



Increased early growth rates decrease longevity of conifers in subalpine forests

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For trees, fast growth rates and large size seem to be a fitness benefit because of increased competitiveness, attainment of reproductive size earlier, reduction of generation times, and increased short-term survival chances. However, fast growth rates and large size entail reduced investment in defenses, lower wood density and mechanical strength, increased hydraulic resistance as well as problems with down-regulation of growth during periods of stress, all of which may decrease tree longevity. In this study, we investigated the relationship between longevity and growth rates of trees and quantified effects of spatial environmental variation (elevation, slope steepness, aspect, soil depth) on tree longevity. Radial growth rates and longevity were determined from tree-ring samples of 161 dead trees from three conifer species in subalpine forests of the Colorado Rocky Mountains (*Abies lasiocarpa*, *Picea engelmannii*) and the Swiss Alps (*Picea abies*). For all three species, we found an apparent tradeoff between growth rate to the age of 50 years and longevity (i.e. fast early growth is associated with decreased longevity). This association was particularly pronounced for larger *P. engelmannii* and *P. abies*, which attained canopy size, however, there were also significant effects for smaller *P. engelmannii* and *P. abies*. For the more shade-tolerant *A. lasiocarpa*, tree size did not have any effect. Among the abiotic variables tested only northerly aspect significantly favored longevity of *A. lasiocarpa* and *P. engelmannii*. Trees growing on south-facing aspects probably experience greater water deficits leading to premature tree death, and/or shorter life spans may reflect shorter fire intervals on these more xeric aspects. Empirical evidence from other studies has shown that global warming affects growth rates of trees over large spatial and temporal scales. For moist-cool subalpine forests, we hypothesize that the higher growth rates associated with global warming may in turn result in reduced tree longevity and more rapid turnover rates.

Trees share attributes of great size, longevity, and long-term reproductive output that are fundamental to their ecological success (Petit and Hampe 2006). Fast growth rates and large size both seem unequivocally to benefit the fitness of trees (Arendt 1997, Lanner 2002). Tall trees achieve an increased competitiveness due to shading of neighbors, enhanced seed dispersal over greater distances, and mitigation against disturbances such as surface fire and ground-based herbivory (Landis and Peart 2005, Petit and Hampe 2006). Fast growth rates early in the life history of a tree allow trees to reach reproductive size earlier, which reduces generation times. However, fast growth rates and large tree size come with some costs (Arendt 1997). Fast growth rates are generally linked to reduced investment in defense (Coley et al. 1985, Loehle 1988, Herms and Mattson 1992), which results in more frequent infestations by insects (Price 1991) or infections by fungi (LaMarche Jr. 1969, Bleiker and Uzunovic 2004). Fast growth rates are also associated with features such as low wood density, reduced mechanical strength, and high ratios of above- to below-ground biomass, all of which increase risk of breakage and damage from wind (Loehle 1988, Larson 2001, King et al.

2006). Large and tall trees are increasingly limited by hydraulic resistance (Ryan and Yoder 1997). Furthermore, large, fast-growing trees might experience problems with down-regulation of growth-related processes during periods of suboptimal conditions; examples include inertia in reducing respiration, transpiration, and nutrient needs when nutrient and water supplies fall short (Arendt 1997, McDowell et al. 2008).

An apparent tradeoff between longevity and growth rates or metabolic rates of trees has long been noted (Rudenschöld 1746, Molisch 1929, Backman 1943, Schulman 1943, 1954). This tradeoff has been extensively described across species; tree species with intrinsically low growth rates tend to live longer than fast-growing tree species (Loehle 1988). Although short-term survival chance is generally known to decrease as growth rates fall below critical levels (Keane et al. 2001, Bigler and Bugmann 2004, Das et al. 2007), the potential relationship between early growth rate and long-term survival has rarely been investigated within the same tree species (Backman 1943, Ward 1982). It has been commonly observed and generalized that particularly old and slow-growing trees are often associated with unfavorable

environmental conditions (e.g. low temperatures, drought or wind) (Schulman 1943, 1954, LaMarche Jr. 1969, Laberge et al. 2000, Larson 2001, Lanner 2002). Although low site productivity reduces the probability of death from fire or insect attack in some environments, the general association of delayed tree death with extreme environments also suggests that lower metabolism extends longevity.

The objective of this study was to investigate the tradeoff between longevity and growth rates of trees and to quantify effects of environmental conditions on tree longevity. For dead trees of three conifer species from subalpine forests in the Colorado Rocky Mountains and the Swiss Alps we test for relationships of tree longevity to both early growth rates and to spatial variation in abiotic environmental conditions (elevation, slope steepness, aspect, and soil depth).

Material and methods

Study areas

Data were collected in the Rocky Mountains (Roosevelt National Forest in northern Colorado, USA) and in the Alps (Davos in eastern Switzerland). The study area in Roosevelt National Forest is located near Cameron Pass and is centered on 40°33'N and 105°50'W. Trees were sampled in an area extending over 11 × 5.8 km and elevations ranged from 2930 to 3320 m (Bigler et al. 2007). These unmanaged, subalpine forests are dominated by Engelmann spruce *Picea engelmannii*, subalpine fir *Abies lasiocarpa*, lodgepole pine *Pinus contorta* var. *latifolia* and quaking aspen *Populus tremuloides*. The stands sampled were not affected by logging or any other silvicultural management. The climate is continental with mean temperatures of -10.1°C in January and 10.8°C in July; mean annual precipitation is 697 mm (estimated for the mean elevation of 3141 m in the study area; for details see Bigler et al. 2007). In Davos, trees were sampled on south-west facing slopes in the Dischma and Flüela valleys (Bigler and Bugmann 2003). The study area is centered on 46°47'N and 9°53'E extending over 4 × 5 km and elevations ranged from 1600 to 2000 m. These subalpine forests are dominated by Norway spruce *Picea abies* and at higher elevations interspersed with some European larch *Larix decidua* and Swiss stone pine *Pinus cembra*. Some of these extensively managed stands were probably planted in the 19th century to mid-20th century and were selectively logged (Price and Thompson 1997). However, the sampled trees represented a wide range of tree ages, which allowed testing of relationships between longevity and early growth rates. The continental to suboceanic climate reaches mean temperatures of -5.3°C in January and 11.3°C in July and annual precipitation of 1082 mm (climate station Davos-Dorf, 1590 m; located ca 2 km away from field sites).

Sampled tree species

Three tree species were sampled: subalpine fir and Engelmann spruce in Roosevelt National Forest, and Norway spruce in Davos. Subalpine fir, a very shade-tolerant species, and Engelmann spruce, a shade-tolerant species, both dominate subalpine, old-growth stands in the

central Rocky Mountains (Veblen 1986a, Peet 2000). These co-existing species share similar regeneration niches, but in general subalpine fir is more abundant in the understory and Engelmann spruce is more abundant in the canopy (Veblen 1986a, Peet 2000). Both species may regenerate in open sites as well as under relatively dense canopy (Knapp and Smith 1982). For both species, sexual reproduction may start at 20–25 years (Loehle 1988, Schütt et al. 2006). Adult trees reach an average longevity of about 300–400 years for subalpine fir and 400–600 years for Engelmann spruce (Veblen 1986a, 1986b, Loehle 1988, Schütt et al. 2006). Norway spruce is a semi shade-tolerant species that has an increasing light demand with increasing age, which often dominates subalpine forests in the Swiss Alps (Ellenberg 1988, Schütt et al. 2006). Regeneration occurs beneath small to large canopy gaps. Earliest reproduction occurs at 20–30 years (Schütt et al. 2006). Adult Norway spruce reach an average longevity of 250–440 years (Schütt et al. 2006).

Sampling design

The sampling design slightly differed between the study areas in Colorado and Davos. In Colorado, trees were sampled at 16 sites in the year 2004 (Bigler et al. 2007). All standing dead trees ≥ 20 cm DBH (diameter at breast height; including bark, where present) were selected in transects of approximately 10 to 50 m width and variable length. The data set used in this study contains subalpine fir from 13 sites and Engelmann spruce from 14 sites. Two increment cores were extracted at breast height. For each tree, elevation (unit: m), slope steepness (degree $^{\circ}$), soil depth (cm), and north-based azimuth (degree $^{\circ}$) were measured (Bigler et al. 2007). Elevation was measured using an altimeter. Soil depth, which was measured using a soil auger with a maximum length of 70 cm, was assigned to three classes (< 40 cm, 40–69 cm, ≥ 70 cm). Azimuth was transformed into east-west aspect using a sine transformation (gradient from +1 representing east to -1 representing west) and into north-south aspect using a cosine transformation (gradient from +1 representing north to -1 representing south). In Davos, trees were sampled in different stands within the study area in the year 2000 (Bigler and Bugmann 2003). All standing dead trees ≥ 10 cm DBH (including bark, where present) were included in the sample. From each tree, two increment cores were removed at breast height. In both study areas, only trees were sampled that had not been killed by disturbance events such as blowdown, avalanches, fire, large-scale insect outbreaks, mechanical damage or cutting by humans. Stem sections with eroded wood were avoided, however, the cool climate in both study areas generally preserved the wood for a long time (Bigler and Bugmann 2003, Bigler et al. 2007). Increment cores were taken at breast height, because near the ground surface growth patterns are often affected by reaction wood. At the time of tree sampling, the trees were classified regarding the canopy position (dominant > codominant > subdominant > suppressed; in order of decreasing dominance).

Processing of increment cores and tree rings

After gluing and sanding the increment cores, tree rings were measured on a tree-ring measurement system with a resolution of 0.01 mm (Velmex for cores from the study area in Colorado, Lintab 3 for cores from the study area in Davos). Tree rings were visually and quantitatively cross-dated using the software COFECHA (Holmes 1983) and TSAP (Rinntech, Heidelberg, Germany); thus, growth patterns were compared between dead trees and existing tree-ring chronologies to assign each tree ring to the correct calendar year and to detect missing and false tree rings. Chronologies had been developed using tree-ring series of live trees from the study areas and are available from the International Tree-Ring Data Bank (ITRDB; chronologies CO635 for subalpine fir, CO633 for Engelmann spruce, and SWIT181 for Norway spruce). Only crossdated cores without any eroded tree rings at the outermost ring were further considered.

For each tree, we estimated longevity based on counting the tree rings and – for those increment cores that missed the pith – additionally on estimating the distance and number of missing rings between pith and first complete tree ring. Because we used different data sources, the methods to estimate longevity slightly differed between the study areas in Colorado and Davos. For Colorado, we estimated the number of missing rings using a geometric and growth-rate method by Duncan (1989). Only cores with an estimated 20 or fewer missing rings were considered. If two cores were available for a given tree, the core with more tree rings was used. For the analyses, we finally included 70 trees for subalpine fir (61.9% of the trees sampled in the field) and 50 trees for Engelmann spruce (39.1%) in the data set. For Davos, the number of missing rings was estimated using a visual method (Applequist 1958). Only cores with an estimated distance <3.0 cm between pith and first complete tree ring were used resulting in an approximated maximum of 12 missing rings for Norway spruce. If two cores were available for a given tree, the ring widths of both cores were averaged. Finally, we included 41 Norway spruce (68.3%) in the data set.

Analysis

To analyze relationships between growth rate and longevity, we calculated average ring width (unit: mm year⁻¹) over the first 50 years of each tree's life. We decided on using the first 50 years, because this age represents an early stage in each tree's life. Similar and significant ($p < 0.002$) effects were obtained by using shorter periods (30 or 40 years) or longer periods (60–100 years), however the significance decreased with shorter periods and sample sizes decreased with longer periods. Ring width over 50 years correlated strongly with ring width over shorter or longer periods (ranges of pairwise Pearson's correlations: subalpine fir = 0.931–0.995, Engelmann spruce = 0.942–0.995, Norway spruce = 0.793–0.991). To quantify the effects of predictor variables on longevity, we used a log-linear model with a quasipoisson error structure. The link function of the log-linear model is written as:

$$\log(\mathbf{Y}) = \mathbf{X}\boldsymbol{\beta} \quad (1)$$

where $\mathbf{Y}$ is a vector with the variable longevity, $\mathbf{X}$ is a matrix with the predictor variables and $\boldsymbol{\beta}$ is a vector with the regression coefficients (Faraway 2006). The log-transformation ensures that predicted longevity is >0 . The quasipoisson error structure adds an additional parameter (the dispersion parameter ϕ) to the variance function, which is used for modeling overdispersion (i.e. the variance is larger than the mean; Faraway 2006).

In a first step, we used all tree species (subalpine fir, Engelmann spruce, Norway spruce) to relate longevity to growth rate based on log-linear models (basic models; Eq. 1). When plotting tree size with age (Fig. 1), we observed that some slower-growing, smaller-sized trees died relatively early, whereas other slower-growing trees reached larger tree sizes and relatively long lifespans. This pattern was particularly apparent for Engelmann spruce and Norway spruce, and we assumed this effect to be related to whether growing conditions remained adverse or whether they improved (Landis and Peart 2005). Therefore, we fitted models that included increasingly larger trees only (i.e. we fitted all possible models that included only trees larger than a given tree size, which we increased in steps of 1 cm). Tree size as represented by DBHBB (diameter at breast height beneath the bark) was calculated as $2 \times$ cumulative ring width. The resulting DBHBB was typically smaller than the DBH determined in the field, because bark was not included and because of stem asymmetries. For each species, the model with the highest significance of the growth rate was selected (subalpine fir ≥ 14 cm DBHBB, $n=69$; Engelmann spruce ≥ 23 cm DBHBB, $n=36$; Norway spruce ≥ 31 cm DBHBB, $n=14$). For the two spruce species, we additionally calculated basic models for smaller trees (Engelmann spruce < 23 cm DBHBB, $n=14$; Norway spruce < 31 cm DBHBB, $n=27$). Most of the larger Engelmann spruce and Norway spruce turned out to belong to the canopy, whereas smaller Engelmann spruce and Norway spruce were more likely to be in the lower canopy positions as will be shown in the results.

In a second step, we used only the tree species from Colorado (subalpine fir, Engelmann spruce) to relate longevity to growth rate, elevation, slope steepness, soil depth, east-west aspect, and north-south aspect (extended models; Eq. 1). We included only trees $\geq$ DBHBB thresholds determined in the previous analysis (subalpine fir ≥ 14 cm DBHBB, $n=69$; Engelmann spruce ≥ 23 cm DBHBB, $n=36$). For the extended models, we started with full models (i.e. including all predictor variables) and then successively removed the least significant variables based on F tests of nested models until only significant variables remained (Faraway 2006). For Engelmann spruce, we additionally calculated an extended model for smaller trees (DBHBB < 23 cm, $n=14$) using the same predictor variables as in the model calculated for larger trees.

Additionally, we compared the log-linear models with negative binomial models. For the extended models, identical model structures resulted (i.e. the same predictor variables were included in the final models) using information-theoretic methods (AIC) for model selection of the negative binomial models. The regression coefficients of the log-linear models and the negative binomial models were very similar for both the basic and extended models. In the following, only results of the log-linear models are

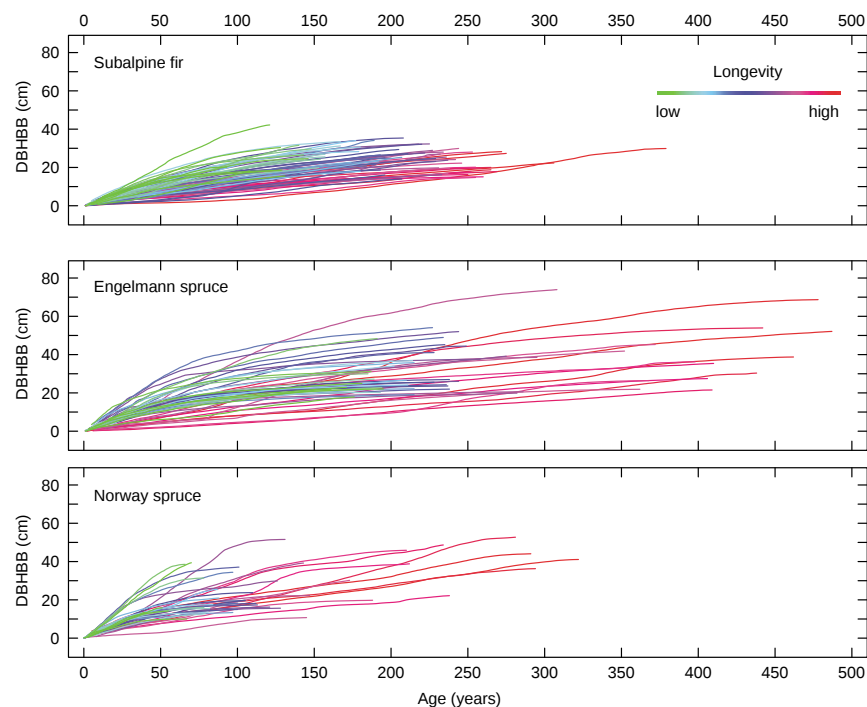


Figure 1. Development of tree size, as represented by DBHBB (diameter at breast height beneath the bark), with age at breast height. Tree size was calculated as $2 \times$ cumulative ring width. Sample sizes: subalpine fir, $n = 70$; Engelmann spruce, $n = 50$; Norway spruce, $n = 41$. Colors indicate gradients from lowest longevity (green) to highest longevity (red).

reported. Regression diagnostics of all final models were checked. We used the R software (ver. 2.7.0) to carry out the analyses.

Results

Maximum longevity of the sampled tree species decreased from Engelmann spruce (longevities ranged between 413–487 years for trees above the 90% quantile), subalpine fir (261–379 years) to Norway spruce (238–322 years) (Fig. 1). The year a tree attained breast height – as indicated by the distribution of the first year of the sampled trees – ranged from 1602 to 1896 for subalpine fir, from 1512 to 1842 for Engelmann spruce, and from 1673 to 1960 for Norway spruce (Fig. 2). Mortality occurred from 1920 to 2003 for subalpine fir, from 1928 to 2003 for Engelmann spruce, and from 1968 to 2000 for Norway spruce (Fig. 2).

For subalpine fir ($n = 70$), 40.0% were in the codominant canopy class, 48.6% in the subdominant canopy class, and only 5.7% in the dominant canopy class. For Engelmann spruce ≥ 23 cm DBHBB ($n = 36$), 36.1% were classified as dominant and 44.4% as codominant, whereas for Engelmann spruce < 23 cm DBHBB ($n = 14$), 92.9% were classified as subdominant and 7.1% as suppressed. For Norway spruce ≥ 31 cm DBHBB ($n = 14$), 42.9% were in the dominant and 57.1% in the codominant canopy class, whereas for Norway spruce < 31 cm DBHBB ($n = 27$), 85.2% were in the suppressed class. Thus, the size thresholds, which were determined in the regression analysis to separate larger from smaller trees, were relatively consistent with upper and lower canopy positions (notably for Engelmann spruce and Norway spruce).

The log-linear models (basic models) revealed significant negative effects of early growth rate on longevity for subalpine fir (≥ 14 cm DBHBB), Engelmann spruce (≥ 23 cm DBHBB), and Norway spruce (≥ 31 cm DBHBB) (Table 1, Fig. 3). Increased growth rate to the age of 50 years was associated with decreased longevity. For example an increase of the growth rate from 1 mm to 2 mm decreases the expected longevity for subalpine fir from 195 years to 127 years, for Engelmann spruce from 326 years to 229 years, and for Norway spruce from 301 years to 158 years (Fig. 3). We verified these basic models by calculating correlations between observed and predicted longevity. The correlations were significant for subalpine fir ≥ 14 cm DBHBB (Pearson's correlation $r = 0.62$, $p < 0.001$, $n = 69$), Engelmann spruce ≥ 23 cm DBHBB ($r = 0.69$, $p < 0.001$, $n = 36$), and Norway spruce ≥ 31 cm DBHBB ($r = 0.86$, $p < 0.001$, $n = 14$). The basic models calculated for smaller trees also resulted in significant negative effects of early growth rate (β_1) for both Engelmann spruce < 23 cm DBHBB (estimate $\pm$ standard error of $\beta_1 = -0.577 \pm 0.154$, $p < 0.003$; $n = 14$) and Norway spruce < 31 cm DBHBB (estimate $\pm$ standard error of $\beta_1 = -0.433 \pm 0.170$, $p < 0.02$; $n = 27$).

For the extended models, growth rate and north–south aspect turned out to be the only significant variables for subalpine fir (≥ 14 cm DBHBB) and Engelmann spruce (≥ 23 cm DBHBB) (Table 2). For both species, increased growth rates were associated with decreased longevity, and trees growing on north-facing aspects had an increased longevity as compared to trees growing on south-facing aspects. For example, if we compare two trees with a fixed growth rate to the age 50 (1 mm year^{-1}) but one tree is growing on a north-facing slope and one on a south-facing

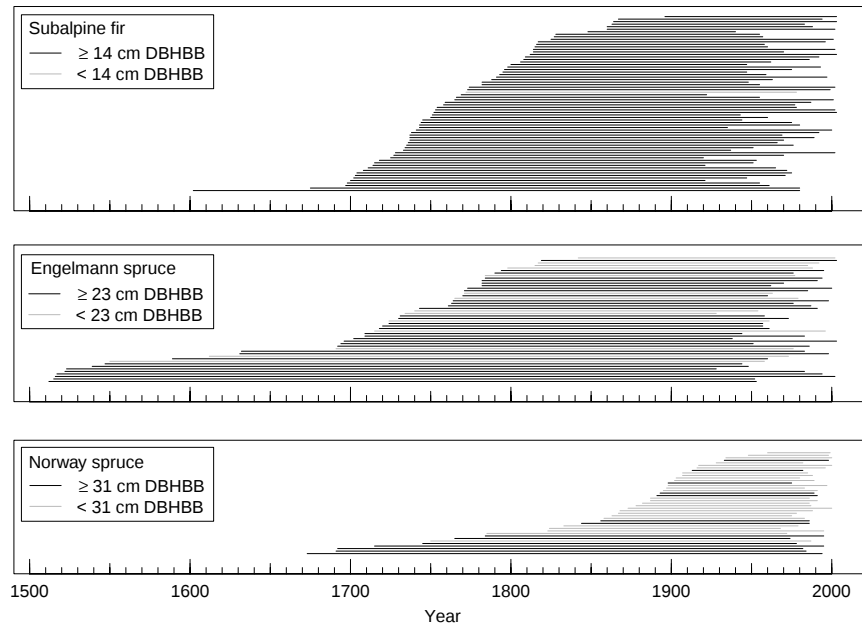


Figure 2. Results of dendrochronological dating of dead trees. Each horizontal line ranges from the first year (corrected for missing rings) to the last year of a dead tree. Shown are trees larger than the species-specific DBHBB (diameter at breast height beneath the bark) (black lines) and trees smaller than the species-specific DBHBB (grey lines).

slope, expected longevity decrease for subalpine fir from 218 years to 157 years and for Engelmann spruce from 352 years to 237 years. For both subalpine fir and Engelmann spruce, there was only weak collinearity between growth rate and north-south aspect as indicated by variance inflation factors (VIF) close to 1 (VIF subalpine fir = 1.015, VIF Engelmann spruce = 1.196; Fox and Monette 1992). Extending the basic models by including north-south aspect improved the predictive power of the models, i.e. the Pearson correlations between observed and predicted longevity increased for subalpine fir ≥ 14 cm DBHBB ($r = 0.71$, $p < 0.001$, $n = 69$) and Engelmann spruce ≥ 23 cm DBHBB ($r = 0.74$, $p < 0.001$, $n = 36$). The extended model calculated for Engelmann spruce < 23 cm DBHBB also resulted in significant effects of early growth

Table 1. Log-linear models with quasipoisson error structure (basic models; Eq. 1). The variable longevity is 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 over-dispersion.

Tree species	Coefficient	Estimate	SE	p
Subalpine fir (n = 69)	β_0	5.694	0.060	<0.001
	β_1	-0.423	0.065	<0.001
	ϕ	8.010		
Engelmann spruce (n = 36)	β_0	6.142	0.096	<0.001
	β_1	-0.353	0.067	<0.001
	ϕ	17.604		
Norway spruce (n = 14)	β_0	6.348	0.176	<0.001
	β_1	-0.642	0.100	<0.001
	ϕ	10.826		

The models were calculated for subalpine fir ≥ 14 cm DBHBB (diameter at breast height beneath the bark), Engelmann spruce ≥ 23 cm DBHBB, and Norway spruce ≥ 31 cm DBHBB. The number of trees (n) is shown in parentheses; SE is the standard error; p is the p-value.

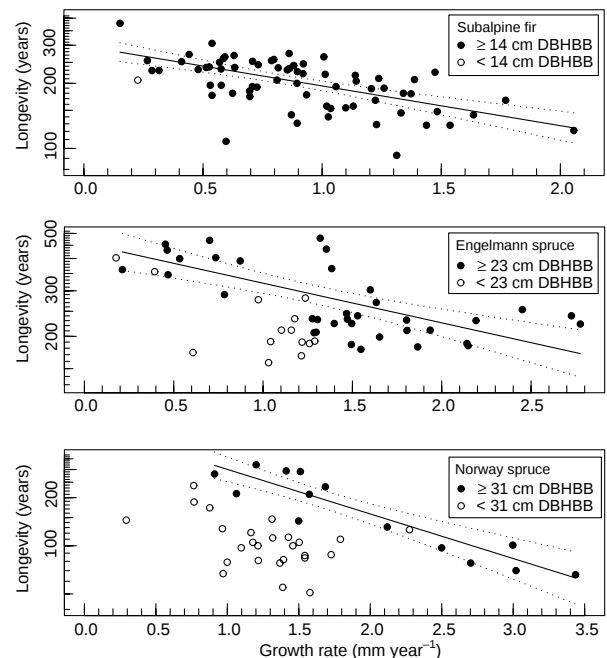


Figure 3. Relationships between average growth rate to the age of 50 years and longevity. Shown are trees larger than the species-specific DBHBB (diameter at breast height beneath the bark) (solid circles) and trees smaller than the species-specific DBHBB (circles). The regression lines (solid lines) and 95% confidence intervals (dotted lines) were calculated for trees larger than the species-specific DBHBB and were derived from the coefficients of the log-linear models in Table 1. Longevity is shown on a logarithmic scale. Note that the scales for the three species differ.

Table 2. Log-linear models with quasipoisson error structure (extended models; Eq. 1). The variable longevity is related to the predictor variables intercept (regression coefficient β_0), growth rate to the age of 50 years (β_1), and north-south aspect (β_2); the dispersion parameter ϕ models overdispersion.

Tree species	Coefficient	Estimate	SE	p
Subalpine fir (n = 69)	β_0	5.616	0.060	<0.001
	β_1	-0.394	0.061	<0.001
	β_2	0.163	0.042	<0.001
	ϕ	6.722		
Engelmann spruce (n = 36)	β_0	5.949	0.119	<0.001
	β_1	-0.283	0.067	<0.001
	β_2	0.199	0.081	<0.02
	ϕ	15.049		

The models were calculated for subalpine fir ≥ 14 cm DBHBB (diameter at breast height beneath the bark) and Engelmann spruce ≥ 23 cm DBHBB. The variable north-south aspect represents a gradient from north (+1) to south (-1). The number of trees (n) is shown in parentheses; SE is the standard error; p is the p-value.

rate (β_1) and north-south aspect (β_2) (estimate $\pm$ standard error of $\beta_1 = -0.523 \pm 0.077$, $p < 0.001$; estimate $\pm$ standard error of $\beta_2 = 0.355 \pm 0.063$, $p < 0.001$; $n = 14$).

Discussion

For subalpine fir, Engelmann spruce and Norway spruce, average growth rates over the first 50 years are negatively related to longevity (Table 1, Fig. 3). Trees with slow growth during the first 50 years tend to live longer, and vice versa fast-growing trees tend to die younger. For Engelmann spruce and Norway spruce, we found size-dependent effects. Larger trees, which are mostly canopy trees, show a different growth-longevity pattern than smaller trees, which are mostly sub-canopy trees (Fig. 1, 3). For subalpine fir, tree size does not have any distinct effects (Fig. 3). Considering dead trees of all size classes, it is striking that there are no old trees among the initially most rapidly growing trees; however, among the slow-growing trees there are younger and older trees, especially of Engelmann spruce (trees with growth rate < 1.3 mm year $^{-1}$) and Norway spruce (trees with growth rate < 1.8 mm year $^{-1}$) (Fig. 3). Many of the slow-growing, relatively short-lived Engelmann spruce and Norway spruce belong to smaller size classes and were classified in the field as subdominant or suppressed. We assume that for these trees growth conditions have deteriorated following the initial period of slow growth (Fig. 1) probably related to local neighborhood effects (Das et al. 2008). Most slow-growing subalpine fir, independent of their size or canopy position, tend to reach high longevity (Fig. 1, 3), which agrees with the higher shade tolerance of this species (Knapp and Smith 1982). For the two species in our study that may dominate the canopy (Engelmann spruce and Norway spruce), fast early growth rates increase the success of reaching the canopy (Engelmann spruce with DBHBB ≥ 23 cm and growth rates > 1.4 mm year $^{-1}$; Norway spruce with DBHBB ≥ 31 cm and growth rates > 1.8 mm year $^{-1}$; Fig. 3). However, these fast-growing canopy trees have lower longevity (mean $\pm$ standard deviation of longevity: Engelmann spruce = 226.5 ± 33.5 years, $n = 19$; Norway spruce = 90.5 ± 24.4 years, $n = 6$) than slower-growing canopy trees (Engelmann spruce = $354.8 \pm$

98.7 years, $n = 17$; Norway spruce = 248.4 ± 59.1 years, $n = 8$) (Fig. 3). The diverging growth strategies (fast versus slow growth) result in a diverse age structure of canopy trees in subalpine forests of Colorado and Switzerland (Fig. 1, 3).

Similar relationships between diameter growth and longevity were obtained for juniper *Juniperus communis* in England (Ward 1982), and a more recent study of various deciduous and evergreen tree species in North America has shown that older trees tend to show slower growth trajectories than younger trees (Black et al. 2008). Furthermore, the findings of our study empirically support Backman's (1943) early generalization that higher maximum growth and earlier maximum growth are associated with reduced tree longevity. Analogously, interspecific comparisons have shown that low tree growth rates are associated with high longevity for gymnosperms (excluding fast-growing, long-lived tree species that occur on very favorable sites) and angiosperms (Loehle 1988). The ecophysiological explanations of the intra-specific relationship between growth rate and longevity may partially correspond to those used to explain inter-specific variability (Black et al. 2008). In the study by Loehle (1988), only angiosperm species showed a negative effect of chemical defense (as measured by volumetric energy content of wood) on growth rates. Gymnosperm species did not reveal a significant effect, perhaps because they grow in cooler climates that are less favorable to fungal pathogens and herbivorous insects, where less investment in chemical defense is needed. For gymnosperm species, however, passive defenses involved in compartmentalization is associated with extended longevity (Loehle 1988). We assume that at the tree level, increased investment in chemical defenses such as phenolics, tannins, or resins and into structural defenses such as fibres, lignins, thick bark, or dense wood reduces pathogen or insect attacks and/or reduces the risk of breakage (Coley et al. 1985, Herms and Mattson 1992, Larson 2001). Resistance to pathogens seems to be a key factor in increasing longevity: fast-growing, short-lived conifers on favorable sites are more likely to be affected by pathogens than slow-growing, old conifers on unfavorable sites (Schulman 1954, LaMarche Jr. 1969, Larson 2001). However, this apparent intra-specific tradeoff between allocation of resources to growth and to defense, as well as its implications for longevity, needs more research. Related to this issue, there is also a need to identify the relative impacts of the environment and genetic constitution on defenses.

The observed negative relationships between early growth rate and longevity complement numerous studies on tree mortality, which generally found positive relationships between growth rates during the last ca 3–40 years prior to tree death and short-term survival probabilities (Keane et al. 2001, Wyckoff and Clark 2002, Bigler and Bugmann 2003, Das et al. 2007, Wunder et al. 2008). Sudden decreases in growth rates related to changing growth conditions generally indicate an increased probability of tree death in the short term (Bigler and Bugmann 2004, Das et al. 2007). However, in the current study, the negative relationship between early growth rate and longevity shows that initially slowly growing trees are expected to reach a greater longevity. Nevertheless, deteriorating growth conditions several or many decades later for those initially slowly growing individuals also may result in

growth rates below critical values that increase mortality risk in the short term. We note that trees with permanently very low growth rates (i.e. below the lowest observed growth; Fig. 1) were not included in our samples, because they died before attaining the necessary minimum size. Although initially fast growing trees have increased short-term survival probabilities (Bigler and Bugmann 2004), expected longevity may be lowered due to the long-term effects of factors such as reduced investment in defenses and increased risk of breakage. Furthermore, growth of these initially fast growing trees often declines rapidly when these trees reach a certain size (Fig. 1), probably as a result of increased hydraulic resistance related to increased xylem path length in larger trees (Ryan and Yoder 1997), which in turn decreases short-term survival chances.

The longevities of subalpine fir and Engelmann spruce are significantly associated with north-south aspect (Table 2). Thus, in addition to average growth rates over the first 50 years, trees growing on south-facing aspects in the Colorado study area tend to die younger than trees on north-facing aspects. This effect is apparent for subalpine fir of all size classes as well as for larger (≥ 23 cm DBHBB) and smaller (< 23 cm DBHBB) Engelmann spruce. Trees growing on south-facing aspects may be more prone to premature tree death, because water deficits are greater due to higher solar radiation compared to north-facing aspects and negatively affect annual growth variability (Villalba et al. 1994). For both subalpine fir and Engelmann spruce at our study sites, drought has been shown to decrease survival of trees (Bigler et al. 2007). Despite this local-scale association of longevity of subalpine fir and Engelmann spruce with aspect that is consistent with drought-induced growth declines and reduced survival probability, it is difficult to rule out other possible explanations. At coarse spatial scales, low resource availability either directly or indirectly through its influence on fuel quantity and fire regime has often been associated with greater tree longevity (Schulman 1954, LaMarche Jr. 1969). In our study, coarse-scale differences in fire regime related to aspect also may contribute to greater tree longevity on north-facing slopes. In northwestern Colorado, subalpine forests on drier south-facing aspects experience considerably more frequent fires than on north-facing aspects (Bebi et al. 2003), which reduces expected stand ages and maximum tree ages and could easily apply at the multi-kilometer scale of our sampling.

One methodological issue that needs to be addressed is the time a tree takes to reach coring height. Coring height in our study was higher than the root-shoot boundary, which introduces a potential error in estimating total tree age. For Norway spruce, where trees have established in stands with a relatively open canopy (Price and Thompson 1997), we assume that the bias is likely to be small. However, some of the Engelmann spruce and subalpine fir trees might have grown up under a relatively dense canopy. Particularly for subalpine fir, the number of missed rings to coring height can be several decades (Veblen 1986b). Because trees established in stands with different stand structures, during different periods, and some of them a long time ago (Fig. 2), estimates of true tree age would require tree-by-tree estimations of the age at coring height rather than general relationships between tree height and age. Correcting age estimates would not substantially

change the results for Norway spruce. For subalpine fir and Engelmann spruce, the relationship between longevity and growth rate might be even stronger, because trees that were growing slowly for the first 50 years at coring height were also likely growing slowly until they reached coring height. Another source of underestimating longevity is related to the fact that production of annual tree rings on dying trees may cease a few years prior to tree death. However, the number of missing rings is small (Bigler et al. 2007) and the effect on estimating longevity would be negligible.

The findings of our study provide a means for long-term predictions of tree death; based on radial growth rates of young trees and information on the spatial environment, it is possible to project life expectancy. Intra-specific maximum longevities may be estimated for very slowly growing trees, e.g. using the lowest observed growth rate to the age 50 (subalpine fir ≥ 14 cm DBHBB = $0.151 \text{ mm year}^{-1}$; Engelmann spruce ≥ 23 cm DBHBB = $0.213 \text{ mm year}^{-1}$; Norway spruce ≥ 31 cm DBHBB = $0.910 \text{ mm year}^{-1}$; Fig. 3) combined with north-facing aspect (subalpine fir and Engelmann spruce only). Given the estimated regression coefficients (Table 2 for subalpine fir and Engelmann spruce; Table 1 for Norway spruce), we expect for subalpine fir a maximum longevity of 275–337 years (approximate 95% confidence interval), of 378–512 years for Engelmann spruce that reach the canopy, and of 263–386 years for Norway spruce that reach the canopy. These predictions are found within or overlap with the range of longevities observed for these species.

Conclusions

Tree growth rates are reported to have increased over broad areas of North America and Europe in recent decades in relation to complex interactions of factors that vary regionally but include increases in temperature and precipitation, nitrogen deposition, rising CO_2 concentrations, and land-use changes (Spiecker et al. 1996, Ryan et al. 2008). For three conifer species from subalpine forests of the Colorado Rocky Mountains and the Swiss Alps, we have shown that more rapid initial growth rates are related to reduced longevity. For moist-cool subalpine forests, we hypothesize that the higher growth rates associated with global warming (Rolland et al. 1998) may in turn result in reduced tree longevity and more rapid turnover rates. This hypothesis is consistent with a recent study showing that temperature is positively correlated with turnover rates of conifer forests along an elevational gradient with relatively uniform precipitation regime in the California Sierra Nevada (Stephenson and van Mantgem 2005). We suggest that the direction of changes in tree longevity and forest turnover rates associated with broad-scale climate warming will be contingent on the nature of limiting climatic factors (cool temperatures versus moisture limitation; Villalba et al. 1994) and their interactions with site conditions such as topographic position. Influences of climate change on growth and turnover rates may be further complicated by non-linear and threshold effects potentially operating over large areas (Breshears et al. 2005, Reich and Oleksyn 2008, van Mantgem et al. 2009). To improve understanding of

long-term effects of climate warming on forest ecosystems, further investigations are needed of relationships between growth rate, tree longevity, and forest turnover rates, which take into account meso-scale topographic variation.

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