Tree regeneration in a Norway spruce snag stand after tree die-back caused by *Ips typographus*

Andrea D. Kupferschmid, Walter Schönenberger and Ulrich Wasem

WSL Swiss Federal Research Institute, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland.
andrea.kupferschmid@wsl.ch; walter.schoenenberger@wsl.ch; ulrich.wasem@wsl.ch

Abstract

In a managed *Picea abies* mountain forest on Gandberg (northern Swiss Pre-Alps), almost all trees were killed by a European spruce bark beetle outbreak in 1993 and left unharvested. As we assumed the large amount of bark litter would have a negative effect on tree regeneration, we investigated natural tree regeneration in 12 permanent plots after bark removal and in 12 control plots with a bark cover of 50%. In half of the plots, 200 *Picea abies* seeds were sown per plot in 1995.

No advance tree regeneration was present. Three *Picea abies* seedlings m^{-2} germinated naturally in 1994. 3.8% of the 2400 sown *Picea* seeds germinated in 1995, resulting in 7.5 seedlings m^{-2}, with equal numbers in plots with and without bark litter. We assume pieces of bark to have no effect on *Picea* germination. The mortality of naturally germinated *Picea* was 25% each year, regardless the age of the saplings (1–7 year). *Acer pseudoplatanus* saplings were almost as numerous as *Picea* (0.58 m^{-2}) in 2001, but pioneer trees such as *Betula pendula* (0.29 m^{-2}), *Sorbus aucuparia* (0.16 m^{-2}) and *Salix caprea* (0.04 m^{-2}) were rare. These low numbers together with extensive ungulate browsing indicate it is unlikely that a closed pioneer or *Acer* stand will be formed. We anticipate that a *Picea* forest will replace the current Rubus idaeus-association on the Gandberg.

Keywords: Forest regeneration, snags, *Picea abies*, experimental sowing, seed source, Switzerland

1   Introduction

Disturbances are important processes in forest dynamics. Disturbances, such as heavy storms, cause direct damage at the level of the forest stand (including complete blowdown) and at the level of the individual tree (e.g. root destabilisation, branch breakage), as well as indirect damage such as bark beetle outbreaks (FORSTER 1998; NÜSSLEIN und FAISST 1998). An example of such a large disturbance was the wind-storm event Vivian in 1990, which struck large parts of Western Europe (BUWAL 1994; FORSTER 1993). In the following years, large-scale tree die-back of weak *Picea abies* stands, caused by the European spruce bark beetle *(Ips typographus)*, occurred (FORSTER 1993; WERMELINGER *et al.* 1999). Given the high cost of tree harvesting in the steep mountains of the Swiss Alps, the question arose whether some of these snag stands could be left unharvested. However, the decision to leave formerly managed forests unharvested after tree death is not without risks (FREY *et al.* 1995). This is particularly the case because little is known about natural tree regeneration in large snag stands (ROSS *et al.* 2001).

In interior Alaska, a spruce bark beetle (*Dendroctonus rufipennis* Kirby) epidemic left large snag stands with little natural spruce regeneration (COLE *et al.* 1999). Due to the low levels of spruce regeneration, many of the repeatedly infested areas underwent a forest type conversion (BAKER and KEMPERMAN 1974). In the Rocky Mountains, spruce-dominated

snag stands which had more than 10% fir changed into fir forests, while other stands with less than 10% fir remained spruce forests (SCHMID and FRYE 1977). In the steep Swiss Alps natural tree regeneration is also low in dense living spruce forests (BRANG and DUC 2002). It is possible that tree regeneration may be even lower in snag stands since the ground becomes quickly covered with large quantities of needles and bark dropped after tree death. Assuming a growing stock of about 880 m^3/ha and a bark thickness of 2 cm, the total bark litter volume of 44 m^3/ha would cover about 22% of the soil surface. It is therefore important to establish whether bark litter hinders or promotes tree regeneration.

In the rather flat highlands of the Bavarian National Park in south-eastern Germany, tree regeneration shortly after the death of the Norway spruce trees was found to have slowed down because tree seedlings and saplings were covered by bark litter (HEURICH 2001). However, the large deposits of needles (20 t dry needles/ha) and bark pieces mulched the zones around the snags and led to an accumulation of nutrients in the soil (BEUDERT 1999), thus leading to favourable regeneration sites for *Picea* and many ground-vegetation species (HEURICH 2001; SINNER 1999). REIF and PRZYBILLA (1995) found 0.28–0.82 Norway spruce saplings m^{-2} on sites with bark litter in the Bavarian National Park. However, it is unclear whether bark is also an important factor for tree regeneration in steep mountain forests.

To understand the mechanisms of tree regeneration in a steep snag stand in the Swiss Alps, we investigated the natural tree regeneration and the germination of sown *Picea abies* on plots with varying degrees of bark removal.

2 Materials and methods

2.1 Study site

The study site is situated on the north face of the Gandstock, south of Schwanden (canton of Glarus, Switzerland) at an elevation of 1220–1260 m a.s.l. The Gandberg inclines towards the North at an angle of about 30–50%, and the site receives no direct sunshine between October and April as a result of orographic shading. Geologically, the Gandberg is composed of red conglomeratic Verrucano (OBERHOLZER and HEIM 1900–1908). The soil is an acid brown soil with a tendency to podsol (ROTH 1996). Its depth varies greatly due to the presence of boulders deposited by rockfall. Precipitation and temperature were not recorded directly on the Gandberg site, but nearby in Glarus (470 m) and Linthal/Tierfehd (812 m, MeteoSchweiz data). The estimated mean annual precipitation for the Gandberg forest is 1600–2000 mm and the mean annual temperature 2–3°C. This relatively mild climate is due to the influence of the frequent föhn, a strong, very warm wind from the southern Alps. Since 1548 the Gandberg has been a part of the 102 km^2 wildlife sanctuary "Freiberg Kärpf". 680 chamois *(Rupicapra rupicapra)*, 173 red deer *(Cervus elaphus)* and 143 roe deer *(Capreolus capreolus)* were present in this area in 1997 (MÜLLER and ZOPFI 1999). The Gandberg forest is a main distribution area in summer for chamois (SCHMIDT 1983).

2.2 Stand structure

The entire Gandberg forest used to be dominated by Norway spruce *(Picea abies)*. Only a few silver fir *(Abies alba*, 1%) and sycamore maple *(Acer pseudoplatanus*, 3%) trees were present. The site belongs to the Galio-Abieti-Piceetum association (KÄGI 1992). The stands developed after being clear-cut in 1842–1846, and were later subject to some high-thinning (Forstverwaltung Kt. Glarus 1949). The forest had a growing stock of about 880 m^3/ha in 1990 (Kupferschmid

unpublished) and was dominated by middle-aged timber trees of 35–50 cm dbh. In 1993, a large-scale European spruce bark-beetle (*Ips typographus* L.) outbreak, triggered by the windthrow event Vivian in 1990, caused the death of almost all *Picea abies* trees not only in the Gandberg forest but also in adjacent forests (till 1997 a total area of 100 ha). Only about 2% of the *Picea* trees and all *Abies alba* and *Acer pseudoplatanus* trees survived, scattered throughout the snag stand. In 1994, it was decided to leave the snag stands unharvested above 1100 m a.s.l., and to actively convert the forest into a deciduous beech forest below this elevation.

In 1992, the ground-vegetation in the Gandberg forest was patchy and dominated by the mosses *Dicranum scoparium*, *Polytrichum formosum* and by *Oxalis acetosella* (KÄGI 1992). After *Picea abies* tree death the ground-vegetation changed into a Rubetum idaei association (KUPFERSCHMID 2002a). The *Rubus idaeus* had reached a mean height of 150 ± 40 cm and covered 75% of the sites in 2001. Underneath these *Rubus* plants moss covered 40% of the soil surface, *Oxalis acetosella* 25%, fern 28%, *Epilobium angustifolium* and *Rubus fruticosus* 7% (KUPFERSCHMID 2000a).

2.3   Methods

In 1994, we started a pilot experiment with 24 permanent plots of 1 x 1 m in the montane zone of the Gandberg (1220–1260 m a.s.l.). The plots were at least 1 m away from the next snag or tree stump to prevent unequal shading. The plots were arranged in six main blocks. Each block contained two plots with bark litter and two plots without bark litter (randomised block design with the factor bark removal). In the 12 plots without bark, bark pieces were removed twice a year in 1994 and 1995. 200 *Picea abies* seeds per plot were sown on 8 May 1995 in one plot with and one without bark litter per block (total 12 plots). Seeds were sown at a density of two seeds per 10 cm^2 on bark strips or on the soil surface. The seeds were collected at Kerns, which is located 1460 m a.s.l. and with a North-East inclination, germination ability was 60%. The position and number of establishing tree seedlings and saplings was recorded annually in July/August on a grid map. We measured annual shoot growth and height (the current terminal shoot was not included) of the tree sapling and noted if terminal shoots were browsed. Young trees were classified as seedlings up to the age of one year, and as saplings if they were older than one year with heights shorter than 1.5 m (which is the height of *Rubus*).

Of the ground vegetation only *Polytrichum formosum* and *Oxalis acetosella* were more abundant when bark litter was absent. All the other mosses and herbs had the same cover with or without bark litter (KUPFERSCHMID 2000a). It was therefore not considered necessary to take the ground vegetation into account in analysing the influence of bark litter on tree regeneration. The tree data were analysed after a square root transformation with ANOVA, fitting the factors "block" and "bark removal". Mortality was compared with the Wilcoxon Rank Sum Test for unpaired data (R: Version 1.3.0).

For naming the ground vegetation and tree species we used the nomenclature of LAUBER and WAGNER (1996); for the mosses that of JAHNS (1995); for the herbaceous plant associations that of OBERDORFER (1993) and for the forest associations that of OTT *et al.* (1997).

3   Results

3.1   Natural tree regeneration

In the 24 permanent plots seeds of six tree species germinated naturally between 1994 and 2001 and the saplings of five species have survived (Fig. 1): *Picea abies* (seedlings N = 88, surviving saplings N = 13), *Acer pseudoplatanus* (29, 15), *Sorbus aucuparia* (8, 4), *Betula pendula* (8, 7), *Salix caprea* (1, 1) and *Abies alba* (1, 0). There was no advance tree regeneration in any of the plots or in the immediate neighbourhood of the plots, i.e. none of the tree seedlings or saplings were present before the death of the Norway spruce stand.

Picea abies seedlings germinated in 1994 and in 1996 on the Gandberg (Fig. 2), while regional crop years were found in autumn 1992 and 1995 (see discussion). The mortality of the *Picea abies* saplings that germinated in 1994 was 73% in the first five years and 88% in the whole 1994–2001 period (Fig. 4). The mean mortality rate per year was 26% (Fig. 4). Similar results were found for the *Picea abies* saplings that germinated in 1996, with 75% dead by 2001 (first five years) and in average 30% mortality per year. However, in contrast to the 1994 seedlings, the 1996 seedlings had a higher mortality rate (42%) than the saplings in later years (mean of white column 1997–2001 is 27%, see Fig. 4). The average height of the 13 surviving *Picea abies* saplings was 13.6 ± 6.8 cm in 2001 (not including the shoot of 2001). The terminal shoots of all but 4 out of 13 living *Picea abies* saplings were browsed in 2001.

Acer pseudoplatanus seedlings were found every year after 1994 (Fig. 3), stemming from some trees that fruited annually in the surrounding area. The mean height of the 15 *Acer pseudoplatanus* saplings was only 10.3 ± 5.6 cm in 2001 due to ungulate browsing.

Betula pendula, on the other hand, was up to 2.3 m high with an average of 143.3 ± 78.6 cm. Surprisingly, the eight *Betula pendula* saplings were only found in plots without bark litter.
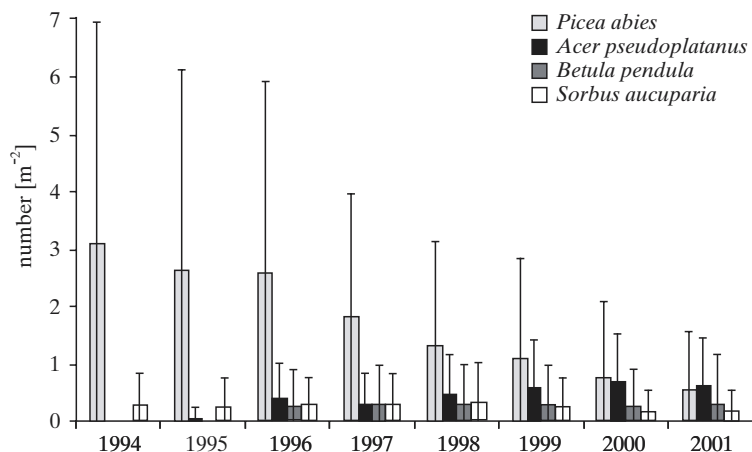

Fig. 1. Mean number ± standard deviation of naturally germinated and surviving tree seedlings and saplings in all 24 permanent plots from 1994 to 2001.
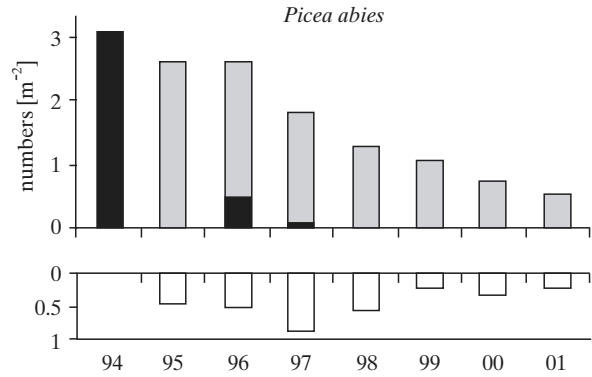
Fig. 2. Number of newly germinated (black), surviving (grey) and dead (white) seedlings and saplings of *Picea abies* in all 24 permanent plots from 1994 to 2001.
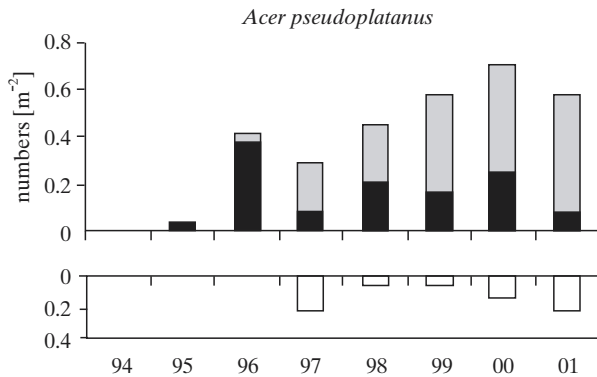

Fig. 3. Number of newly germinated (black), surviving (grey) and dead (white) seedlings and saplings of *Acer pseudoplatanus* in all 24 permanent plots from 1994 to 2001.
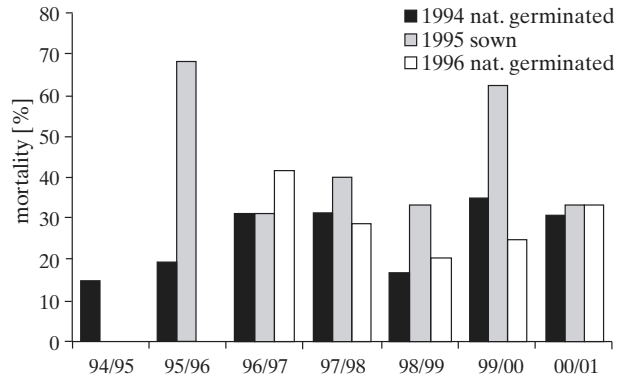

Fig. 4. Mortality of *Picea abies* seedlings and saplings germinated naturally in 1994, after sowing in 1995 or naturally in 1996.

3.2   Sowing experiment

91 of the 2400 *Picea abies* seeds sown in May 1995 germinated and survived until July 1995 (3.8%), resulting in 7.5 ± 4.2 seedlings m^{-2} (Fig. 5). *Picea abies* germinated almost equally well in plots with bark litter (9.1 ± 5.1 seedlings m^{-2}) as in plots without bark litter (6 ± 2.7 seedlings m^{-2}, Fig. 5, ANOVA m.s. = 0.788, p = 0.327). However, in the plots with bark litter, only 50% of the soil was actually covered with bark (Fig. 5), therefore the seedlings may have partially germinated on soil rather than on bark. If there is less germination because of bark, there should be fewer seedlings in plots with bark litter than in those without. As we found equal numbers or even slightly more seedlings in plots with bark pieces (Fig. 5), we assume that bark litter does not have a negative effect on *Picea* germination.

In the first months after sowing, the mortality of the sown seedlings (68%) was higher than that of the naturally germinated seedlings (15–42%, Fig. 4, W = 28.5, p <0.01). Over the first five years, 97% of the sown *Picea abies* saplings died (Fig. 4), resulting in only two surviving saplings in 2001 (Fig. 5). Mortality was therefore higher for sown (97%) than for naturally germinated saplings (74%) in the first five years (W = 45.5, p <0.01). Generally, we could not determine the causes of death, although sometimes being covered with pieces of bark may have played a role.
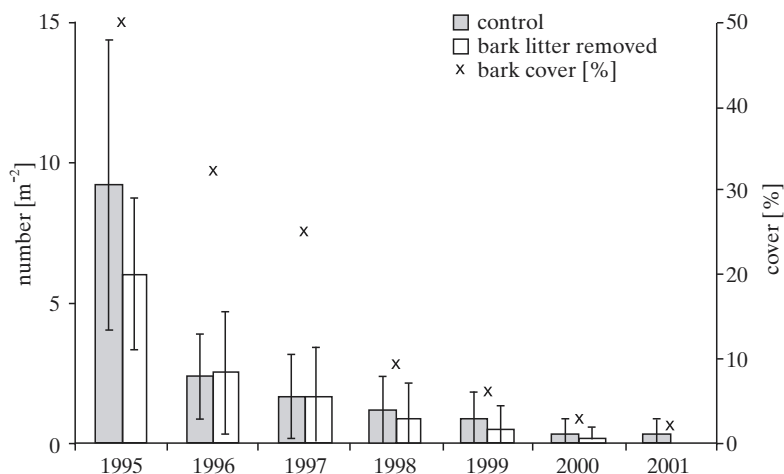

Fig. 5. Mean number ± standard deviation of germinated and surviving *Picea abies* seedlings and saplings sown in May 1995 on 12 permanent plots with bark removal in 1995 and on 12 control plots. X marks the % mean cover of bark litter (right axis) in the 12 control plots in each year.

4   Discussion

4.1   Development of the snag stand

What plant community will develop on a given site after a spruce beetle infestation depends on several factors including the species that were present on the site before the tree die-back, the distance away from seed sources, the seedbed conditions and the weather conditions after tree death (ROSS *et al.* 2001). In our study, the ground vegetation of the former *Picea abies* forest of the Gandberg, which used to be dominated by mosses (i.e. *Polytrichum formosum* and *Dicranum scoparium*) and *Oxalis acetosella*, changed into a Rubetum idaei association five years after tree death (KUPFERSCHMID 2002a). The high quantity of needles and bark deposited might have stimulated this succession via nitrogen release in the first years after tree die-back (BEUDERT 1999). But what vegetation will come after the Rubetum idaei association?

Generally, the forest structure prior to disturbance plays an important role in influencing post-disturbance tree succession (e.g. COOPER-ELLIS *et al.* 1999). Wind and insect disturbances differ from fire disturbances in the sense that advance regeneration is allowed to survive (DROBYSHEV 1996). After beetle-caused tree mortality there is often a release of co-dominant or understory trees (HOLSTEN *et al.* 1995; VEBLEN *et al.* 1991; SCHULZ 1996). This depends on the availability of advance regeneration prior to the disturbance, which is often absent in managed forests due to the dense canopy structures (SCHÖNENBERGER and WASEM 1999). The dense structure of the former *Picea abies* forest on the Gandberg, together with the high pressure from ungulate browsing, explains the lack of advance tree regeneration on the study site.

This initial lack of regeneration can be partially compensated for if new trees rapidly establish. Extrapolating from the numbers found in the permanent plots, it is likely that around 30 000 *Picea* seedlings per ha germinated and survived till July 1994 on the Gandberg. Autumn 1993 was not a crop year in the region, but seed still appears to have dispersed from the fruiting *Picea abies* trees in the neighbouring stands. These neighbouring trees however, also died in 1994 after being attacked by European spruce bark beetles *(Ips typographus)*. As a result only 5000 seedlings per ha germinated and survived in 1996, although seed dispersal had presumably been good, as autumn 1995 was an important crop year in the region. Hence, the small quantities of living *Picea* might restrict rapid forest recovery in the Gandberg forest in future, even though at this time decomposed logs would constitute additional niches (GRUBB 1977) for new tree regeneration (MAI 1998; STÖCKLI 1995; STÖCKLI 1997; ULANOVA 2000a). HOGGET (2000) found that higher levels of regeneration tend to be associated with higher levels of live canopy trees after a hemlock looper infestation in the interior cedar hemlock biogeoclimatic zone in Canada. Usually, the lack of an adequate seed source near disturbed sites has been attributed in the literature to causing low levels of tree regeneration after disturbances (LÄSSIG *et al.* 1995; TIMONEY and PETERSON 1996).

The few *Acer pseudoplatanus* trees (3%) in the Gandberg forest continued to fruit and hence *Acer* seedlings were found every year in the permanent plots. Our findings support the idea that retaining surviving trees (green tree retention) in disturbed sites and clear-cuttings is important for tree regeneration (LEDER and KRUMNACKER 1998; BEACH and HALPERN 2001; HANSEN *et al.* 1995).

Where rapidly growing, long-lived species such as *Betula* sp. and *Populus* sp. established on a site, *Rubus idaeus* brushwood dominated the site after a disturbance only for 5–10 years (RICARD and MESSIER 1996; ULANOVA 2000b; WHITNEY 1982). Closed pioneer-crop stands of *Sorbus aucuparia, Salix* sp. or *Betula* sp., are only expected where the advance regeneration

of such pioneer tree species is abundant or where large vegetation-free gaps are frequent (SCHMIDT-SCHÜTZ 1999). Neither was the case at our study site on the Gandberg. Therefore, we believe either it will take a very long time for a pioneer tree stand to develop, or no such stand will develop at all. For this reason *Rubus idaeus* will probably continue to dominate the Gandberg snag stands until the *Picea abies* trees have grown so much that they provide too much shade to *Rubus idaeus* and thus *Rubus* will disappear.

4.2   High mortality rates

We observed a mean mortality rate of about 25% per year for naturally germinated *Picea abies* saplings in the permanent plots of the Gandberg (Fig. 4). However, only very few seedlings and saplings were found to have been actually covered by bark, probably because bark decomposed rather fast on the soil surface and because little bark fell after 1995 (Fig. 5). It was not, however, possible to determine directly most of the reasons for the mortality of the tree regeneration. According to other studies, we assume some of the following factors may have played a role in the seedling mortality: (i) the dense "canopy" structure of *Oxalis acetosella* and the frequently dry raw humus on which it grows (BRANG 1996); (ii) the horizontally growing mosses like *Hylocomium splendens* and *Thuidium tamariscinum* which inhibit the penetration of seedling roots into the mineral soil layer (HILAIRE and LEOPOLD 1995; HÖRNBERG *et al.* 1997); (iii) the increased shoot growth of *Polytrichum formosum* (BRANG 1998) due to more light and nutrients (POTTER *et al.* 1995); (iv) the low light availability under *Rubus idaeus* and ferns (ISHIZUKA *et al.* 1998; LAUTENSCHLAGER 1999; STAROSTINA 1965; RUEL 1992); (v) mice activity (SCHREINER *et al.* 2000; ODERMATT and WASEM 2001; WASEM and SENN 2000); (vi) pathogen attacks, particularly of *Herpotrichia* sp. (BAZZIGHER 1976); (vii) browsing by ungulates; and (viii) unfavourable weather conditions (BRANG 1998) or (ix) a combination of these stress factors.

The sown *Picea abies* had very low germination rates and even higher mortality rates than naturally germinated *Picea*. Seed predation and weather conditions have been shown to be important factors in influencing the number of germinating seeds (SCHREINER *et al.* 2000; PELLISSIER and TROSSET 1992).

Ungulate browsing on tree saplings can cause mortality, but more often shoot reductions have been reported (EIBERLE and NIGG 1986; LONG *et al.* 1998; SCHÖNENBERGER and WASEM 1999; YLI-VAKKURI 1961). In windthrow areas CRAWFORD *et al.* (1993) found fewer browsed hemlock trees on mounds than in pits. However, logs were found to be less effective as an obstacle against chamois *(Rupicapra rupicapra)* than against red deer (*Cervus elaphus*, LÜTHI 1998). On our study site on the Gandberg, chamois are very frequent and hence we observed a high browsing pressure even on *Picea abies* (70%). No *Abies alba* survived and *Acer pseudoplatanus* remained small or were lost. SCHWEIGER and STERBA (1997) pointed out that ungulates preferentially browse saplings 10–30 cm high, which corresponds to the actual height of our saplings on the Gandberg. Due to heavy winter feeding by chamois on the tree regeneration, *Rubus idaeus*, which is at this season defoliated, could not play a role in protecting saplings against ungulate browsing. It will therefore probably take many years until the Rubetum idaei association currently present on the Gandberg is replaced by a new *Picea abies* forest.

The main question of whether a new *Picea* stand will develop out of the current tree regeneration and how the future stand will be structured is explored in a model we are implementing for this snag stand (KUPFERSCHMID 2002b).

5   Conclusion

Where wind and beetle disturbances are an integral part of forest dynamics, the findings of this study suggest that managers need to be concerned about maintaining stand structures allowing for advance tree regeneration (i.e. allowing more natural development processes [LÄSSIG and MOTSCHALOW 2000]). If stands are too dense and homogeneous, there will not be a rapid forest recovery following bark beetle disturbance. Furthermore, retaining the few surviving trees seems to be important for the fast reforestation of disturbed sites, especially if pioneer trees are almost absent. If the management goal is to ensure there is continuous forest cover, pre-disturbance risk management may be even more important than post-disturbance management.

6   References

BAKER, B.H.; KEMPERMAN, J.A., 1974: Spruce beetle effects on a white spruce stand in Alaska. J. For. 72: 423–425.

BAZZIGHER, G., 1976: Der schwarze Schneeschimmel der Koniferen (*Herpotrichia juniperi* [Duby] Petak und *Herpotrichia coulteri* [Peck] Bose). Eur. J. For. Pathol. 6: 109–122.

BEACH, E.W.; HALPERN, C.B., 2001: Controls on conifer regeneration in managed riparian forests: effects of seed source, substrate and vegetation. Can. J. For. Res. 31: 471–482.

BEUDERT, B., 1999: Veränderungen im Stoffhaushalt eines abgestorbenen Fichtenökosystems im Forellenbachgebiet des Nationalparks Bayerischer Wald. In: Einzugsgebiet Grosse Ohe – 20 Jahre hydrologische Forschung im Nationalpark Bayerischer Wald. Symposiumsbericht, 11.5.1999. Nationalparkverwaltung Bayerischer Wald. 83–106.

BRANG, P., 1996: Experimentelle Untersuchungen zur Ansamungsökologie der Fichte im zwischenalpinen Gebirgswald. Beih. Schweiz. Z. Forstwes. 77.

BRANG, P., 1998: Early seedling establishment of *Picea abies* in small forest gaps in the Swiss Alps. Can. J. For. Res. 28, 4: 626–639.

BRANG, P.; DUC, P., 2002: Zu wenig Verjüngung im Schweizer Gebirgs-Fichtenwald: Nachweis mit einem neuen Modellansatz. Schweiz. Z. Forstwes. 153, 6: 219–227.

BUWAL, 1994: Sturmschäden 1990 im Schweizer Wald. Bern, Bundesamt für Umwelt, Wald und Landschaft.

COLE, E.; NEWTON, M.; YOUNGBLOOD, A., 1999: Regeneration white spruce, paper birch and willow in south-central Alaska. Can. J. For. Res. 29, 7: 993–1001.

COOPER-ELLIS, S.; FOSTER, D.R.; CARLTON, G.; LEZBERG, A., 1999: Forest response to catastrophic wind: results from an experimental hurricane. Ecology 80, 8: 2683–2696.

CRAWFORD, H.S.; LAUTENSCHLAGER, R.A.; STOKES, M.R.; STONE, T.L., 1993: Effects of forest disturbance and soil depth on digestible energy for moos and white-tailed deer. USDA Forest Service Research Paper NE-682.

DROBYSHEV, I.V., 1996: Role of natural disturbances in regeneration of Norway spruce in differ-
ent types of European south boreal forests. In: BERGERON, Y.; FRISQUE, G. (eds) Second
International Workshop on Disturbance Dynamics in Boreal Forest, Rouyn-Noranda, Québec,
Canada, August 1996: Workshop abstracts. Québec, Université de Québec. 75–78.

EIBERLE, K.; NIGG, H., 1986: Untersuchung über den Verbiss durch die Gemse (*Rupicapra
rupicapra* L.) an Fichte *(Picea abies)*. Ber. Bot.-Zool. Ges. Liecht.-Sargans-Werdenberg 15:
15–36.

FORSTER, B., 1993: Entwicklung der Borkenkäfersituation in den Schweizer Sturmschaden-
gebieten. Schweiz. Z. Forstwes. 144, 10: 767–776.

FORSTER, B., 1998: Storm damages and bark beetle management: how to set priorities. In:
Methodology of Forest Insect and Disease Survey in Central Europe. Proc. First Workshop of
the IUFRO WP7.03.10, April 21–24, 1998. Ustron-Jaszowiec (Poland). Warszawa, Forest
Research Institute. 161–165.

Forstverwaltung Kt. Glarus, 1949: Wirtschaftsplan über die Gemeindewaldungen von Schwanden
(1. Revision). Glarus, Forstverwaltung Kt. Glarus.

FREY, W.; FORSTER, B.; GERBER, W.; GRAF, F.; HEINIGER, U.; KUHN, N.; THEE, P., 1995: Risiken
und Naturgefahren auf Windwurfflächen. Schweiz. Z. Forstwes. 146, 11: 863–872.

GRUBB, P.J., 1977: The maintenance of species richness in plant communities: the importance of
the regeneration niche. Biol. Rev. 52: 107–145.

HANSEN, A.J.; GARMAN, S.L.; WEIGAND, J.F.; URBAN, D.L.; MCCOMB, W.C.; RAPHAEL, M.G.,
1995: Alternative silvicultural regimes in the Pacific Northwest: simulations of ecological and
economic effects. Ecol. Appl. 5, 3: 535–554.

HEURICH, M., 2001: Waldentwicklung im montanen Fichtenwald nach grossflächigem Buch-
druckerbefall im Nationalpark Bayerischer Wald. In: HEURICH, M. (ed) Waldentwicklung
im Bergwald nach Windwurf und Borkenkäferbefall. Grafenau, Nationalparkverwaltung
Bayerischer Wald. 99–176.

HILAIRE, L.R.S.; LEOPOLD, D.J., 1995: Conifer seedling distribution in relation to microsite con-
ditions in a central New York forested minerotrophic peatland. Can. J. For. Res. 25: 261–269.

HOGGET, A., 2000: Western hemlock looper and forest disturbance in the ICHwk3 of the Robson
Valley; Stage 2: The Effects of western hemlock looper – Report and silviculture recommen-
dations. Faculty of Forestry, University of British Columbia.

HOLSTEN, E.H.; WERNER, R.A.; DEVELICE, R.L., 1995: Effects of a spruce beetle *(Coloptera:
Scolytidae)* outbreak and fire on Lutz spruce in Alaska. Environ. Entomol. 24, 6: 1539–1547.

HÖRNBERG, G.; OHLSON, M.; ZACKRISSON, O., 1997: Influence of bryophytes and microrelief
conditions on *Picea abies* seed regeneration patterns in boreal old-growth swamp forests. Can.
J. For. Res. 27: 1015–1023.

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. J. Sust. For. 6, 3/4: 367–388.

JAHNS, H.M., 1995: BLV Bestimmungsbuch Farne Moose Flechten; Mittel-, Nord- und West-
europa. München, BLV Verlagsgesellschaft mbH.

KÄGI, B., 1992: Pflanzensoziologische Karte des Gandbergwaldes. Glarus, Forstdirektion Kt.
Glarus.

KUPFERSCHMID, A.D., 2002a: Bark influence on vegetation development in a dead *Picea abies*
mountain forest. In: BOTTARIN, R.; TRAPPEINER, U. (eds) Interdisciplinary Mountain
Research. Berlin, Vienna, Blackwell. 242–247.

KUPFERSCHMID, A.D., 2002b: Decay and regeneration of a Norway spruce mountain forest after a
large-scale die-back caused by bark beetles in the northern Swiss Alps. [Published online, last
Update 10 Jan. 2002]. Available from World Wide Web ‹http://www.wsl.ch/staff/andrea.kupfer-
schmid/Gandberg-en.html› Birmensdorf, Swiss Federal Research Institute WSL.

LÄSSIG, R.; EGLI, S.; ODERMATT, O.; SCHÖNENBERGER, W.; STÖCKLI, B.; WOHLGEMUTH, T., 1995:
Beginn der Wiederbewaldung auf Windwurfflächen. Schweiz. Z. Forstwes. 146, 11: 893–911.

LÄSSIG, R.; MOTSCHALOW, S.A., 2000: Frequency and characteristics of severe storms in the Urals
and their influence on the development, structure and management of the boreal forests. For.
Ecol. Manage. 135: 179–194.

LAUBER, K.; WAGNER, G., 1996: Flora Helvetica. Bern, Haupt.

LAUTENSCHLAGER, R., 1999: Environmental resource interactions affect red raspberry growth and its competition with white spruce. Can. J. For. Res. 29, 7: 906–916.

LEDER, B.; KRUMNACKER, J., 1998: Zur Vegetations- und Gehölzentwicklung auf Sukzessionsflächen nach Fichtenwindwurf. LÖBF-Mitt. 1: 64–72.

LONG, Z.T.; PETERSON, C.J.; CARSON, W.P., 1998: Can disturbance create refugia from herbivores: an example with hemlock regeneration on treefall mounds. J. Torrey Bot. Soc. 125, 2: 165–168.

LÜTHI, C., 1998: Einfluss verschiedener Räumungsvarianten auf die Nutzung der ehemaligen Sturmschadenfläche Schwanden durch Schalenwild. Diplomarbeit. ETH, Institut für Forstwiss. Zürich. unpublished.

MAI, W., 1998: Naturverjüngung auf Moderholz. Allg. Forst Z. Waldwirtsch. Umweltvorsorge 11: 591.

MÜLLER, P.; ZOPFI, P., 1999: Vom Wildschutz zum Naturschutz. In: 450 Jahre Freiberg Kärpf. Linthal, Verlag Neujahrsbote. 11–17.

NÜSSLEIN, S.; FAISST, G., 1998: Waldentwicklung im Nationalpark Bayerischer Wald 1998: Totholzflächen und Waldverjüngung. Freising, Bayerische Landesanstalt für Wald und Forstwirtschaft.

OBERDORFER, E., 1993: Süddeutsche Pflanzengesellschaften, Teil II: Sand- und Trockenrasen, Heide- und Borstgrasgesellschaften, alpine Magerrasen, Saum-Gesellschaften, Schlag- und Hochstauden-Fluren. Jena, Gustav Fischer Verlag.

OBERHOLZER, J.; HEIM, A., 1900–1908: Geologische Karte der Glarneralpen (Spezialkarte Nr. 50).

ODERMATT, O.; WASEM, U., 2001: Mäuseschäden bei der Wiederbewaldung von Windwurfflächen. [Published online, last Update 28 Nov. 2001] Available from World Wide Web ‹http://www.wsl.ch/forest/wus/pbmd/› Birmensdorf, Eidgenössische Forschungsanstalt WSL. 3 pp. [pdf]

OTT, E.; FREHNER, M.; FREY, H.-U.; LÜSCHER, P., 1997: Gebirgsnadelwälder: Ein praxisorientierter Leitfaden für eine standortgerechte Waldbehandlung. Bern, Stuttgart, Wien, Verlag Paul Haupt.

PELLISSIER, F.; TROSSET, L., 1992: Les difficultés de régénération naturelle des pessières subalpines: prédation des graines au sol et blocages dus à l'humus. Ann. sci. for. 49: 383–388.

POTTER, J.A.; PRESS, M.C.; CALLAGHAN, T.V.; LEE, J.A., 1995: Growth responses of *Polytrichum commune* and *Hylocomium splendens* to simulated environmental change in the sub-arctic. New Phytol. 131: 553–541.

REIF, A.; PRZYBILLA, M., 1995: Zur Regeneration der Fichte *(Picea abies)* in den Hochlagen des Nationalparks Bayerischer Wald. Hoppea 56: 467–514.

RICARD, J.-P.; MESSIER, C., 1996: Abundance, growth and allometry of red raspberry (*Rubus idaeus* L.) along a natural light gradient in a northern hardwood forest. For. Ecol. Manage. 81, 1: 153–160.

ROSS, D.W.; DATERMAN, G.E.; BOUGHTON, J.L.; QUIGLEY, T.M., 2001: Forest health restoration in south-central Alaska: a problem analysis. Gen. Tech. Rep. USDA For. Serv. PNW-GTR-523: 1–38.

ROTH, I., 1996: Untersuchungen über die forstliche Ansamung in einem abgestorbenen Fichtenbestand, Objekt: Gandberg oberhalb Schwanden GL. Diplomarbeit. ETH, Institut für Forstwiss. Zürich. unpublished.

RUEL, J.-C., 1992: Impact de la compétition exercée par le framboisier (*Rubus idaeus* L.) et les feuillus de lumière sur la croissance du sapin (*Abies balsamea* [L.] Mill.) en régénération. Can. J. For. Res. 22, 9: 1408–1416.

SCHMID, J.M.; FRYE, R.H., 1977: Spruce beetles in the Rockies. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. RM-49:1–38.

SCHMIDT, A., 1983: Der Freiberg Kärpf; Das älteste Wildschutzgebiet der Schweiz in den Glarner Alpen. Glarus, Buchhandlung Baeschlin.

SCHMIDT-SCHÜTZ, A., 1999: Wiederbewaldung von Fichten-Sturmwurfflächen auf vernässenden Standorten mit Hilfe von Pioniergehölzen. Forstl. Forsch.ber. München, 176: 120–130.

SCHÖNENBERGER, W.; WASEM, U., 1999: Der Beginn der Wiederbewaldung von Sturmwurfflächen im Gebirge – Ein Zwischenbericht. Forstl. Forsch.ber. München, 176: 102–110.

SCHREINER, M.; BAUER, E.-M.; KOLLMANN, J., 2000: Reducing predation of conifer seeds by clear-cutting *Rubus fruticosus* agg. in two montane forest stands. For. Ecol. Manage. 126, 3: 281–290.

SCHULZ, B., 1996: Response of residual spruce in beetle-impacted stands in Resurrection Creek Drainage, Kenai Peninsula, Alaska. USDA Forest Service Technical Report-62. 21pp.

SCHWEIGER, J.; STERBA, H., 1997: A model describing natural regeneration recruitment of Norway spruce (*Picea abies* [L.] Karst.) in Austria. For. Ecol. Manage. 97, 2: 107–118.

SINNER, K.F., 1999: Aktuelle Konflikte im Nationalpark Bayerischer Wald als Beispiel für unseren gesellschaftlichen Umgang mit Wildnis. Bayer. Akad. Natursch. Landschaftspfl. Laufener Semin.beitr. 2: 11–13.

STAROSTINA, K.F., 1965: Experimental data on the effect of *Rubus idaeus* on the growth of *Picea abies* seedlings on clear fellings. Bot. Zhurn. Leningrad 50, 7: 971–974.

STÖCKLI, B., 1995: Moderholz für die Naturverjüngung im Bergwald: Anleitung zum Moderanbau. Merkbl. Prax. 26: 8 S.

STÖCKLI, B., 1997: Moderholzverjüngung, Hilfsmassnahme zur Kadaververjüngung. Allg. Forst Z. Waldwirtsch. Umweltvorsorge 2: 85.

TIMONEY, K.P.; PETERSON, G., 1996: Failure of natural regeneration after clearcut logging in Wood Buffalo National Park, Canada. For. Ecol. Manage. 87, 1–3: 89–105.

ULANOVA, N.G., 2000a: The effects of windthrow on forests at different spatial scales: a review. For. Ecol. Manage. 135: 155–167.

ULANOVA, N.G., 2000b: Plant age stages during succession in woodland clearings in Central Russia. In: Proceedings IAVS Symposium. Uppsala, Schweden, I.A.V.S. Opulus Press. 80–83.

VEBLEN, T.T.; HADLEY, K.S.; REID, M.S.; REBERTUS, A.J., 1991: The response of subalpine forests to spruce beetle outbreak in Colorado. Ecology 72, 1: 213–231.

WASEM, U.; SENN, J., 2000: Fehlende Weisstannenverjüngung: Hohe Schalenwildbestände können die Ursache sein. Wald Holz 9: 11–14.

WERMELINGER, B.; OBRIST, M.K.; DUELLI, P.; FORSTER, B., 1999: Development of the bark beetle (Scolytidae) fauna in windthrow areas in Switzerland. Mitt. Schweiz. Entomol. Ges. 72: 209–220.

WHITNEY, G.G., 1982: The productivity and carbohydrate economy of a developing stand of *Rubus ideaus*. Can. J. Bot. 60: 2687–2703.

YLI-VAKKURI, P., 1961: Kokeellisia tutkimuksia taimien sytymiséstä ja ensi kehityksestä kuusikoissa ja männiköissä (Experimental studies on the emergence and initial development of tree seedlings in spruce and pine stands). Acta For. Fenn. 75: 1–122.