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Does individual-tree biomass growth increase continuously with tree size?

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ABSTRACT

Relationships between tree size and growth are sometimes assumed to show increasing growth with increasing size only until intermediate sizes are reached, followed by a phase where growth rates decline with further increases in size. However, this "rise-and-fall" pattern has been challenged by studies suggesting continuously increasing growth with size. This study examined relationships between tree diameter and above-ground biomass (AGB) growth and how such relationships can differ depending on whether they represent an individual tree through time (longitudinal analyses) or whether the relationship was fit to many trees within a stand at a single point in time (cross-sectional analyses). Using 949 long-term plots in Switzerland (measured between 1888 and 2014) including several species, sites and management regimes, segmented regressions were used to describe the longitudinal and cross-sectional relationships between stem diameter and AGB growth. The slopes of the last segments of cross-sectional analyses indicated that AGB growth generally increased with tree diameter. However, last-segment slopes of longitudinal analyses showed that AGB growth of 12% of trees had actually declined for several decades. This number increased to 44%, when considering only the last growth periods for each tree, corresponding to about 16 years of growth. The contrast between cross-sectional and longitudinal patterns results because declines in tree growth occur at different times or sizes for different individuals (longitudinal analyses), but this is averaged out and rarely evident from cross-sectional analyses unless many individuals decline at similar times or sizes.

The last-segment slopes of individual trees were positively correlated with the last-segment slopes of relationships between diameter and tree light absorption or light-use efficiency (AGB/light absorption). Interestingly, last-segment slopes were not correlated with light absorption, only the change in light absorption. This reiterates the potential of thinning to delay the onset of growth declines. When all data were combined (e.g. an aggregated longitudinal analysis), AGB growth was most strongly influenced by diameter, followed by relative height, neighbourhood basal area, climatic conditions, silviculture, and lastly, tree species diversity.

Cross-sectional analyses often show AGB growth continuously increasing with diameter, because firstly, they represent patterns averaged across may trees within a stand and secondly, because they represent only one point in time. However, the AGB growth of individual trees doesn't always continuously increase with tree diameter (longitudinal analyses). This highlights the importance of carefully considering which type of analysis (cross-sectional or longitudinal) is appropriate to the question being addressed.

1. Introduction

Whether or not the growth rates of large trees continue to increase as their size increases, or instead follow a unimodal "rise-and-fall" pattern, remains the subject of confusion (Stephenson et al., 2014; Sheil et al., 2017). Large trees are important due to their contribution to wood production, carbon stocks (Clark and Clark, 1996; Slik et al., 2013; Ligot et al., 2018; Lutz et al., 2018), their provision of high-quality wood (Benneter et al., 2018), for quantifying stand structural attributes (McElhinny et al., 2005), as sources of fruits and seeds (Sist et al., 2003)

and habitat or shelter (Florence, 1996; Lindenmayer et al., 2012). The disproportionate influence large trees can have on these characteristics highlights the value of better understanding their growth dynamics.

Several approaches are used to examine tree size-growth relationships (Fig. 1). These can lead to different size-growth patterns (Sheil et al., 2017) and warrant clear definitions to avoid confusion. One important consideration is the type of analysis used in terms of whether the size-growth relationship is intrinsic, cross-sectional or longitudinal. An intrinsic relationship could refer to growth when there were few or no external factors reducing growth from its potential under ideal
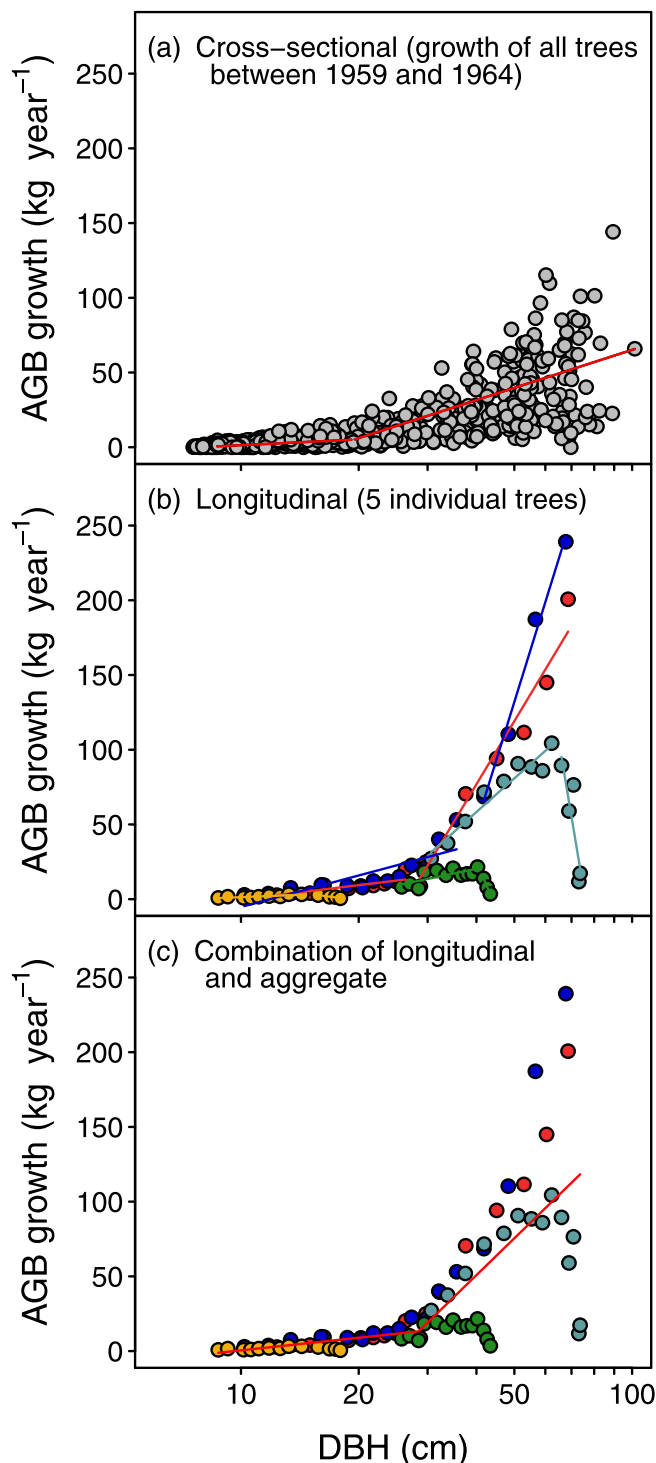
Fig. 1. Examples of a cross-sectional DBH-AGB growth relationship where all trees are examined for the same growth period (a), longitudinal relationships where individual trees are examined for many growth periods (b), and a relationship for a combined longitudinal and cross-sectional data set (c). These may also be referred to as aggregate relationships (a & c) or individual relationships (b). Each colour in (b) and (c) represent a different tree. The lines are segmented regressions (see methods section). All data are for *Abies alba* trees in a single-tree selection plot dominated by *Abies alba* and *Picea abies* in Niederhünigen, Switzerland. Note the trees in (b) and (c) were not randomly sampled and were chosen to illustrate their contrasting size-growth patterns.

conditions for much of the tree's lifetime, e.g. no competition or pests and a favourable climate combined with non-limiting resource availability. Intrinsic relationships are rarely measured. A cross-sectional relationship (Fig. 1a) represents a given point in time, such that many trees within a given stand are compared, but each tree is represented only once (e.g. two successive diameter measurements per tree). Cross-sectional analyses control for differences in climate and changes in stand conditions, such as density. They show which sizes within the stand are currently growing the fastest but do not show how the individual trees developed or why different sizes grow differently, e.g. were the slower growing trees in shadier and denser neighbourhoods? In contrast, a longitudinal relationship (Fig. 1b) shows how the growth of an individual tree has changed with its size and is based on data from many growth periods. However, temporal effects of environmental changes or stand conditions on growth will be confounded with the effects of changes in individual tree size (Foster et al., 2016).

A second important consideration is whether the size-growth relationship is for a single tree (Fig. 1b) or represents the mean of several trees (Fig. 1a & 1c), which is sometimes referred to as an aggregate relationship (Sheil et al., 2017). Aggregate relationships average out the different size-growth patterns of individuals.

Size-AGB growth patterns have received little attention but some common findings have emerged that differ between cross-sectional and longitudinal analyses. Cross-sectional analyses have shown a dominance in continuously increasing AGB growth with diameter at breast height (1.3 m; DBH). For example, in a study based on 403 tropical and temperate tree species, cross-sectional (aggregate) analyses showed that 97% of species had continuously increasing AGB growth (Stephenson et al., 2014). In tropical forests of the Central African Republic, cross-sectional AGB growth continuously increased for 45 of 52 species (87%) (Ligot et al., 2018). In tropical forests of Bolivia, Cameroon and Thailand, cross-sectional (aggregate) patterns showed increasing AGB growth with DBH for 13 of 14 species (93%) (Sheil et al., 2017). In contrast, longitudinal analyses using the same data, showed a broader range of results, with up to 7 of 14 species (50%) showing declining AGB growth in the larger size classes (Sheil et al., 2017). Very few studies appear to have examined longitudinal AGB growth patterns.

It is important to note that growth-DBH patterns also depend on whether growth is quantified in terms of AGB, as in this study, or DBH, basal area, height etc. While the studies reviewed above indicate that cross-sectional AGB growth-DBH are generally positive, cross-sectional DBH growth, height growth or basal area growth patterns may be more likely, than AGB growth, to show "rise-and-fall" patterns. Consequently, DBH growth, height growth and basal area growth are often incorporated as "rise-and-fall" relationships in forest growth models (Vanclay, 1994; Canham et al., 2004; Pretzsch, 2009; Weiskittel et al., 2011; Burkhart and Tomé, 2012). This is consistent with theoretical relationships. Biomass increases continuously with DBH, with biomass $\propto DBH^{8/3}$ according to metabolic scaling theory (West et al., 1999, 2009) or with biomass $\propto DBH^3$ according to geometric scaling theory (Yoda et al., 1963; Gorham, 1979; Pretzsch et al., 2012). The exponents for other variables are lower e.g. geometric scaling predicts linear tree dimensions (e.g., DBH) are related to quadratic or area-related dimensions (e.g., basal area, leaf area) as quadratic $\propto linear^2$. The higher exponents for biomass (or volume) relationships means that longitudinal or cross-sectional analyses of DBH growth, height growth or basal area growth are likely to plateau or decline before biomass (or volume) growth.

Gaining a mechanistic understanding of the cross-sectional and longitudinal growth patterns can be aided by examining stand conditions (basal area, species composition), tree physiology, and tree architecture. Declines in AGB growth might refer to a rise-and-fall shape of longitudinal or cross-sectional size-growth relationships or to the difference between intrinsic growth under optimal conditions compared with the longitudinal or cross-sectional relationships. There may be no predominant cause across species and sites, given that different climatic,

edaphic, intrinsic or extrinsic factors limit growth (Lee and Muzika, 2014). Frequently suggested causes of individual tree growth decline relate to structural and physiological limits to tree size, such as hydraulic limitations relating to tree height and an exponential decline in the ratio of foliage to branch biomass as stand leaf area approaches its maximum (Ryan and Yoder, 1997; Warren and Adams, 2000; Koch et al., 2004; Mencuccini et al., 2005; Ryan et al., 2006; Bennett et al., 2015; Waring et al., 2016). This is associated with reductions in growth efficiency (growth per unit leaf area) (Waring et al., 2016). However, growth may still continue to increase if leaf area, and the implied absorption of photosynthetically active radiation, increases with tree size faster than the decline in growth per unit leaf area (Sheil et al., 2017). Little attention has been given to longitudinal relationships between individual tree size and light absorption or between size and light-use efficiency (growth per light absorption). In contrast, there have been many studies on cross-sectional or aggregate longitudinal relationships, which show that light absorption typically increases with tree size, while light use efficiency can increase, remain unchanged and occasionally declines with tree size (Binkley et al., 2010, 2013; Forrester and Albrecht, 2014; Forrester et al., 2019b).

To examine the differences between longitudinal and cross-sectional DBH-AGB growth relationships as well as the tree or stand conditions associated with longitudinal changes in AGB growth, this study addressed the following three questions: (1) Are cross-sectional analyses more likely than longitudinal analyses to show that AGB growth increases continuously with DBH, such that the slopes of the last segments of DBH-AGB growth relationships are predominantly positive (Fig. 1a), while the last-segment slopes of longitudinal (i.e. individual) relationships are sometimes also negative (Fig. 1b) (e.g. for approx. 50% of trees (Sheil et al., 2017))?; (2) Do the last-segment slopes of longitudinal DBH-AGB growth relationships depend on stand basal area, climatic conditions and changes in individual tree light absorption in terms of the last-segment slopes of longitudinal DBH- light absorption relationships?; (3) When combining all data (e.g. Fig. 1c), which tree and stand variables reduce growth most from a potential intrinsic growth rate?

2. Materials and methods

2.1. Experimental sites

The data were obtained from the Experimental Forest Management (EFM) plots in Switzerland (Forrester et al., 2019a), which are designed to examine silvicultural treatments across a range of species, climatic and edaphic conditions. The plots used in this study were located at altitudes between 375 and 1950 m. For the periods when the tree growth data were collected, mean daily minimum temperature in January ranged from −12.2 °C to 0.1 °C and the mean daily maximum temperature in July ranged from 14.5 °C to 26.7 °C. Mean annual precipitation was between 691 and 2484 mm.

For this study, 949 plots (646 sites) were used (Table 1). The earliest inventories occurred in 1888 and the latest in 2014. Mean plot area was 0.32 ha (0.02–3.06 ha) and the measurement intervals were often between five and 12 years, depending on silvicultural treatments and growth rates. Two main groups of plots were used: single-tree selection plots and plots where a given species is even-aged. Given that these plots are managed, trees are often, but not always, removed by thinning when they are considered likely to die before the next thinning operation.

2.2. Individual-tree measurements and calculations

The diameter at 1.3 m (DBH) was measured for all trees with DBH ≥ 8 cm. The height, four crown radii, height to the lowest main-crown branch and stem diameter at 7 m were measured for a sample of trees (the 100 largest-diameter trees and 20% of the rest), and were predicted for all other trees using plot-, year- and species-specific regressions as described in Forrester et al. (2019a). The aboveground biomass (stems, branches and foliage) and leaf area of each tree was predicted using species-specific relationships that incorporate the effects of stand basal area (Forrester et al., 2017). Individual tree growth rates (per year) were calculated as the change in size between measurements, divided by the number of years between measurements. The structure of individual tree neighbourhoods was quantified in terms of the basal area ($m^2\ ha^{-1}$) of all trees within a 10-m radius, the relative height of all trees within the same radius (height of target tree divided by the mean height of all trees

Table 1
Description of the plots used for each type of analysis.

Species	Number of plots where species occurred	First/last measurement	Mean plot size (ha; min/max)	Mean basal area ($m^2\ ha^{-1}$; min/max)	Mean trees per ha (min/max)
Cross-sectional analyses					
Picea abies	480	1888/2014	0.51 (0.02/3.06)	44.7 (2/107.2)	1497 (178/4990)
Abies alba	124	1890/2012	0.91 (0.05/2.47)	43.9 (12.6/78.3)	941 (204/3377)
Pinus sylvestris	96	1893/2011	0.23 (0.02/1.15)	36.3 (8.8/86.6)	1463 (176/4814)
Pseudotsuga menziesii	36	1906/2013	0.25 (0.02/0.61)	40.9 (2/78.9)	943 (264/2500)
Fagus sylvatica	263	1889/2013	0.52 (0.03/3.06)	32 (2/78.3)	939 (114/2750)
Quercus petraea or Q. robur	59	1891/2010	0.46 (0.04/3.06)	24.9 (6.2/51.5)	1123 (192/2311)
Longitudinal analyses (only for trees with at least 15 measurements)*					
Picea abies	17	1890/2010	1.16 (0.2/1.99)	37.7 (2/57)	660 (146/2348)
Abies alba	14	1905/2010	1.58 (0.27/1.99)	36.6 (2/55.1)	610 (146/2186)
Pinus sylvestris	2	1906/2005	0.3 (0.2/0.5)	27.9 (3/42.8)	776 (215/2006)
Pseudotsuga menziesii	2	1924/2002	0.36 (0.25/0.42)	64.3 (36/91.2)	630 (268/1339)
Fagus sylvatica	23	1890/2010	0.39 (0.17/1.99)	31.3 (0.1/65)	932 (10/2348)
Quercus petraea or Q. robur	3	1914/2003	0.89 (0.22/1)	30.7 (3.6/42.9)	909 (130/2186)
Light absorption analyses (only for trees with at least 5 measurements that are associated with tree position data)					
Picea abies	2	1935/2005	0.37 (0.25/0.5)	46.2 (35.1/54.5)	446 (373/616)
Abies alba	1	1981/2004	1.18 (1.18/1.18)	35.1 (33.1/36.4)	631 (588/700)
Fagus sylvatica	2	1937/1999	0.25 (0.25/0.25)	34.4 (25.5/47.1)	359 (224/540)
Intrinsic growth analyses**					
Picea abies	170	1930/2014	1.02 (0.03/3.06)	42.7 (11.1/104.4)	669 (112/2990)
Abies alba	96	1941/2013	1.56 (0.03/3.06)	40.4 (15.2/78.3)	565 (114/3193)
Fagus sylvatica	177	1931/2014	1.15 (0.02/3.06)	34.7 (11.1/89)	498 (99/2376)

* The same data were used for longitudinal analyses of the last segments and for the last periods.
** The basal area for the intrinsic analyses is the neighbourhood basal area rather than the plot basal area.

within the radius, including the target tree) and the tree species richness (number of tree species within a 10-m radius).

2.3. Estimation of light absorption

Individual-tree light absorption (GJ tree^{-1} year^{-1}) was calculated in plots where tree positions were recorded. Mapping of tree positions was done in 1935 at the earliest, but usually not until about the 1970′s. The light absorption was predicted using the 3D tree-level model Maestra (Grace et al., 1987; Wang and Jarvis, 1990; Medlyn, 2004; Duursma and Medlyn, 2012). Maestra light absorption predictions have been validated in several mixed and monospecific forests (Wang and Jarvis, 1990; Charbonnier et al., 2013; le Maire et al., 2013; Forrester et al., 2018, 2019b).

Individual-tree light absorption is predicted while considering the crown architecture (crown width and length, leaf area and leaf angle distributions), species-specific differences in leaf optical properties and leaf area density distributions. To account for shading by neighbours, the canopy is represented as an array of tree crowns whose positions are defined by x and y coordinates and with slope and aspect considered in both the x and y directions. Parameter values were obtained from the literature and described in Forrester (2019).

For evergreen species, the individual tree light absorption was total annual light absorption, while for deciduous species, growing season light absorption was calculated. The growing season for each species was calculated as a function of altitude (Dittmar and Elling, 2006; Vitasse et al., 2009; Čufar et al., 2012; Pellerin et al., 2012; Cornelius et al., 2013; Schuster et al., 2014).
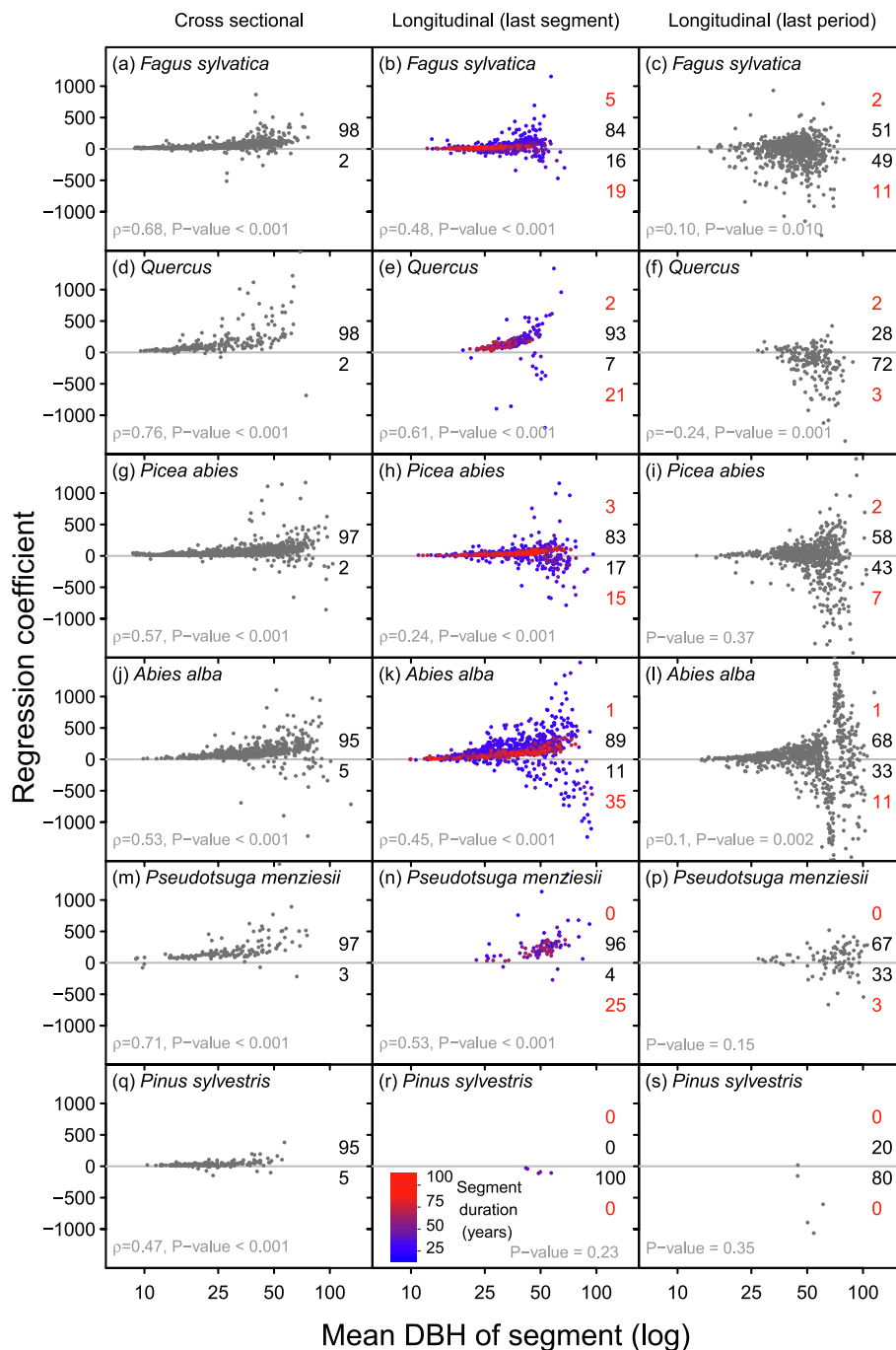

Fig. 2. The last-segment slopes of log(DBH)-AGB growth relationships plotted against the mean DBH of the last segment for cross-sectional analyses (left column), longitudinal analyses based on the last segments (middle column), and the longitudinal analyses based on only the last two growth periods (about 16 years of growth in total) (right column). Spearman rank correlation ρ and P-values are provided at the bottom of each pane. The percentage of trees with positive and negative slopes are shown on the right of each pane immediately above or below the grey horizontal line (y = 0). The percentage of those trees that died at their last measurement are shown in red text. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

To avoid edge effects, light absorption predictions were not used for trees within 10 m of plot boundaries. In case this 10-m buffer was too narrow, an additional 20-m-wide buffer was simulated around each plot. The simulated buffer contained the average tree spacing, species composition and tree dimensions of the given plot.

2.4. Climatic and edaphic data

Climatic data were collected by the federal office of meteorology and climatology MeteoSwiss (Bundesamt für Meteorologie und Klimatologie MeteoSchweiz) and was interpolated for each plot location using the methods described by Thornton et al. (1997). These data included solar radiation data for the Maestra light absorption calculations. Topographic variables, including altitude, were obtained using the Land suitability models from the Swiss Federal Statistical Office. To determine the temperature and precipitation climatic variables most highly correlated with growth, the AGB growth of each species was regressed against climatic variables that have been found to influence growth in central Europe (Babst et al., 2012; Carrer et al., 2012; Rohner et al., 2016; Klesse et al., 2018; Harvey et al., 2020). These variables included annual averages, seasonal averages (spring, summer, autumn, winter), growing season averages, and averages based on the climate of the previous year. The most highly correlated temperature variable was the mean growing season temperature (March to October), and the most highly correlated precipitation variable was the previous summer precipitation (June to October). Therefore these were calculated for each inventory period and plot.

2.5. Calculations of slopes of longitudinal and cross-sectional relationships

Piecewise regressions were used to examine the longitudinal and cross-sectional DBH-AGB growth relationships. Each segment had to contain at least 10% of the data and at least five data points, i.e. 6 measurements. Six measurements was typically representative of 48 years because the average measurement interval between inventories was 8 years. For longitudinal analyses, individual trees were only examined when there were at least 15 measurements (14 growth periods). When there were no break points, a single (non-segmented) line was fitted to all data for the given tree (longitudinal) or a given plot-year combination (cross-sectional). For each longitudinal and cross-sectional relationship, the slope of the last segment was recorded, or when no break points existed, the slope of the line fitted to all data was recorded as the last-segment slope. Piecewise regression models were fitted using the R-package *Segmented* (Muggeo, 2008). Breakpoints were identified using the *breakpoints* function of the R package *strucchange* (Zeileis et al., 2002, 2003). Longitudinal DBH-light absorption and DBH-light use efficiency relationships were also fit to the last-segment slope period of the DBH-AGB growth relationships. Less light absorption data were available than growth data because tree coordinates (required for light absorption calculations) had usually only been recorded since the 1970's. Therefore, the last-segment slopes of DBH-light absorption and DBH-light use efficiency relationships required a minimum of four points (compared with five for growth).

For longitudinal analyses, the length of time represented by the last segment will probably influence the likelihood of finding negative slopes of DBH-AGB growth relationships. The last segments of longitudinal relationships calculated above typically represent about 48 years or more of growth. Therefore, as a comparison, the slope of the DBH-AGB growth relationships for only the last two growth periods were also calculated for all trees included in the longitudinal analyses. These last two periods typically represented much shorter time periods, about 16 years in total.

2.6. Linear regressions

Linear mixed models were used to examine how last-segment slopes of longitudinal relationships changed in relation to DBH, temperature, precipitation, basal area, relative height, tree species richness, silviculture (even-aged vs. single-tree selection) and all two-way interactions with DBH. Each explanatory variable represented the period when the growth of the last segment occurred. All variables were standardised by subtracting the mean from the variable value and then dividing it by the standard deviation of the given variable. The standardised independent variables then each have a mean (μ) of 0 and a standard deviation (σ) of 1. If the variable was ln-transformed, then the transformed values were standardised to $\mu = 0$ and $\sigma = 1$. The slope parameters were used to provide the effect size for each variable. These are scale free, and quantify how many standard deviations the response variable (Y) will change per standard deviation increase in the explanatory variable (X) and provide effect size estimates (Peterson and Brown, 2005; Nieminen et al., 2013). Starting models that included all explanatory variables were in the form of Eq. (1).

$$y_i = X_i\beta + Z_i b_i + \varepsilon_i \tag{1}$$

With random effects $b_i \overset{iid}{\sim} N(0, \sigma_i^2)$ where y_i is the response variable (standardised last-segment slopes), X_i is the dependent variables matrix (fixed effects matrix), Z_i is the random effects matrix, β and b are the parameters' vector of fixed and random effects, i is the index for plot and ε_{ij} is the within group error vector. Linear mixed models were also used to examine whether the last-segment slopes of DBH-AGB growth relationships were correlated with the last-segment slopes of DBH-light absorption or DBH-light use efficiency relationships.

Linear mixed models were used to examine which factors influenced tree growth of the three most abundant species in the data set (*Picea abies, Fagus sylvatica* and *Abies alba*) after combining all individual tree data (as in Fig. 1c). That is, although intrinsic relationships could not be examined, this analysis was used to identify some of the factors that could have caused a reduction in growth relative to the potential. All variables were standardised and fit to the model described by Eq. (1).
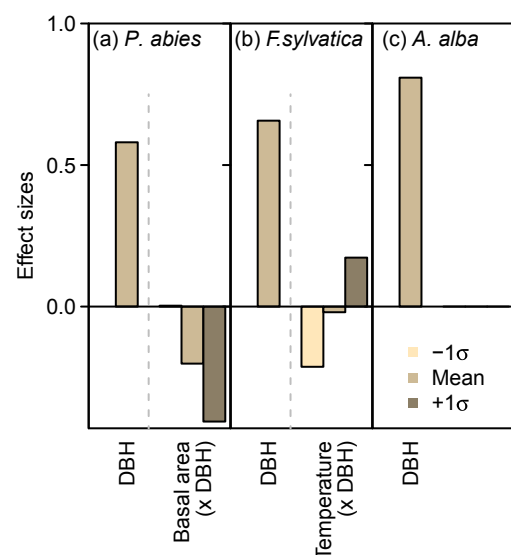

Fig. 3. The effect sizes of DBH, stand basal area (m² ha⁻¹), and mean temperature during the growing season, on the regression coefficients of the last-segment slopes of longitudinal DBH-AGB growth relationships for *Picea abies* (a), *Fagus sylvatica* (b) and *Abies alba* (c). The statistical information is in Table A1. For the interactions between independent variables, the effects are shown for the mean DBH and + or – 1 standard deviation.
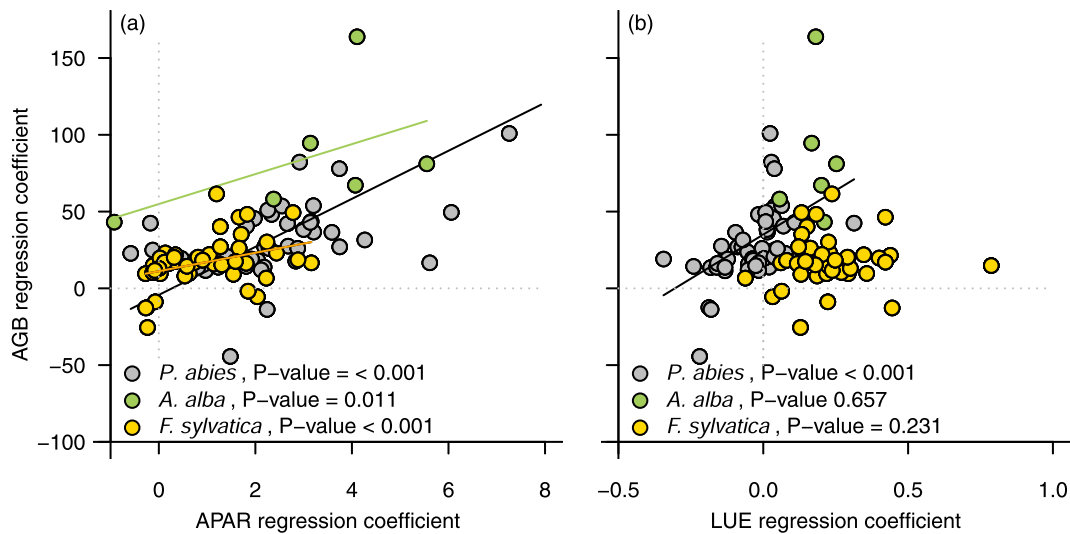
Fig. 4. Relationships between regression coefficients of the last-segment slopes of longitudinal DBH-AGB growth relationships and last-segment slopes of DBH-light absorption relationships (a), or DBH-light use efficiency relationships (b).

Mixed models (Eq. (1)) were fitted as hierarchical mixed-effects models using the R package *nlme* (Pinheiro et al., 2018) and R 3.5.1 (R Core Team, 2019). Initially all fixed effect variables were included before all non-significant (P > 0.05) variables were removed in order of decreasing P-value. Residual and normal quantile plots were assessed to ensure that residuals were centred at zero and approximately normally distributed. Plot was included as a random effect.

3. Results

For all six species examined, the last-segment slopes of cross-sectional DBH-AGB growth relationships were positive for at least 95% of all plot-year combinations (Fig. 2). The last-segment slopes of cross-sectional relationships generally increased with DBH (Fig. 2). The

last-segment slopes of longitudinal relationships were also often positive, but there was a higher proportion of negative last-segment slopes (12% of all trees) compared with the cross-sectional analyses. The last-segment slopes of longitudinal relationships represent approximately 48 years of growth. The slopes calculated only for the last two growth periods (16 years), were negative for 44% of all trees. The most extreme case was *P. sylvestris*, which had a very small sample size (n = 5), where all trees had negative last-segment slopes. Each of these trees was a dominant tree, and the stand basal area was 29–37 m² ha⁻¹.

For the three species with the most data (*P. abies, A. alba* and *F. sylvatica*) the last-segment slopes of longitudinal relationships were positively correlated with the DBH (Fig. 3; Table A1). The last-segment slopes were also negatively correlated with stand basal area, and interacted with DBH for *P. abies*, such that the larger the DBH, the larger
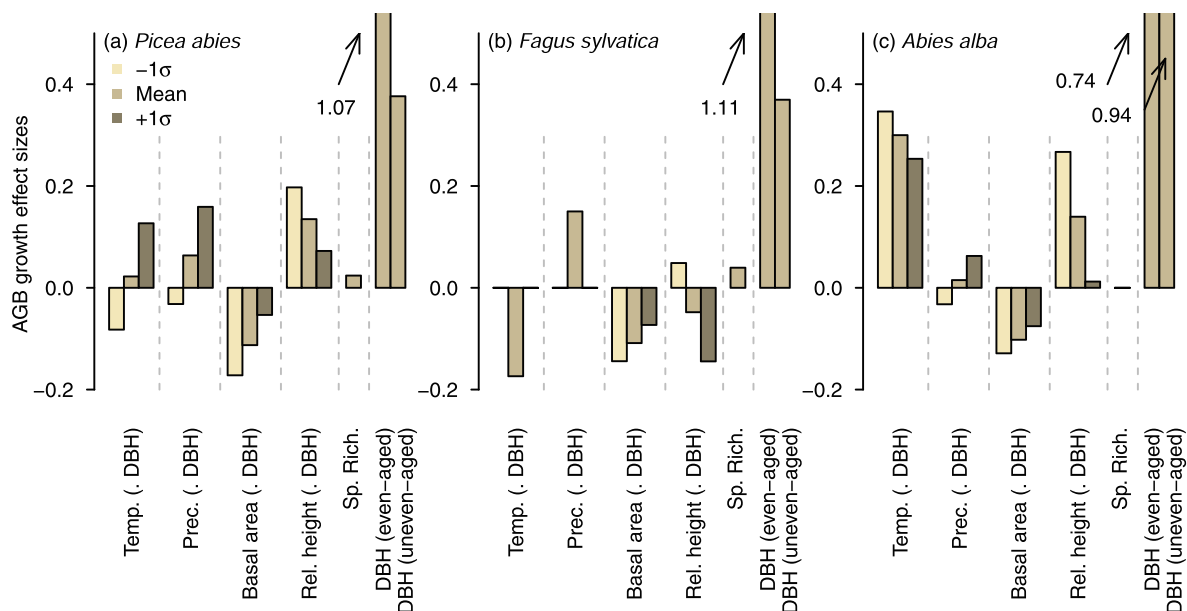

Fig. 5. The effect sizes of all independent variables used to predict AGB mass growth for *Picea abies* (a), *Fagus sylvatica* (b) and *Abies alba* (c), including (ln) DBH, mean temperature during the growing season, mean precipitation during the previous summer, (ln) basal area (within 10 m of the tree), (ln) relative height (tree height divided by mean height of all other trees within 10 m), (ln) tree species richness (Sp. Rich; number of species within 10 m), silviculture (even-aged vs. single-tree selection), and all 2-way interactions with DBH (all standardised). The effect sizes are quantified as the slopes of the variables on the x-axis, all of which have been standardised (mean = 0 and standard deviation = 1). The statistical information is in Table A2. The interactions between DBH and other independent variables are shown for the mean and + or − 1 standard deviation of the standardised DBH.

the effect of stand basal area. The last-segment slopes were also correlated with growing season temperature for *F. sylvatica*, and interacted with DBH, such that for larger DBH, temperature had a positive effect, while for smaller DBH, temperature had a negative effect on last-segment slopes. The precipitation and silviculture were not significantly correlated with the last-segment slopes.

The change in AGB was correlated with changes in light absorption and light use efficiency, such that the last-segment slopes of the DBH-AGB growth relationships was positively correlated with the slope of the DBH-light absorption or DBH-light use efficiency relationships that occurred during the same period of the DBH-AGB growth last-segment slopes (Fig. 4). The exception was the light use efficiency slopes for *A. alba* and *F. sylvatica*.

For the three most abundant species in the data (*P. abies, A. alba* and *F. sylvatica*), after combining all data together, AGB growth of each species was most positively influenced by DBH and negatively influenced by neighbourhood basal area (Table A2; Fig. 5). Relative height also had a positive effect, except for medium and large sized *F. sylvatica* trees, where the effect was negative. The effects of temperature and precipitation were also significant but varied between species. Tree species richness had the smallest (always positive) effects.

4. Discussion

4.1. Cross-sectional and longitudinal DBH – AGB relationships

There appears to be a broad generality where most species show continuously increasing AGB growth based on cross-sectional analyses i. e. when averaging across many trees at a single point in time (Fig. 1a). In this study, cross-sectional analyses showed that AGB growth of all species continuously increased for at least 97% of cases. Similarly, 13 out of 14 species from tropical forests of Bolivia, Cameroon and Thailand had continuously increasing AGB growth (Sheil et al., 2017), as did 97% of 403 tropical and temperate tree species (Stephenson et al., 2014) and 45 out of 52 species from tropical forests of the Central African Republic (Ligot et al., 2018). Exceptions may occur when an environmental change significantly reduces the growth of larger trees but has a much smaller or even positive impact on intermediate and smaller trees. Nevertheless, any other aggregated analyses (e.g. cross-sectional or aggregated longitudinal, Fig. 1c) appear more likely to show continuously increasing AGB growth.

In contrast to cross-sectional (or other aggregated analyses), longitudinal analyses, which examine single individual tree patterns (Fig. 1b), are more likely to show some trees that do not have continuously increasing AGB growth. In this study, longitudinal analyses revealed that 12% of trees eventually had declining AGB growth (negative last-segment slopes) while up to 7 out of 14 species in tropical forests of Bolivia, Cameroon and Thailand had declining AGB growth (negative S_L) (Sheil et al., 2017).

The lower proportion of trees with negative last-segment slopes in this study (12%) compared with Sheil et al. (2017) (50%) at least partly reflects a longer period between measurements in this study. To reliably fit the last segments of each tree, at least five data points were used for this study, which generally represented several decades, often about 48 years or more, as indicated by the purple points in Fig. 2. For the same trees, a much higher proportion (44%) had negative slopes when only the last two growth periods were used to calculate the slope (16 years of data; Fig. 2), which is still a longer period than the 5-year period used in Sheil et al. (2017).

Two additional reasons for the lower proportions of trees that eventually had negative last-segment slopes compared with Sheil et al. (2017) are a higher management intensity in this study, and environmentally driven declines in growth of the tropical species. Regarding management, the forests in this study were managed. Trees considered to have a low potential for future growth are more likely to be thinned and trees that eventually died were much more likely to have negative

last-segment slopes. Many more may have been thinned much earlier before significant declines in last-segment slopes became evident. Trees can have declining basal area growth in the years before they die (Cailleret et al., 2017) and therefore, the management of the forests examined in this study may have removed trees that would otherwise have had low or negative last-segment slopes.

Regarding the environmentally driven declines, another study that used the same data set as Sheil et al. (2017), showed that the basal area growth rates of all size classes had been declining for the past 30–50 years due to changing environmental conditions, and the relative declines were greater for the larger size classes (an aggregated longitudinal analysis; Nock et al., 2011). This may also have increased the probability of finding single trees with declining growth rates.

4.2. Correlations between light absorption and growth

Determining which trees are most likely to be declining in any given stand is useful when managing and modelling growth. A longitudinal analysis showed that the last-segment slopes of AGB growth was positively correlated with the last-segment slopes of light absorption for *A. alba*, *P. abies* and *F. sylvatica* and the last-segment slopes of light use efficiency for *P. abies*. Similarly, thinning or artificial illumination can increase growth due to increases in individual tree light absorption, based on longitudinal or aggregated longitudinal analyses (Forrester et al., 2013; Graham et al., 2003). The negative last-segment slopes of AGB growth, light absorption or light use efficiency show that even if trees continue to grow larger (more AGB), there can still be declines in growth, light absorption (due to shading) and light use efficiency. Since the correlations between the last-segment slopes of AGB and light absorption were weak and since last-segment slopes declines even occurred for the largest trees, changes in light absorption could only be partly responsible. Other causes have been suggested, for example hydraulic limitations related to tree height and branch lengths (Ryan and Yoder, 1997; Warren and Adams, 2000; Mencuccini et al., 2005).

The longitudinal analysis also showed that the last-segment slopes of AGB growth were positively correlated with DBH for *A. alba*, *F. sylvatica* and *P. abies*, indicating that the rate at which AGB growth increased with DBH, was higher for larger the trees. Long-term studies of tree structure, tree physiology and neighbourhood structure will be required to identify the relative importance of different factors such as hydraulic limitations, light absorption and light use efficiency. That is, does the relative importance depend on tree size, with smaller trees more likely to be limited by light absorption and larger trees more likely to experience hydraulic limitations?

4.3. Silvicultural implications

It is important to distinguish between a low growth rate and a declining growth rate. Trees with declining growth rates, may still have very high AGB growth relative to most other trees in the stand. For example, a 60-cm-DBH *Carpinus betulus* tree that grows 3 cm will grow nearly 333 kg of additional stem mass, which alone is equivalent to the entire stem mass of >15 trees with a DBH of 10 cm. It is also important to note these size-growth relationships cannot be extrapolated to stand level growth without considering other stand structural characteristics such as stand density and tree size distributions, as well as mortality and recruitment (Forrester, 2019). In even-aged forests, stand growth generally follows a uni-model pattern with age (Ryan et al., 1997).

The positive correlations between longitudinal last-segment slopes of growth and last-segment slopes of light absorption are consistent with many other studies showing that growth and growth efficiency (growth per leaf area) can be increased or maintained by thinning, which increases individual-tree light absorption, light use efficiency and growth efficiency, by reducing competition for light and other resources (Stape and Binkley, 2010; Forrester, 2013; Forrester et al., 2013; Gspaltl et al., 2013; Waring et al., 2016). Thus thinning from above or below could

create conditions that will improve or maintain individual tree growth rates. Interestingly, light absorption was not a significant determinant of longitudinal last-segment slopes (data not shown) indicating that changes in light absorption or light use efficiency are more important than the actual light absorption in determining the last-segment slopes of longitudinal size-growth relationships.

While the potential intrinsic AGB growth could not be analysed, the effect sizes of potential factors that influenced growth indicated that tree size was by far the most important, followed by relative height, basal area and climate. Tree species richness had the smallest effect. This is consistent with aggregate analyses, where tree size and age have much greater effects on individual tree biomass growth, than climatic variability (Foster et al., 2016) and with stand level studies showing that stand density can have greater effects on stand growth than climate or tree species diversity (Zhang et al., 2015; Jucker et al., 2016; Ouyang et al., 2019). It is important to note that the climate impacts might have been underestimated in this study by using inventory data with approximately 8-year measurement intervals, instead of annual or monthly measurement intervals that reflect seasonality of climate.

4.4. Modelling implications and methodological considerations

The difficulty and importance of using accurate biomass estimates when studying individual-tree AGB growth relationships has been reviewed by Sheil et al. (2017). While, the AGB biomass equations used were not developed from these plots, they were obtained from a meta-analysis of European biomass studies, including 973 equations and > 60,000 sample trees (Forrester et al., 2017), and the tree dimensions, stand structures, and site conditions were similar to the stands in this study.

Rise-and-fall size-growth relationships are an important component of many tree-level forest models, and equations describing these relationships for diameter growth and basal area growth often include tree, stand and site variables to define when peaks in the rise-and-fall occur, and how high the peaks are (Vanclay, 1994; Canham et al., 2004; Weiskittel et al., 2011; Burkhart and Tomé, 2012). If DBH to AGB growth relationships are included in models, consideration may need to be given to whether continuously increasing shapes are possible within the model structure. The differences between the last-segment slopes of longitudinal and cross-sectional analyses reiterate the importance of considering whether individual tree (longitudinal), averaged (cross-sectional) or intrinsic size-growth relationships are required for a given model. Furthermore, the effect of temporal resolution on longitudinal analyses, shows the importance of considering the interval between measurements (or time step of the forest model), because shorter intervals (e.g. annual growth measurements examined for 5 year segments) are more likely to pick up growth declines before a tree dies, or is thinned, than longer intervals (e.g. 10-yearly growth measurements examined for several decades).

5. Conclusions

AGB growth generally increased with DBH when averaged across all trees within a plot, based on cross-sectional analyses. In contrast, the AGB growth of individual trees (longitudinal analyses) was more variable with about 12% of trees having declining AGB growth with increasing DBH, based on the last segments, and 44% of trees having declining AGB growth when considering only the last two growth periods. This shows the importance of considering the type of analysis used to examine tree growth dynamics and the temporal resolution of the measurements. The last-segment slopes of longitudinal DBH-AGB growth was positively correlated with the corresponding last-segment slopes of longitudinal DBH-light absorption relationships, indicating that growth responses may have partly resulted from changes in light absorption, and that thinning might be used to maintain positive last-segment slopes.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118717.

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