**Large-tree growth follows a unimodal cascading pattern under the combined effect of allometric scaling and growth plasticity**

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**Abstract**:

The continuously increasing trend of large-tree growth challenges the assertion of the unimodal pattern in classical growth theories. Here, we considered the effect of phenotypic plasticity on growth and extended classical growth equations (i.e., Gompertz and logistic curves) to reconcile this contradiction. Tree growth is indeterminate and modular, and we speculated that a trajectory of tree growth should be viewed as a combination of a series of different unimodal curves, termed cascading growth. Mathematically, the increasing growth trend may be attributable to the later emergence of larger-scale unimodal curves, which depend on some beneficial change of functional traits relative to tree size. To test this hypothesis, we determined tree growth in four plots across the subalpine *Abies fabri* forest belt on Gongga Mountain in the eastern Tibetan Plateau of China, and then analyzed the effects of some important functional traits (i.e., leaf and stem economics and morphological traits) on the growth curve. Our results indicate that the ideal growth trajectory that is composed of the maximum growth increment of different trees follow a unimodal curve with a cascade characteristic. At individual levels, the emergence of a larger unimodal curve is caused by an increase in the relative amount of canopy and a decrease in the relative amount of sapwood. This study clarifies the general growth rule of large trees, offers a concise way to link traits and growth performance, and reveals the complexity and sustainability of a old forest acting as a carbon sink to some extend.

**Key words:** *Abies fabri*; large-tree growth; tree ring; aboveground biomass; unimodal pattern; logistic and Gompertz curves; cascading growth

Symbolic meaning

*M*: biomass

*M*a: aboveground biomass

*b:* metabolic exponent, usually equal to 0.75 for trees

*T*:the time of development of unit tissue, controlled by genes and physiological activity, independent of size, such as cell, callus or organ formation time

*f*(*M*): discrete biomass increment (∝ total amount of new tissue) during time *T*

*F*(*M*): discrete biomass increment

*cM*: average *f*(*M*) throughout the growth process, related to the average resource acquisition and respiration consumption during time *T*

*M*max and *M*amax: tree maximum biomass and tree maximum aboveground biomass

*mr*:maintenance respiration coefficients, i.e., the rate of maintenance respiration rate per unit of tissue

*gr*: growth respiration coefficient, i.e., the amount of respiration needed to produce a unit of tissue, usually considered as a constant

*λ+*1: intrinsic growth rate

*o*: initial biomass

# 1. Introduction

Plant growth is a fundamental ecological process that is affected by physiology, community dynamics, and ecosystem properties (Paine et al., 2012). For a forest ecosystem, the large-tree growth trend determines the carbon budget of forests, especially old forests. Tree growth has been thought to follow a ‘rise-and-fall’ unimodal pattern (i.e., the tree biomass increment per unit time first increases and then decreases with tree size), thus presenting a sigmoidal trajectory of biomass over the lifetime of a tree (e.g., Ryan and Yoder, 1997). Most of the data from chronosequence-based studies supports a decline in biomass accumulation at the community scale (e.g., Acker et al., 2002; Ryan et al., 1997). However, some studies of very old trees suggested an increase in the growth increment with tree size or age (e.g., Sillett et al., 2010; Johnson et al., 2009), which directly contradict the unimodal or sigmoidal growth model. Although there is obvious inconsistency in both aggregate and individual growth trends (Sheil et al., 2017), the root cause of the conflict remains unknown. Overall, technical or/and theoretical limitations have limited a more comprehensive understanding of the growth behavior of large trees (Sheil et al., 2017).

Plant biomass accumulation represents the balance of photosynthetic gains and respiratory losses. Increased total respiratory expenditure is the main cause of productivity decline, which is generally considered to conform to von Bertalanffy paradigm (Von Bertalanffy, 1957; West et al., 2001; Shi et al., 2013). Gompertz and/or logistic equations based on the this theoretical framework (see below) reasonably explain the growth of most small plants (e.g., crops) (e.g., Shi et al., 2013; Karadavut et al., 2008). These results support the rationality of the unimodal pattern, and impels us to consider some significant differences between trees and other small plants. Compared with small plants, large trees have larger-scale physiological and ecological activities, resulting in stronger and more flexible self-regulation ability. For instance, for an average stand, tree height growth, as a game-theory problem (Falster et al., 2003), depends on the presence of the height strategies of other trees. Compared with large trees, the shorter life history of small plants means there are fewer opportunities to be affected by external factors (e.g., disturbances). Thus, small plants are more likely to maintain their inherent growth strategies, thus presenting a growth pattern that is consistent with the theory. More flexible growth strategies, in contrast, may delay achievement of photosynthetic-respiration balance.

Plant functional traits are measurable morphological and physiological attributes that significantly affect whole-plant performance (Enquist et al., 2007). Classical life history theory indicates that at least four independent trait-defined axes (leaf-height-seed-stem) (Baraloto et al. 2010b) can shape the core strategies plants use to acquire and invest resources (Falster et al., 2018). For example, wood density is related to biomass allocation and photosynthetic carbon gain (Santiago et al., 2004) and stem economics and adult stature largely explained interspecific differences in growth strategies for rain forest tree species (Héraul et al., 2011). To maximize the efficiency of using system resources, increased size may shift the benefits and costs of some trait-based trade-offs, resulting in a size-dependent change in the net effect of a particular trait on growth (Falster et al., 2011). A recent meta-analysis supported this idea, showing that trait-growth correlations change with plant size (Gibert et al., 2016). Moreover, functional balance allows an individual to adjust its growth strategy to effectively respond to its immediate environment within the envelope of possibilities defined by allometry (Chen et al., 2013). For example, trees may make substantial plastic adjustment in morphology and anatomy of newly developing leaves, xylem, and fine roots to respond to environment stress (West 2019). If an increase in the investment of valuable traits, plant resource use efficiency may increase as a result. Meanwhile, for trees with obvious changes in size, the relationship between these traits and plant size will change significantly. Due to the indeterminate and modular growth of plants (Weiner 2004), we speculated that the growth trajectory of large trees may include two or more unimodal curves with different scales (i.e., cascading growth). On the whole, the downward trend of the former unimodal trajectory may be obscured by the larger upward trend of the latter trajectory. In essence, cascading growth is result from plant exhibit a range of phenotypes depending upon its environment (acclimation) (i.e., phenotypic plasticity).

The measurement of tree biomass remains a difficult challenge. Researchers have used multiple indicators (e.g., diameter and tree height) or a specific empirical equation to estimate tree biomass. However, the range of a measured indicator limits the applicability of empirical equations (Sileshi 2014). Variation in architecture and form, ontogeny, bark thickness, wood density, damage, and rot all contribute to variation within and among species (Sheil et al., 2017). Thus, it is appropriate to estimate the biomass of trees with fitness and competitive advantage (termed ideal trees) using calibrated equations. These ideal trees grow in relatively ideal environments, so they can invest more resources in growth and approach the ideal growth pattern. The functional traits of these trees must be optimal to promote growth. Obviously, if the growth trajectories of ideal trees are unimodal, then other non-unimodal growth trajectories may represent the incomplete expression of a unimodal pattern. This may be related to the relatively weak influence of functional traits on growth. The ideal growth pattern should be considered separately rather than included in the average results.

We tried to determine whether the observed continuous growth uptrend can be attributed to cascading growth. We hypothesized that: 1) the ideal growth pattern of trees is unimodal (H1); 2) tree growth trajectories may follow unimodal curves with cascade characteristics, and the scale of new curves should increase with tree size (H2), and 3) cascading growth is due to the beneficial change of functional traits relative to tree growth (H3). Based on extended classical growth equations, these hypotheses were specifically tested by analyzing the growth dynamics of different subalpine *Abies fabri* forests in western China.

# Materials and Methods

## *2.1 Classical growth equations for the rising growth trend*

The Gompertz and logistic equations are two important types of sigmoidal trajectories. In order to better describe the unimodal trajectory, here, we discretized these two equations. For the Gompertz model, we first introduced a time parameter *T* to re-describe growth rate, where *T* refer to the formation time of unit tissue. Although still considered conceptual, *T* is not biologically arbitrary, but describes the time during which tissue development is controlled by genes and physiological activity, independent of size. Assuming *f*(*M*)is the total biomass of new tissues during time *T*, then the expression term of growth rate is *f*(*M*)/*T* in this period of time. In mathematics, *T* can also be infinitely small so that *f*(*M*)/*T* →d*M*/dt. So the introduction of *T* has a broader significance. Applying this concept and the Bertalanffy paradigm, we not only can obtain the discrete Gompertz equation, but also extend it further. The discrete logistic equation can be directly derived from the population model based on the intrinsic growth rate and reproductive generations. See supplementary information for the detailed derivation steps of all equations. The resulting discrete growth expressions can be written as:

 (1a)

 (2)

Eq. 1a is the extension of the discrete Gompertz equation, and can be simplified to

 (1b)

Where *f*(*M*)/*T* representthegrowth rate; (ignore *o*) and parameter *o* ensures that the growth equation can move along the transverse axis, reflecting the modular strategy of tree growth. The vertex of Eq. 1b is (, ).

Since *T*, *gr* and *b* are relatively stable, *M*max is mainly determined by *cM*/*mr*. By definition, *cM* ∝ resource uptake, 1/*mr* and 1/*gr*.Obviously, Eqs. 1a and 2 belong to the Bertalanffy family.

The effects of parameters *cM*, *b*, *T*×*mr*/*gr,* *M*max and *λ* on growth curves are shown in Figs. 1a and b. Note that the parameter *cM* reflects the average levels of resource uptake and respiration consumption. The change of *T*×*mr*/*gr* mainly depends on *mr*, because *mr* is more sensitive to the environment (Van Iersel 2003). Mathematically, unimodal curves connected in series can be divided into types *α* and *β,* as shown in Fig. 1c. Type *α* indicates that unimodal curves in series have the same starting point. In type *β*, the starting point of the new curve can be anywhere on the old curve, reflecting modular growth. Biologically, the difference between *α* and *β* types lies in the involvement of the old tissues in the new growth pattern. Considering Eq. 1 as an example, continuous changes in parameters (*cM* and *T*×*gr*/*m*r ) may result in a mixed trajectory, as shown in Fig. 1d. We referred to this type as type γ.

We speculated that changes in the relationship between functional traits and tree size may affect cascading growth, with both positive and negative effects (PE and NE) on growth. The effects of PE and NE on Eqs. 1 and 2 are related to changes in functional traits such as module and overall performance, as shown in Table. 2. On the module scale, we considered both leaf and stem economics (Table. 2), which are related to photosynthesis, hydraulic transport, and respiration consumption. These traits are important for tree ontogeny (Westoby 1998; Weiher et al. 1999; Poorter et al. 2008; Héraul et al., 2011). On a more comprehensive scale, we considered the number of trait modules relative to size, where some morphological traits that are related to the total amount of photosynthesis and respiration deserve special attention. The product of average crown width/(DBH+crown width) (abbreviated as CW/(D+CW)) and crown height/tree height (i.e., crown ratio) (abbreviated as CH/H) can be considered a proxy of canopy/size. Note that the size in this indicator is not biomass but volume. Higher canopy/size means a resource intake strategy, then increase *cM* and *M*max. The attenuation of light within the canopy will cause a decrease in light utilization after the canopy closes, so the uptake rate of trees to resources is not directly proportional to their canopy.

Sapwood is the living, outermost portion of a woody stem or branch, and heartwood is the dead, inner wood, which often comprises the majority of a stem's cross-section. Sapwood, not heartwood, serves as a sink tissue that consumes sugars for daily metabolism through respiration (Lehnebach et al., 2016; Bamber et al., 1976). Because heartwood is not active, the *mr* of the trunk could decrease with a decreasing sapwood/heartwood ratio. Given that the tree trunk accounts for most of the tree biomass, we calculated the sapwood area to heartwood area ratio to assess the change of tree *mr*. Obviously, the change of *mr* can affect maintenance respiration (= *mr* × biomass) from the scaling relationship with biomass. In fact, sapwood maintenance respiration may also be a significant cause of growth decline with increasing tree age (Tatuo and Shidei, 1967; Ryan and Yoder, 1997; Sillett et al., 2010). Overall, these two ratios have great effects on plant growth.

## *2.2 Site description and experimental design*

We studied four subalpine primeval *Abies fabri* forests located in the Gongga Mountain, in the southeastern Tibetan Plateau, and at altitudes of 2,900 m, 3,000 m, 3,300 m, and 3,600 m (treeline). The mean annual temperature was 4 °C, and the mean annual precipitation was 1,938 mm, with roughly 50% of the annual total rainfall occurring from June to September in 2015. The characteristics of these survey plots are described in Wang et al (2017).

*Abies fabri* trees havelarge stature and long life history, and we expected to observe significant biomass changes on the century scale. First, we estimated the ideal and average growth trajectories (with respect to size) of this species by the DBH sequence of all sampled trees and biomass equations. These results can be used to test H1 and H2. Note that the ideal growth trajectory is composed of the maximum growth increment of different trees along the size gradient. Then, we focused on changes in some important functional traits with tree size. This can be achieved by analyzing the functional traits of different trees. Some variable functional traits may be the key to cascading growth. Finally, we tried to quantify the effects of these variable functional traits on unimodal growth to test H3. Sampled functional traits is current, so they are only valid for recent growth dynamics. Thus, some individual trees that follow the unimodal trajectory only in recent growth would be selected, all located at an altitude of 3,100 m. We expect that the height and length of these unimodal trajectories (related to parameters *cM*, *mr*, *λ* and *M*max) are determined by some current functional traits (Tab. 1).

## *2.3 Data collection, processing and analysis*

In September 2015, we measured the tree ring sequence and DBH (> 10cm) of each tree in four large plots along elevation gradients. For details of the method, see Wang et al. (2017). In June 2019, we sampled and measured the relevant functional traits of trees belonging to different DBH classes. DBH classes are in the 5 cm interval. These randomly sampled trees covered more than half of the sample areas surveyed in 2015. Meanwhile, the functional traits of the selected trees were sampled separately. For leaf and stem economics (listed in Tab. 1), we sampled three times at the south and north sides of trees, and at different heights (e.g., 5m, 10m,15m). The number of leaves sampled each time ranged between 20 and 60. Some leaves were used for element analysis. Leaf N concentrations were analyzed with a Vario MAX CN element analyzer (Elementar, Hanau, Germany). The vanadium molybdate yellow colorimetric method was used to measure Leaf P, and flame photometry was used to measure Leaf K. We used foliar dry matter content to locate different trees on a resource use axis rather than specific leaf area (SLA) (Wilson et al., 1999) due to the large vertical span of the fir canopy and sampling difficulty. Details of trait measurement are described in Wilson et al. (1999) for foliar dry matter content. For stem economics, trunk xylem density was calculated as the ratio of mass of samples dried for 72 h at 105℃ after the removal of bark, to their fresh volume as calculated by the displacement of liquid volume (water). Trunk bark thickness was measured by vernier caliper. Trunk wood moisture was determined by the fresh mass and dry mass of the wood, and was expressed as fresh mass/dry mass-1. We determined the sapwood width using diameter increment borers. Sapwood and heartwood areas are equal to π×(DBH/2)2－π×(DBH/2-sapwood width)2 and π×(DBH/2－sapwood width)2, respectively. Other morphological traits were obtained by direct forestry survey.

We used the actual tree ring sequence to determine the aboveground biomass dynamic of individual trees. To reduce error, the minimum time interval for describing growth dynamic was set to 10 years. The increase in DBH for each decade can be derived from the current DBH and tree-ring data. Based on previous results (Zhou et al., 2013), we established the aboveground biomass equation of individual trees dependent on DBH, which allows us to obtain the growth trajectory of individual trees (see supplementary information). From these results, we can determine the best and average DBH or biomass increment within different DBH classes (> the maximum diameter increments) to reveal the growth dynamic along along the DBH or size gradient. The emphasis of maximum increment is on species upper-quantile growth change (95% percentile) (Wright et al., 2010), reflecting a relatively ideal growth state.

For Eq. 1b, *f*(*M*)/*T* canrepresent the annual average growth rate over a decade. Thus, the 10-year aboveground biomass increment can be approximately equal to 10*f*(*M*)/*T*.

 (3)

Where *b* = 0.75. Assuming a constant ratio of aboveground to underground biomass (Shu et al., 2019), individual growth equations can also be used directly to describe the change of aboveground biomass. We used Eqs. 3 and 2 and their extended forms (see supplementary information) to fit the growth dynamics of aboveground biomass and DBH to directly test the validity of classical growth equations. If these equations are valid for the selected trees, we can get the length and height of two type of unimodal curves (Figs. 1a and b), which are closely related to parameter *λ*, *M*amax 10*mr*/*gr* and *cM*. According to Tab. 1, we can directly test the effect of selected variable traits on the formation of unimodal curve.

# Results

## *3.1 Underlying growth pattern of trees*

We revealed the growth trajectories of trees on the century scale, at the aggregate, and individual levels. With DBH as the gradient, the maximum tree ring increment of fir communities at different altitudes was determined and the results are presented in Fig. 2, which reflects the inherent or ideal growth law independent of the environment. The radial growth of ideal trees at altitude of 2,900m, 3,100m and 3,300m exhibit unimodal (Figs. 2b and c) or bimodal (Fig. 2a) characteristics. For a range of DBH less than 80 cm, the fir radial growth at all altitudes except at the treeline exhibit a unimodal curve extended by Gompertz pattern (Eq. 1b) (Tab. S2). We also directly observed a unimodal curve based on logistic pattern in the larger DBH interval (>80 cm) (Tab. S2). The growth also shows an initial increase and then a linear decreasing pattern, as shown in Fig. 2d. Trees at the altitude of the treeline are subjected to a harsher environment, and the observed linear growth pattern may indicate the incomplete expression of a unimodal pattern.

The aboveground biomass measurements also reveal the unimodal growth of ideal trees, as shown in Fig. 3. These unimodal curves are as obvious as those corresponding to radial growth. The unimodal parts are still well explained by Eqs. 3 and 2 (R2>0.7, P<0.01. Tab. S3). From a more complete growth curve, it can be seen that the growth trajectory of trees can transit from one smaller unimodal curve to a larger one, as shown in Fig. 3a. Not only that, the average increment dynamics may be unimodal or multimodal because of the covariant relationship with the ideal increment dynamics (Fig. S2). For the same reason, the biomass dynamic near the forest line (Fig. 3d) was similar to that of DBH (Fig. 2d). To a large extent, these results directly support H1.

The growth trajectories of selected trees were determined and are shown in Fig. 4. Clearly, these unimodal curves vary in size and do not fully cover the entire growth process, as some independent growth changes occur before and after the unimodal curve. In fact, there may be more than one unimodal curve, as shown in Fig. 4e. The maximum heights and lengths of the unimodal curves increase with tree size. For example, the lengths of unimodal trajectories of trees with biomass 1412 kg and 4855 kg are 510 kg and 2053 kg respectively, and the heights of those are 115 kg and 180 kg respectively (Figs. 4h and i). These trajectories driven by radial and tree height growth conform to the Gompertz curve. See Tab. S4 for fitting results.These results support H2.

## *3.2 Change of functional traits with growth*

Due to the lack of significant difference in module traits (i.e., leaf and stem economics) of individual trees, here, we only presented the traits corresponding to different size intervals (Ⅰ, Ⅱ, and Ⅲ), as shown in Figs. 5 and 6. However, structural indicators (canopy/size and SWA/SHA) are not stable. Except for trees located at the treeline (Fig. 7d), the canopy/size and size of other trees at other elevations should conform to the logistic relationship. The SWA/SHA and sizes of all trees show an obvious inverse relationship (see Tab. S5 for fitting results). According to our hypothesis, increasing canopy/size and decreasing SWA/SHA would result in a greater growth increment and maximum biomass (Fig.1 and Tab. 1). Thus, these two traits may be related to cascading growth. In practice, in accordance with the actual biomass intervals in Figs. 3a and c where the Gompertz curves are located (i.e., left side of vertical solid line in Figs. 3a and c), the SWA/SHA and canopy/size of ideal trees can be estimated by the size of ideal trees (dotted line in Fig. 7) and the size-traits function. The calculated SWA/SHA and canopy/size are 0.28 and 0.75 (2,900m), 0.30 and 0.79 (3,100m) and 0.47 and 0.70 (3,300m).

## *3.3 Changes in canopy and sapwood relative to size are the main causes of cascading growth*

With very stable leaf and stem economics, we next tested whether canopy /size and SWA/HWA can affect the formation of unimodal curve. According to Fig. 1 and Tab. 1, we tested canopy /size ∝ maximum growth rate (∝ *cM*), SWA/HWA ∝ *mr* and SWA/HWA∝ 1/maximum growth rate (∝ 1/*cM*). In addition to individual trees at an elevation of 3,100m, these analyses also included ideal trees at different altitudes (black dots). All relationships are confirmed well (R2>0.56, p<0.01), as shown in Figs. 8a, b and c. Due to *M*max ∝*cM*/*mr* (Fig. S3),we expected a positive correlation between canopy /size ×HWA/SWA and *M*amax. When *M*amax is less than 2100kg, this correlation tends to be linear (R2= 0.93, p<0.01), as shown in Fig. 8d. Overall, this relationship is closer to power function (R2= 0.93, p<0.01). Obviously, the the height and length of the growth curve can be largely explained by the morphological traits, consistent with H3.

# Discussion

It is difficult to study large-tree growth due to the limitation of relevant theories and practical measurement tools. Tree rings accurately record the radial growth dynamics of trees, and we can estimate tree biomass dynamics based on the obvious DBH-height relationship for a suitable time scale (e.g., decade interval). Although there has not been sufficient analysis of the use of logistic curves (right side of vertical solid line in Fig. 3), current results are supportive of our hypotheses (H1, H2 and H3).

## *4.1 Control of tree size on growth*

Our results highlight the interaction between functional traits and size, as shown in Figs. 7 and 8. On the one hand, canopy/size and SWA/HWA change with size; and the other hand, they can futher affect the growth rate and maximum biomass of trees, which highlights the size-driven growth mechanism. In fact, tree size acts in organism design and function (Gibert et al., 2016). In some experiments, size has a greater effect on age-related declines in relative growth and net assimilation rates than cellular senescence (Mencuccini et al., 2005). Environmental factors, such as temperature and precipitation, can also affect production indirectly through variation in plant size (Michaletz et al., 2014), suggesting size-dependent tree growth should be quite common in nature. Mathematically, growth can be formulated as a series of spontaneous iteration cyclic equations with an initial input of some starting biomass *M*0, *M*0→*f*(*M*0)+*M*0→*f*(*f*(*M*0)+*M*0)*+f*(*M*0)+*M*0...→*M*max, causing the biomass *M*0 to approach *M*max. Achieving balance between photosynthesis and respiration stops the iteration mapping. At least two types of unimodal curvesare associated with this control (i.e., Eqs. 1 and 2).

## *4.2 Cause of Abies fabri cascading growth*

We found that the most common cascading growth types are *β* and *γ* (data not fully shown)(e.g., Fig. 4c)*.* Modular proliferation and gradual physiological adaptation provide a more moderate and conservative growth strategy to mitigate the risk of drastic change. In this process, Canopy/size and SWA/HWA reflect the relative number relationship between photosynthetic and respiration modules and the changed of plant compounds, respectively, which determines the balance of photosynthesis and respiration. Thus, Canopy/size × HWA/SWA, physiologically, are closely related to *cM*/*mr* (∝*M*amax) (linear part in Fig. 8d). It should be noted that the effect of Canopy/size × HWA/SWA on *cM*/*mr* may weaken due to the shading and wear of leaves in the canopy of very large trees (nonlinear part in Fig. 8d). Trees may offset this loss by adjusting other functional traits. Overall, as trees grow, the higher canopy/size and lower SWA/HWA can result in a higher ratio of resource uptake to respiratory expenditure, which is the main reason for the increase in the scale of the unimodal curve.

Canopy growth has genetic and environmental limitations. Except for species-specific, shoot ramification patterns, sylleptic and proleptic growth or the ratio of long and short shoots show clear dependence on light quantity or quality (Kull and Tulva, 2000). Species that attain large sizes may intercept more light, so that canopy/size should increase with tree height. However, increased height-related hydraulic constraints (Ryan et al., 2006) stimulate a slower sapwood-to-heartwood transition rate (McDowell et al., 2002), resulting in a lower SWA/HWA. These changes may be the main mechanism to form the larger unimodal curve. Of course, the limits of canopy /size and SWA/HWA mean that there is an upper limit to the scale of the unimodal curve. If this change is not regular, there may not be a unimodal trend, as shown in Figs. 3d and 7d.

Since this study is only for *Abies fabri* distributed in same region, some important module traits, such as leaf and wood economics, do not show significant differences. Nevertheless, some results are still predictable. For example, higher wood density not only increase *gr*, but also may decrease *mr* because certain plant compounds require little or no maintenance (e.g. lignin and Cellulose) (Johnson 1990; Van Iersel 2003). From the view of result, a decrease in *mr*/*gr* will increase the kurtosis of the growth curve (Fig. 1), which is consist with the views of Hérault et al (2011).

The change of *b* is also an important reason for cascading growth. In our model, *b* is the key to control the transition of growth trajectory from Gompertz to logistic patterns. Mathematically, the Gompertz and logistic patterns require the metabolic scaling exponent of trees < 1 (also need >0) and = 1 (i.e., *Mb* where*b* = 0.75 or =1). In practice, the diameter growth of old trees may continue long after the height growth has slowed (Phillips et al., 2008a), which means tree biomass is proportional to both tree diameter and leaf area. Due to leaf area ∝ respiration rate ∝ *Mb* (Wang et al., 2015), then in the later period of growth, *b* may indeed equal to 1. Under the effect of competition, the logistic growth pattern is more suitable to describe tree growth (right side of the vertical solid line in Fig. 3).

## *4.3 Implications of larger tree growth*

Many investigations have aimed to identify the sources of interannual variation in NPP, and focused on environmental conditions that affect growth rate to better predict carbon sources and/or sinks of the community. However, estimates of the carbon sequestration capacity of individuals or the community through short-term measurements of the growth rates or NPP are not conclusive. On the one hand, the growth of large trees has strong growth plasticity; and other hand tree size heterogeneity also complicates the carbon sequestration of community. If the maximum and average growth increments of trees still have a clear pattern (Fig. 3a), individual size distribution seems to be the key factor for carbon sequestration.

Our results also show that the largest unimodal growth trajectory is incomplete for study of trees with the largest time span (>390 years) (Fig. 3a). We speculated the largest individuals may have died before achieving growth balance due to disturbance or/and competition (Shu et al., 2019). These external factors may be particularly important for carbon sequestration in old forests, because they can promote the formation of stable tree size heterogeneity and the continuous entry of carbon into the soil. In fact, U-shaped size-mortality trends are common in natural old forests (e.g., Lorimer et al., 2001 Foster et al., 2014, Coomes and Allen, 2015; Pillet et al., 2017).

# Conclusions

We proposed a model of cascading growth to try to bridge the gap between the actual growth performance of large trees and classical theory. Cascading growth is caused by tree phenotypic plasticity and is constrained by allometric scaling. For *Abies fabri*, changes in functional traits, such as decreased SWA/HWA and increased canopy/size, can result in a larger unimodal growth curve.

# Acknowledgements

This work was supported by the National key research and development program of China (2017YFC0505004); by IMHE of CAS, 135 directional project: ecological restoration and security maintenance technology in the alpine gorge region of Western Sichuan; by the National Natural Science Foundation of China (41601206). We thank Mr. Zhi-qiang Xiao and Mr. George kontsevich for their important advice to the theories and text.

# Data accessibility statement

All data generated or analyzed during this study are included in this article.

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**Figure legends**

**Figure. 1. Conceptual diagram illustrating two types of unimodal curves and cascading growth.** a and b: red and green arrows represent the effects of parameters *cM* (or *M*max) and *Tmr*/*gr* (or λ) onunimodal curves; - and + represent the negative and positive correlation between parameters and the curve characteristics (height, kurtosis and length). c and d: the growth trajectories that trees may follow, i.e., cascading growth. Here, we only illustrate the concept of cascading growth. The green line in Figs. c and d represents the unimodal pattern that growth should follow. Dotted lines represent not fully realized trajectories. Blue or red lines represent two new and larger unimodal curves. The solid portions of lines may be in series with the green solid lines, which means growth will follow the new trajectories, resulting in a continuous increase in growth trend (*α* and *β*). The dotted lines in the graph represent growth trajectories that do not occur. The lines with an arrow indicate growth trends. Another indistinguishable cascading trajectory (*γ*) caused by a continuous increase of *cM* and decrease of *Tmr*/*gr*.

**Figure. 2. Tree ring maximum increment along DBH gradient for subalpine *Abies fabri* forest sites at different altitudes on Gongga Mountain.** Circles represent the DBH maximum increment for each decade. Hollow circles represent the growth dynamics with certain regularity. Solid circles represent limited scattered data, and are not included in the fitting. The yellow line indicates 95% confidence interval.

**Figure. 3. The aboveground biomass increments along tree size gradients for subalpine *Abies fabri* forest sites at different altitudes on Gongga Mountain.** Green and white dots represent maximum and average aboveground biomass increments, respectively. The scatter points on the left side of the vertical solid line conform to the Gompertz equation, on the right side conform to the logistic equation or are not fitted. Roman numerals I, II, and III represent the size intervals corresponding to rising, falling and other trends of growth. The yellow line indicates 95% confidence interval.

**Figure. 4. Growth trajectory of *Abies fabri* individuals at elevation of 3,100m.** Hollow circles represent growth dynamics with obvious regularity. The change trend of solid circles is different from that of hollow circles, so is not included in the analyses.

**Figure. 5. Elements and dry matter content in leaves of trees under different growth trends.** Ⅰ, Ⅱ and Ⅲ indicate different size intervals, corresponding to those in Figure 3. Different lowercase letters indicate significant difference at P<0.05 level

**Figure. 6. Stem economics and leaf dry matter content** **under different growth trends.** Here, xd, wm, bt, and dc represent xylem density, wood moisture, bark thickness, and leaf dry matter content, respectively. Different lowercase letters indicate significant difference at the P<0.05 level. Ⅰ, Ⅱ and Ⅲ indicate different size intervals, corresponding to those in Figure 3.

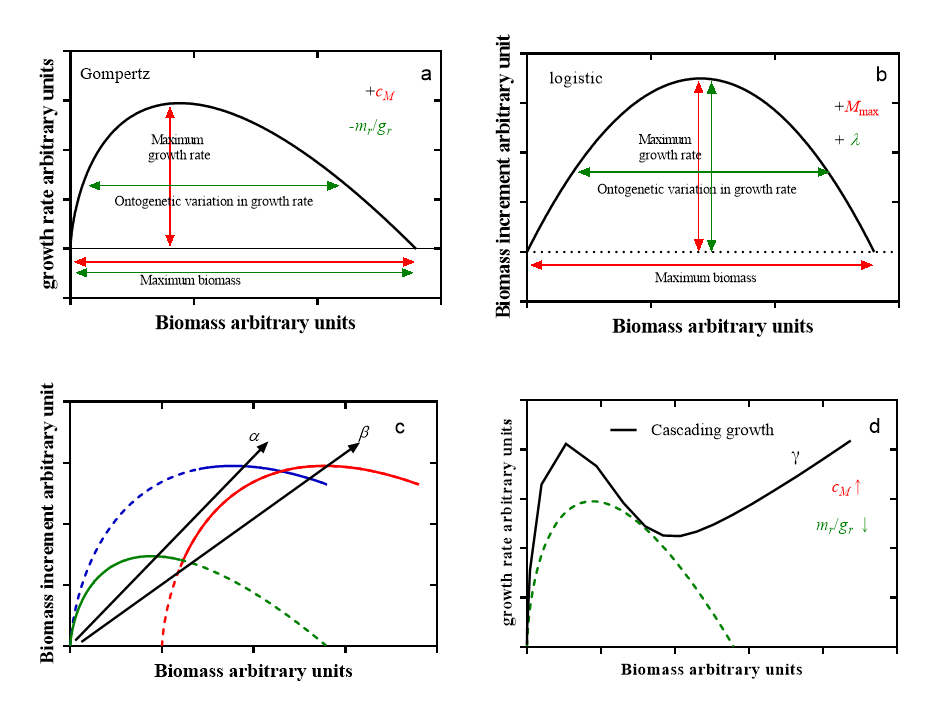
**Figure. 7. Relationships between morphological traits and tree size.** The black rectangles or circles in Fig. 7b represent SWA/HWA and canopy/size, respectively, for individual trees with recent growth trajectories that exhibit a unimodal pattern (i.e., Fig. 4). The intersections of the fitting functions and horizontal dashed lines represent the sizes of ideal trees and the corresponding functional traits.

**Figure. 8. Effects of morphological traits on equation parameters.** The black dots and hollow circles represent ideal trees (i.e., green dots to the right of the vertical solid line in Figs. 3a, b and c) and individual trees (i.e., black symbols in Fig. 4b), respectively. The yellow line indicates the 95% confidence interval.

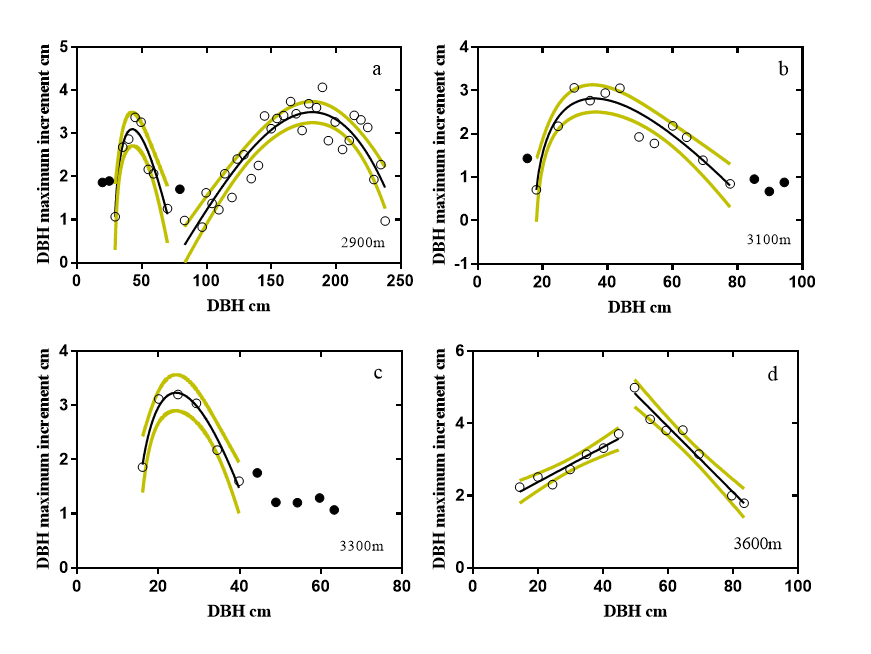
**Table 1. Functional traits related to growth**

|  |  |  |  |
| --- | --- | --- | --- |
| Indicators | Main Role | For Eq. 1 | For Eq. 2 |
| Leaf economics (module scale) | | | |
| Foliar Km (K) (g/kg) | Maintaining water potential; promoting photosynthesis (Ashraf et al., 2001) (PE) | ∝ *cM* | ∝*λ* and *M*max |
| Foliar Nm (N) (g/kg) | Increasing photosynthetic capacity (Takashima et al., 2004; Reich and Walters 1994) (PE) | ∝ *cM* | ∝*λ* and *M*max |
| Foliar Pm (P) (g/kg) | P deficiency could restrict photosynthesis and leaf growth (Mollier and Pellerin 1999) (PE or none) | ∝ *cM* or none | ∝*λ* and *M*max |
| Foliar dry matter content (g/g) | Indicating conservative resource use strategy (NE) | ∝1/*cm* | ∝1/*λ* and 1/*M*max |
| Stem economics (module scale) | | | |
| Trunk bark thickness (Bark) (cm) | Defence (Héraul et al., 2011) (PE) | ∝ *cM* | ∝*λ* and *M*max |
| Trunk wood moisture content (g/g) | Relating to transport and structure (Héraul et al., 2011) (PE) | ∝ *cM* | ∝*λ* and *M*max |
| Trunk xylem density (g/ml) | Defence (Héraul et al., 2011) but more increasing stem growth cost (King et al., 2006) (NE) | ∝*gr*  and 1/*cM* | ∝1/*λ* and 1/*M*max |
| Morphological traits (overall scale) | | | |
| Crown width/(DBH+crown width) (abbreviated as CW/(D+CW)) | Reflecting the ratio of source uptake to consumption (PE) | ∝ *cM* | ∝*λ* and *M*max |
| Crown height/tree height  (abbreviated as CH/H) | Reflecting the ratio of source uptake to consumption (PE) | ∝ *cM* | ∝*λ* and *M*max |
| CW/(D+CW)CH/H  (termed Canopy /size) | Reflecting the proportion of canopy volume to tree volume (PE) | ∝ *cM* | ∝*λ* and *M*max |
| Sapwood area / heartwood area (abbreviated as SWA/HWA) | Relating tohydraulic conduction and respiration consumption (Carbone et al. 2013) (NE) | ∝ *mr*  and 1/*cM* | ∝1/*λ* and 1/*M*max |

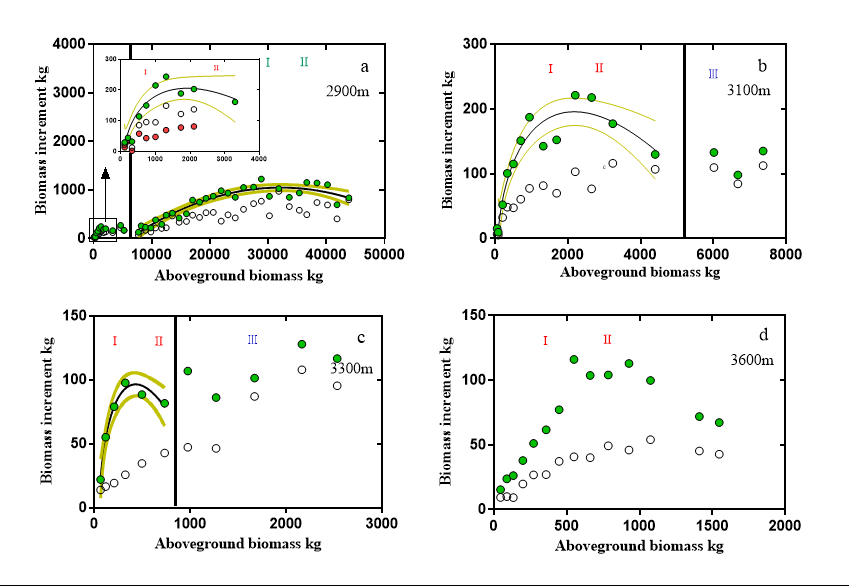
Some functional traits may regulate growth in multiple ways and here we listed only the main effects on tree growth. For example, leaf nitrogen content also increases leaf respiration. However, for individual trees, tree respiration also includes the trunk and root parts, so the increase of leaf respiration may not match the increase of net photosynthesis. PE and NE represent positive and negative effects of functional traits on growth, respectively.



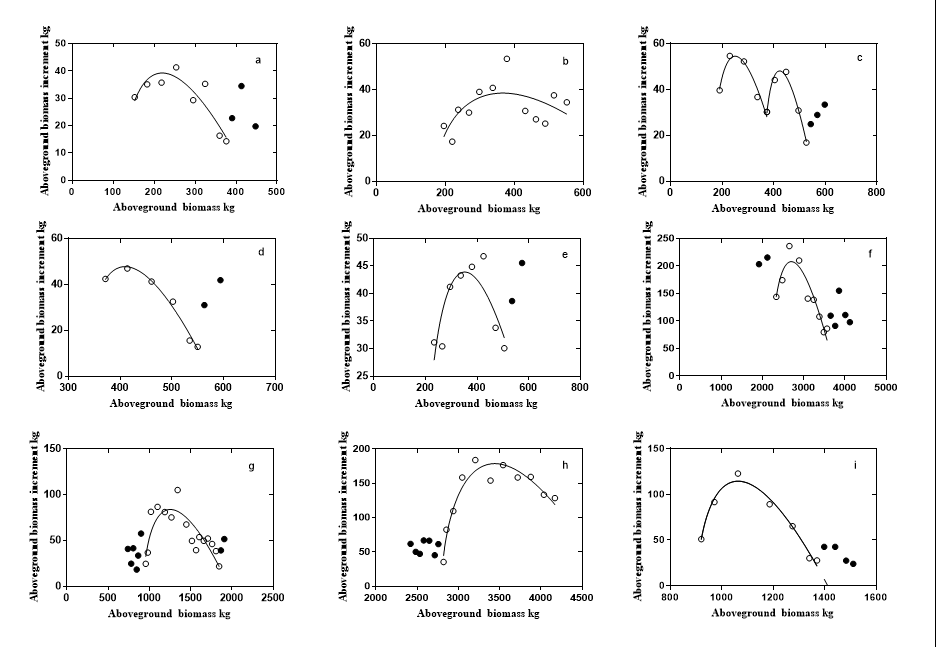
**Fig. 1**



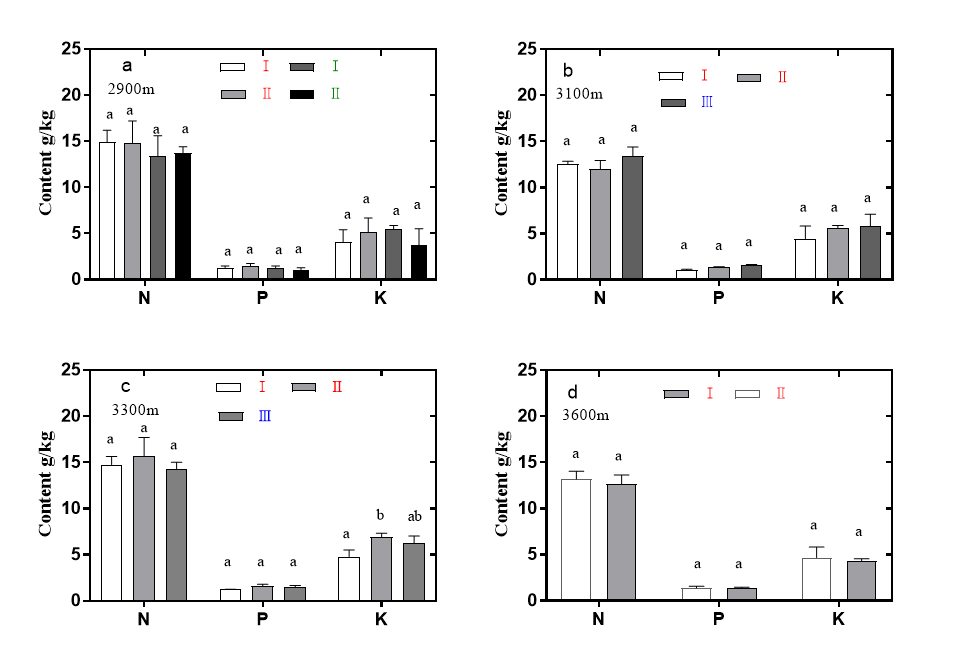
**Fig. 2**



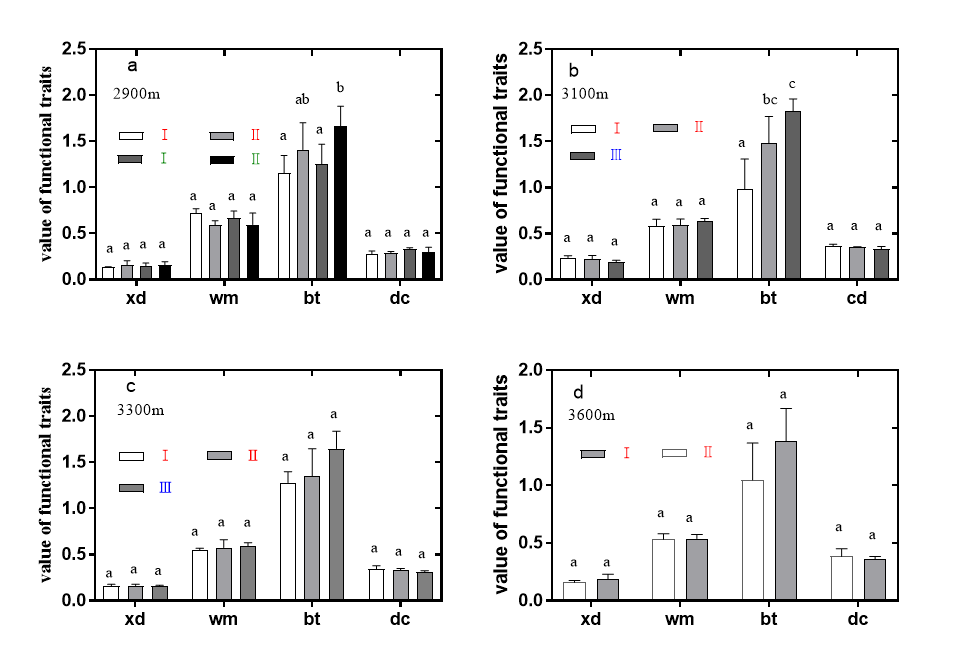
**Fig. 3**



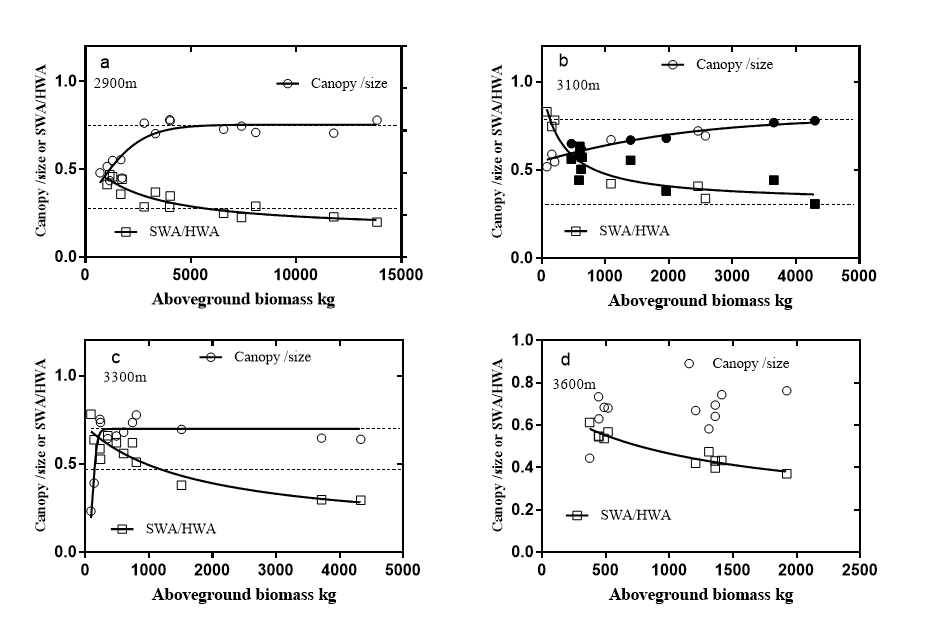
**Fig. 4**



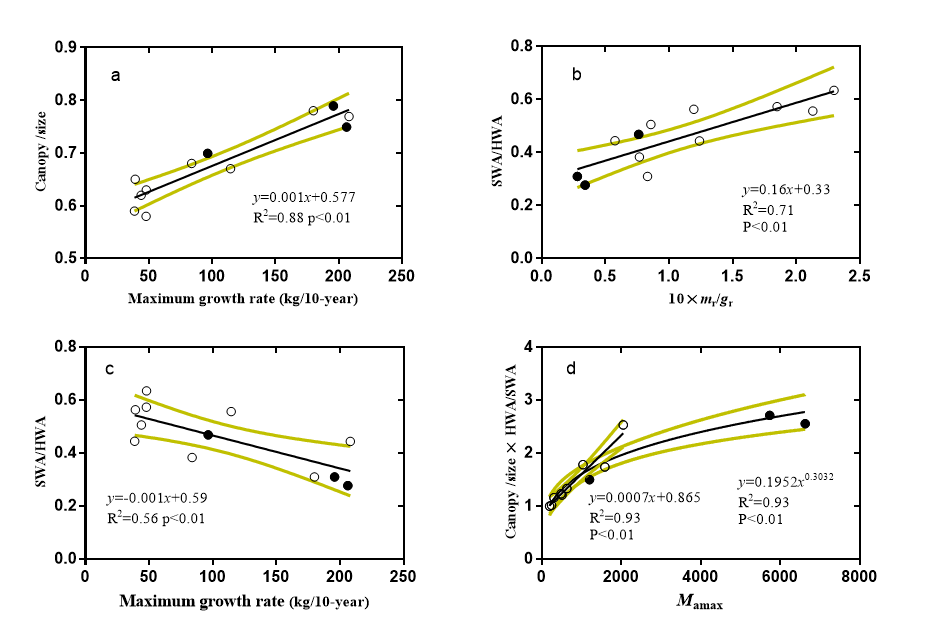
**Fig. 5**



**Fig. 6**



**Fig. 7**



**Fig. 8**