus* in Scottish oakwoods .1. Competition from *Pteridium aquilinum*. J Appl Ecol 34: 577-584.

Huntley B, Bartlein PJ, Prentice IC (1989) Climatic control of the distribution and abundance of beech (*Fagus* L.) in Europe and North America. J Biogeogr 16: 551-560.

Inderjit (2001) Soil: Environmental effects on allelochemical activity. Agron J 93: 79-84.

Jefries H (1917) On the vegetation of four Durham coal-measure fells. III. On water-supply as an ecological factor. J Ecol 5: 129-154.

Keller W, Wohlgemuth T, Kuhn N, Schütz M, Wildi O (1998) Waldgesellschaften der Schweiz auf floristischer Grundlage. Mitt. Eidgenöss. Forsch.anst. WSL.

Koop H, Hilgen P (1987) Forest dynamics and regeneration mosaic shifts in unexploited beech (*Fagus sylvatica*) stands at Fontainebleau (France). Forest Ecol Manag 20: 135-150.

Kupferschmid AD, Bugmann H (2005) Predicting decay and ground vegetation development in *Picea abies* snag stands. Plant Ecol 179: 247-268.

Long HC, Fenton EW (1938) The story of the bracken fern. Journal of the RASE 99: 15-36.

Marrs RH, Watt AS (2006) Biological flora of the British isles: *Pteridium aquilinum* (L.) Kuhn. J Ecol 94: 1272-1321.

Martin DJ, Sparke CJ (1982) Field trials in south-west Scotland. Proceedings of the Royal Society of Edinburgh Section B Biological Sciences, 81: 117-123.

Norby RJ, Kozlowski TT (1980) Allelopathic potential of ground cover species on *Pinus resinosa* seedlings. Plant Soil 57: 363-374.

Packham JR, Thomas PA, Atkinson MD, Degen T (2012) Biological flora of the British Isles: *Fagus sylvatica*. J Ecol 100: 1557-1608.

Petritan AM, von Lüpke B, Petritan IC (2007) Effects of shade on growth and mortality of maple (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*) saplings. Forestry 80: 397-412.

Royo AA, Carson WP (2006) On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Can J For Res-Rev Can Rech For 36: 1345-1362.

Schelhaas MJ, Nabuurs GJ, Schuck A (2003) Natural disturbances in the European forests in the 19th and 20th centuries. Glob Change Biol 9: 1620-1633.

Schreiner M (2000) Vorkommen und Ausbreitung von Brombeeren sowie ihre Bedeutung für die Naturverjüngung von Tannen-Fichten-Wäldern - dargestellt am Beispiel der Region „Oberer Neckar“. Ph.D. thesis, University of Freiburg im Breisgau, Germany.

Smith RT, Lockwood JG (1990) Bracken invasion and bracken replacement: guidelines for the prediction of hydrological changes. In: Thomson JA, Smith RT (eds) Bracken Biology and Management. Australian Institute of Agricultural Science, Sydney.

Stewart RE (1975) Allelopathic potential of Western bracken. J Chem Ecol 1: 161-169.

Storey INJ (1991) Allelopathy in bracken *Pteridium aquilinum* (Dennstaedtiaceae: Pteridophyta). Fern Gaz 14: 51-53.

Thomas H, Webb DP, Wareing PF (1973) Seed dormancy in Acer - Maturation in relation to dormancy in *Acer pseudoplatanus* L. J Exp Bot 24: 958-967.

Tolhurst KG, Turvey ND (1992) Effects of bracken (*Pteridium esculentum* (Forst f.) Cockayne) on eucalypt regeneration in west-central Victoria. Forest Ecol Manag 54: 45-67.

Usbeck T, Wohlgemuth T, Dobbertin M, Pfister C, Burgi A, Rebetez M (2010) Increasing storm damage to forests in Switzerland from 1858 to 2007. Agric For Meteorol 150: 47-55.

van Hees AFM (1997) Growth and morphology of pedunculate oak (*Quercus robur* L) and beech (*Fagus sylvatica* L) seedlings in relation to shading and drought. Ann Sci For 54: 9-18.

Wang HH, Chen BJ, Hsu LM, Cheng YM, Liou YJ, Wang CY (2011) Allelopathic effects of bracken fern (*Pteridium aquilinum* L. Kuhn) in Taiwan. Allelopathy J 27: 97-110.

Webb DP, Wareing PF (1972) Seed dormancy in *Acer pseudoplatanus* L. - Role of covering structures. J Exp Bot 23: 813-&.

Weidenhamer JD (1994). Distinguishing resource competition and chemical interference: Overcoming the methodological impasse. In: Symposium on Allelopathy in Cropping Systems, at the ASA-CSSA-SSSA Annual Meeting. Amer Soc Agronomy, Seattle, Wa, pp. 866-875.

Wohlgemuth T, Moser B, Brändli UB, Kull P, Schütz M (2008) Diversity of forest plant species at the community and landscape scales in Switzerland. Plant Biosyst 142: 604-613.

Synthesis

The main objective of this thesis was to quantify natural tree regeneration in large forest gaps (≥ 3 ha) originating from wind disturbance in Switzerland, and to identify factors influencing succession dynamics of trees. Of particular interest was the influence of the post-storm treatments ‘salvage-logging’ and ‘no intervention’ on tree species composition (*Chapter I*), on deadwood amount and quality (*Chapter II*), and the role of bracken (*Pteridium aquilinum* L.; Marrs and Watt 2006) as an often rapidly extending early colonizer for the regeneration success of deciduous beech (*Fagus sylvatica* L.) and sycamore (*Acer pseudoplatanus* L.; *Chapter III*).

Main findings

Tree regeneration after wind disturbance

The study presented in *Chapter I* is novel with respect to the diversity of windthrow areas that encompassed an exceptionally wide range of ecological conditions. In contrast to many previous studies on small numbers of windthrow areas, the large sample of 90 windthrow areas in my study builds a sufficient statistical basis to evaluate the importance of several predictors for post-storm tree regeneration, and it may serve as reference data for a wide range of forest stands.

Natural post-storm regeneration (stem density ha^{-1}) 20 years after Vivian (1990; 3614 ± 616 ha^{-1}; mean ± SE) and 10 years after Lothar (1999; 6941 ± 951 ha^{-1}) is mainly influenced by soil pH and ground vegetation cover, with high sapling densities on substrate with neutral to weakly alkaline soils and with a small cover of competing species. Further, higher sapling densities are found in salvage-logged than in unharvested forest gaps 10 and 20 years after a storm event. In contrast to my expectation, the influence of elevation is less pronounced, which was probably due to the disproportionately high number of soils with neutral to weakly alkaline soils at higher elevations, a fact that coincides with the predominance of limestone bedrock in the Northern Pre-Alps and the high incidence of windthrow damage in that region. However, the significantly smaller sapling density in older Vivian compared to younger Lothar gaps can statistically be explained by elevation, since gaps of the storm Vivian were, on average, 570 m higher than those of the storm Lothar. In this respect, many growth relevant factors change with elevation such as vegetation period, mean and extreme temperature or species pool.

Soil pH, vegetation cover, post-storm treatment (‘salvage logging’ or ‘no intervention’), and elevation are the four main predictors explaining the variation in sapling densities in windthrow gaps in beech (*Fagus sylvatica* L.), fir (*Abies alba* Mill.)-beech, fir-spruce (*Picea abies* (L.) H. Karst.) and spruce forests in Switzerland. Beyond the distinct patterns explaining the variability in sapling density, tree succession in individual gaps can deviate greatly from the general trends. This pattern of regeneration heterogeneity in the sample confirms recent studies of post-disturbance succession (see *Chapter I*).

The observed general trends are confirmed by other studies. For example, Gough et al. (2000) found higher plant density on higher soil pH in Alaskan arctic tundra, Schreiner (2000) observed a lower number of established fir and spruce saplings in dense *Rubus fruticosus* stands, and Peterson and Pickett (1990) and van Mantgem et al. (2006) found elevation to be negatively correlated with sapling density. Similar to Schönenberger (2002) and Ilisson et al. (2007), I also detected higher regeneration densities in salvage-logged than unharvested forest gaps, although it is known that deadwood can be decisive for tree regeneration. Especially in moist coniferous forests, e.g. in North America (McKee et al. 1982; Harmon and Franklin 1989), Switzerland (Imbeck and Ott 1987) or the Czech Republic (Svoboda et al. 2010), deadwood was found to be crucial for regeneration success. By far the majority of deadwood in my study was caused by the storms Vivian (1990) or Lothar (1999), and this is why most of the deadwood pieces were younger than 20 years. Decaying wood in 10-year-old wind-disturbed Lothar forests was not yet an appropriate seedbed, but its importance for tree regeneration increased in the older Vivian gaps (*Chapter II*). Nevertheless, I could not find a positive effect of deadwood on regeneration in the first 10 to 20 years after a disturbance, which is in line with Zielonka (2006), who showed that it takes a few decades until deadwood turns into an appropriate seedbed.

In contrast to the assumption that salvage-logged windthrow areas differ in species composition from unharvested ones for decades, in particular with more early colonizing pioneer species (Močalov and Lässig 2002; Schönenberger 2002), I found tree species composition to be similar among treatments. Pioneer species were equally frequent in both salvage-logged and unharvested forest gaps, and late-successional species like beech and Norway spruce dominated tree numbers after both storm events (except in Lothar spruce forests). Conversely, pioneer species grew faster than the late-successional species, and thus pioneer species occupy the upper story of the young forests, and late-successional species the understory. This visually confirms the classical succession theory by Clements (1936). Given that these gaps are relatively young, my data demonstrate the simultaneous establishment of early- and late-successional species. Egler (1954) hypothesized that merely different growth rates of plant species that had established simultaneously, i.e. at the very beginning of secondary succession, are responsible for the observed successional stages (‘Initial Floristic Composition’ hypothesis), which means that the developing forests in the gaps 10 or 20 years after the wind disturbance are already on their way to stands dominated by late-successional species. In a surprisingly high number of gaps (n=24) of my study, late-successional species are already equally tall or even taller than the pioneer species, which resembles the phenomenon of ‘direct re-growth’ (Romme et al. 2011). In the context of Egler’s initial floristic composition hypothesis, the phenomenon of ‘direct re-growth’ is merely a successional stage where the pre-disturbance species show the highest growth rates, and therefore dominate the upcoming vegetation. Linking the early successional stage of my study with life cycles of (forest) communities, several theories can be considered for potential pathways of vegetation succession, e.g. the monoclimax theory by Clements (1936), the polyclimax theory by Tansley (1920, 1935), the individualistic approach by Gleason (1927) or the initial floristic composition hypothesis by Egler (1954; incomplete enumeration of succession theories). Clements (1936) stated that especially regional macroclimatic conditions are crucial, leading to a linear development toward the climatic climax. In contrast Tansley (1920, 1935) declared that beside macroclimatic conditions also factors like fire, particular soil conditions, or the influence of animals are decisive and can prevent an area from reaching the climax condition. Gleason (1927), however, emphasized the importance of the individual species (but obviously can be misinterpreted; see Nicolson et al. 2002) and Egler (1954) formulated the significance of “who gets there first”. Even though all of the above mentioned theories appeal, none of the theories fully explains the tree regeneration patterns and processes found in the forest gaps. It is highly unlikely that a single theory about succession will apply equally well with respect to great variety of ecosystems (Kimmins 2004), even if we focus on forest succession only. Considering the overall heterogeneity found in the gaps after wind disturbance, I conclude that a mixture of early- and late-successional species in terms of height and numbers appears to reflect 'normality' 10 to 20 years after wind disturbance, and that this heterogeneity will very likely still be apparent in the following decades. The attempt to apply one of the classical succession theories to explain vegetation development after windthrow is not appropriate when considering a large sample of different windthrow areas in temperate forests.

Deadwood quantity and quality after wind disturbance

Only a few large-scale studies have been conducted worldwide on both deadwood quantity and quality after fire or windthrow. The study presented in *Chapter II* is, to my knowledge, the first in Central Europe to investigate the amount and quality of deadwood at a large spatial scale after windthrow.

In salvage-logged forest gaps deadwood volume was surprisingly high, with 76.4 m^3 ha^{-1} on average 20 years after Vivian and 73.8 m^3 ha^{-1} 10 years after Lothar. These values exceed the target deadwood volumes by a factor two for close-to-nature forests in the context of biodiversity conservation (Müller and Bütler 2010). The average deadwood volume in unharvested forest gaps amounted to 284.7 m^3 ha^{-1} in Vivian and 266.1 m^3 ha^{-1} in Lothar gaps. These values are rather small compared to the average growing stock in Swiss forests, which ranges from 327 m^3 ha^{-1} in the Alps to 475 m^3 ha^{-1} in the Pre-Alps (Cioldi et al. 2010). I presume that among the unharvested forest gaps, stands with a low growing stock were overrepresented because windthrown stands with a high growing stock probably had mostly been harvested. A low growing stock, indicating poor site conditions, may have been an obvious reason for leaving the thrown or broken timber in place. In both salvage-logged and unharvested forest gaps the range of deadwood diameter classes was large, as well as the variety of decay stages and the variety of deadwood types (lying and standing deadwood). This suggests considerable habitat diversity for deadwood-associated species independent of the treatment.

The remarkably large deadwood volumes left and the wide variety of deadwood stages after salvage logging demonstrate the importance of wind disturbance for biodiversity, quite independent of the post-storm treatment. I conclude that in Switzerland, the current logging practices after wind disturbance are likely to leave enough deadwood to ensure a wide diversity of deadwood-associated species.

Bracken interference with tree seedlings

Bracken is known to suppress plant growth by the release of phytotoxic compounds (e.g. Gliessman and Muller 1972; Dolling et al. 1994; Wang et al. 2011). Since regeneration failure of beech (*Fagus sylvatica* L.) and sycamore (*Acer pseudoplatanus* L.) in dense bracken stands has not been investigated for allelopathy yet, I tested if germination and early seedling growth of these two species are susceptible to allelochemicals released by dead bracken fronds or rhizomes (*Chapter III*).

Based on my results from a greenhouse and a common garden experiment, regeneration failure of beech and sycamore in dense bracken stands cannot be attributed to an allelochemical influence of bracken. I found only weak evidence for the existence of phytotoxic compounds, that is, a slightly but ecologically irrelevant reduction in the germination rate of beech. Conversely, I found strong evidence for light competition as probably one of the most important factors causing regeneration failure of beech and sycamore in dense bracken stands. Differences in susceptibility to allelopathic effects from bracken have been reported frequently between species or functional groups such as grasses (Gliessman and Muller 1972), conifers (Dolling et al. 1994; Den Ouden 1995) and broadleaved trees (Dolling et al. 1994). My results are similar to those of many other studies, which did not find allelopathic effects of bracken leachates on other plant species, either (see Table 1 in *Chapter III*); even bioassays that probably feature much higher concentrations compared to natural conditions did not consistently yield allelopathic effects. In contrast, several studies found a high correlation between light availability in dense bracken stands and the reduced growth performance of seedlings (e.g. Tolhurst and Turvey 1992; Gaudio et al. 2011).

My results thus suggest that beech and sycamore are unsusceptible to phytotoxic compounds released from dead bracken fronds and rhizomes, and that light is one of the most important factors causing regeneration failure during the first vegetation period.

In the context of successional pathways, the rate at which succession proceeds is important and determines how fast a disturbed forest will again result in the reestablishment of a closed forest (Kimmins 2004). Bracken can invade rapidly from close by propagules or rhizomes if light availability is abruptly and greatly increased (Marrs and Watt 2006). Once established bracken can suppress tree regeneration for decades (Koop and Hilgen 1987). In this case succession is delayed, since bracken dominates a serial stage for many years. Bracken has a large ecological amplitude, which is why it can grow under many different ecological conditions, from boreal forests in America to Sub-Saharan regions in Africa (review in Marrs and Watt 2006). Due to its effectiveness in competing for resources (Evans et al. 1990; Tolhurst and Turvey 1992; Gaudio et al. 2011), bracken is an aggressive competitor after disturbances. After a windthrow in temperate forests it is difficult to predict, which early colonizing herbaceous species may invade, whether it is bracken, and for how long the species in concern would prevail. Occasional predominance of single plant species is another factor that makes predictions of successional pathways after windthrow in temperate forests difficult. In the literature, an event that causes a successional change in vegetation has been described as a vegetation switch (Wilson and Agnew 1992). Single competitive species may effect a delay situation in terms of forest growth.

Concluding remarks and further research

The large sample of 90 windthrow gaps covering a wide ecological amplitude enabled me to derive generalizations regarding tree regeneration in windthrow-damaged forests of Switzerland. My results support management decisions by identifying the general driving forces of natural regeneration. In general, planting is not required to ensure regeneration success 10 to 20 years after windthrow, in most of the gaps at low elevation, on substrate with neutral or weakly alkaline pH, in gaps with low understory vegetation cover during the first years after the disturbance, and where timber was harvested. There are, in contrast, interacting factors that result in a full or partial lack of regeneration. Here, the question arises whether such transiently treeless gaps eventually turn into closed forests, and how long such a delay may last. The species composition emerging in windthrow gaps with delayed regeneration may also be of interest as a starting point for possible succession trajectories. Since I did not distinguish between tree species in the analysis when I searched for predictors influencing tree regeneration, it would be of considerable interest to investigate if the individual tree species follow the detected general patterns, and if not, which are the differences between tree species. Further, a comparison of the present results regarding fully damaged forests with areas of only partial wind damage would also be of particular interest.

My results show that logging practices in Switzerland provide a wide variety of deadwood in salvage-logged gaps and ensure diverse habitats for deadwood-associated species. Moreover, deadwood in an advanced decay stage is a favorable habitat for tree seedling establishment in moist high-elevation forests, but it has not been decisive for sapling density in my study yet, as the major part of the saplings had established on the forest floor. The visual determination of the species of deadwood specimen was often ambiguous, which is why I did not attempt to record the species. However, many deadwood dwellers depend not only on particular deadwood structures, but also on particular deadwood tree species, which is why further studies should focus on the tree species composition of deadwood and the specific decay time involved. Regarding deadwood quantity and quality, our findings are representative for the climatically and edaphically diverse forests of Switzerland, but should not be generalized for other regions and larger scales. Questions remain regarding how the wide range of logging practices, i.e. from practices in lowland forests to practices in mountain forests, compares to logging practices in other countries of Central Europe.

The greenhouse and common garden experiments revealed that light competition and not allelopathy is one of the main factors driving interference of bracken with beech and sycamore during the first vegetation period. Seedling establishment in dense bracken stands is, therefore, highly correlated with light availability. Based on my results, beech and sycamore are not susceptible to the leachates released by dead bracken fronds or rhizomes, but further studies are needed to evaluate my findings under field conditions. Additionally, there may be several other factors distinctly influencing tree regeneration success or failure in dense bracken stands: i) bracken litter as a barrier for seeds to reach the soil, ii) competition for nutrients and water with regard to the efficient rhizome system, iii) smothering effect through dying bracken fronds may cause high seedling mortality, and iv) bracken is generally not affected by herbivory, in contrast to trees and shrubs. Further studies should include these factors when studying the reasons causing regeneration failure of beech and sycamore in dense bracken stands.

If herbaceous plants dominate both below and above ground resources, Kimmins (2004) suggests that soil disturbance and disruption of herb and shrub roots and rhizomes will result in the reestablishment of closed forests. A preliminary study to the greenhouse and common garden experiment, however, showed that even bracken rhizomes that were cut into pieces of only 10 cm length were able to resprout rapidly, which is why this measure would probably not yield the required effect. I assume that for successful tree seedling establishment in dense bracken stands, the aboveground living biomass of bracken has to be reduced mechanically (fronds should be cut) several times during the vegetation period in order to increase light availability for the emerging seedlings.

References

Cioldi F, Baltensweiler A, Brändli U-B, Duc P, Ginzler C, Bonardi AH, Thürig E, Ulmer U (2010) Waldressourcen. In: Brändli U-B (ed) Schweizerisches Landesforstinventar Ergebnisse der dritten Erhebung 2004-2006. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft WSL, Birmensdorf. Bundesamt für Umwelt BAFU, Bern, pp. 31-114.

Clements FE (1936) Nature and structure of the climax. J Ecol 24: 252-284.

Den Ouden J (1995) Allelopathy in bracken in the Netherlands. In: Smith RT, Taylor JA (eds) Bracken: An Environmental Issue Contributions to an international conference, July 1994, University of Wales, Aberystwyth, pp. 43-46.

Dolling AHU, Zackrisson O, Nilsson MC (1994) Seasonal variation in phytotoxicity of bracken (*Pteridium aquilinum* L. Kuhn). J Chem Ecol 20: 3163-3172.

Egler FE (1954) Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4: 412-417.

Evans GR, Nordmeyer AH, Kelland CM (1990) Biomass and nutrient pools of bracken growing under radiata pine, Nelson, New Zealand. In: Thomson JA, Smith RT (eds) Bracken Biology and Management. Australian Institute of Agricultural Science, Sydney.

Gaudio N, Balandier P, Philippe G, Dumas Y, Jean F, Ginisty C (2011) Light-mediated influence of three understorey species (*Calluna vulgaris*, *Pteridium aquilinum*, *Molinia caerulea*) on the growth of *Pinus sylvestris* seedlings. Eur J For Res 130: 77-89.

Gleason HA (1927) Further views on the succession-concept. Ecology 8: 299-326.

Gliessman SR, Muller CH (1972) The phytotoxic potential of bracken, *Pteridium aquilinum*. Madrono 21: 299-304.

Gough L, Shaver GR, Carroll J, Royer DL, Laundre JA (2000) Vascular plant species richness in Alaskan arctic tundra: the importance of soil pH. J Ecol 88: 54-66.

Harmon ME, Franklin JF (1989) Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. Ecology 70: 48-59.

Ilisson T, Koster K, Vodde F, Jogiste K (2007) Regeneration development 4-5 years after a storm in Norway spruce dominated forests, Estonia. Forest Ecol Manag 250: 17-24.

Imbeck H, Ott E (1987) Verjüngungsökologische Untersuchungen in einem hochstaudenreichen subalpinen Fichtenwald, mit spezieller Berücksichtigung der Schneeablagerung und der Lawinenbildung. Eidgenösschische Forschungsanstalt für Wald, Schnee und Landschaft WSL, Birmensdorf.

Kimmins JP (2004) Forest Ecology: a foundation for sustainable forest management and environmental ethics in forestry, 3rd Edition. Prentice Hall, NJ, USA.

Koop H, Hilgen P (1987) Forest dynamics and regeneration mosaic shifts in unexploited beech (*Fagus sylvatica*) stands at Fontainebleau (France). Forest Ecol Manag 20: 135-150.

Marrs RH, Watt AS (2006) Biological flora of the British isles: *Pteridium aquilinum* (L.) Kuhn. J Ecol 94: 1272-1321.

McKee A, LaRoi G, Franklin JF (1982) Structure, composition and reproductive behavior of terrace forests, south Fork Hoh River, Olympic National Park. In: Starkey EE, Franklin JF, Matthews JW (eds) Ecological research in national parks of the Pacific Northwest. Oregon State University, Forest Research Laboratory, Corvallis, Oregon, USA, pp. 22-29.

Močalov SA, Lässig R (2002) Development of two boreal forests after large-scale windthrow in the Central Urals. For Snow Landsc Res 77: 171-186.

Müller J, Bütler R (2010) A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. Eur J For Res 129: 981-992.

Nicolson M, McIntosh RP, Nicholson M (2002) H. A. Gleason and the individualistic hypothesis revisited. Bulletin of the Ecological Society of America 83: 133-142.

Peterson CJ, Pickett STA (1990) Microsite and elevational influences on early forest regeneration after catastrophic windthrow. J Veg Sci 1: 657-662.

Romme WH, Boyce MS, Gresswell R, Merrill EH, Minshall GW, Whitlock C, Turner MG (2011) Twenty Years After the 1988 Yellowstone Fires: Lessons About Disturbance and Ecosystems. Ecosystems 14: 1196-1215.

Schönenberger W (2002) Post windthrow stand regeneration in Swiss mountain forests: the first ten years after the 1990 storm Vivian. For Snow Landsc Res 77: 61-80.

Schreiner M (2000) Vorkommen und Ausbreitung von Brombeeren sowie ihre Bedeutung für die Naturverjüngung von Tannen-Fichten-Wäldern - dargestellt am Beispiel der Region „Oberer Neckar“. Ph.D. thesis, University of Freiburg im Breisgau, Germany.

Svoboda M, Fraver S, Janda P, Bace R, Zenáhlíková J (2010) Natural development and regeneration of a Central European montane spruce forest. Forest Ecol Manag 260: 707-714.

Tansley AG (1920) The classification of vegetation and the concept of development. J Ecol 8: 118-149.

Tansley AG (1935) The use and abuse of vegetational concepts and terms. Ecology 16: 284-307.

Tolhurst KG, Turvey ND (1992) Effects of bracken (*Pteridium esculentum* (Forst. f.) Cockayne) on eucalypt regeneration in west-central Victoria. Forest Ecol Manag 54: 45-67.

van Mantgem PJ, Stephenson NL, Keeley JE (2006) Forest reproduction along a climatic gradient in the Sierra Nevada, California. Forest Ecol Manag 225: 391-399.

Wang HH, Chen BJ, Hsu LM, Cheng YM, Liou YJ, Wang CY (2011) Allelopathic effects of bracken fern (*Pteridium aquilinum* L. Kuhn) in Taiwan. Allelopathy J 27: 97-110.

Wilson JB, Agnew ADQ (1992) Positive-feedback switches in plant communities. Adv Ecol Res 23: 263-336.

Zielonka T (2006) When does dead wood turn into a substrate for spruce replacement? J Veg Sci 17: 739-746.

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