

# Growth response of Norway spruce saplings in two forest gaps in the Swiss Alps to artificial browsing, infection with black snow mold, and competition by ground vegetation

Catherine Cunningham, Niklaus E. Zimmermann, Veronika Stoeckli, and Harald Bugmann

**Abstract:** Black snow mold (*Herpotrichia juniperi* (Duby) Petr.) infection and browsing by ungulates influence the growth of Norway spruce (*Picea abies* (L.) Karst.) saplings in subalpine forests in the European Alps. To isolate the impacts of artificial browsing (clipping of shoots) and snow mold infection on growth, we conducted a 2 year field experiment with planted saplings in two forest gaps in the subalpine zone of the Swiss Alps. In the first year (2003) saplings responded slightly positively to clipping and negatively to snow mold infection; sapling growth behavior was site-specific (ANOVA,  $r^2 = 0.35$ ). In 2004, saplings responded negatively to clipping, snow mold infection, long-lasting snow cover, and shading by ground vegetation (ANOVA,  $r^2 = 0.59$ ). The difference in mean annual growth rates between noninfected and infected saplings was large; long-lasting snow was found to enhance snow mold coverage. Removing these variables from general linear models strongly reduced model performance ( $d^2 = 0.32$  for the full model,  $d^2 = 0.23$  for no clipping,  $d^2 = 0.16$  for no snow cover). Sapling growth was negatively related to shading by ground vegetation, especially in 2004. We conclude that these biotic factors have a strong impact on growth, both individually and in combination, and that their effect is enhanced by interaction with environmental factors such as snow duration.

**Résumé :** L'infection causée par le noir (*Herpotrichia juniperi* (Duby) Petr.) et le broutage des ongulés influencent la croissance des gaules d'épicéa commun dans les forêts subalpines des Alpes européennes. Pour isoler les impacts du broutage artificiel (taille des pousses) et du noir sur la croissance, nous avons réalisé une expérience sur le terrain pendant deux ans avec des gaules plantées dans des trouées dans la zone subalpine des Alpes suisses. Durant la première année, (2003), les gaules ont légèrement répondu de façon positive à la taille et de façon négative au noir; le comportement des gaules était différent selon la station (ANOVA,  $r^2 = 0,35$ ). En 2004, les gaules ont réagi négativement à la taille, à l'infection causée par le noir, à la longue période d'enneigement et à l'ombre fait par la végétation au sol (ANOVA,  $r^2 = 0,59$ ). La différence dans la croissance annuelle moyenne entre les gaules infectées et saines était importante; une longue période d'enneigement favorise le développement du noir. L'élimination de ces variables dans les modèles linéaires généraux a fortement diminué la performance des modèles ( $d^2 = 0,32$  pour le modèle complet,  $d^2 = 0,23$  sans taille des pousses,  $d^2 = 0,16$  sans couvert de neige). La croissance des gaules était négativement reliée à l'ombre que faisait la végétation au sol, particulièrement en 2004. Nous concluons que ces facteurs biotiques ont un impact important sur la croissance, tant individuellement que combinés, et que leur effet est accentué par l'interaction avec les facteurs environnementaux tels que la durée de la période d'enneigement.

[Traduit par la Rédaction]

## Introduction

Mountain forests provide water, resources, and habitat for flora and fauna (Bisaz et al. 1997) and protect human infra-

structure against landslides, rockfall, and avalanches (Schönenberger 2001). Regeneration of Norway spruce (*Picea abies* (L.) Karst.) is an essential component of forest dynamics in the European Alps (Kräuchi et al. 2000). For example, this species dominates a large fraction (83%) of the forested area in the Swiss Alps (Brändli 1999), often occurring naturally in pure stands. Thus, Norway spruce regeneration has been studied extensively. Browsing by ungulates (Bergquist et al. 2003a), infection by black snow mold (*Herpotrichia juniperi* (Duby) Petr.) (Bazzigher 1976), and competition by ground vegetation (Frehner 2002) were found to be important biological factors influencing growth.

Browsing on Norway spruce saplings by ungulates was identified as an important factor in the dynamics of Swiss montane forests (e.g., Eiberle 1978; Kupferschmid and Bugmann 2005), German mountain forests (e.g., El Kateb et

Received 17 November 2005. Accepted 30 May 2006.  
Published on the NRC Research Press Web site at  
<http://cjfr.nrc.ca> on 22 November 2006.

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al. 2004), and southern Swedish forests (e.g., Bergquist et al. 2003a), and in many other regions around the globe. A large number of field studies have focused on the impacts of ungulate browsing on spruce sapling growth. Typically, light to moderate browsing was found to stimulate height and branch growth (Welch et al. 1992) even when repeated (Bergquist et al. 2003b), whereas severe browsing strongly reduced stem diameter and branch growth (Eiberle 1978; Bergquist et al. 2003a). Similar effects were found for other conifers (e.g., Saunders and Puettmann 1999). Thus, depending on the intensity and frequency of browsing (Canham et al. 1994), a long-term reduction of sapling growth may be induced. Evidence of the impact of browsing acting in isolation has been used to project long-term forest dynamics under enhanced ungulate browsing (e.g., Kienast et al. 1999). In reality, however, browsing interacts with many other biotic factors, and to our knowledge no study has analyzed the impact of severe clipping on Norway spruce sapling growth in combination with other biotic factors, such as snow mold infection and competition by ground vegetation.

In addition to ungulate browsing, infection by pathogens is considered a key factor for growth and mortality of Norway spruce saplings (Bazzigher 1976). Some researchers have used planting (Imbeck 1983; Mayer 1999; Frehner 2002) and sowing (Brang 1998) experiments to investigate (mostly qualitatively) the host–pathogen relationship between young Norway spruce and black snow mold, and have suggested that snow mold coverage is negatively correlated with growth. The ecology of black snow mold has been described in the literature (Simms 1967; Hartig 1988), yet in only one laboratory experiment (Gäumann et al. 1934) and one 10 year field study (Zolbrist 1950) have its development, growth, and spread been rigorously investigated. Snow mold spreads most rapidly at high temperatures (15 °C) accompanied by high relative humidity (Gäumann et al. 1934) in a laboratory setting, but this combination of factors is impossible to find in a natural snow environment. Thus, questions remain regarding the behavior of snow mold and the conditions necessary for snow mold infection and spread in a natural setting. In addition, to the best of our knowledge there has been no field investigation in which host saplings were artificially inoculated to track infection subsequent infection.

Ground vegetation competes with tree saplings for light, water, and nutrients (Grace and Tilman 1990; Oliver and Larson 1990), and may have an even stronger impact on sapling growth than overstory trees (Lundqvist and Fridman 1996) because tall herbs compete for light with saplings and reduce soil warming (Brang 1998; Michalet et al. 2003). Ground vegetation also competes with saplings for soil moisture and nutrients (Nilsson and Örlander 1995; Bergh et al. 1999). For example, dense ground vegetation restrained diameter growth (and to a lesser extent height growth) of Engelmann spruce saplings by reducing soil temperature and moisture (Coates et al. 1991). However, spruce planted in peat pots (with no fertilizer added) were found to grow slightly better with increased cover of ground vegetation (cf. Dolling 1996; Frehner 2002). This indicates that when soil resources are not limiting, or planted saplings are growing not in native soil but in peat pots, the influence of shading on growth is not conclusive.

Thus, further research is needed in two areas. First, the combined impact of browsing, snow mold infection, and competition by ground vegetation on Norway spruce sapling growth should be investigated. The spatial pattern of browsing and snow mold infection is quite complex in nature, so these factors are difficult to isolate in the field, which makes a controlled field experiment desirable. Second, snow mold occurrence was analyzed in Norway spruce (Imbeck 1987; Mayer 1999; Frehner 2002) and Engelmann spruce forests (Hessl and Baker 1997) where trees had been infected naturally. No study to date has looked at the spread of snow mold from known infection sources (inoculated saplings) in a controlled field experiment.

With the present research we aim to answer two questions. First, what is the individual and combined effect of artificial browsing (clipping), snow mold infection, and competition by ground vegetation on aboveground growth of Norway spruce saplings? Second, what biotic and abiotic conditions promote snow mold infection and thus the spread of this biotic agent in Norway spruce sapling populations?

## Material and methods

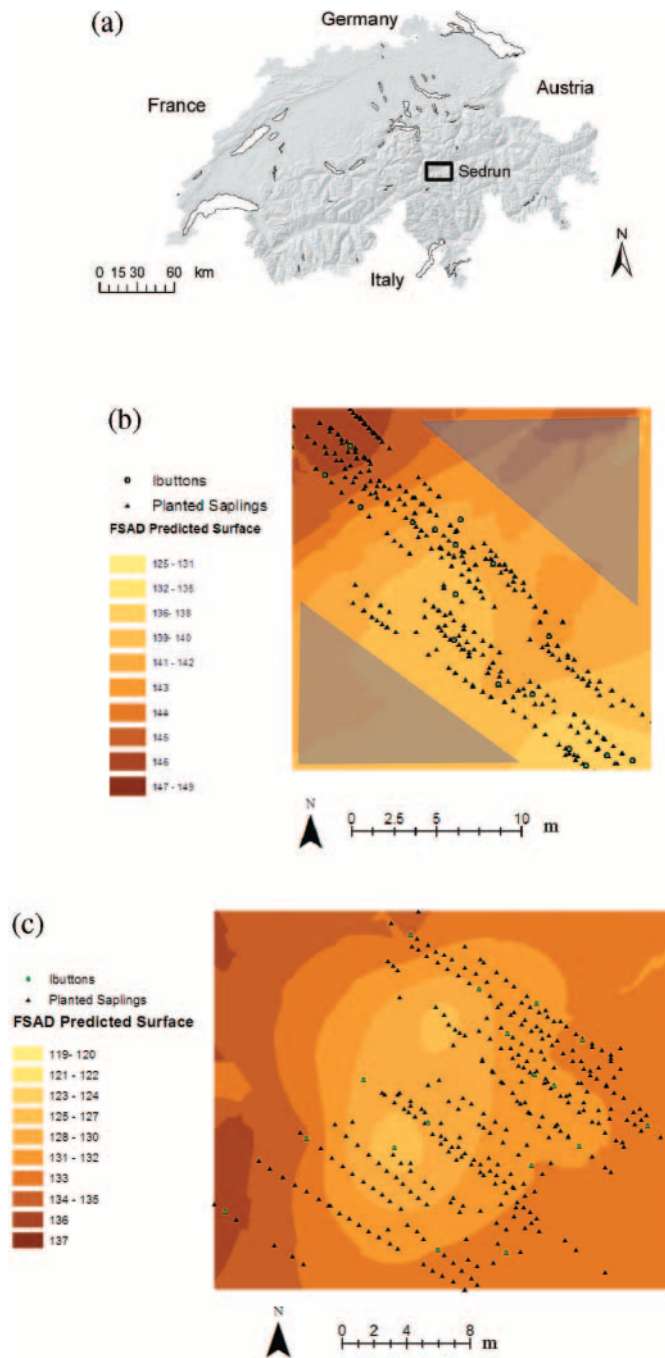
### Study site and experimental design

We conducted a field experiment in two similar forest openings near the ETHZ Research Forest in the community of Sedrun (Canton of Graubünden, Switzerland; Fig. 1a). Summer and winter temperatures were higher and precipitation and maximum snow depth were lower in the second year of investigation (2004) than in the first year (2003) (Table 1). Maximum snow height (average for 2002–2005) was 86 cm at the Disentis snow station (1190 m), whereas it was 203 cm at the Gütsch station (2287 m). The snow finally melted on 15 May (average for 2002–2005) in Disentis and persisted until 15 June in Gütsch.

The two forest openings ( $\approx 350 \text{ m}^2$ ) are located on the same north-facing (305°) slope in the subalpine zone at 1590 and 1750 m a.s.l., respectively, and were selected because of their proximity and similar aspects. Struck by the 1990 Vivian windstorm, these forests then experienced an outbreak of the European spruce bark beetle (*Ips typographus* L.) and were cleared of overstory trees. Slope inclination averaged 23° and 18° in the upper and lower openings, respectively. Vegetation in the upper opening included highly abundant *Adenostyles alliariae* (Gouan) Kerner and ferns such as *Dryopteris dilatata* (Hoffm.) Gray and *Athyrium distentifolium* Tausch ex Opiz, whereas vegetation in the lower opening was dominated by *Rubus idaeus* L., *Epilobium angustifolium* L., and *Equisetum sylvaticum* L. Soils in both openings are characterized by humo-ferric podzols on slate rock (Frehner 2002).

In the center of each opening we created an experimental site (Figs. 1b and 1c) to minimize forest-edge influences (Drobyshev 1999). The size of site 1 (1750 m a.s.l.) was 15 m × 35 m and the size of site 2 (1590 m a.s.l.) was 20 m × 20 m. Prior to planting, resident ground vegetation was cleared. However, to investigate the impacts of shading on growth we allowed it to reestablish. Permanent wire fences (1.5 m tall) were constructed around the perimeter of each site to prevent browsing by ungulates. We observed no damage caused by small mammals on the planted trees and

**Fig. 1.** (a) Hillshade map of Switzerland showing the location of Sedrun. (b and c) Surfaces of final snow ablation date (FSAD) in Julian days (2004) for planting site 1 (1750 m a.s.l.) and site 2 (1590 m a.s.l.), respectively. Ordinary kriging (cf. Cressie 1991) was used for interpolation. The calculated surfaces were cropped to the core sampling area (cf. shaded area in b). Measured values from iButton temperature loggers were used to calculate the FSAD surface and to provide temperature values for each planted sapling.



found no evidence of mice, hare pelts, or fox droppings within the sites.

#### Planted Norway spruce saplings

In June 2002 we purchased 661 three-year-old spruce saplings (3/1) of the Frauenkirch provenance (1600–1900 m

a.s.l.) that were approximately 15–20 cm tall (from a nursery in Rodels, Switzerland, situated at 797 m a.s.l.). Saplings were refrigerated and remained dormant until they were transported into degradable peat pots to reduce planting shock (Nilsson and Örlander 1995) and avoid contamination by insects (e.g., large pine weevil, *Hylobius abietis* L.) (Thorsen et al. 2001) or root pathogens (Piri 2003). Although we transferred saplings to a considerably higher elevation (ca. +650 m), no signs of stress were detected after transport, and the potted saplings were stored at 1500 m a.s.l. for 2 months before planting.

The saplings were planted in July–August 2002 along a fixed grid (oriented northeast–southwest) and in staggered rows (across the slope), but slash piles and tree stumps within both sites prevented the creation of a strict grid design (Figs. 1b and 1c). We attempted to reduce spatial autocorrelation among neighbors by planting at approximately 1 m intervals and to reduce the edge effect of the fence by creating a 1 m wide buffer zone around the perimeter. We planted trees to the depth of the pots (~15 cm), with 5 cm deep wells to trap water (Turner et al. 1982), and took care to exclude air pockets around the root zone (Nilsson and Örlander 1995). Summer 2002 was fairly wet, and saplings received rain immediately after planting. The combination of high-quality planting stock, careful manual planting, and favorable weather may partly explain why sapling mortality reached only 2% in 2002–2003 and less than 1% in 2003–2004. For comparison, in the study by Frehner (2002), saplings in the same region exhibited a 7.4% mortality rate 5 years after planting. We used distance and azimuth readings from a baseline point in the upper left (northwest) corner of each site to determine the exact location of each sapling.

As a proxy for aboveground growth, we measured the annual elongation (cm) of all the branches of the uppermost two whorls of each sapling. The sum of these measurements per sapling is referred to as primary growth (cf. Cunningham et al. 2006). Growth was recorded in late September of 2003 and 2004, i.e., at the end of the growing season (Bergh et al. 1999). Measurements were taken with a metric ruler from the base of the previous year's bud scar to the tip of the terminal bud.

#### Biological treatments and competition by ground vegetation

Each sapling received one of four stochastically assigned treatments: (1) clipping of all new shoots (artificial browsing), (2) inoculation with black snow mold, (3) a combination of clipping and snow mold inoculation, and (4) no treatment (control). Trees assigned to the browsing treatment were clipped of all new growth 3 weeks after snowmelt in the first sampling year (2003) to simulate early-spring browsing by ungulates (Bergstrom and Danell 1987; Canham et al. 1994). Trees assigned to the snow mold treatment were inoculated with a strain of black snow mold from Sedrun (strain 00522.4 preserved as a pure culture in the ETHZ Forest Pathology Laboratory). Pieces of mycelium from this strain were cultivated on malt-extract agar (2% w/v malt extract, 1.5% w/v agar) in Petri dishes at 4 °C for 2.5 months. A bundle of spruce needles on a branch section (4 cm long) was then overgrown with snow mold by incubat-

**Table 1.** Average summer (15 April – 15 October) and winter (16 October – 14 April) temperatures and precipitation.

Year and station <sup>a</sup>	Elevation (m a.s.l.)	Summer/winter temp. (°C)	Summer/winter precipitation (mm/day)
2002–2003			
Disentis	1190	11.4/–0.8	2.3/4.0
Gütsch/Andermatt	2287	6.4/–5.1	2.7/4.8
2003–2004			
Disentis	1190	14.5/1.0	1.0/1.1
Gütsch/Andermatt	2287	11.1/–1.3	1.1/1.8

<sup>a</sup>Meteo Swiss ANETZ stations from which the data were obtained.

**Table 2.** Summary statistics for final snow ablation date (FSAD) in 2003 and 2004 for site 1 (1750 m a.s.l.) and site 2 (1590 m a.s.l.).

Year	Site	FSAD (Julian days)				Ordinary kriging					
		Mean	Min.	Max.	Min. – max.	Range	Sill	Nugget	Lag distance	Lag No.	SE <sup>a</sup>
2003	1	117	114	120	6	3.53	4.13	3.22	0.52	12	2.48
	2	122	117	126	9	4.03	5.28	3.30	0.73	12	2.56
2004	1	141	125	149	24	27.74	34.07	15.03	2.56	10	4.08
	2	132	119	137	18	27.00	34.00	9.00	2.50	10	4.58

**Note:** Values are given for models of the FSAD surface determined by ordinary kriging (cf. Cressie 1991) for each site for each year. For a further description of parameters see the text.

<sup>a</sup>Standard error of the model.

ing it for 2 months at 4 °C and 1 month at 15 °C before field application in autumn 2002. The infected branch sections were securely (but loosely) attached with thin, flexible wire to the main stem directly below the crown of each sapling. Infection of the saplings (i.e., symptomatic evidence in the form of black felt-like mats) was assessed as the fraction of the sapling crown covered by black felt-like mats to 5% accuracy.

The density of reestablished ground vegetation within the experimental sites was recorded in August 2003. Coarse levels of shading were defined as 100%, 50%, or 0%, based on the area within a 0.5 m radius around each sample tree that was shaded by ground vegetation. We did not intend to evaluate competition for nutrients and water between saplings and ground vegetation, and thus did not measure belowground sapling growth or soil conditions.

Snow mold and clipping treatments were not reapplied in 2003–2004, but the levels of shading by ground vegetation were estimated again in August 2004. In 2004 we performed laboratory tests on a randomly selected subsample of 25 trees taken from the planting sites to evaluate the viability of the black snow mold inoculum and to confirm infection (where evident) with black snow mold. Viability was tested by inoculating water agar plates with infested branch sections, incubating them at 4 °C, transferring the hyphae to malt-extract agar (2% w/v malt extract, 1.5% w/v agar) and inspecting colony morphology after 2 months. Genetic analyses to distinguish wild strains of black snow mold from the inoculated strain were not performed.

#### Determination of snow duration at the sites with planted saplings (2003 and 2004)

In late autumn 2002 we placed iButton temperature loggers (Anonymous 2005) on the soil surface at random points

in the planting areas (94 loggers at 1750 m a.s.l., and 71 loggers at 1590 m a.s.l.). Because the number of available loggers was limited in 2004 and snow cover was relatively homogeneous in 2003 (Table 2, Figs. 1b and 1c), we placed only 18 loggers randomly throughout each of the planting sites in 2004.

The loggers were programmed to record ambient temperature (°C) every 3 h for a period of 285 days beginning on 15 October each year. After 15 June each year we collected them from the planting sites and transferred the time and temperature information to a PC using the iButton Viewer software (Anonymous 2005). Coordinates of the loggers were also calculated at the time of recovery with reference to a baseline point. Temperature readings for all iButtons at room temperature exhibited a precision of  $\pm 1$  °C with an error probability of 0.001. Logged temperature data were processed with a Visual Basic macro in Microsoft Excel<sup>®</sup> to calculate a Julian date for final snow ablation (i.e., snowmelt). Loggers record high daily temperature amplitudes on days with little (<10 cm depth) or no snow cover, so it is possible to determine the presence or absence of snow on a daily time step (Gottfried et al. 2002; Cunningham et al. 2006).

We created a surface of final snow ablation dates (FSAD) for each of the planting areas and for each year (2003 and 2004) by interpolating FSAD with ordinary kriging in ArcGIS<sup>®</sup> version 8.2 geospatial analyst (Cressie 1991). Kriging is based on semivariograms and allows for fitting three basic parameters (nugget, sill, range; cf. Table 2, Figs. 1b and 1c) to optimize the prediction to the given surface (the experimental sites) between measured points. A general but detailed description of kriging and its application is given in Cressie (1991), and a study in which the method was used specifically in the context of snow-cover dynamics

**Table 3.** Summary information for continuous variables (C) and ordinal variables (O) used in ANOVA models.

Code	Description	Type of variable	Range	Level 1	Level 2	Level 3	Level 4
PG2003	Primary growth in 2003 (cm)	C	0–49.5				
PG2004	Primary growth in 2004 (cm)	C	0–124				
FSAD2003	Final snow ablation date (Julian day)	C	114–126				
FSAD2004	Final snow ablation date (Julian day)	C	119–149				
SM2004	Amount of snow mold infection (5% classes)	C	0–100				
SURFT	Soil-surface temp. (°C) after FSAD <sup>a</sup>	C	3.3–13				
SITE	Experimental site	O	—	1750 m (264) C (144)	1590 m (327) SM (142)	C and SM (135) Control (209)	Control (138)
TREAT	Biological treatment in 2002–2003	O	—	~100% (114)	~50% (237)		
COMP2003	Ground vegetation cover in 2003	O	—	~100% (225)	~50% (187)		
COMP2004	Ground vegetation cover in 2004	O	—				

**Note:** Values in parentheses are corresponding numbers of observations for each level of each factor. Levels of treatment are clipping (C), snow mold inoculation (SM), clipping plus snow mold inoculation (C and SM), and control. Sample sizes represent the population after the removal of dead and non-relocated trees.

<sup>a</sup>Mean daily surface temperature for the 2 week period following final snow ablation.

can be found in Erickson (2004). Lastly, a few trees that were located outside the interpolated area in 2003 were not used in the analysis.

### Statistical analyses

We used ANOVA to analyze sapling growth in response to treatments with black snow mold and simulated browsing for 2003 and 2004 separately. Ground vegetation (classified into three levels of shading) and planting site (upper and lower) were used in the models as well. FSAD in 2003 and 2004, the percentage of the crown infested by snow mold (SM2004), and primary growth in 2003 (PG2003, only relevant for 2004) were the continuous variables in the ANOVA (Table 3). Initial tree size was a strong predictor of growth for large (22–62 cm tall) black spruce saplings 8 years after planting (Jobidon et al. 2003), and aboveground biomass was positively correlated with growth for several conifer species (Mitchell et al. 2003). However, we did not consider initial tree size in the analysis for 2003 because size variation among the saplings in our planting experiment was small (all were ca. 15–20 cm tall), and tree size was not found to be a significant predictor of the primary growth of Norway spruce saplings of similar sizes (Cunningham et al. 2006).

We ran type III ANOVA models using a sum of squares approach for an unbalanced design because the ranking of variables remains stable regardless of their order in the linear equation (Sokal and Rohlf 1995). The sample sizes were not identical within levels for all tested factors (Table 3), but ANOVAs are robust with respect to moderate inequality of sample size within factor levels (Zar 1999). We also ran models with transformations of the continuous explanatory variables, but they did not improve the model fit and thus were not considered further. Outliers were not removed because their inclusion did not compromise model results. Model summaries for 2003 and 2004 included ANOVA test results and the estimated coefficients for each continuous variable as well as for each level of all significant factors (Table 4). Multiple pairwise comparisons for the treatment factor were performed using Scheffé's method, which allows for simultaneous comparison among multiple combinations of factor levels (Zar 1999). Tukey–Anscombe plots (Anscombe and Tukey 1963) were consulted to evaluate the distribution of residuals for all models.

To analyze black snow mold infection (evident on many trees only in 2004), we employed generalized linear models (GLMs) of the binomial family (Sokal and Rohlf 1995). Presence/absence of snow mold infection (SM) was related to a combination of snow duration (FSAD, continuous variable), clipping (simulated browsing, binary), soil-surface temperature 2 weeks after final snowmelt (SURFT, continuous), and competition by ground vegetation (COMP, binary). Model statistics that we report here include  $d^2$  (equivalent to  $R^2$  in linear regression) as a measure of calibration strength to the training data set (Guisan and Zimmermann 2000). Leave-one-out cross-validation (LOU-CV) was used to evaluate the predictive power of the selected models (Bühlmann 2005). We report the correct classification rate (CCR) and  $\kappa$  as measures of accuracy (Fielding and Bell 1997);  $\kappa$  is especially useful because it is sensitive to prevalence (Fielding and Bell 1997). We determined the cut level of the binary re-

**Table 4.** Summary results from ANOVAs for growth of planted saplings in 2003 (model 1) and in 2004 (model 2).

	df	<i>p</i>	Coefficient <sup>a</sup>			
			1	2	3	4
Model 1, 2003 ( <i>r</i> <sup>2</sup> = 0.35)						
Intercept			37.7			
TREAT	3	<0.001	4.34	-5.50	-4.60	0
COMP2003	2	0.220	-0.78	0.10	0	
FSAD2003	1	0.493	-0.20			
SITE	1	0.008	-9.21	0		
SITE × FSAD2003	1	0.009	0.77			
Residuals	425					
Model 2, 2004 ( <i>r</i> <sup>2</sup> = 0.59)						
Intercept			72.1			
TREAT	3	0.003	-1.71	-3.19	-2.90	0
COMP2004	2	0.034	-1.25	-1.18	0	
FSAD2004	1	0.023	-0.70			
SITE	1	0.161	2.27	0		
SM2004	1	0.002	-1.93			
PG2003	1	0.005	0.55			
FSAD × SM2004	1	0.010	-0.01			
TREAT × SM2004	3	0.019	-0.06	0.05	0.06	0
Residuals	515					

**Note:** Estimated coefficients are for continuous variables (FSAD, SM, PG) and for levels of factors (SITE, TREAT, COMP; for descriptions see Table 3). Levels of factors (1–4) correspond to levels 1–4 in Table 3. <sup>a</sup>0 indicates the level used as the baseline for calculating the coefficients.

**Table 5.** Summary results from GLMs for predicting presence/absence of black snow mold (*Herpotrichia juniperi*) in 2004 (inoculated and noninoculated trees).

	Full model	No clipping	No FSAD
Model-fit criterion			
<i>n</i>	561	561	561
Adjusted <i>d</i> <sup>2</sup>	0.31	0.23	0.16
Correct classification rate (CCR)	0.78	0.77	0.72
κ	0.56	0.55	0.44
Threshold	0.55	0.45	0.6
Model fit (parameter estimates)			
Clipping (yes/no)	1.65***		1.37***
FSAD	0.22***	0.2***	
SURFT	-0.16**	-0.14*	-0.3***
COMP2004 (yes/no)	0.57*	0.49*	1.08***

**Note:** The *d*<sup>2</sup> value is reported as a measure of calibration strength. The correct classification rate (CCR) and κ are measures of model accuracy. Parameter estimates with corresponding *p* values are given. See Table 3 for descriptions of variables. Significance levels are as follows: \*, *p* = 0.05–0.01; \*\*, *p* = 0.01–0.001; \*\*\*, *p* < 0.001.

sponse for the predicted probabilities in LOU-CV by varying the cut level in 5% steps and evaluating model output for each cut level using κ (Table 5).

## Results

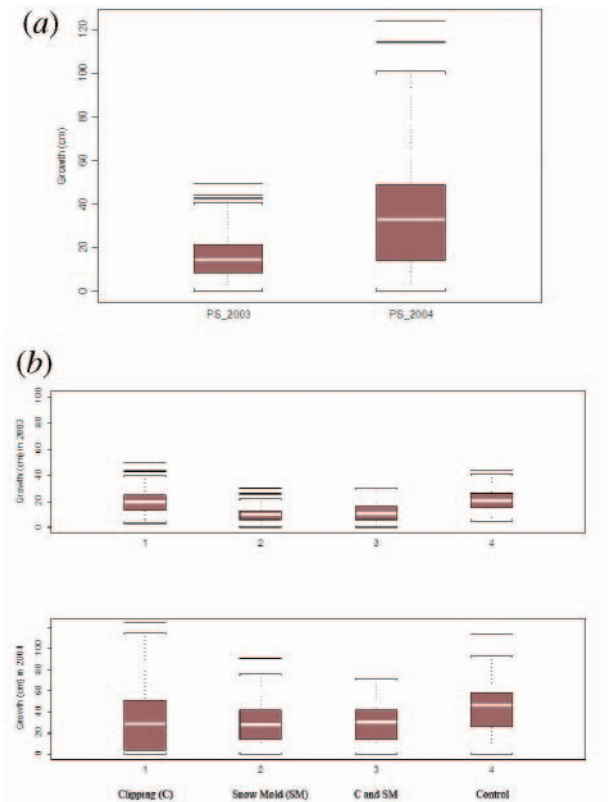
### Primary growth in 2003

Maximum primary growth of planted saplings in 2003 was 50 cm, but most saplings grew between 5 and 20 cm (Fig. 2a). The treatment and planting site significantly influenced sapling growth in 2003 (Table 4). Interaction terms were highly insignificant (*p* > 0.75) in most cases, with the

exception of the planting site combined with FSAD (SITE × FSAD). Tukey–Anscombe plots (Anscombe and Tukey 1963) suggested a normal distribution of residuals for the 2003 growth model.

Clipped saplings grew slightly more and saplings inoculated with snow mold grew less than control trees (model 1; Table 4). In the first year, clipped saplings were predicted to grow more (≈9 cm/year) than saplings assigned both the inoculation treatment and the clipping treatment (≈7 cm/year) (Figs. 3a and 3b). However, for the bulk of clipped saplings growth was similar to that of control trees, with a few exceptions (Fig. 2b). Conversely, the predicted rate of growth of

**Fig. 2.** Box plots identifying the middle 50%, the median (white line), and the extremes (whiskers) of primary growth (raw values) in 2003 and 2004 for all planted saplings ( $n = 591$ ) (a) and for all saplings according to treatment level (b).



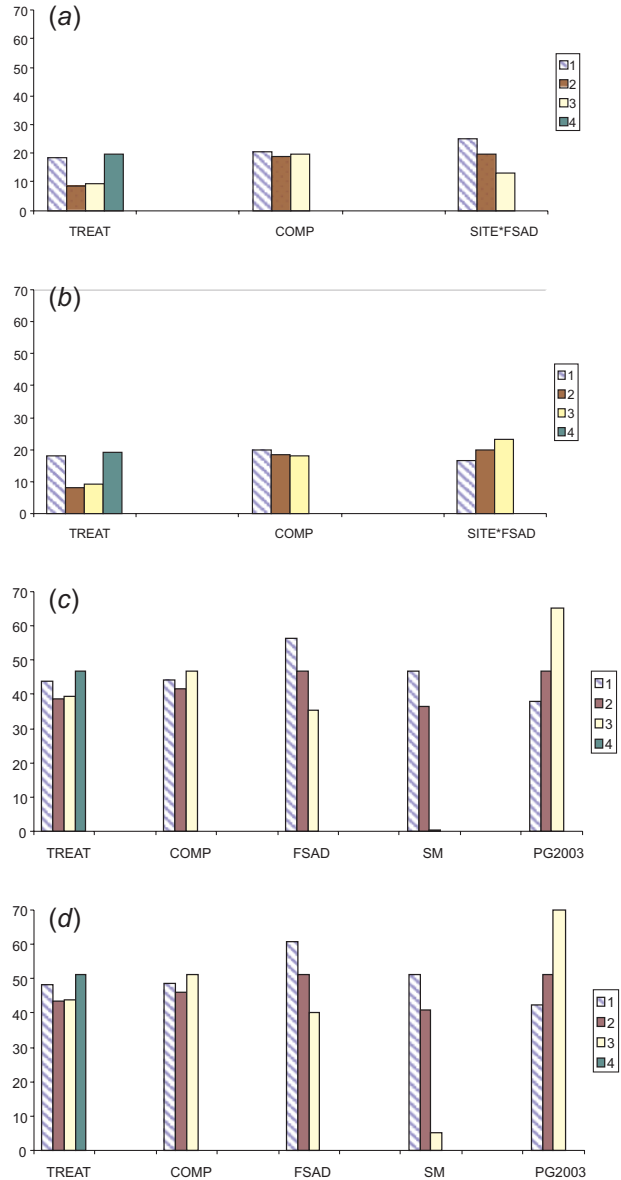
inoculated saplings was noticeably lower than that of control trees (Figs. 3a and 3b), even though infection of only two inoculated saplings was visible in 2003. A pairwise comparison among treatment levels (using Scheffé’s method for multiple comparisons (not shown)) revealed significant differences in 2003 between all treatment levels and control trees, with the exception of “clipped only” saplings and control saplings, and “clipped only” saplings and “clipped and inoculated” saplings.

In August 2003, 114 saplings were 100% shaded and 237 saplings were 50% shaded by ground vegetation (Table 3). However, ground vegetation did not significantly influence their growth in the first growing season (model 1 in Table 4). FSAD was only significant for growth in relation to the site (cf. factor SITE × FSAD,  $p = 0.01$ ; Table 4). Early snowmelt corresponded to higher sapling growth rates in the upper site (1), whereas later snowmelt corresponded to slightly higher growth rates in the lower site (2) (Figs. 3a and 3b). Thus, in the first growing season the primary growth of saplings was slightly enhanced by clipping, restrained by snow mold inoculation, though few saplings showed visible symptoms, and only marginally affected by ground vegetation and snow duration.

**Primary growth in 2004**

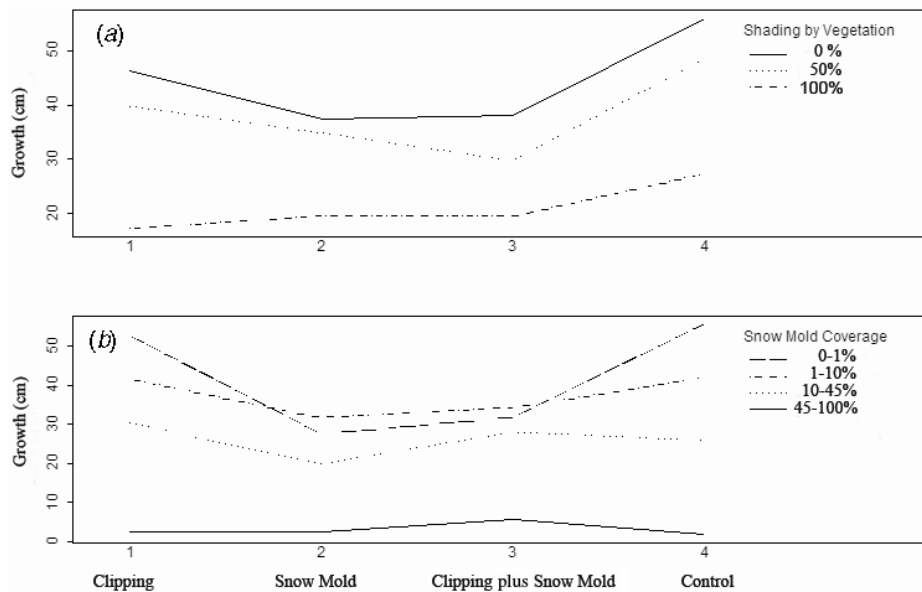
In general, saplings grew better in 2004 than in 2003. Maximum primary growth increased in the second year from 50 cm in 2003 to 124 cm in 2004, and median primary

**Fig. 3.** Predicted primary growth (cm) of saplings in 2003 for site 1 (1750 m a.s.l.) (a) and site 2 (1590 m a.s.l.) (b) and in 2004 for site 1 (c) and site 2 (d). Predictions are based on the best fitting ANOVA for each year (Table 4). Median values for explanatory variables constitute the baseline model. Growth values are for levels 1–4 for treatment (TREAT) and levels 1–3 for competition (COMP), and are minimum (level 1), mean (level 2), and maximum (level 3) for the continuous variables (FSAD, SM, and PG2003). For a description of codes see Table 3.



growth shifted from 15 to 35 cm (Fig. 2a). Additionally, mean annual growth per branch (leader shoot and uppermost two whorls) increased more than twofold (from 3.0 to 6.6 cm) and from 6.3 to 13.0 cm, respectively). Shading by ground vegetation, snow duration, and snow mold infection significantly influenced sapling growth (model 2 in Table 4). Most interaction terms did not contribute to a better fit of the models to the data (e.g., FSAD × SITE;  $p = 0.67$ ), with the exception of SM2004 × TREAT and SITE × SM2004

**Fig. 4.** Interaction plots of treatment levels 1–4 (clipping, snow mold inoculation, clipping plus snow mold inoculation, and control) according to % shading by ground vegetation (a) and % snow mold coverage (infection) (b) in 2004 plotted against primary growth.



(model 2 in Table 4). Tukey–Anscombe plots generally exhibited a normal distribution of residuals.

In 2004, primary growth was predicted to be 8 cm lower for inoculated trees (and for inoculated and clipped trees) than for control trees in both sites (Figs. 3c and 3d). Primary growth of clipped trees was higher in 2004 (mean 26 cm) than in 2003 (mean 9 cm), but growth of clipped trees in 2004 was significantly lower ( $\approx 8$  cm) than that of control trees (cf. Table 4, Fig. 2b). Clipped trees also exhibited increased branching in the second year; the maximum number of branches was 9 in 2003 and 45 in 2004.

The number of saplings visibly infected by snow mold increased from 2 in 2003 to 287 in 2004. Both inoculated trees (145 out of 277) and noninoculated trees (142 out of 385) were infected in 2004, and infection contributed significantly to the reduction in sapling growth (cf. SM2004; model 2 in Table 4). Inoculated trees exhibited only a slightly stronger tendency toward infection (cf. the interaction between treatment level and infection; model 2 in Table 4). While the difference in predicted primary growth rates between saplings whose crowns were not covered by snow mold (0%) and those with average coverage (22%) was only 11 cm for both sites; the difference in growth between saplings with 0% and 100% coverage was ca. 45 cm for both sites (Figs. 3c and 3d). Saplings showed a threshold for snow mold infestation at about 45% crown coverage (Fig. 4b), meaning that at higher percentages of snow mold coverage, very low growth rates were found. No fruiting bodies of snow mold were observed in the field or in the laboratory, but re-isolations in the laboratory from randomly selected saplings with visible snow mold symptoms (8 inoculated and 17 noninoculated saplings) indicated cultures typical of *H. juniperi*.

The number of saplings exposed to  $>50\%$  shading by ground vegetation was larger in 2004 (Table 3), and increased shading was significantly correlated with reduced

growth of saplings relative to that of nonshaded trees in the second year (model 2 in Table 4). Increased shading corresponded to reduced growth for all treatments, but especially for the snow mold treatment and the combination of snow mold and clipping (Fig. 4a). This can be interpreted as an example of the effect of a combination of biological stress factors on growth. However, predicted primary growth of saplings that were 100% shaded was not very different ( $<5$  cm at both sites) from that of nonshaded saplings (Figs. 3c and 3d).

From 2003 to 2004 the main period of snow ablation (mean) shifted to later in spring by 24 and 10 days in the upper and lower sites, respectively (Table 2). Snow duration (FSAD) was correlated negatively with growth in 2004, and when combined with snow mold infection, it also had a negative impact (model 2 in Table 4). Predicted growth of saplings that were snow-free early, i.e., at the minimum FSAD (6 May for site 1, 30 April for site 2), was higher by 21 cm than that of saplings that were snow-free only at the maximum FSAD (30 May for site 1, 18 May for site 2; cf. Fig. 3).

Finally, primary growth of saplings in 2003 was significantly correlated with growth of saplings in 2004 (Table 4). Because large saplings tend to have higher growth rates than small saplings, primary growth in 2003 is also a proxy of tree size, which renders this result unsurprising. Saplings that grew most in 2003 ( $\max[\text{PG}_{2003}] \approx 50$  cm) were predicted to grow 27 cm more in 2004 than saplings that grew least in 2003 ( $\min[\text{PG}_{2003}] \approx 16$  cm). Therefore, although saplings grew more in the second year, their growth was restrained by the clipping and snow mold inoculation treatment (performed in 2002), infection by snow mold, shading by ground vegetation, and increased snow duration. In addition, the combination of competition and snow mold infection and infection and browsing further compromised the growth of saplings.

### Factors that determine the presence of snow mold

GLMs that included simulated browsing (clipping), snow duration (FSAD), soil-surface temperature 2 weeks after snowmelt (SURFT), and competition (shading) by ground vegetation (COMP\_2004) best explained the presence of snow mold ( $d^2 = 0.31$ ; Table 5). Longer snow duration, lower soil-surface temperatures, clipping, and (to a lesser extent) shading by ground vegetation were conducive to snow mold infection (Table 5). Removing simulated browsing (clipping) or snow duration (FSAD) from the full model reduced model performance much more than removal of the other tested variables ( $d^2 = 0.23$  and  $d^2 = 0.16$ , respectively; Table 5).

The measures of model accuracy (CCR and  $\kappa$ ) were similar between the full model and the model without clipping, which suggests that removing clipping did not strongly affect model accuracy (Table 5). The optimized threshold for the model without snow duration was slightly farther from 0.50 (at 0.60) than in the other models, and model accuracy was slightly lower (CCR = 0.72 and  $\kappa = 0.44$ ; Table 5). These results indicate that snow duration is more important to snow mold occurrence than the other variables tested. Taken together, clipping, late-lying snow, and to a lesser extent low soil-surface temperatures and shading by ground vegetation contributed to the enhanced snow mold occurrence in this field experiment.

## Discussion

### Relative importance of biotic factors for sapling growth in 2003 and 2004

The higher primary growth rates for saplings in 2004 than in 2003 may have been due partly to carbon allocation below ground in the first year after planting and partly to the larger size of the trees in the second year. The results of our study document the importance of ungulate browsing (simulated by clipping in our study) and snow mold infection for the growth of planted saplings. To a lesser extent, shading by ground vegetation and long snow duration were also found to restrain growth.

Although the clipping treatment consisted of removing all new growth from the leader shoot removed, saplings appear to have responded initially by compensating for the lost foliage, only exhibiting a marked reduction in aboveground growth compared with control trees in the second year. In the first year, saplings may have benefited from clipping because the treatment was done early in the growing season, so the amount of foliage lost was rather small (Canham et al. 1994), which led to strong (over)compensatory growth. Also, the treatment reduced the amount of transpiring tissue, hence it may have reduced susceptibility to drought. However, the northern slopes studied here are characterized by mesic soils, transplanting techniques were aimed at minimizing planting shock, and growth conditions were quite good in the subalpine zone of the Swiss Alps in 2003 (Jolly et al. 2005). Therefore, another explanation for the difference in response to clipping in the two years may be that clipping initially stimulated sapling height growth (overcompensation for the lost foliage, as was documented, for example, for Scots pine (*Pinus sylvestris* L.) and eastern white pine (*Pinus strobus* L.); cf. Saunders and Puettmann 1999). The

reduction in growth in the following year could have been due to the subsequent allocation of carbon to stem-diameter growth, and particularly root growth, as was shown for Scots pine and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) (Edenius et al. 1995; Vila et al. 2003). Finally, the increased branching of clipped trees observed in our study in 2004 may have contributed to the reduction in growth in the second year, as other researchers found for Norway spruce (Bergquist et al. 2003a) and Sitka spruce (Welch et al. 1992).

The negative correlation between snow mold inoculation (without signs of infection) and sapling growth in 2003 is difficult to explain. We surmise that growth inhibition by snow mold through unknown chemically induced processes or latent infection may have occurred. Regarding the latter, evidence of canopy infection by pathogenic fungi may be difficult to detect in the field without magnification (cf. Senn 1999). Therefore, it is possible that minor infection was present in 2003 on inoculated trees (and even on noninoculated trees, as ascospores can spread at any time; cf. Simms 1967), but it was not evident macroscopically until extensive spread occurred in 2004. Regarding the former, latent infection that negatively affects growth by means of toxins may have occurred (O. Holdenrieder, ETHZ, personal communication, 2005). However, to our knowledge little research has been conducted on the behavior of black snow mold that would support this hypothesis. Finally, it is not likely that tying the infected branch sections to host stems caused physical damage because the inocula were attached only loosely, and no stem damage was observed in 2004. To rule out this possibility, it would have been preferable to tie uninfected branch pieces to the saplings in the control group.

The extensive spread of snow mold in 2004 was strongly correlated with a reduction in sapling growth in our study. This is consistent with the results of other field investigations of Norway spruce (e.g., Brang 1998; Mayer 1999; Frehner 2002) and other species (e.g., Hessel and Baker 1997; Brang et al. 2003). However, the latent infection (or the delay of extensive macroscopic symptoms) by black snow mold that we observed has not yet, to our knowledge, been described and deserves further research. Other snow-dependent pathogens such as low-temperature basidiomycetes (Orr et al. 1996), *Gremmeniella abietina* (Lagerb.) Morrelet (Senn 1999), and *Heterobasidion parviporum* Niemelä & Korhonen (Piri and Korhonen 2001; Piri 2003) have exhibited a similar delay, hence it is reasonable to hypothesize that this mechanism may be operating also in the case of black snow mold.

The weak response of saplings to shading by ground vegetation in 2003 was most likely due to the very low abundance of competing vegetation at the sites. By removing ground vegetation before planting in 2002, we minimized the impact of shading on sapling growth in 2003 because re-establishment only occurred during summer. The negative correlation between increased ground vegetation cover and sapling growth that we found for 2004 is in agreement with textbook descriptions (Grace and Tilman 1990; Oliver and Larson 1990) and the results of field studies (Munson et al. 1993; Bergh et al. 1999; Kubner et al. 2000). However, the difference in growth between shaded and nonshaded trees in 2004 was only slight and may be explained by our coarse es-

timate of shading. Also, the weak (albeit significant) difference in growth between shaded and nonshaded saplings may have been partly due to the fact that we focused on shading effects and did not consider competition for soil resources (cf. Dolling 1996; Lundqvist and Fridman 1996). Finally, this result may reflect, in part, reduced sensitivity of above-ground primary growth (in contrast to estimates of stem-diameter growth or root growth) to the impacts of ground vegetation (in terms of light, nutrients, and water; cf. Munson et al. 1993), as was shown for black spruce (*Picea mariana* (Mill.) BSP) saplings (Kubner et al. 2000).

The significant influence of snow duration on growth in the second year is best explained, first, by the slightly later snowmelt and, second, by heavier snow mold infection induced by the late-laying snow. In 2004, late-lying snow in our study area, especially at the upper site (1750 m a.s.l.), probably overrode the difference in elevation between the sites, and thus contributed to the reduction in growth at both sites by shortening the growing season. This effect of late-lying snow was also found in observational studies (Cunningham et al. 2006) and modeling investigations (Bergh et al. 1998). In addition, the range of snowmelt dates within the two sites was larger for 2004 than for 2003, and thus provided a stronger signal. Also, snow mold infection is mediated by snow duration. Therefore, infection observed only in 2004 may partly explain the significant relationship between snow duration and sapling growth. This explanation is supported by results from a 20 year planting experiment in Switzerland (Senn 1999) in which 59.8% of planted Swiss stone pine (*Pinus cembra* L.) and 45.6% of Swiss mountain pine (*Pinus mugo* Turra) were killed by *G. abietina*, and mortality was highly correlated with snow duration.

### Factors conducive to snow mold infection

Artificially inoculated saplings showing symptoms of snow mold coverage (52% of the saplings treated with the inoculum) were likely infected by direct contact with the mycelium that was tied to the stems. Infected saplings that had not been artificially inoculated (142 trees) were likely infected by the Surrein strain from inoculated neighbors, either via contact or via ascospores. Since the distance between saplings was at least 0.5 m and no mycelium mats connecting one host with the other were observed, it seems most likely that this infection was induced by ascospores rather than by direct contact. Infection by a wild strain cannot be excluded for either group, but very little infection was observed on saplings in the surrounding forests.

Our results do not support the conclusion that the primary driver of snow mold infection is proximity to infected saplings, but rather that it is site conditions (e.g., snow duration or soil-surface temperature) and host susceptibility (e.g., weakening due to browsing). Although we can only partly explain the presence of snow mold on saplings with the factors included in the GLMs, the reduced explanatory power and the lower  $\kappa$  value of the model without the FSAD variable as compared with the full model clearly suggest a dependence of snow mold on snow cover. This result is in line with that reported by Simms (1967) for *H. juniperi*. Similar findings were also obtained in experimental studies for low-temperature basidiomycetes and *Plenodomus meliloti* Dearn. and GB Sanford (Orr et al. 1996). Further, reduced sapling

vigor due to clipping and (or) to a lesser extent to competition by ground vegetation may have been an important precondition for snow mold infection. Finally, the negative relationship between soil-surface temperatures 2 weeks after final snowmelt (SURFT) and snow mold infection is consistent with descriptions of *H. juniperi* (Hartig 1988) and suggests that higher temperatures are unfavorable to the growth of the mycelium in exposed environments.

### Implications and recommendations for further research

With this field experiment we aimed, ultimately, to quantify the influence of biotic factors on the growth of Norway spruce saplings and evaluate the interactions among these factors and with factors of the abiotic environment, primarily snow duration. An improved understanding of how browsing and competition by ground vegetation impact the susceptibility of saplings to snow mold infection would help forest managers make appropriate management decisions concerning, for example, the creation of forest gaps or the afforestation of sites.

Our results clearly show that as an example of a biotic stress factor for sapling growth, snow mold infection cannot be evaluated independently of site environmental conditions or host susceptibility to infection, which in turn are determined partly by abiotic and biotic influences. Since the climate will change over the coming decades because of anthropogenic trace gas emissions, it becomes crucial to better understand the interactions of the abiotic environment with biotic drivers of tree growth, such as snow mold infection and browsing. We recommend that future efforts to model long-term forest stand dynamics under the impacts of global climate change in mountainous regions include these interactions among abiotic and biotic factors influencing tree regeneration (cf. Bugmann 2001).

Finally, we recommend that future laboratory investigations focus on the infection behavior of snow mold to test the latent-infection hypothesis that we invoked to explain the observed negative response to inoculation, i.e., the lack of symptomatic evidence of infection. We also suggest that future field experiments include a dummy (sterile) inoculum to rule out the possibility of physical impacts of the inoculum that is attached to the stems of the saplings. In the long run, a subsample of the planted trees in our study should be destructively analyzed to investigate the responses of root biomass and radial growth to both clipping and competition by ground vegetation, as additional (and perhaps more sensitive) means to evaluate the impact of the biotic environment on the growth of Norway spruce saplings.

### Acknowledgements

This study has been funded by the Swiss Federal Institute of Technology (ETH) Zurich. The fencing costs were met by the ETH Department of Forest Science. A special thank you is extended to Adrian Deragisch and Corsin Flepp for permitting the study to be carried out in the forests they manage, for helping with site preparation, and for constructing the fences around the study areas. Andrew Quinn, Ingeborg Kump, Henrik Peel, and Simon Walbaum deserve credit for their contribution to tree planting and field measurement. We are grateful to Christof Birrer for his review of the statistical

methods used. We thank Ottmar Holdenrieder for allowing us to use the ETHZ pathology laboratory, for technical support in the laboratory, and for comments on the manuscript. Finally, we are grateful to Dr. Josef Senn, Dr. Felix Kienast, and three anonymous reviewers for their comments on an earlier version of the manuscript.

## References

- Anonymous. 2005. Revolutionary iButton temperature and humidity data loggers: iButton user's manual. Maxim Dallas Semiconductor, Dallas, Tex.
- Anscombe, F., and Tukey, J.W. 1963. The examination and analysis of residuals. *Technometrics*, **5**: 141–160.
- Bazzigher, G. 1976. Schwarzer Schneeschimmel der Koniferen [*Herpotrichia juniperi* (Duby) Petr. und *Herpotrichia coulteri* (Peck) Bose]. *Eur. J. For. Pathol.* **6**: 109–122.
- Bergh, J., Linder, S., Lundmark, T., and Elfving, B. 1999. The effect of water and nutrient availability on the productivity of Norway spruce in northern and southern Sweden. *For. Ecol. Manage.* **119**: 51–62.
- Bergh, J., McMurtrie, R.E., and Linder, S. 1998. Climatic factors controlling the productivity of Norway spruce: a model-based analysis. *For. Ecol. Manage.* **110**: 127–139.
- Bergquist, J., Bergstrom, R., and Zakharenka, A. 2003a. Responses of young Norway spruce (*Picea abies*) to winter browsing by roe deer (*Capreolus capreolus*): effects on height growth and stem morphology. *Scand. J. For. Res.* **18**: 368–376.
- Bergquist, J., Örlander, G., and Nilsson, U. 2003b. Interactions among forestry regeneration treatments, plant vigour and browsing damage by deer. *New For.* **25**: 25–40.
- Bergstrom, R., and Danell, K. 1987. Effects of simulated winter browsing by moose on morphology and biomass of two birch species. *Ecology*, **75**: 533–544.
- Bisaz, A., Escher, F., Grosjean, M., Ives, J.D., Messerli, B., and Price, M. 1997. Mountains of the world: challenges for the 21st century [booklet]. Paul Haupt Verlag, Bern, Switzerland.
- Brändli, U.B. 1999. Survey and interpretation of stand structure in the second Swiss National Forest Inventory. Swiss Federal Research Institute for Forest, Snow, and Landscape Research (WSL), Birmensdorf, Davos, Switzerland.
- Brang, P. 1998. Early seedling establishment of *Picea abies* in small forest gaps in the Swiss Alps. *Can. J. For. Res.* **28**: 626–629.
- Brang, P., Moran, J., Puttonen, P., and Vyse, A. 2003. Regeneration of *Picea engelmannii* and *Abies lasiocarpa* in high-elevation forests of south-central British Columbia depends on nurse logs. *For. Chron.* **79**: 273–279.
- Bugmann, H. 2001. A review of forest gap models. *Clim. Change*, **51**: 259–305.
- Bühlmann, P. 2005. Computational statistics. Seminar für Statistik, ETHZ, Zürich, Switzerland.
- Canham, C.D., McAninch, J.B., and Wood, D.M. 1994. Effects of the frequency, timing, and intensity of simulated browsing on growth and mortality of tree seedlings. *Can. J. For. Res.* **24**: 817–825.
- Coates, K.D., Emmingham, W.H., and Radosevich, S.R. 1991. Conifer-seedling success and microclimate at different levels of herb and shrub cover in a *Rhododendron-Vaccinium-Menziesia* community of south central British Columbia. *Can. J. For. Res.* **21**: 858–866.
- Cressie, N. 1991. Statistics for spatial data. John Wiley & Sons, New York.
- Cunningham, C., Bugmann, H., Zimmermann, N., and Stoeckli, V. 2006. Norway spruce sapling growth in Swiss mountain forests: Does spring climate matter? *For. Ecol. Manage.* **228**: 19–32.
- Dolling, A.H.U. 1996. Interference of bracken (*Pteridium aquilinum* L. Kuhn) with Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L. Karst.) seedling establishment. *For. Ecol. Manage.* **88**: 227–235.
- Drobyshev, I.V. 1999. Regeneration of Norway spruce in canopy gaps in *Sphagnum-Myrtillus* old-growth forests. *For. Ecol. Manage.* **115**: 71–83.
- Edenius, L., Danell, K., and Nyquist, H. 1995. Effects of simulated moose browsing on growth, mortality, and fecundity in Scots pine: relations to plant productivity. *Can. J. For. Res.* **25**: 529–535.
- Eiberle, K. 1978. Folgewirkungen eines simulierten Wildverbisses auf die Entwicklung junger Waldbäume. *Schweiz. Z. Forstwes.* **129**: 757–768.
- El Kateb, H., Benabdellah, B., Ammer, C., and Mosandl, R. 2004. Reforestation with native tree species using site preparation techniques for the restoration of woodlands degraded by air pollution in the Erzgebirge, Germany. *Eur. J. For. Res.* **123**: 117–126.
- Erickson, T.A. 2004. Development and application of geostatistical methods to modeling spatial variation in snowpack properties, Front Range, Colorado. University Press of Colorado, Boulder, Colo.
- Fielding, A.H., and Bell, J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* **24**: 38–49.
- Frehner, M. 2002. Untersuchungen über den Einfluss unterschiedlicher Kleinstandorte und der Pflanztechnik auf Fichtenpflanzungen in subalpinen Lawinenschutzwäldern. Ph.D. thesis, Swiss Federal Institute of Technology, Zürich, Switzerland.
- Gäumann, V.E., Roth, C., and Anliker, J. 1934. Über die Biologie der *Herpotrichia nigra* Hartig. *Z. Pflanzenkr. Pflanzenschutz*, **44**: 97–116.
- Gottfried, M., Pauli, H., Reiter, K., and Grabherr, G. 2002. Potential effects of climate change on alpine and nival plants in the Alps. *In Mountain biodiversity. Edited by C. Körner and E. Spehn.* The Parthenon Publishing Group, London. pp. 213–222.
- Grace, J.B., and Tilman, D. 1990. Perspectives on the determinants of competitive success. *In Perspectives on plant competition. Edited by J.B. Grace and D. Tilman.* Academic Press, San Diego, Calif. pp. 3–7.
- Guisan, A., and Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. *Ecol. Modell.* **135**: 147–186.
- Hartig, R. 1988. *Herpotrichia nigra*. *Allg. Forst Jagdztg.* **1**: 15–17.
- Hessl, A.E., and Baker, W.L. 1997. Spruce and fir regeneration and climate in the forest-tundra ecotone of Rocky Mountain National Park, Colorado, U.S.A. *Arct. Alp. Res.* **29**: 173–183.
- Imbeck, H. 1983. Schneeuntersuchungen in subalpinen Fichtenwäldern. *Schweiz. Z. Forstwes.* **134**: 925–928.
- Imbeck, H., and Ott, E. 1987. Verjüngungsökologische Untersuchungen in einem hochstaudenreichen subalpinen Fichtenwald, mit spezieller Berücksichtigung der Schneeablagerung und der Lawinenbildung. *Mitt. Eidgen. Inst. Schnee-Lawinenforsch.* **42**: 1–202.
- Jobidon, R., Roy, V., and Cyr, G. 2003. Net effect of competing vegetation on selected environmental conditions and performance of four spruce seedling stock sizes after eight years in Quebec (Canada). *Ann. For. Sci.* **60**: 691–699.
- Jolly, W.M., Dobbertin, M., Zimmermann, N.E., and Reichstein, M. 2005. Divergent vegetation growth responses to the 2003 heat wave in the Swiss Alps. *Geophys. Res. Lett.* **32**: 1–4.

- Kienast, F., Fritschi, J., Bissegger, M., and Abderhalden, W. 1999. Modeling successional patterns of high-elevation forests under changing herbivore pressure – responses at the landscape level. *For. Ecol. Manage.* **120**: 35–46.
- Kräuchi, N., Brang, P., and Schönenberger, W. 2000. Forests of mountainous regions: gaps in knowledge and research needs. *For. Ecol. Manage.* **132**: 73–82.
- Kubner, R., Reynolds, P., and Bell, F. 2000. Growth response of *Picea mariana* seedlings to competition for radiation. *Scand. J. For. Res.* **15**: 334–342.
- Kupferschmid, A.D., and Bugmann, H. 2005. Effect of microsites, logs, and ungulate browsing on *Picea abies* regeneration in a mountain forest. *For. Ecol. Manage.* **205**: 251–265.
- Lundqvist, L., and Fridman, E. 1996. Influence of local stand basal area on density and growth of regeneration in uneven-aged *Picea abies* stands. *Scand. J. For. Res.* **11**: 364–369.
- Mayer, A.C. 1999. Verjüngung in Bestandeslücken eines subalpinen Hochstauden-Fichtenwaldes. *Schweiz. Z. Forstwes.* **150**: 171–177.
- Michalet, R., Rolland, C., Joud, D., Gafta, D., and Callaway, R. 2003. Associations between canopy and understory species increase along a rainshadow gradient in the Alps: habitat heterogeneity or facilitation? *Plant Ecol.* **165**: 145–160.
- Mitchell, A.K., Dunsworth, B.G., Bown, T., and Moran, J.A. 2003. Above-ground biomass predicts growth limitation in amabilis fir and western hemlock seedlings. *For. Chron.* **79**: 285–290.
- Munson, A.D., Margolis, H.A., and Brand, D.G. 1993. Intensive silvicultural treatment: impacts on soil fertility and planted conifer response. *Soil Sci. Soc. Am. J.* **57**: 246–255.
- Nilsson, U., and Örlander, G. 1995. Effects of regeneration methods on drought damage to newly planted Norway spruce seedlings. *Can. J. For. Res.* **25**: 790–802.
- Oliver, C.D., and Larson, B.C. 1990. *Forest stand dynamics*. McGraw-Hill Inc., New York.
- Orr, D.D., Piening, L.J., Baron, V.S., and Burnett, P.A. 1996. Winter survival of snow mold inoculated alfalfa under varying levels of snow cover. *Can. J. Plant Pathol.* **18**: 242–246.
- Piri, T. 2003. Early development of root rot in young Norway spruce planted on sites infected by *Heterobasidion* in southern Finland. *Can. J. For. Res.* **33**: 604–611.
- Piri, T., and Korhonen, K. 2001. Infection of advance regeneration of Norway spruce by *Heterobasidion parviporum*. *Can. J. For. Res.* **31**: 937–942.
- Saunders, M., and Puettmann, K.J. 1999. Effects of overstory and understory competition and simulated herbivory on growth and survival of white pine (*Pinus strobus*) seedlings. *Can. J. For. Res.* **29**: 536–546.
- Schönenberger, W. 2001. Trends in mountain forest management in Switzerland. *Schweiz. Z. Forstwes.* **152**: 152–156.
- Senn, J. 1999. Tree mortality caused by *Gremmeniella abietina* in a subalpine afforestation in the central Alps and its relationship with duration of snow cover. *Eur. J. For. Pathol.* **29**: 65–74.
- Simms, H. 1967. On the ecology of *Herpotrichia nigra*. *Mycologia*, **59**: 902–909.
- Sokal, R.R., and Rohlf, F. 1995. *Biometry: the principles and practice of statistics in biological research*. W.H. Freeman and Co., New York.
- Thorsen, A., Mattsson, S., and Weslien, J. 2001. Influence of stem diameter on the survival and growth of containerized Norway spruce seedlings attacked by pine weevils (*Hylobius* spp.). *Scand. J. For. Res.* **16**: 54–66.
- Turner, H., Häsler, R., and Schönenberger, W. 1982. Contrasting microenvironments and their effects on carbon uptake and allocation by young conifers near alpine treeline in Switzerland. *In Proceedings of a IUFRO Workshop: Ecology of Subalpine Zones. Edited by R.H. Waring*. Forest Research Laboratory, Oregon State University, Corvallis, Oreg. pp. 22–30.
- Vila, B., Torre, F., Guibal, F., and Martin, J.L. 2003. Growth change of young *Picea sitchensis* in response to deer browsing. *For. Ecol. Manage.* **180**: 413–424.
- Welch, D., Staines, B.W., Scott, D., and French, D.D. 1992. Leader browsing by red and roe deer on young sitka spruce trees in western Scotland. II. Effects on growth and tree form. *Forestry (Oxf.)*, **65**: 309–330.
- Zar, J.H. 1999. *Biostatistical analysis*. Prentice Hall, Englewood Cliffs, N.J.
- Zolbrist, L. 1950. Zehn Jahre Versuche zur Bekämpfung des Schwarzen Schneeschimmels *Herpotrichia nigra* Hartig. *Schweiz. Z. Forstwes.* **101**: 632–642.