Effects of growth rates, tree morphology and site conditions on longevity of Norway spruce in the northern Swiss Alps

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Elisabeth Rötheli · Caroline Heiri · Christof Bigler

Abstract Longevity of trees is known to be associated with growth rates, but also with tree morphology and spatial influences. However, very little quantitative information is available on the effects of these biotic and abiotic influences on maximum ages of trees. The objectives of this study were to investigate the trade-off between longevity and growth rates of Norway spruce (*Picea abies*) and to quantify the effects of tree morphology and abiotic site conditions on longevity of this species. Data were collected along different topographical and climatic gradients in a 20 × 25 km study area in the northern part of the Swiss Alps (Glarus). The ages of the more than 100 sampled dead Norway spruces ranged between 50 and 367 years. Longevity of these trees was negatively related to tree growth, i.e. slow-growing trees tended to grow older than fast-growing trees. Tree height was positively associated with longevity for both upper and lower storey trees. Longevity of lower storey trees was increased with large crown diameter, but decreased with long crown length.

Upper storey trees growing at higher altitude tended to get older than at lower altitude. We conclude that the combined effects of growth rates, variability in site conditions and different traits of tree morphology determine tree longevity of Norway spruce in the Swiss Alps. Because longevity is tightly linked to mortality rates of tree populations, our study may improve our understanding of long-term processes of forest dynamics under current and future climate.

Keywords Norway spruce · Radial growth rates · Longevity · Upper storey · Lower storey · Tree morphology

Introduction

The remarkably long lifespan of trees has always fascinated researchers and nature lovers alike, and also nature conservancy has discovered the value of very old or large trees as flagships for protected areas. The lifespan of the oldest giant sequoias (*Sequoiadendron giganteum*) and bristlecone pines (*Pinus longaeva*) in the U.S. Southwest may extend over more than 3000 or 4000 years, respectively (Schulman 1954). In Europe, sessile oak (*Quercus petraea*) may grow for more than 800 years and Norway spruce (*Picea abies*) can achieve an age of 600–650 years (Amann 2004; Brang and Duc 2002). The question 'Which site- and tree-specific factors influence the long lifespan of trees?' has been of major interest to foresters and ecologists for a long time (Backman 1943; Leibundgut 1976; Molisch 1929; Møller 1957). Tree mortality processes, which characterize the last stage of a tree's life history, ultimately determine the length of the lifespan (i.e. longevity) of a tree. However, the underlying causes of tree mortality—in the absence of any disturbances such as fire or

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blowdown—are difficult to detect due to the sequence of interacting stressors such as competition, drought or fungi (Franklin et al. 1987; Keane et al. 2001). Thus, we currently lack a mechanistic understanding of long-term tree mortality processes. In the face of impending climate change, which will affect forest ecosystems and their goods and services to a yet unknown degree, a better understanding of site- and tree-specific influences on longevity and their effects on forest structures and dynamics is needed (Bugmann and Bigler 2011).

For different tree species in Europe and North America, a negative association between lifespan and radial growth has been indicated, i.e. slow-growing trees are likely to reach a higher lifespan than fast-growing trees (Bigler and Veblen 2009; Black et al. 2008; Larson 2001; Reynolds and Burke 2011; Ward 1982). Early hypotheses by Backman (1943) suggested that maximum growth rate is negatively related to longevity, and the age, when maximum growth rate is reached, is positively related to longevity. The allocation of resources into growth, into wood structures to increase mechanical stability and into defence mechanisms to prevent pathogen attacks may affect longevity. On the one hand, a higher investment in wood structures and defences entails a reduction of the growth rate and therefore a lower metabolism (Loehle 1988). Recently, lower metabolism activity in trees, which reflects the balance between respiration and photosynthesis, has been suggested as a potential mechanism to explain increased tree longevity (Issartel and Coiffard 2011). On the other hand, a lower investment in wood structures and defences may result in higher growth rates. Fast-growing trees benefit from competitive advantages, because rapid growth reduces the duration of the vulnerable period (Arendt 1997), during which the risk of damages related to browsing by deer or sapling mortality related to high shading is increased. However, a decreased investment of resources into the above or below ground biomass might increase the risk of uprooting because of a poorly developed root system or of windbreak because of low investment in mechanical stability (Larson 2001; Loehle 1988). In addition, fast-growing trees are more likely infected by pathogens (Reynolds and Burke 2011) and might reach their species-specific maximum tree height relatively early related to increased hydraulic resistance (Ryan and Yoder 1997), thus resulting in premature tree death.

Longevity is not only associated with growth rates, but also with morphological characteristics of trees such as stem or crown morphology and spatial influences such as abiotic site conditions (Bigler and Veblen 2009; Matthes et al. 2008). Specific features of tree morphology such as a low ratio of height to diameter growth, sparse foliage or stunted size seem to be indicators of high lifespan in some conifer species (Matthes et al. 2008; Schulman 1954). Site conditions that prevail at extreme sites, for instance strong wind, low soil moisture and nutrients or low temperature, are known to create conditions, which are beneficial for reaching old ages (LaMarche 1969; Lanner 2002; Larson 2001; Schulman 1954). However, morphological characteristics and spatial influences have not been systematically included in studies on maximum ages of trees. Currently the only study we know of which relates ages of living trees (i.e. minimum longevities) to different influences of environmental heterogeneity and morphological characteristics of trees has been published by Matthes et al. (2008), which focussed on eastern white cedar (*Thuja occidentalis*) growing on cliffs in southern Ontario (Canada).

The objective of our study was to quantitatively investigate the trade-off between longevity and growth rates of dead Norway spruce (*Picea abies*) in the northern part of the Swiss Alps and to quantify the effects of morphological characteristics of trees and of abiotic site conditions on longevity of this species. We addressed the following research questions in our study:

1. Are different parameters of radial growth (i.e. early and late growth, maximum growth) associated with longevity of Norway spruce?
2. Does longevity of Norway spruce vary with tree morphology (i.e. tree height, crown diameter, crown length) and site conditions (i.e. altitude, slope steepness, aspect, relief)?

Materials and methods

Study area and tree species

Data were collected in the canton of Glarus in the northern Swiss Alps. The 14 stands sampled were distributed over an area of approximately 20 × 25 km and were located in the montane and subalpine belt between 1,180 and 1,920 m a.s.l. (Table 1). The climate is oceanic and affected by the foehn (warm and dry fall wind from the south); however, the climate becomes increasingly continental when moving southwards within the study area (Table 1). The mean January temperature ranges from −5.4°C to −3.2°C and the mean July temperature from 9.8°C to 13.5°C; mean annual precipitation ranges from 1,714 to 2,712 mm (Table 1). Climate data were interpolated based on the average from 1960 to 2006 applying the methods described by Thornton et al. (1997). The interpolated Daymet data were obtained from the research unit Landscape Dynamics at the Swiss Federal Institute for Forest, Snow and Landscape Research WSL (Birmensdorf, Switzerland).

The most frequent phyto-sociological forest associations found in the vicinity of the sampled trees are *Homogyno-*

Table 1 Site properties of the investigated spruce forests. Coordinates represent the centre of the forest stand

Forest name	Coordinates (northing, easting)	Altitude (m)	Aspect (°)	Temperature January mean (°C)	Temperature July mean (°C)	Precipitation annual sum (mm)
Flüewald	47° 7′ 31″, 8° 58′ 27″	1,210–1,480	360–100	−3.3	13.0	2,606
Grappliwald	47° 4′ 44″, 9° 0′ 25″	1,310–1,580	320–20	−3.6	12.5	2,515
Saften	47° 3′ 57″, 8° 59′ 8″	1,510–1,685	250–34	−4.5	11.0	2,712
Glarnerwald	46° 58′ 21″, 9° 8′ 26″	1,410–1,680	20–90	−3.5	12.9	1,954
Heulochwald	46° 59′ 28″, 9° 13′ 36″	1,600–1,760	240–360	−5.0	10.4	2,158
Fitteren	46° 58′ 41″, 9° 11′ 36″	1,650–1,930	180–260	−5.4	9.8	2,250
Raminerwald	46° 55′ 35″, 9° 13′ 14″	1,420–1,755	140–230	−4.7	11.1	1,898
Gamperdunwald	46° 55′ 36″, 9° 12′ 17″	1,450–1,655	140–200	−4.3	11.7	1,875
Burst	46° 53′ 53″, 9° 7′ 30″	1,320–1,610	100–140	−3.2	13.5	1,714
Etzel	46° 57′ 14″, 9° 4′ 9″	1,400–1,760	330–30	−4.2	11.7	2,080
Ischtwald/Hüttenwald	46° 57′ 14″, 9° 4′ 18″	1,380–1,720	55–140	−3.6	12.7	1,975
Tüfenwald	46° 57′ 27″, 9° 3′ 55″	1,180–1,810	270–20	−4.6	11.1	2,148
Haaggenwald	46° 56′ 42″, 9° 3′ 44″	1,680–1,780	200–220	−5.1	10.3	2,203
Schwamm	47° 0′ 3″, 9° 10′ 37″	1,555–1,890	340–10	−4.7	10.8	2,213

Altitude and aspect represent the range, where dead trees were sampled. The values for temperature and precipitation are interpolated climate data, based on averages between 1960 and 2006

Piceetum vaccinietosum myrtilli (concerns 28% of the sampled trees) followed by *Asplenio Abieti-Piceetum* (25%) and *Adenostylo alliariae-Abieti-Piceetum typicum* (14%), as classified by Frey (1995). The majority of stands sampled show a cool, humid climate and acidic soils (Table 1).

The forest stands are dominated by Norway spruce and have been managed extensively. Many of the investigated stands are remote protection forests in which silvicultural interventions focus on maintaining stand stability (Frehner et al. 2005). Harvesting of wood in these forest stands is economically of no interest, i.e. forest management had only minor effects on the age structure and stand density. Promoting decayed wood and stands rich in structure are two primary policies of the forest service for subalpine spruce forests in the canton of Glarus, thus standing dead trees are generally not cut in the investigated stands (*personal communication*, Jürg Walcher). Furthermore, we observed relatively many standing and lying dead trees in the field, which reflects the naturalness of the forest stands. The sites selected for this study were situated in the natural distribution area of spruce, which—due to the boreal character of this tree species—lies mainly in the subalpine belt of the Swiss Alps.

Field sampling

In 2008, a total of 128 dead, standing spruce trees were sampled between 50 and 100 cm above ground with an increment borer (Suunto, Finland). Sample height was chosen as low as possible to include as many tree rings as possible, but evading the root collar. Two cores per tree were extracted from different directions. Only trees with a diameter of at least 20 cm

at breast height were sampled. Dead trees, which were obviously killed by storms, avalanches, fire, rock fall, bark beetles or management, were not considered. Because relatively many dead trees were in advanced decay, 43% of all attempts to extract cores were unsuccessful. For each sampled tree, diameter at breast height (DBH), crown length (percentage of tree height), crown diameter, state of decay and percentage of remaining bark were recorded. Additionally, altitude (metre), slope steepness (degree °), aspect (north-based azimuth; degree °), relief (ridge, slope or plain) and canopy position within a radius of 10 m were recorded for each sampled tree. Applying a modified classification scheme of Kraft (1884), which determines the social position of a tree within the forest canopy based on tree height and crown size/vitality, the trees were classified as dominant, co-dominant, subdominant or suppressed. We denoted dominant and co-dominant trees as 'upper storey', subdominant and suppressed trees as 'lower storey'. The canopy position as assessed during the field sampling likely reflects the competitive situation during the time of tree death fairly well due to the slow growth rates at these high elevations and because more than 80% of the sampled trees died after 1990. To develop a tree-ring chronology for the study area in Glarus, additional 35 living spruce trees were cored.

Processing of increment cores and measurement of tree rings

All sampled increment cores were prepared for measurement and dating. However, just one increment core per tree was finally measured. The selection criteria were the

proximity to the pith and the general condition of the core (e.g. cores with eroded tree rings or gaps between segments of tree rings were avoided). The second increment core was used in case the first one could not be dated.

The individual ring widths were measured with an accuracy of 0.01 mm on the tree-ring measurement system LINTAB 5 (Rinn 2004) and cross-dated using the software COFECHA (Holmes 1983) and TSAPWin 0.55 (Rinn 2003). To assign tree rings to the correct calendar year, growth patterns of dead trees were compared with the chronology of the study area in Glarus and a nearby spruce chronology from Bödmerenwald in the canton of Schwyz (Bigler and Bugmann 2003).

If a core did not reach the pith, the number of missing rings and the distance between pith and the first complete ring were estimated using the geometric method by Duncan (1989). The estimated number of missing rings was added to the number of measured rings to obtain the corrected tree age. Only cores were used that met the following criteria: (1) ≤25 missing rings; (2) number of missing rings ≤25% of the measured rings and (3) The estimated distance was ≤25% of the measured radius. Finally, 107 trees with one core per tree were included in the further analyses (83.6% of the successfully sampled trees).

Data analysis

To relate longevity and radial growth rate in an early stage of a tree's life, we calculated the average ring width (unit: mm/year) over the first 50 years (variable AG.50) for each tree. To relate longevity and radial growth rate in a late stage of a tree's life, we calculated the average ring width (unit: mm/year) over the last 10 years (AG.END) for each tree. The hypotheses of Backman (1943) were tested by calculating the relationships between maximum growth rate and longevity as well as between the age of the maximum growth rate (i.e. tree age when maximum growth rate occurred) and longevity. For each tree the average maximum growth rate was determined by calculating moving averages over five ring widths and extracting the maximum value.

Because the response variables are count data, we used a Poisson regression to model longevity. The probability density function of the Poisson distribution is defined as:

$$f(y; \mu) = \frac{\mu^y \times e^{-\mu}}{y!} \tag{1}$$

with mean μ and integer $y \geq 0$, which reflects the probability of obtaining a count y given μ. The effects of growth rates, site variables and morphological variables on expected longevity were quantified using:

$$\log(\mu) = \beta_0 + \beta_1 x_1 + \ldots + \beta_k x_k \tag{2}$$

with predictor variable x_i and regression coefficient β_i (Faraway 2006). To relax the assumption of equal mean and variance in Eq. (1), we allowed overdispersion (i.e. the variance is larger than the mean) by adding a dispersion parameter ϕ to the variance function (Faraway 2006). Regarding model selection, we used backward elimination of variables, i.e. we included all predictor variables in the models and then removed the least significant predictor variables consecutively—based on F tests—until only significant variables ($P < 0.05$) remained in the models (Sachs and Hedderich 2009). Although backward elimination of variables may cause compounded errors, this model selection approach was justified in our study, because the relationships between predictor and response variables were largely unknown (Stauffer 2008).

In the models of longevity at the age of 50, all predictor variables, which were known at the age of 50 years, were included: one growth variable (AG.50) and different site-specific variables (altitude, slope steepness, aspect, relief). Separate models were computed for the upper storey ($n = 76$) and the lower storey ($n = 31$).

In the models of longevity at the end of a tree's life, all predictor variables, which were known at the time of tree death, were included: growth variables (AG.50, AG.END), morphological variables (tree height, crown diameter, crown length) and site-specific variables (altitude, slope steepness, aspect, relief). DBH was excluded from the models due to its high correlation with tree height. Models were computed for both the upper and lower storey.

Because trees growing at the same site were not independent, we also checked for variability between sites using mixed-effects models, i.e. we included the intercept as a random effect (Pinheiro and Bates 2000). However, including random effects did not improve the models compared to fixed-effects models.

The quality of the resulting fixed-effects models was verified by checking residual diagnostics and by calculating correlations between observed and predicted longevities. To check for multicollinearity between predictor variables, we calculated variance inflation factors for all final models with more than one predictor variable (Fox and Monette 1992). All statistical analyses were carried out with the R software (version 2.7.0; R Development Core Team 2008).

Results

The first calendar year at sampling height ranged from 1629 to 1953 (Fig. 1). Mortality occurred from 1912 to 2008 (Fig. 1): 19% ($n = 20$) of the sampled Norway spruces died before 1990, 38% ($n = 41$) died in the 1990s and 43%

($n = 46$) from 2000 to 2008. Lifespan ranged from 50 to 367 years: 53 trees were older than 150 years (thereof 23 older than 200 years) and 54 trees were younger than
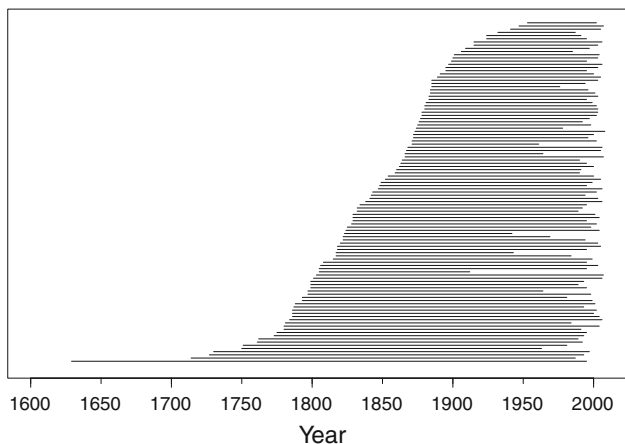

Fig. 1 Results of the dendrochronological dating of 107 analysed dead trees. Each horizontal line represents the lifespan from the first to the last year of a tree

150 years (thereof 14 younger than 100 years). The sampling height of 50 to 100 cm above ground implies that tree age was slightly underestimated, thus the calculated longevities must be interpreted as minimum longevities.

The negative relationship between AG.50 and longevity was significant for the upper storey trees (Spearman rank-order correlation; $r_s = -0.49$, $P < 0.001$) as well as for the lower storey trees ($r_s = -0.51$, $P < 0.004$; Fig. 2a), i.e. slow-growing trees reached a higher lifespan than fast-growing trees. The Poisson regression models confirmed the significant negative effects of AG.50 on longevity (Table 2; Table 3). Pearson correlations between observed and predicted longevities were significant (upper storey: $r = 0.50$, $P < 0.001$, $n = 76$; lower storey: $r = 0.48$, $P < 0.01$, $n = 31$).

The relationship between AG.END and longevity turned out to be significantly negative for both upper and lower storey trees (upper storey: $r_s = -0.23$, $P < 0.05$; lower storey: $r_s = -0.55$, $P < 0.002$; Fig. 2b), i.e. increased radial growth rates during the last 10 years of a tree's life
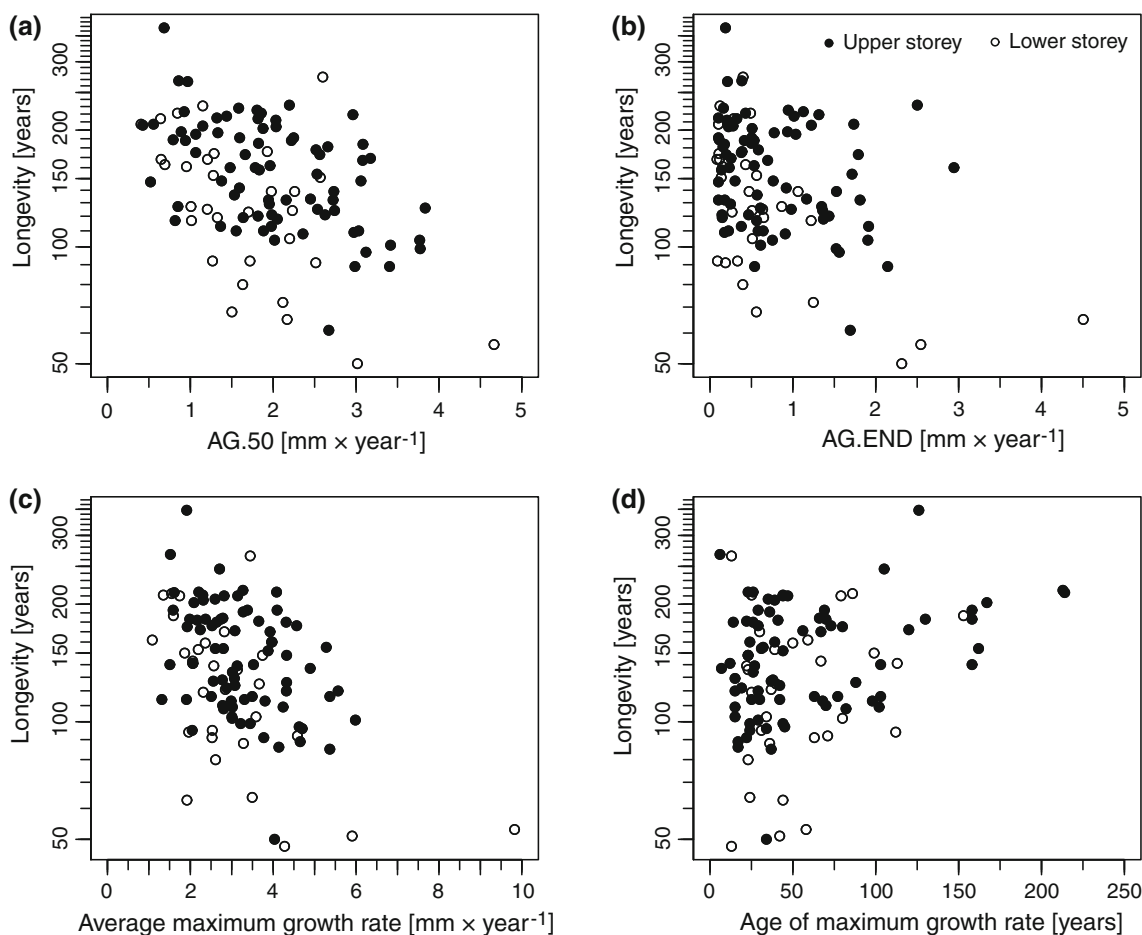

Fig. 2 Relationship between **a** AG.50 (average ring width over the first 50 years) and longevity; **b** AG.END (average ring width over the last 10 years) and longevity; **c** average maximum growth rate and longevity; **d** age of average maximum growth rate and longevity. The relationships are shown for the upper storey ($n = 76$) and the lower storey ($n = 31$)

Table 2 Poisson regression models to the age of 50 years fitted to upper and lower storey trees

Trees	Coefficient	Estimate	SE	P
Upper storey	β_0	5.461	0.078	<0.001
($n = 76$)	β_1	−0.193	0.038	<0.001
	ϕ	11.933		
Lower storey	β_0	5.306	0.153	<0.001
($n = 31$)	β_1	−0.244	0.091	<0.02
	ϕ	19.905		

The variable longevity was related to the predictor variables intercept (regression coefficient β_0) and growth rate to the age of 50 years (β_1). The dispersion parameter ϕ models overdispersion

n number of spruce trees, *SE* standard error, *P*: *P* value

Table 3 Poisson regression models at the end of life fitted to upper and lower storey trees

Trees	Coefficient	Estimate	SE	P
Upper storey	β_0	4.366	0.358	<0.001
($n = 76$)	β_1	−0.238	0.034	<0.001
	β_2	−0.158	0.045	<0.001
	β_3	0.032	0.006	<0.001
	β_6	0.0004	0.0003	<0.04
	ϕ	8.294		
Lower storey	β_0	5.236	0.330	<0.001
($n = 31$)	β_1	−0.222	0.079	<0.01
	β_2	−0.206	0.089	<0.03
	β_3	0.037	0.012	<0.004
	β_4	0.079	0.392	<0.06
	β_5	−0.008	0.005	<0.08
	ϕ	10.925		

The variable longevity was related to the predictor variables intercept (regression coefficient β_0), growth rate to the age of 50 years (β_1), growth rate at the end of life (β_2), tree height (β_3), crown diameter (β_4), crown length (β_5) and altitude (β_6). The dispersion parameter ϕ models overdispersion

n number of spruce trees, *SE* standard error, *P*: *P* value

were related to decreased longevity. This relationship was also confirmed by the Poisson regression models (Table 3). Correlations between observed and predicted longevities were significant (upper storey: $r = 0.71$, $P < 0.001$, $n = 76$; lower storey: $r = 0.75$, $P < 0.001$, $n = 31$).

The relationship between the maximum radial growth rate and longevity was significantly negative (upper storey: $r_s = -0.41$, $P < 0.001$; lower storey: $r_s = -0.57$, $P < 0.001$; Fig. 2c), i.e. trees with a higher maximum ring width died earlier than trees with a lower maximum ring width. The correlation between the age, when maximum growth rate occurred, and longevity was significant only for the upper storey trees ($r_s = 0.27$, $P < 0.02$; Fig. 2d) but not for the lower storey trees ($r_s = 0.15$, $P < 0.5$; Fig. 2d).

For upper storey trees, this implies that the later in a tree's life maximum growth occurred the higher the lifespan.

In the regression models of longevity to the age of 50 years, the site parameters (altitude, slope steepness, aspect, relief) did not significantly affect longevity (Table 2). However, there was a significantly positive effect of altitude on longevity for the upper storey trees in the model of longevity at the end of life (Table 3). Upper storey trees situated on higher altitude grew older than upper storey trees on lower altitude. The regression models of longevity at the end of life resulted further in a significantly positive effect of tree height on longevity for both the upper and lower storey trees (Table 3), which means that taller trees were older than shorter trees. The positive effect of crown diameter and the negative effect of crown length (percentage of tree height) on longevity were marginally significant for the lower storey trees (Table 3). Lower storey trees with a wider crown diameter reached a higher longevity than those with a smaller crown diameter, and longevity decreased with increasing crown length. For both models at the end of life (Table 3), the variance inflation factors for all variables were below 1.6, thus there was no indication of collinearity between predictor variables.

We calculated expected maximum longevities by combining the estimated regression coefficients of the regression models to the age of 50 years (Table 2) and of the regression models at the end of life (Table 3) with extreme observations for the predictor variables (e.g. very slow growth, high altitude, etc.). For the regression models to the age of 50 years, the expected maximum longevities ranged between 189 and 243 years for upper storey trees and between 139 and 225 years for lower storey trees (approximate 95% confidence interval). According to the regression models at the end of life, the predictions increased to 331–642 years for upper storey trees and to 219–583 years for lower storey trees. The expected longevities of the regression models to the age of 50 years are closer to the observed average longevities in the study area of 162 ± 52 years (mean ± standard deviation) for upper storey trees and of 137 ± 55 years for lower storey trees. The observed median longevities differed between upper and lower storey trees (Kruskal–Wallis test; $\chi^2 = 5.2120$, $P < 0.03$).

Discussion

Growth rates and longevity

The investigation of dead Norway spruce trees in the montane and subalpine belt of Glarus revealed that trees with early slow growth (AG.50) lived longer than fast-growing trees (Fig. 2a; Table 2; Table 3). Similar

relationships between growth rate and longevity were found by Bigler and Veblen (2009) for subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) in Colorado (USA) and for Norway spruce in Davos (eastern Switzerland), by Ward (1982) for common juniper (*Juniperus communis*) in England, and by Reynolds and Burke (2011) for American chestnut (*Castanea dentata*) in Virginia (USA). Furthermore, our study revealed a weaker negative effect of early growth on the lifespan of upper storey trees than on lower storey trees. Tree size was unlikely to bias the variable AG.50, because between-tree variability of DBH during the first 50 years is low.

Similar to the findings of early tree growth, trees growing slowly during the last 10 years (AG.END) tended to get older than fast-growing trees (Fig. 2b; Table 3). The low correlation between DBH and AG.END ($r = 0.17$, $P = 0.082$) indicates that there is no size-dependent effect affecting these results. In contrast to the influence of early growth rate, the negative effect of a high growth rate at the end of life on longevity was stronger for lower storey trees than for upper storey trees. A recent study on American chestnut indicates that trees infected with chestnut blight (*Cryphonectria parasitica*) had higher growth rates over 10 years prior to tree death (Reynolds and Burke 2011). Such fungal infestations might point to a potential explanation for the reduced lifespan with increased growth found for Norway spruce, since spruce is known to be susceptible for root rot (*Heterobasidion annosum* or *Armillaria* sp).

The observed negative relationship between growth prior to tree death and longevity (Table 3) seems to disagree with results of a large body of studies on tree mortality that indicate a negative relationship between growth over 3–40 years prior to tree death and mortality probability (e.g. Bigler and Bugmann 2003; Wyckoff and Clark 2002). Threshold effects may explain why very slowly growing trees have a strongly increased mortality probability compared to trees with slightly higher growth rates (Bigler and Veblen 2009). Thus, if whole-tree respiration becomes larger than photosynthesis, the carbon balance turns negative, which strongly increases the mortality risk (Keane et al. 2001).

The analysis of absolute ring widths and of the age when maximum growth occurred revealed two distinct relationships with longevity: first, trees with smaller maximum ring width were older than trees with larger maximum ring width (Fig. 2c), and second, trees reaching their maximum growth earlier in life died younger than trees reaching their maximum growth later (Fig. 2d). These findings agree with the theoretical considerations of Backman (1943), which were originally based on maximum height growth. Applying Backman's hypothesis to radial growth data is appropriate, since well-established allometric relationships between DBH and tree height exist (Mitscherlich 1970;

Prodan 1961), which are also reflected by the strong correlation between DBH and tree height of dead spruce trees in our study ($r = 0.69$, $P < 0.001$). The hypothesis of Backman (1943), postulating that trees reaching their maximum (height) growth later grow older, could only be confirmed for upper storey trees, but not for lower storey trees (Fig. 2d). Many of the sampled upper storey trees ($n = 48$, 63%) reached their maximum growth before the age of 50 and achieved an average age of 152 years. 37% ($n = 28$) reached their maximum growth after 49 years and achieved an average age of 178 years. The high percentage of upper storey trees reaching maximum growth before the age of 50 years suggests that long-term success in reaching the canopy seems to be strongly affected by a fast early growth rate (Landis and Peart 2005). Still, more than one-third of the upper storey trees reached maximum growth later, but grew older than trees with early maximum growth. For lower storey trees, the relationship between the age of maximum growth and longevity is highly dispersed and thus not significant (Fig. 2d). 58% of the lower storey trees reached the age of maximum growth before 50 years ($n = 18$) and achieved an average age of 127 years. 42% reached maximum growth after 49 years ($n = 13$) and achieved on average the age of 151 years. Lower storey trees of both groups (i.e. trees reaching maximum growth before 50 years or after 49 years, respectively) did not reach the canopy and died younger than upper storey trees.

Tree morphology and longevity

Different morphological characteristics of trees at the time of tree death have turned out to be useful indicators for the estimation of longevity. (1) Tall trees tended to live longer than short trees, and vice versa (Table 3). This might be a logical deduction from observations based on individual trees that with every year trees get taller. However, this relationship does not necessarily apply to tree populations, because ancient trees, which often grow at extreme sites, have been observed to show stunted growth (LaMarche 1969; Larson 2001). (2) Lower storey trees with large crown diameters tended to grow older than lower storey trees with small crown diameters (Table 3). Low stand densities favour wider crown diameters (Schütz 2003), because more light may be intercepted, which increases the amount of carbohydrates produced that can be invested in crown structure. We assume that lower storey trees with small crown diameters are more likely to die prematurely due to an unfavourable carbon balance. (3) Lower storey trees with a short crown length tend to grow older than trees with a long crown (Table 3). These findings are congruent with those of Matthes et al. (2008) reporting on increased tree age with higher relative height to the first branch. Strong competition leads to the dieback of lower

branches (Schütz 2003), and thus, results in a shorter crown. We assume that trees with shorter crowns grow more slowly because of lower photosynthetic activity, which—in agreement to our findings—results in older ages. Lower storey trees with longer crowns likely experience self-shading of the lower branches, which may not acquire sufficient resources in the long term. These results do not contradict the previously discussed findings of lower storey trees with large crown diameters getting older, because a wider crown also reduces self-shading of branches, and trees featuring a wide crown usually have more growing space, thus experience less light competition from the surrounding trees.

Site conditions and longevity

Longevity of upper storey trees increased with increasing altitude (Table 3). In the northern part of the Swiss Alps, spruce is common in the upper montane and subalpine belts (altitude approx. 1,200–1,900 m) (Frehner et al. 2005). Increasing altitude implicates harsher conditions such as lower temperatures, frequent frosts, shorter growing periods and stronger wind. In the subalpine belt the growing period is considerably shorter than in the upper montane belt, thus resulting in reduced annual growth. Also, for the lower storey trees, we found a decreasing growth rate with increasing altitude. However, lower storey trees are not only influenced by shorter growing periods, but also by the lack of light due to competition, which may result in very small growth rates falling below lethal threshold levels (Bigler and Bugmann 2004). Site factors such as altitude or aspect are known to affect growth rates of trees, which in turn are associated with tree longevity. However, site factors may impact tree longevity not only via influences on growth rates, but also for example by decreasing soil moisture, which may increase the risk of drought-induced mortality at lower altitudes or on south-facing slopes (Bigler and Veblen 2009). By including variables in the regression models that represent tree growth, tree morphology and site conditions, we assess the combined effects of these variables on longevity. Additional site conditions such as soil moisture or nutrient content may affect tree longevity as well. However, because of the time-varying character of these influences, their effects on longevity may not be easily reconstructed.

Conclusions

For the northern Swiss Alps, we quantified effects of growth rates, tree morphology and site conditions on longevity of dead Norway spruce trees that were growing along different topographical and climatic gradients: (1) As expected, longevity was negatively related to tree growth, i.e. slow-growing trees tended to grow older than fast-growing trees; (2) Tree height was positively associated with longevity for both upper and lower storey trees; (3) Longevity of lower storey trees was increased with large crown diameter, but decreased with long crown length; and (4) Upper storey trees were growing older with increasing altitude. These findings reveal how tree-specific traits but also site conditions operate on tree longevity. For some of the investigated factors, we found differential effects for trees in different canopy layers, which indicate that stand dynamics, particularly competitive relationships among neighbouring trees, is an important determinant of variability in tree longevity. Even in the absence of any further information related to the causes of tree mortality, the resulting models allow to predict what age Norway spruce in our study area may reach. Because longevity is linked to mortality rates of tree populations (Clark 2007), our study may ultimately improve the understanding of long-term processes of forest dynamics under current and future climate (Bugmann and Bigler 2011). While experimentally increased atmospheric CO_2 leads to species-specific growth stimulations of trees at treeline (Dawes et al. 2011), climate warming has been demonstrated to result in increased growth rates of Norway spruce at high elevations in the Alps (Rolland et al. 1998). Provided the observed trade-off between growth rates and longevity remains valid under climate change, future increased growth rates may in turn lead to reduced longevity and increased mortality rates at higher altitudes.

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