RESEARCH PAPER

CrossMark

Is tree age or tree size reducing height increment in *Abies alba* Mill. at its southernmost distribution limit?

Pasquale A. Marziliano[1] (iD) · Roberto Tognetti[2] · Fabio Lombardi[1]

Abstract
· *Key message* Conventional methods for estimating the current annual increment of stand volume are based on the uncertain assumption that height increment decreases with tree age. Conversely, size, rather than age, should be accounted for the observed senescence-related declines in relative growth rate and, consequently, implemented in silvicultural manuals. Results stem from a study on *Abies alba* Mill. at its southern limit of distribution.
· *Context* Many factors limit height increment when age and size increase in large-statured tree species. Height–diameter allometric relationships are commonly used measures of tree growth.
· *Aims* In this study, we tested if tree age was the main factor affecting the reduction in height increment of silver fir trees (*Abies alba* Mill.), verifying also whether tree size had a significant role in ecophysiological-biomechanical limitations to tree growth.
· *Methods* The study was carried out in a silver fir forest located in Southern Italy, at the southernmost distribution limit for this species. Through a stratified random sampling, 100 trees were selected. All the selected trees were then felled and the total tree height, height increments (internode distances), diameter at breast height, and diameter increments (ring widths) were measured.
· *Results* The analyses of allometric models and scaling coefficients showed that the correlation between tree age and height increment was not always significant.
· *Conclusion* We may conclude that tree age did not statistically explain the decrease in height increment in older trees. Instead, the increase in tree size and related physiological processes (expressed as product between diameter at breast height and tree height) explained the reduction in height increment in older trees and was the main factor limiting height growth trends in marginal population of silver fir.

1 Introduction

The observation that for most tree species mass growth rate of individual trees increases continuously with tree size has triggered new interest in the ecology of old and tall organisms

✉ Pasquale A. Marziliano
  pasquale.marziliano@unirc.it

[1] Dipartimento di Agraria, Università Mediterranea di Reggio Calabria, Loc. Feo di Vito, 89065 Reggio Calabria, Italy

[2] Dipartimento di Agricoltura, Ambiente e Alimenti, Università degli Studi del Molise, Via Francesco De Sanctis, 86100 Campobasso, Italy

(Stephenson et al. 2014). Indeed, this outcome implies that accumulation of carbon would continue as trees increase in size and age rather than decrease as trees mature. Nevertheless, evidence exists that size accounts for the observed age-related declines in relative height growth and net assimilation rates (Mencuccini et al. 2005). Discrepancies may also derive from the mechanics of curve fitting, linear vs. nonlinear models of tree growth (Paine et al. 2012). The growth of trees continues for years by continuously increasing both diameter and height, though it is unclear whether mature trees have static linear diameter–height trajectories or curved trajectories in relation to neighbor effects (Henry and Aarssen 1999). In addition, the allometric relationship between stem diameter at breast height and tree height does not always represent stem-mass growth patterns (Sillett et al. 2010).

Many studies have focused on the mechanisms regulating the maximum height that trees are able to reach (e.g., Koch et al. 2004; Meng et al. 2006; Ryan et al. 2006; Givnish et al.

2014; Larjavaara 2014; Socha et al. 2017; Jiang et al. 2018). These mechanisms involve both biomechanical and physiological challenges (Larjavaara 2014). Decreasing capacity to produce photosynthates in old trees (Bond 2000; Kenzo et al. 2006), as well as mechanical constraints (Meng et al. 2006; Feldpausch et al. 2011), have been observed. Leaves located in the upper part of the crown of tall trees have shown a reduction in photosynthetic efficiency (Murty et al. 1996; Koch et al. 2004; Ryan et al. 2006; Givnish et al. 2014). The hydrostatic component of the water potential drops from soil to leaves may decrease gas exchange and carbon assimilation (Woodruff et al. 2004; Koch et al. 2004; Ambrose et al. 2010), which can be partially compensated by adjustments in leaf area to sapwood area ratio (McDowell et al. 2002). Yet, this hydraulic connection does not always hold true (Barnard and Ryan 2003; Ryan et al. 2004) and a potential role of tree age on height growth, nutrient availability, and carbon metabolism has been envisaged (Day et al. 2001; Mencuccini et al. 2005; Bond et al. 2007).

Although the precise signals that limit height increment are still a topic of debate, it is clear that maximum tree height is an important feature in scaling of forest quantities and a major indicator for understanding stand biomass and resource use (Kempes et al. 2011). Allometric relationships may be used to interpret physiological traits relevant to forest dynamics and structure, which have been often found to be correlated with tree size following approximate power laws (Niklas and Spatz 2004). Intrinsic properties of the vascular system and genetic factors, as well as climate and competition factors, contribute to the final height and shape of a tree species (Jensen and Zwieniecki 2013). Although the overall efficiency of the water transport system may have a primary role in determining the maximum height of individual trees (Mencuccini 2003; Anfodillo et al. 2006; Du et al. 2008; Magnani et al. 2002), the efficiency of the water transport trough the xylem in relation to the tree dimension has been questioned (Becker et al. 2000a; Ryan et al. 2006; Netting 2009).

Tallest trees are often the oldest ones and, then, the lower assimilation rates can be linked to tree age (Yoder et al. 1994; Gower et al. 1996; Bond 2000; Day et al. 2001; Day et al. 2002; Binkley et al. 2002). However, there is no clear evidence of a degeneration in the meristematic tissues over time (Wareing and Seth 1967; Woolhouse 1972; Lanner and Connor 2001; Onate and Mussè-Bosch 2008). Indeed, meristems of branches cut from mature trees are able to normally resume the longitudinal growth if grafted into young plants (Mencuccini et al. 2005; Bond et al. 2007; Mencuccini et al. 2007; Petit et al. 2008). In addition, the decline in tree growth with age can be reversible when mature trees are released from competition by thinning (Martínez-Vilalta et al. 2007). Again, deviation from the optimal temperature (e.g., seasonal temperature oscillation) may reduce tree height increment (Larjavaara and Muller-Landau 2012, 2013). Allometric

scaling rules and mechanisms are fundamental not only to explain patterns in tree growth but also to manage stand productivity and carbon storage in forests (e.g., setting the rotation age based on the decline in annual production of wood after canopy closure).

The debate on factors causing the reduction of height increment as trees age has practical consequences, being related to tree allometry and forest mensuration. Methods usually applied for estimating the current increase in volume of forest stands consider tree height and stem diameter increments (Assmann 1970; Avery and Burkhart 2002; Husch et al. 2003; van Laar and Akca 2008). Indeed, tree stems show increments of wood as a series of overlapping cones derived from annual radial increments and apical elongations (Sumida et al. 2013). Temporal trends in the diametric and hypsometric tree growth differ among tree species or forest stands (Sumida et al. 1997). In fact, while the radial growth never stops throughout the tree lifetime, the tree height may only reach a maximum, typical of each tree species (Woolhouse 1972; Ryan and Yoder 1997; Midgley 2003; Koch et al. 2004; Niklas and Spatz 2004; Niklas 2007). However, starting from a specific age or size, the height increment usually decelerates and eventually culminates (Weiner and Thomas 2001; Zens and Webb 2002; Larjavaara 2014), but stem elongation may also stop when tree crown reaches a certain position within the vertical canopy profile (Becker et al. 2000a).

In forest management, this simplification can be misleading and may lead to even significant errors in the evaluation of forest stand productivity (in terms of volume or biomass), since many methods applied in Central and Southern Europe for estimating the current annual increment (CAI) are all based on the assumption that height increment decreases with tree age. Based on the simplification proposed by Schneider in 1853 (see Prodan and Holzmesslehre 1965), the estimate of the percentage current annual increment (PCAI) is calculated from the ratio between the K coefficient (Schneider's coefficient) and the number of tree rings included in the outer centimeter of the core sampled at the stem breast height, multiplied by the diameter at breast height. According to this method, tree age is the main factor influencing the relationship between height increment (Δh) and tree height (h), but also between radial growth (Δd) and stem diameter at breast height (dbh). From this method originates the so-called chronological criterion according to which the Schneider's coefficient K is related to tree age and equals 400 for old trees (i.e., $\Delta h/h = 0$), 600 for mature trees (i.e., $\Delta h/h = \Delta d/dbh$) and 800 for young trees (i.e., $\Delta h/h = 2 \cdot \Delta d/dbh$).

The main objectives of this study were (i) to test if tree age is the main factor affecting the reduction in height increment and (ii) to verify if tree size has a significant role in declining height increment as tree matures. Resultant aims were to (iii) provide an allometric framework for the revision of current methods to evaluate forest stand productivity, which is

assumed to decline with tree age and (iv) to reconsider the use of Schneider's coefficient K, assigning values in relation to tree size rather than to tree age. Measurements were conducted on silver fir (*Abies alba* Mill.) at its southernmost geographical limit (Calabria, Southern Italy). These marginal populations at the East-West Mediterranean Sea divide provide a test-bed for understanding the pattern of growth in silver fir trees and their resilience (Antonucci et al. 2018), in response to increasing wind loading and drought stress, and related hydraulic and mechanical restraints, as a consequence of climate change.

2 Materials and methods

2.1 Study area and field survey

The study area is located in Calabria, Southern Apennines, Italy, on the watershed divide between Tyrrhenian and Ionian seas, separating the wind and thermally driven circulation of eastern and western Mediterranean Sea. The investigated stand refers to the "Archiforo" forest (38° 32′ 24″ N; 16° 18′ 24″ E), a silver fir (*Abies alba* Mill.) even-aged forest of approximately 120 years extending approximately 800 ha and located at an altitude of about 1150 m a.s.l. Climate is temperate. According to the USDA soils taxonomy (USDA 1999), soils (fertile loamy) belong to the Great Group of Dystrudepts. The site morphology is mainly flat.

Field surveys were carried out in three plots, each extending 0.2 ha, representative of the overall structure of the studied forest stand. The diameter at breast height (*dbh*) of all trees with *dbh* > 12.5 cm was measured. In 2015, 100 silver fir trees were selected through a stratified random sampling, in relation to the frequency of the *dbh* classes to the 0.2 ha plot-level. The sample size was determined examined the trees height variability, with the following formula:

$$n = \left(\frac{CV}{Err\%} \cdot t \right)^2 \tag{1}$$

where *n* is the number of trees sample, *CV* is the coefficient of variation of tree height when cut, *Err%* is the acceptable sampling error (4%), and *t* (Fisher's exact test) equals 2 (95% confidence). According to this, the statistical sample size was 100.

Furthermore, increment cores at breast height were collected from each sampled tree, using a Pressler borer, and all sample trees have about the same age, ranging from 115 to 125 years.

All the selected trees were then felled and the total tree height (*h*) and height increments (*Δh*) were measured. Values of height increments were obtained by measuring the stem internodes distance, starting from the tree top. Height

increment corresponds to the length of the last apical growth at the end of the vegetative season. Considering that silver fir is characterized by a monopodial growth, the annual height increments were easily measurable. Table 1 summarizes the main descriptive statistics of the measured attributes, all revealing a normal distribution of data.

2.2 Analyses and data processing

Tree-ring widths were measured with a resolution of 0.01 mm using the LINTAB measurement equipment (Frank Rinn, Heidelberg, Germany) fitted with a Leica MS5 stereoscope (Leica Microsystems, Germany); tree ring widths were cross-dated following standard procedures and statistically verified with the TSAP software package (Fritts 1976).

Subsequently, for each tree, starting from the current *dbh* and height measured in the field, the *dbh* and height of previous years were calculated. For all sample trees, it was thus possible to obtain the diameter and height for each previous year of its growth.

Values of *Δd* and *dbh*, and of *Δh* and *h*, measured on sample trees, were used for establishing the relationships between *Δd* and *dbh*, and between *Δh* and *h*. In these relationships, *Δd* was calculated as $2 \cdot r_{10}/10$ where r_{10} is the increment of the radius occurred in the last 10 years and *dbh* is the diameter at the final age; *Δh* was calculated as $\Delta h = l_{10}/10$, where l_{10} is the stem length corresponding to the height increment in the last 10 years and *h* is the height at the final age. This procedure was used only for relationships between *Δd* and *dbh*, and between *Δh* and *h*. The aim was to evaluate the relationship between *dbh* or *h* of the sample trees in 2015 and mean *dbh* or *h* increment in the last 10 years.

The height–diameter relationship (i.e., the hypsometric curve) was also derived at different tree ages, on the basis of the 100 sample trees. In general, tree height can be explained by variables such as diameter, soil fertility, stand density, and age of trees (Clutter et al. 1983; Parresol 1999; Pommerening 2002). Height–diameter relationships with a combination of these variables have been included in several modeling approaches of tree growth (Curtis 1967; Bennett and Clutter 1968; Clutter et al. 1983; Corona et al. 2002; Marziliano et al. 2013).

Considering that our experimental plots were located in the same study area, with limited variations in soil and microclimate, the site index was excluded from the equation. Yet, the stand density (number of trees per hectare) did not vary between plots and, consequently, was also excluded from the equation. Therefore, a model that allows for computing tree height as a function of age and dbh was applied:

$$h = f(\text{Age}, dbh) \tag{2}$$

where *h* = total tree height; Age = tree age; *dbh* = tree diameter at breast height.

Table 1 Descriptive statistics of the attributes measured on the sampled trees

Attribute	Mean	Min	Max	SD	Skewness	Kurtosis
dbh (cm)	53.0	15.0	94.0	18.48	− 0.20	− 0.65
Current annual increment of dbh (cm year^{-1})	0.39	0.13	0.63	0.13	0.06	− 0.39
Height (m)	29.3	16.1	44.2	5.85	− 0.05	− 0.40
Current annual increment of height (cm year^{-1})	0.20	0.04	0.39	0.07	0.26	− 0.19

SD standard deviation

The analysis was carried out by comparing different transformations and combinations of the equation variables, suitable to express the relationship between tree height and age and *dbh*. The process involved a regression analysis with a stepwise procedure (in each step, a variable is considered for addition to or subtraction from the set of explanatory variables based on F tests). We evaluated fit of the final model using and analyzing the value of root mean square error (RMSE) and the R^2 value. In addition, residual plots were used to assess homogeneity of variance and normality of residuals and the Shapiro-Wilk test to verify the normality of error distribution.

For each sample tree, we calculated the time-trajectory relationship between tree age (Age) and height increment (Δh). For each Age-Δh relationship, we quantified the share of variance for Δh explained by the variable Age with respect to total variance through R^2. Finally, considering the whole sample (100 trees), we used a linear mixed-effect model to test the effects of Age and Size on Δh, evaluating the significance of the estimated coefficients. In this analysis, tree size was expressed as the product between *dbh* (cm) and h (m) (*dbh* · h). Therefore, age (Age) and size (*dbh* · h) and their interaction term (Age ·(*dbh* · h)) were employed as fixed-effect explanatory variables in the model. The tree ID was incorporated as a random effect to account for the nesting of correlated annual observations within a tree. For the linear mixed-effect model analysis, the nlme package for the R programming language (R Core Team 2016) was used. We evaluated and compared the following two models:

$$\Delta h = \beta_0 + \beta_1 \cdot \text{Age} + \beta_2 \cdot (dbh \cdot h)$$
$$+ \ (\text{tree } ID \text{ as random effect}) \tag{3}$$

$$\Delta h = \beta_0 + \beta_1 \cdot \text{Age} + \beta_2 \cdot (dbh \cdot h) + \beta_3 \cdot \text{Age} \cdot (dbh \cdot h)$$
$$+ \ (\text{tree } ID \text{ as random effect}) \tag{4}$$

In order to evaluate and then compare annual tree growth increments at different ages, we also used the relative growth rate (RGR), as it provides a measure of tree growth relative to initial size between any two intervals. The analysis of RGR provides indication if inherent differences in growth potential are associated to tree ages, or if the differences in absolute growth derive from effects associated with differences in tree size (Mencuccini et al. 2007). Mean RGR was calculated using the following equation (Mencuccini et al. 2007):

$$\text{RGR} = \frac{\ln(h_2) - \ln(h_1)}{t_2 - t_1} \tag{5}$$

where h_2 and h_1 are the measured heights at times t_2 and t_1, respectively, and RGR is the relative growth rate. The time interval for calculating RGR was 1 year.

As reported in Mencuccini et al. (2007), although RGR systematically changed through time, decreasing as the initial tree height increased, such a decline did not invalidate the use of RGR in assessing tree growth performance and efficiency; trees of the same population growing in similar environmental conditions often show similar growth patterns, with curves forming almost parallel lines, but with different absolute RGR values (Pommerening and Muszta 2015).

The effect of age on RGR was assessed with covariance analysis (ANCOVA), using the initial tree height (h) between any two intervals as covariate, to account for the negative effect of increasing size on RGR.

3 Results

The studied stand was characterized by a tree density of 245 individuals per hectare, without significant differences between plots, in terms of number of trees per hectare, and tree *dbh* and height. Figure 1 shows the trees distribution among *dbh* classes in the stand and the sample trees distribution among diameter and height classes. The tree distribution had the typical bell-shaped pattern, with a quadratic mean *dbh* (qmd) of 59 cm; the tree height corresponding to qmd was about 30 m, while the living volume was 1032 m^3 ha^{-1}.

For the relationship between Δd and *dbh*, for all sample trees, the quadratic function proved to be the most suitable (in terms of higher value of R^2 and in terms of lower value of S.E.E.) (Fig. 2):

$$\Delta d = 0.0838 + 0.0047 \cdot dbh + 0.00002 \ dbh^2 \tag{6}$$

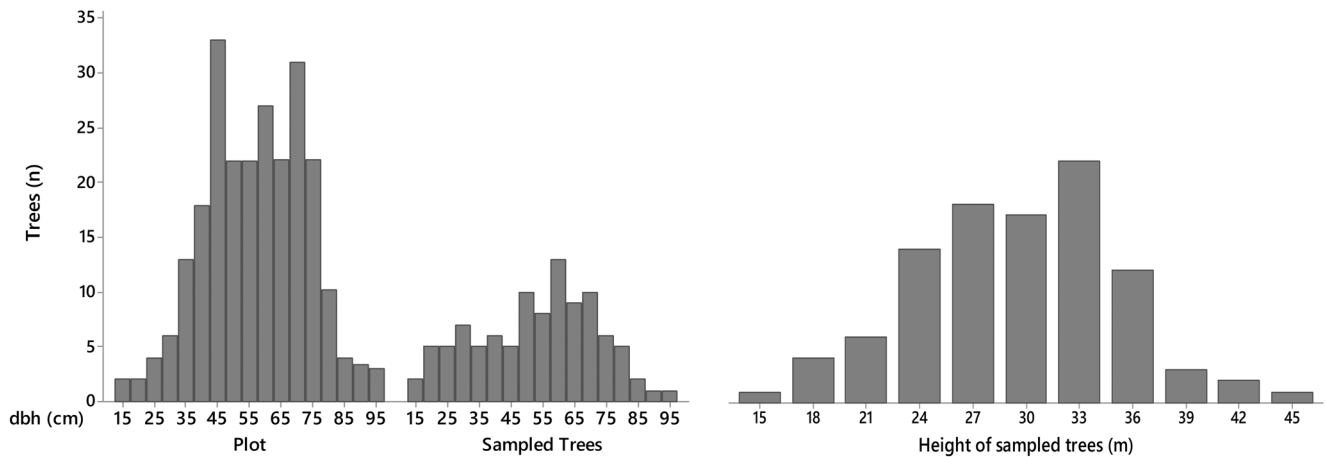where $R^2 = 0.78$ and S.E.E. = 0.064 cm year^{-1}.

Fig. 1 Tree distribution among diameter classes in the study site and tree distribution among diameter and height classes in the sample trees

In the examined stand, *dbh* increment raised as tree *dbh* increased (Fig. 2). In detail, Δd ranged from 0.14 to 0.21 cm year^{-1} for the smallest *dbh* class (15–20 cm) and from 0.56 to 0.63 cm year^{-1} for the largest one (85–90–95 cm).

For the relationship between Δh and h, among various functional approaches, the linear form proved to be the most suitable (in terms of higher value of R^2 and in terms of lower value of S.E.E.) (Fig. 3):

$$\Delta h = 0.485 - 0.010\, h \tag{7}$$

with $R^2 = 0.60$ and S.E.E. $= 0.048$ cm year^{-1}.

In this case, height increment decreased as tree height increased (Fig. 3). Yet, the measured Δh ranged from 0.27 to 0.39 m year^{-1} for the smallest height category (15–17.5 m) and from 0.05 to 0.08 m year^{-1} for the largest one (42.5–45 m).

Furthermore, considering the hypsometric curve at different tree ages, starting from the Eq. 2, the variables were combined in the following model:

$$\ln(h) = 3.818$$
$$+ 1.722 \cdot \frac{1}{\text{Age}} - 0.335 \cdot \frac{1}{dbh} - 975.461 \cdot \frac{1}{dbh \cdot \text{Age}} \tag{8}$$

Fit statistics were good. Root mean square error (RMSE) was 0.1488 and R^2 was 0.54.

Figure 4a provides the height–diameter correlation (i.e., the hypsometric curve) at different tree ages. The analysis covered a time lapse of 100 years: from tree age of 20 to 120 years. As expected, the hypsometric curve appeared steeper during the first decades of their lifetime, than the other curves (tree age from 80 to 120 years). Residual plot (deviations vs. predictions) displayed a uniform distribution (Fig. 4b), allowing for the model to be validated (homogeneity of variance and

Fig. 2 Measured and estimated current annual increment of *dbh* values (Δd) in relation to the measured *dbh*. The age of trees was approximately 120 years
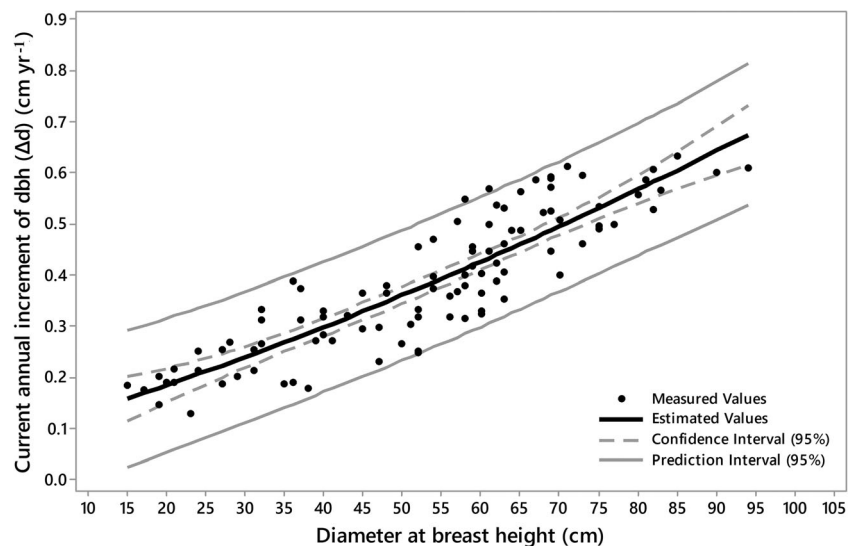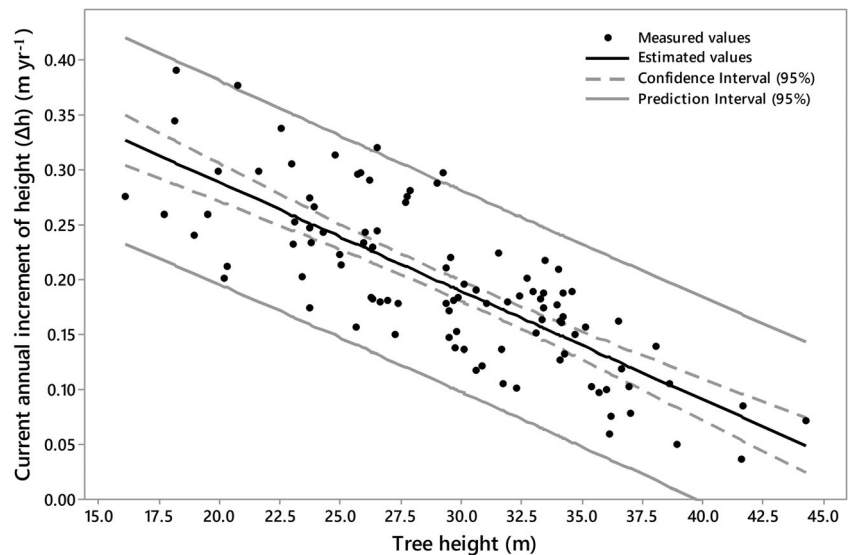
Fig. 3 Measured and estimated current annual increment of tree height (Δh) in relation to the measured height. The age of trees was approximately 120 years

normality of residuals). Besides, the Shapiro-Wilk normality test ($W = 0.9263$; $p = 0.087$) confirmed the absence of deviation from normality.

Figure 5 shows the scatterplot and the regression lines of the Age-Δh relationship for some sample trees, all with age of about 120 years. In general, the linear regressions of these relationships showed very low R^2, with the slope of regression lines almost never significant. More specifically, results revealed that only 6% of regression lines were statistically significant ($p < 0.05$) and with high R^2 (Fig. 6). In addition, for all sample trees, the sign of the slopes was always negative.

Table 2 shows the results of the linear mixed-effect model for examine the possible influence of the fixed effects Age, Size, and their interaction) on height increment (Δh). In both models (Eqs. 3 and 4), the tree size ($dbh \cdot h$) was a significant predictor ($p < 0.001$) and was negatively related to height increment, while the tree age ($p = 0.1022$ in Eq. 3 and $p = 0.0902$ in Eq. 4) and the interaction term ($p = 0.0892$ in Eq. 4) were not significant predictors to Δh.

RGR for height decreased with increasing initial tree size (Fig. 7). However, in order to verify the age effects, we examined RGR for height referred to each age class. Therefore, we analyzed if differences in RGR across age classes (but at constant size) were indicative of an age-related trend. Figure 7 shows RGR values for tree height of three age classes against initial height and initial dbh. For each value of the initial tree height or initial dbh, and for each age class, RGR indicates the mean value of RGR of all trees with the same initial height (Fig. 7a) or the same initial dbh (Fig. 7a). Being equal the initial tree height or initial dbh, RGR for height values were independent of tree age. This was confirmed by the ANCOVA. Although significant differences were seen for different heights ($F_{1;81} = 469.328$; $p = < 0.001$) and for different diameters ($F_{1;285} = 376.867$; $p = < 0.001$), age class did not significantly affect yearly RGR, being the differences across age classes not significant with initial tree height ($F_{2;81} = 1.103$; $p = 0.337$) and initial dbh ($F_{2;285} = 0.174$; $p = 0.841$). However, RGR for tree height values diverged slightly from
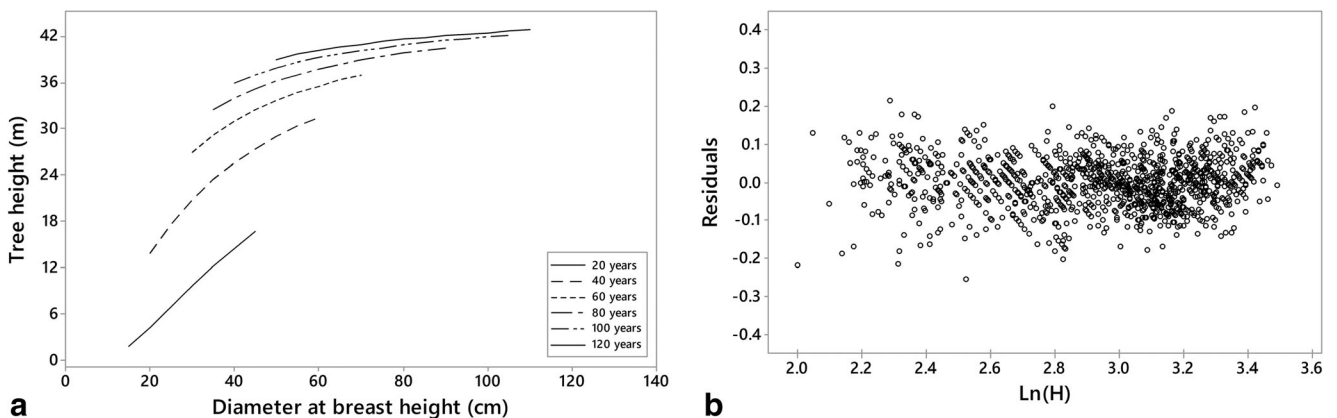

Fig. 4 Tree height-diameter curves observed at different mean stand age with an interval of 20 years, from 20 to 120-year-old trees (**a**) and residuals from height estimation (Eq. 7) (**b**)
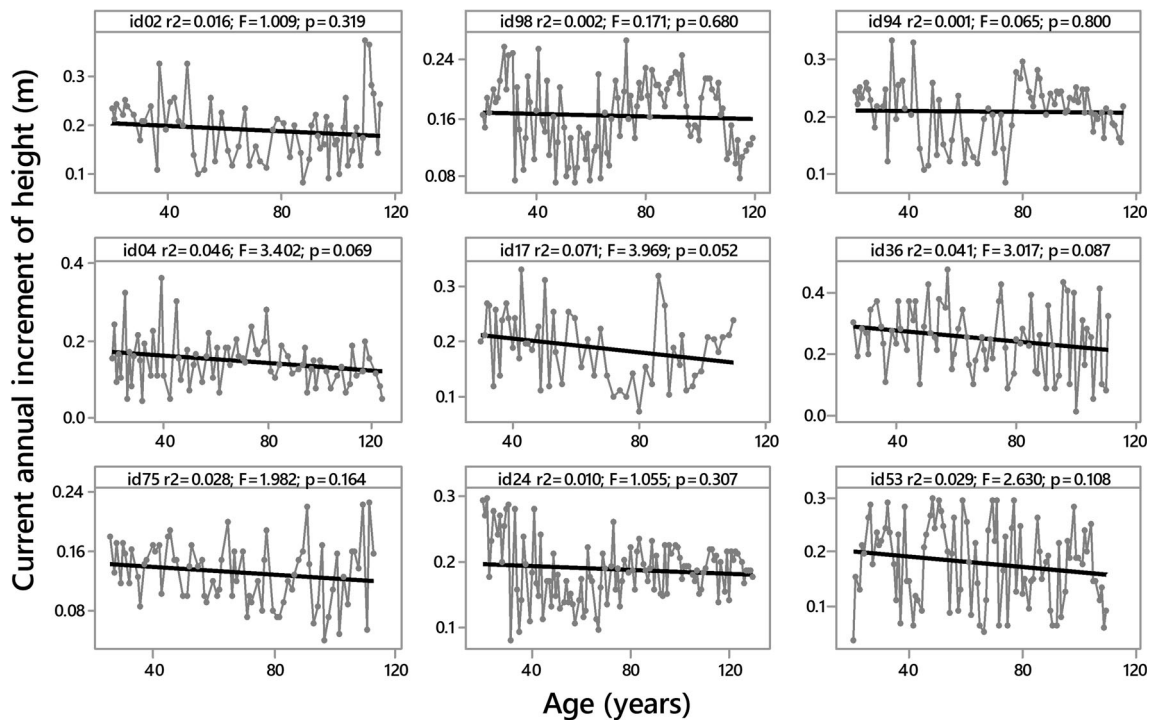
Fig. 5 Relationship between current annual increment of tree height (Δh) and tree age for selected trees. Data were fitted separately with linear functions. Id number is the tree sampled, r^2 is the determination coefficient of regression, F and p value indicate the significance of regression

this rule when trees were of small size. Therefore, younger trees had higher RGR for height values.

4 Discussion

Although limited to silver fir growing at its southernmost distribution limit, we showed that an appropriate choice of allometric models and scaling coefficients allows the resolution of

uncertainties found in silvicultural manuals about the variation in the relationship between tree height and stem diameter as tree age and size increase. For example, Corona et al. (2009) applied the simplification proposed by Schneider for the assessment of growing stock volume, following the conventional technique referred to as forest inventory by compartments. Indeed, methods used to assess CAI may exceed the chronological criterion, often adopted in the Alpine and Mediterranean environments, being based on the negative

Fig. 6 Determination coefficients representing the relationship between height increment and tree age obtained for each sampled tree. Columns colored in blue identify trees with statistically significant regression lines
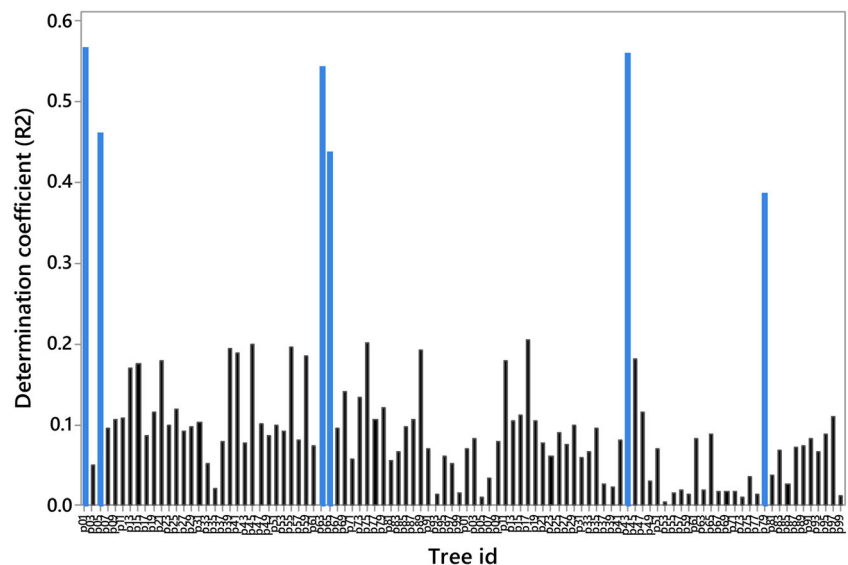
Table 2 Results of the linear mixed-effect model with tree ID as random effect for examining the possible influence of fixed effects (Age, Size, and their interaction) on the response variable (height increment (Δh))

Model	Value	DF	t value	p value
Equation 3				
Intercept	4.3526	2739	22.5541	< 0.0001
Age	− 0.0173	2739	− 1.6349	0.1022
$dbh \cdot h$	− 0.000224	88	− 17.893	< 0.0001
Equation 4				
Intercept	4.9404	2738	12.4781	< 0.0001
Age	− 0.0227	2738	− 1.695	0.09019
$dbh \cdot h$	− 0.000495	88	− 6.791	< 0.0001
Age $\cdot (dbh \cdot h)$	0.000003	2738	1.7000	0.0892

correlation between height increment and tree age. Size-mediated (and not age-dependent) functional processes were the major drivers of height growth reductions in these silver fir trees, which may reflect the preeminent role of hydraulic architecture in limiting carbon uptake in tall conifers (Niklas and Spatz 2004), although mechanical constraints are conceptually thought to rule size-dependent relationships in forest trees (cf. Niklas 1994). Indeed, long pathway-lengths and low maximum water potentials in tall trees may preclude refilling of xylem conduits, although wind-induced tensile and/or compressive stresses may further add to gravity load in setting maximum attainable heights (Niklas 2007).

The hypsometric curves (Fig. 4a) suggest that the increment in height of sample trees was regulated by the interaction of two opposite factors: a rapid longitudinal development during the earlier stage of development and the constraint imposed by external and internal factors (e.g., individual competition, limiting resources, hydraulic stress, ontogenetic aging) as tree age increased. The hypsometric curve, initially steeper, became more flattened with age, indicating a high level of spatial competition between individual trees (Marziliano et al. 2013). As trees aged, such a relationship was affected by the differentiation in stem diameter rather than the variation in tree height. As a consequence, trees grew more in diameter than in height. Therefore, height increment and radial growth of silver fir revealed different temporal patterns (e.g., Sumida et al. 1997). Although a decrease in longitudinal increment was observed, radial growth tended to be constant over time (e.g., Hara et al. 1991). Therefore, at first approximation, it is possible to infer that the tree age was the main factor inducing the decrease in height increment (e.g., Bond 2000; Day et al. 2002; Binkley et al. 2002). Continued stem diameter growth, independently of height increase or decrease, may ensure repair or reconstruction of damaged areas and maintaining of functional sapwood, thus increasing long-term survival in aging dominant trees under disturbance pressure.

Results obtained with the regression lines were in contrast with this hypothesis. Assuming a negative correlation between tree age and height increment, the height increment should have decreased as tree age increased. However, if tree age was the main factor influencing the decrease in height increment of silver fir, significant R^2 values were expected. By contrast, the analysis showed mainly low and insignificant correlation between "Age" and "Height increment." Furthermore, we observed also that the variability in Δh was not fully explained by tree age. Hence, tree age alone was not able to explain the decrease of height increment in silver fir sampled at its southernmost distribution limit. This allometric exercise provides insights to understand adaptations of peripheral silver fir populations to local environment, as well as useful predictions for forest managers that aim to maximize wood production and direct future stand development in central populations under long-term disturbance scenario.

It must be pointed out that the hypsometric curves and the trajectories of *dbh-h* relationships among individual trees may vary trough time, because of variation in long-term patterns of crown-base rise. Crown length, foliage amount, and
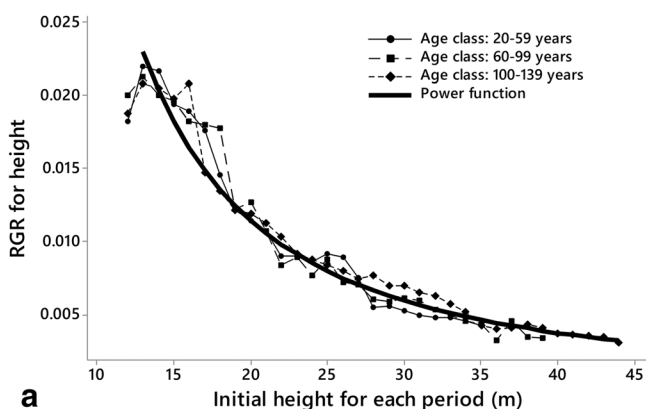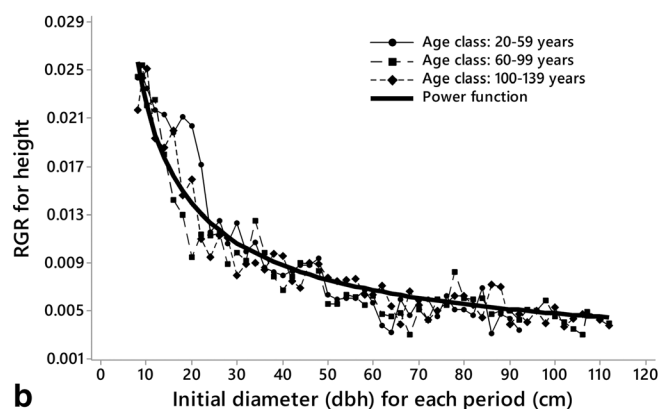
Fig. 7 Relative growth rates (RGR) vs. initial tree height (**a**) and initial tree diameter (**b**) across three age classes, and the power function obtained from the relationship between RGR for height and the initial tree height, **a** (RGR = 1.444 h$^{-1.615}$), and initial tree diameter, **b** (RGR = 1.005 dbh$^{-0.666}$) for all ages

physiological status may vary among individuals, resulting in different growth priority between stem portions. Indeed, the growth rate of the stem cross-sectional area has been found to be low in the stem below the crown base in suppressed conifer trees (Sumida et al. 2013), increasing along the stem upwards, but decreasing in dominant trees. Therefore, since silver fir trees were selected on a random basis, with the aim of representing a range of crown classes, it is possible that overtopped trees at a given age were included in the sampling frame, while taking all samples from the dominant or co-dominant crown classes, at any given age, might have limited potential model bias (Lhotka and Loewenstein 2015). Yet, as reported by Trouvé et al. (2015), the maximum height growth rate can be greater in stands with relatively low tree density than in dense forests, and the height–diameter growth rate ratio can be greater in suppressed than dominant trees. Sustained diameter growth of the upper-trunk of co-dominant trees have been observed in other tall conifer trees (e.g., Ishii et al. 2017). Competition for light most probably affected height–diameter growth relationships in these silver firs, depending on density and social status of trees in the stand, as well as on available water (and other resources). Further research evaluating potential model errors is warranted.

The correlation between Age and Δh was correctly quantified and measured using the determination coefficient (R^2), and the regression analysis showed that Age was not related to height growth decline. Whereas, tree size had a significant effect on Δh and, therefore, a large share of the variability of Δh was most probably related to the size of trees. These results support the hypothesis that the reduction of height increment was mainly driven by functional tree-size constraints (Ryan and Yoder 1997; Enquist et al. 2000), although the limitation caused by tree age cannot be ruled out. When tree height and size increase, the distance between roots and leaves becomes longer, which may induce several hydraulic and mechanical constraints, since the hydrodynamic resistance in xylem conduits grows significantly (Friend 1993; West et al. 1999; Becker et al. 2000a; Becker et al. 2000b; Enquist 2003). Yet, in tall silver fir trees, height–diameter (h-dbh) allometries could be critically determined by wind regimes (e.g., Thomas et al. 2015); locally elevated surface winds are common in the mountain forest environment. Silver fir trees were sampled in the watershed divide between two seas (Tyrrhenian and Ionian), which separates western and eastern thermally driven circulation patterns of the Mediterranean Sea, with strong influence on wind regime. Physiological limitations and biomechanical perturbations would preclude any potential increase in tree size of marginal tree populations operating at their limits, due to their effects on functional and structural traits (Niklas 1992; Enquist 2003).

The observed growth reduction in relation to tree size was also confirmed by the relationships Δh-h (Fig. 3) and Δd-dbh

(Fig. 2). Taller silver fir trees stopped growing in height, while smaller ones, but of the same age, were still characterized by higher height increment. In our study, despite having only few trees over 40 m in height, we observed that these big trees (dbh > 80 cm and height > 40 m) ceased almost completely their height growth, independently of tree age, confirming a major impact of tree size (see Mencuccini et al. 2005). Thus, the chronological rule widely adopted in forest management guidelines in the Alpine region (as well as the Italian Peninsula), where tree age is the main driver of the relationship between $\Delta h/h$ and $\Delta d/dbh$, can be misleading. Marziliano et al. (2012) have shown that the application of this method results in significant errors in tree volume estimation (up to 40%). We, therefore, recommend to assign K values (the Schneider's coefficient used to calculate the percentage current annual increment) based on tree size rather than tree age.

RGR for tree height varied with dbh and height independently of tree age, however, showing relatively higher values when trees were of small size and younger. The power function obtained in the relationship between RGR for height and dbh had exponent 2/3, following mechanical and hydraulic constraints posed by tree size (e.g., Niklas and Spatz 2004). The exponent increased in absolute terms for the relationship between RGR for height and initial tree height, which points to the need of considering flexible scaling rules across these variables and specific environmental settings. In these silver fir trees, RGR for height decreased more rapidly when plotted against the initial height than the initial dbh, which implies to consider size-dependent relationships as constrained not only by mechanical stability but also by hydraulic capacity. As silver fir trees grew taller, RGR for height slowed down (regardless of the age class), showing that size-mediated functional and structural constraints prevailed over age-related factors in ruling tree growth rates. Nevertheless, age-related factors (particularly in early tree/stand development) and environmental disturbance (wind, drought) may still affect scaling relationships (Ryan et al. 2004; Coomes et al. 2011).

Tree height and radial increments did not follow similar trends. In fact, while the radial increment increased with tree size, the height increment decreased, as reported by several authors (e.g., Ryan and Yoder 1997; Mencuccini et al. 2005; Petit et al. 2008). Tree stature reflects environmental factors (air temperature, soil depth, wind speed, snow cover) and adaptation potential of the species to limiting factors (Wang et al. 2017). The stature of silver trees growing at the southernmost distribution margin for the species was, therefore, probably modulated by both latitude-related changes in environmental conditions and other stand-specific factors. Tree height–diameter scaling relationships in silver fir were flexible, varying across age classes, probably due to partitioning patterns and ecological responses to specific environmental conditions. Increasing leaf water stress due to path length

resistance, as well as the tradeoffs between water transport requirement and water column safety may constrain leaf expansion and assimilation rate, and thus height growth, even when soil moisture is not limiting (Koch et al. 2004).

5 Conclusions

Height increment in silver fir was related to tree size independently of tree age. Stem diameter at breast height of this large-sized tree species increased continuously as trees got older and bigger, while height increment decreased and eventually stopped. Clarifying how height–diameter allometric relations vary locally may provide more reliable tree growth estimates to forest managers, as well as regarding the effects of climate change on currently growing forests.

Tree age did not explain the reduction in height growth in older silver fir trees, while tree size was considered the main factor limiting their height increment. However, despite the several hypotheses made for explaining the cessation of height increment in big and tall trees with aging (e.g., hydraulic limitation, mechanical perturbation, temperature constraint), further research is needed to clarify allometric rules for single species and to explore mechanistic links between tree physiology and climate change.

The cessation of height growth in older trees of this large-statured species was well described by the application of hypsometric curve-fitting to model height–diameter allometric relationship. Height–diameter allometric relationships varied with stand age, which may translate in some inconsistencies between stem diameter growth and tree biomass/volume increment and be worth considering in future studies of stand productivity of silver fir populations.

Compliance with ethical standards

References

Ambrose AR, Sillett SC, Koch GW, Van Pelt R, Antoine ME, Dawson TE (2010) Effects of height on treetop transpiration and stomatal conductance in coast redwood (*Sequoia sempervirens*). Tree Physiol 30:1260–1272

Anfodillo T, Carraro V, Carrer M, Fior C, Rossi S (2006) Convergent tapering of xylem conduits in different woody species. New Phytol 169:279–290

Antonucci S, Rossi S, Lombardi F, Marchetti M, Tognetti R (2018) Influence of climatic factors on silver fir xylogenesis along the Italian peninsula. IAWA J in press

Assmann E (1970) The principles of forest yield study. Pergamon Press, Oxford

Avery TE, Burkhart HE (2002) Forest measurements (5th edition). McGraw-Hill

Barnard HR, Ryan MG (2003) A test of the hydraulic limitation hypothesis in fast-growing *Eucalyptus saligna*. Plant, Cell and Environment 26:1235–1245

Becker P, Gribben RJ, Lim CM (2000b) Tapered conduits can buffer hydraulic conductance from path-length effects. Tree Physiol 20:965–967

Becker P, Meinzer FC, Wullschleger SD (2000a) Hydraulic limitation of tree height: a critique. Funct Ecol 14:4–11

Bennett FA, Clutter JL (1968) Multiple-product yield estimates for unthinned slash pine plantation-pulpwood, sawtimber, gum, USDA Forest Service Research Paper SE-35. Southeastern Forest Experimental Station, Ashville, NC

Binkley D, Stape JL, Ryan MG, Barnard HR, Fownes J (2002) Age-related decline in forest ecosystem growth: an individual-tree, stand-structure hypothesis. Ecosystems 5:58–67

Bond BJ (2000) Age-related changes in photosynthesis of woody plants. Trends Plant Sci 5:349–353

Bond BJ, Czarnomski NM, Cooper C, Day ME, Greenwood MS (2007) Developmental decline in height growth in Douglas-fir. Tree Physiol 27:441–453

Clutter JL, Fortson JC, Pienaar LV, Brister GH, Bailey RL (1983) Timber management: a quantitative approach. John Wiley & Sons

Coomes DA, Lines ER, Allen RB (2011) Moving on from metabolic scaling theory: hierarchical models of tree growth and asymmetric competition for light. J Ecol 99:748–756

Corona P, Fattorini L, Franceschi S (2009) Estimating the volume of forest growing stock using auxiliary information derived from relascope or ocular assessments. For Ecol Manag 257:2108–2114

Corona P, Marziliano PA, Scotti R (2002) Top-down growth modelling: a prototype for poplar plantations in Italy. For Ecol Manag 161:65–73

Curtis RO (1967) Height–diameter and height–diameter–age equation for second growth Douglas-fir. For Sci 13:365–375

Day ME, Greenwood MS, Diaz-Sala C (2002) Age and size-related trends in woody plant shoot development: regulatory pathways and evidence for genetic control. Tree Physiol 22:507–513

Day ME, Greenwood MS, White AS (2001) Age-related changes in foliar morphology and physiology in red spruce and their influence on declining photosynthetic rates and productivity with tree age. Tree Physiol 21:1195–1204

Du N, Fan JT, Chen S, Liu Y (2008) A hydraulic-photosynthetic model based on extended HLH and its application to coast redwood (*Sequoia sempervirens*). J Theor Biol 253:393–400

Enquist BJ, Wes GB, Brown JH (2000) Quarter-power scaling in vascular plants: functional basis and ecological consequences. In: Brown JH, West GB (eds) Scaling in biology. Oxford University Press, Oxford, UK, pp 167–199

Enquist BJ (2003) Cope's rule and the evolution of long-distance transport in vascular plants: allometric scaling, biomass partitioning and optimization. Plant, Cell and Environment 26:151–161

Feldpausch TR, Banin L, Phillips OL, Baker TR, Lewis SL, Quesada CA, Affum-Baffoe K, Arets EJMM, Berry NJ, Bird M, Brondizio ES, de Camargo P, Chave J, Djagbletey G, Domingues TF, Drescher M, Fearnside PM, França MB, Fyllas NM, Lopez-Gonzalez G, Hladik A, Higuchi N, Hunter MO, Iida Y, Salim KA, Kassim AR, Keller M, Kemp J, King DA, Lovett JC, Marimon BS, Marimon-Junior BH, Lenza E, Marshall AR, Metcalfe DJ, Mitchard ETA, Moran EF, Nelson BW, Nilus R, Nogueira EM, Palace M, Patiño S, Peh KSH, Raventos MT, Reitsma JM, Saiz G, Schrodt F, Sonké B, Taedoumg HE, Tan S, White L, Wöll H, Lloyd J (2011) Height–diameter allometry of tropical forest trees. Biogeosciences 8:1081–1106

Friend AD (1993) The prediction and physiological significance of tree height. In: Solomon AM, Shugart HH (eds) Vegetation dynamics and global change. Springer, Boston, MA, pp 101–115

Fritts HC (1976) Tree ring and climate. Academic Press, London, UK

Givnish TJ, Wong SC, Stuart-Williams H, Holloway-Phillips M, Farquhar GD (2014) Determinants of maximum tree height in Eucalyptus species along a rainfall gradient in Victoria, Australia. Ecology 95:2991–3007

Gower ST, McMurtrie RE, Murty D (1996) Aboveground net primary production decline with stand age: potential causes. Trends in Ecology and Evolution 11:378–382

Hara T, Kimura M, Kikuzawa K (1991) Growth patterns of tree height and stem diameter in populations of *Abies Veitchii*, *A. Mariesii* and *Betula Ermanii*. J Ecol 79:1085–1098

Henry HAL, Aarssen LW (1999) The interpretation of stem diameter–height allometry in trees: biomechanical constraints, neighbor effects, or biased regressions? Ecol Lett 2:89–97

Husch B, Beers TW, Kershaw JA (2003) Forest mensuration, 4th edn J. Wiley & Sons

Ishii HR, Sillett SC, Carroll AL (2017) Crown dynamics and wood production of Douglas-fir trees in an old-growth forest. For Ecol Manag 384:157–168

Jensen KH, Zwieniecki MA (2013) Physical limits to leaf size in tall trees. Phys Rev Lett 110

Jiang L, Tian D, Ma S, Zhou X, Xu L, Zhu J, Jing X, Zheng C, Shen H, Zhou Z, Li Y, Zhu B, Fang J (2018) The response of tree growth to nitrogen and phosphorus additions in a tropical montane rainforest. Sci Total Environ 618:1064–1070

Kempes CP, West GB, Crowell K, Girvan M (2011) Predicting maximum tree heights and other traits from allometric scaling and resource limitations. PLoS One 6:e20551

Kenzo T, Ichie T, Watanabe Y, Yoneda R, Ninomiya I, Koike T (2006) Changes in photosynthesis and leaf characteristics with tree height in five dipterocarp species in a tropical rain forest. Tree Physiol 26: 865–873

Koch GW, Sillett SC, Jennings GM, Davis SD (2004) The limits to tree height. Nature 428:851–854

Lanner RM, Connor KF (2001) Does bristlecone pine senesce? Exp Gerontol 36:675–685

Larjavaara M (2014) The world's tallest trees grow in thermally similar climates. New Phytol 202:344–349

Larjavaara M, Muller-Landau HC (2012) Temperature explains global variation in biomass among humid old-growth forests. Glob Ecol Biogeogr 21:998–1006

Larjavaara M, Muller-Landau HC (2013) Corrigendum on: temperature explains global variation in biomass among humid old-growth forests (vol. 21, pp. 998, 2012). Glob Ecol Biogeogr 22:772

Lhotka JM, Loewenstein EF (2015) Comparing individual-tree approaches for predicting height growth of underplanted seedlings. Ann For Sci 72:469–477

Magnani F, Grace J, Borghetti M (2002) Adjustment of tree structure in response to the environment under hydraulic constraints. Funct Ecol 16:385–393

Martınez-Vilalta J, Vanderklein D, Mencuccini M (2007) Tree height and age-related decline in growth in Scots pine (*Pinus sylvestris* L.). Oecologia 150:529–544

Marziliano PA, Tognetti R, Lombardi F (2018) Is tree age or tree size reducing height increment in Abies alba Mill. at its southernmost distribution limit? V2. Zenodo. [Dataset]. https://doi.org/10.5281/zenodo.2526274

Marziliano PA, Lafortezza R, Colangelo G, Davies C, Sanesi G (2013) Structural diversity and height growth models in urban forest plantations: a case-study in northern Italy. Urban Forestry and Urban Greening 12:246–254

Marziliano PA, Menguzzato G, Scuderi A, Corona P (2012) Simplified methods to inventory the current annual increment of forest standing volume. iForest 5:276–282

McDowell N, Barnard H, Bond BJ, Hinckley T, Hubbard RM, Ishii H, Köstner B, Magnani F, Marshall JD, Meinzer FC, Phillips N, Ryan MG, Whitehead D (2002) The relationship between tree height and leaf area: sapwood area ratio. Oecologia 132:12–20

Mencuccini M (2003) The ecological significance of long-distance water transport: short-term regulation, long-term acclimation and the hydraulic costs of stature across plant life forms. Plant, Cell and Environment 26:163–182

Mencuccini M, Martınez-Vilalta J, Hamid HA, Korakaki E, Vanderklein D, Lee S, Michiels B (2005) Size, not cellular senescence, explains reduced vigour in tall trees. Ecol Lett 8:1183–1190

Mencuccini M, Martínez-Vilalta J, Hamid HA, Korakaki E, Vanderklein D (2007) Evidence for age- and size-mediated controls of tree growth from grafting studies. Tree Physiol 27:463–473

Meng SX, Lieffers VJ, Reid DEB, Rudnicki M, Silins U, Jin M (2006) Reducing stem bending increases the height growth of tall pines. J Exp Bot 57:3175–3182

Midgley JJ (2003) Is bigger better in plants? The hydraulic costs of increasing size in trees. Trends in Ecology and Evolution 18:5–6

Murty D, McMurtrie RE, Ryan MG (1996) Declining forest productivity in aging forest stands: a modeling analysis of alternative hypotheses. Tree Physiol 16:187–200

Netting AG (2009) Limitations within "the limits to tree height". Am J Bot 96:542–544

Niklas KJ (1992) Plant biomechanics: an engineering approach to plant form and function. In: University of Chicago Press. USA, Chicago, IL

Niklas KJ (1994) Plant allometry: the scaling of form and process. In: University of Chicago Press. USA, Chicago, IL

Niklas KJ (2007) Maximum plant height and the biophysical factors that limit it. Tree Physiol 27:433–440

Niklas KJ, Spatz HC (2004) Growth and hydraulic (not mechanical) constraints govern the scaling of tree height and mass. Proc Natl Acad Sci U S A 101:15661–15663

Onate M, Munne-Bosch S (2008) Meristem aging is not responsible for age-related changes in growth and abscisic acid levels in the Mediterranean shrub, *Cistus clusii*. Plant Biol 10:148–155

Paine CET, Marthews TR, Vogt DR, Purves D, Rees M, Hector A, Turnbull LA (2012) How to fit nonlinear plant growth models and calculate growth rates: an update for ecologists. Methods Ecol Evol 3:245–256

Parresol BR (1999) Assessing tree and stand biomass: a review with examples and critical comparisons. For Sci 45:573–593

Petit G, Anfodillo T, Mencuccini M (2008) Tapering of xylem conduits and hydraulic limitations in sycamore (*Acer pseudoplatanus*) trees. New Phytol 177:653–664

Pommerening A (2002) Approaches to quantifying forest structures. Forestry 75:305–324

Pommerening A, Muszta A (2015) Methods of modelling relative growth rate. Forest Ecosystems 2:5

Prodan M, Holzmesslehre JD (1965) Sauerländer's Verlag. Frankfurt am Main

R Core Team (2016) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna

Ryan MG, Binkley D, Fownes JH, Giardina CP, Senock RS (2004) An experimental test of the causes of forest growth decline with stand age. Ecol Monogr 74:393–414

Ryan MG, Phillips N, Bond BJ (2006) The hydraulic limitation hypothesis revisited. Plant, Cell and Environment 29:367–381

Ryan MG, Yoder BJ (1997) Hydraulic limits to tree height and tree growth: what keeps trees from growing beyond a certain height? BioScience 47:235–242

Sillett SC, Van Pelt R, Koch GW, Ambrose AR, Carroll AL, Antoine ME, Mifsud BM (2010) Increasing wood production through old age in tall trees. For Ecol Manag 259:976–994

Socha J, Pierzchalski M, Bałazy R, Ciesielski M (2017) Modelling top height growth and site index using repeated laser scanning data. For Ecol Manag 406:307–317

Stephenson NL, Das AJ, Condit R, Russo SE, Baker PJ, Beckman NG, Coomes DA, Lines ER, Morris WK, Rüger N, Álvarez E, Blundo C, Bunyavejchewin S, Chuyong G, Davies SJ, Duque Á, Ewango CN, Flores O, Franklin JF, Grau HR, Hao Z, Harmon ME, Hubbell SP, Kenfack D, Lin Y, Makana JR, Malizia A, Malizia LR, Pabst RJ, Pongpattananurak N, Su SH, Sun IF, Tan S, Thomas D, van Mantgem PJ, Wang X, Wiser SK, Zavala MA (2014) Rate of tree carbon accumulation increases continuously with tree size. Nature 507:90–93

Sumida A, Ito H, Isagi Y (1997) Trade-off between height growth and stem diameter growth for an evergreen oak, *Quercus glauca*, in a mixed hardwood forest. Funct Ecol 11:300–309

Sumida A, Miyaura T, Torii H (2013) Relationships of tree height and diameter at breast height revisited: analyses of stem growth using 20-year data of an even-aged *Chamaecyparis obtusa* stand. Tree Physiol 33:106–118

Thomas SC, Martin AR, Mycroft EE (2015) Tropical trees in a wind-exposed island ecosystem: height-diameter allometry and size at onset of maturity. J Ecol 103:594–605

Trouvé R, Bontemps J-D, Seynave I, Collet C, Lebourgeois F (2015) Stand density, tree social status and water stress influence allocation in height and diameter growth of *Quercus petraea* (Liebl.). Tree Physiol 35:1035–1046

USDA (1999) Soil taxonomy. A basic system of soil classification for making and interpreting soil surveys. 2nd Edition. Agriculture Handbook Number 436

van Laar A, Akca A (2008) Forest Mensuration. Springer

Wang X, Yu D, Wang S, Lewis BJ, Zhou W, Zhou L, Dai L, Lei J-P, Li M-H (2017) Tree height-diameter relationships in the alpine treeline ecotone compared with those in closed forests on Changbai Mountain, northeastern China. Forests 8:132

Wareing PF, Seth K (1967) Ageing and senescence in the whole plant. Symp Soc Exp Biol 21:543–558

Weiner J, Thomas SC (2001) The nature of tree growth and the "age-related decline in forest productivity". Oikos 94:374–376

West GB, Brown JH, Enquist BJ (1999) A general model for the structure and allometry of plant vascular systems. Nature 400:664–667

Woodruff DR, Bond BJ, Meinzer FC (2004) Does turgor limit growth in tall trees? Plant, Cell and Environment 27:229–236

Woolhouse HW (1972) Ageing processes in higher plants. Oxford University Press, London

Yoder BJ, Ryan MG, Waring RH, Schoettl AW, Kaufmann MR (1994) Evidence of reduced photosynthetic rates in old trees. For Sci 40:513–527

Zens MS, Webb CO (2002) Sizing up the shape of life. Science 295:1475–1476