Relative plant growth revisited: Towards a mathematical standardisation of separate approaches

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ABSTRACT

The concept of relative growth has independently been developed and pursued in different fields of science and at different locations. It has proved to be useful in comparative studies of plant growth analysis. The purpose of this review is to provide a synthesis of different independent approaches as well as of research applications and to standardise the mathematical notation in order to facilitate future research.

In the context of ecology, we explore and analyse the definitions of absolute and relative growth rates, growth acceleration, growth multipliers and allometry from a mathematical point of view. In addition, we evaluate statements made in the literature, compare different concepts that have been developed separately and show how they relate to each other. We also review and standardise functions of absolute and relative growth, which can be used for analysing and modelling plant growth. Finally, we comment on sampling, growth rate combinations and the recently discussed method of size standardisation.

We conclude that the different approaches to quantifying and modelling relative growth rates can conveniently be integrated in one consistent theoretical concept and as a result provide useful synergies. A harmonisation of different definitions of relative growth rate is straightforward and a consistent, meaningful notation provides a deeper understanding of the concept.

Relative growth rates are key characteristics for assessing growth performance and growth efficiency. Recently they have gained importance for diagnosing and modelling mortality and reproduction processes and they potentially play a crucial role in reconstructing growth processes in dendrochronology, climate change and forest decline research. From a technical point of view, relative growth rates are more straightforward to model than absolute growth rates and more emphasis should be devoted to model development.

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1. Introduction

All living organisms are capable of "growth" in the sense of irreversible change with time, mainly in size, often in form and occasionally in number (Hunt, 1982, p. 5). Growth is indeed a universal and fundamental life process on earth. In plants, both survival and reproduction depend on plant size and growth rate (Bigler and Bugmann, 2003; Shipley, 2006).

Bertalanffy (1951, p. 267) desribed growth as an increase in size of a living system as a result of assimilation. More generally Jørgensen et al. (2000) defined growth as increase in a measurable quantity, often taken in ecology to be some form of mass or energy, such as population size or biomass. The authors distinguish between three forms of growth, i.e., growth to storage, growth to throughflow and growth to organisation. Growth is a common theme in biology, ecology, forestry and agriculture, yet mathematically the topic has been approached separately using different concepts and notation.

In a forestry context, Laar and Akça (2007, p. 201) point out that *growth* is the biological process whilst *increment* is the observed growth of an organism or a population during a given period of time. In production biology and forestry, *yield* is defined as the harvested or harvestable accumulated increment per unit area (Assmann, 1970, p. 1; Laar and Akça, 2007, p. 201). The methods described in this paper are general and can be applied to a wide range of organisms and biological scales, however, we focus here on plant growth.

The term *plant growth analysis* refers to quantitative methods that describe the performance of whole plant systems grown under natural, seminatural or controlled conditions. Plant growth analysis

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provides an explanatory, holistic and integrative approach to interpreting plant form and function. It uses observed primary data such as weights, areas, volumes and contents of plants or plant components to investigate processes involving the whole plant or a population of plants (Hunt, 2003). On the same subject Wenk et al. (1990, p. 20) explain that forest growth and yield science – the corresponding forestry counterpart – is concerned with the experimental and theoretical exploration of ecological growth patterns of individual trees and forest stands and their use for satisfying needs of human society. This suggests an intimate link between field experiments and models.

In the aforementioned areas of plant science, methods of plant growth analysis were developed more or less independently. Boundaries of academic subjects and unhelpful notations (South, 1995) have so far prevented to see that many seemingly different approaches in plant growth analysis can indeed be considered as essentially one approach. In production biology, particularly in forestry, the quantification of the outcome of growth processes has been an important pre-requisite for ensuring sustainability and planning business activities. Thus, the theoretical foundation of forestry activities through a mathematical description of growth processes has had a high priority. First basic population models, the so-called *yield tables*, were already established towards the end of the 18th century and systematic experiments with a view to monitor and quantify the growth of tree populations exposed to different treatments started towards the end of the 19th century (Assmann, 1970, p. 1f.). It did not take long before researchers in this area found that the possibilities for identifying strict growth laws similar to those in physics are limited and that stochastic methods from mathematical statistics are required to identify and to describe growth patterns (Assmann, 1970, p. 205.).

Hunt (1982, p. 1, 16) refers to the *British school of plant growth analysis*, which had its origin in the work of Gregory, Blackman, Briggs, Fisher and colleagues, in their turn drawing some inspiration from 19th-century German work. A detailed history of this school can be found in Evans (1972, p. 190ff.). The methods of this school amount to quantifying the growth of whole plants and populations by means of mathematical-statistical methods and provided a useful framework for ecological, genetical, physiological and agricultural studies.

Together with his colleagues at Tharandt/Dresden Technical University in Germany, G. Wenk founded a quantitative plant science school in forestry, starting in the 1970s approximately at the same time as the British school formed at Sheffield and Aberystwyth Universities. The Tharandt school characterised the growth of trees by using the concept of relative plant growth and here particularly the approach of analysing growth functions, see Section 2.5 in this review. Eventually this school developed a population model and a size class model for predicting the growth of trees (Wenk et al., 1990; Wenk, 1994). There is also evidence of empirical work on relative tree growth by Russian researchers (Antanaitis and Zagreev, 1969) at the same time, however, a theoretical treatment of the subject seems to be lacking. Another parallel and detailed work on relative tree growth has been carried out in Finland by Kangas (1968), but with fairly limited uptake by the international research community. The work of these research schools is unique, as the concept of relative growth has found only few scientific applications in forestry, much in contrast to general plant science.

Modelling growth processes to confirm the results of the analysis and to project future ecological growth patterns has been an important concern of researchers in this field. The mathematical-statistical analysis and modelling of plant growth has started in the middle of the 19th century parallel to the first advances in plant physiology. It was at that time that the first functions describing logistic plant growth were developed and published. One of the oldest growth functions is that by Gompertz (1825), though originally designed for a different purpose. Since then many more functions describing plant growth have been published. For good overviews of growth functions see Hunt (1982), Zeide (1993), Bolker (2008) and Burkhart and Tomé (2012).

Like other parts of quantitative plant science, the concept of relative plant growth, involving the analysis and modelling of plant growth rate relative to plant size, has been developed independently at different locations more or less at the same time. It has provided valuable insights into the growth patterns of plants and has extensively been used in plant physiology and ecology (Grime and Hunt, 1975; Ingestad, 1982; Hunt and Cornelissen, 1997; Shipley, 2006; Houghton et al., 2013). The concept is also closely related to plant mortality and is a pre-requisite for quantifying and modelling allometric relationships in plants (see Section 2.4 of this review). Numerous studies using methods of relative plant growth have been and are still being published and they have also been applied in animal science, for an overview see Shimojo et al. (2002). A particular benefit of studying relative plant growth is the avoidance, as far as possible, of the inherent differences in scale between contrasting organisms so that their performances may be compared on an equitable basis (Hunt, 1990, p. 6). As such relative growth rate is a standardised measure of productive capacity of a plant and allows the comparison of plants that differ in initial size, age or environmental conditions (Larocque and Marshall, 1993).

The objective of this paper is to mathematically review the definitions, concepts and ecological applications of relative growth in plant science with a view to better understand its current state of the art and to present a holistic picture of previously separated approaches. To this end, we have standardised the notation and presented synonyms of certain terms from different research fields so that readers concerned with them can more easily follow this synthesis. Finally, we make suggestions for future research directions in this field.

2. The concept of relative growth

2.1. Basic definition of growth processes

Let $y(t)$ denote the state of a plant characteristic at time t, e.g., the weight, area, volume or biomass of a plant. This is modelled by a strictly increasing continuously differentiable real-valued function, F (Eq. (1)), defined on the interval $[0,\infty)$. This function has at least one inflection point and possesses lower and upper horizontal asymptotes.

$$y(t) = F(t) \text{ with } 0 \le t < \infty \tag{1}$$

The function defined in Eq. (1) represents cumulative growth, e.g., the total biomass attained by a plant at any particular age (Assmann, 1970, p. 41), see Fig. 1.

The first derivative of growth function F is referred to as *instantaneous absolute growth* (AGR) or – to draw an analogy to mechanics – *growth velocity* (Wenk, 1978; Hunt, 1982, p. 16). In forestry, this is often referred to as *current annual increment*, *CAI*:

$$y'(t) = \frac{dy}{dt} = f(t) \tag{2}$$

Function f is equal to the derivative of function F and hence is continuous and positive, see Fig. 1. Function f is positive since the growth function F is strictly increasing and it is continuous because growth function F is continuously differentiable. Growth function F is selected so that its rate of growth, f, displays a sharp increase, followed by a rapid decrease and then followed by a slow tapering-off. As a result, f has an asymmetric shape. The maximum value of function f corresponds to the inflection point of function F. The
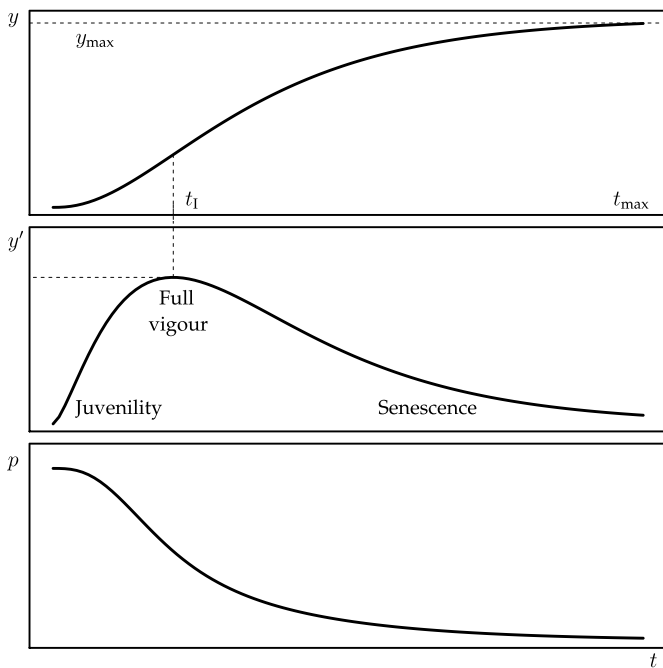
Fig. 1. Relationships between a cumulative, an absolute instantaneous and a relative growth rate function. The symbol t_I denotes the time when the inflection point of the growth curve occurs. The symbol t_{max} corresponds with the upper asymptote denoted y_{max}. Other variables are explained in the text.

value of $f(t)$ is close to zero when t is a very small or very large number, corresponding to the horizontal asymptotes of F.

Absolute growth rate depends on the current state of the plant size characteristic and is therefore not helpful to growth analysts when comparing plants of different sizes (Causton and Venus, 1981, p. 17). In such situations, relative growth, p, is often preferred to absolute growth. *Relative growth velocity* or *instantaneous relative growth rate* (RGR; in forestry termed *relative increment*) is also a function of time and is defined as the increase in size relative to the growth characteristic:

$$p(t) = \frac{y'(t)}{y(t)} = \frac{dy}{dt}\frac{1}{y(t)} = \frac{d}{dt}\log y(t) \tag{3}$$

Thus, we see that relative growth rate is also equal to the derivative of $\log(y(t))$ with respect to time t, see also Fisher (1921), Causton (1977, p. 213) and Kangas (1968, p. 28). Studying the relative growth of $y(t)$ is, therefore, equivalent to studying the absolute growth of $\log(y(t))$, see Appendix 1. This relationship between relative growth and logarithmic size characteristics is an important consideration, which is particularly relevant to allometry as discussed in the corresponding section of this review.

Instantaneous relative growth rate can initially exhibit very large values or with values around 1 (if early growth before the inflection point is exponential) and typically decreases with increasing time. The curve of relative growth rate declines throughout growth in a "reverse sigmoid" manner (Causton, 1977, p. 207): In the first years, function p decreases slowly, then more rapidly followed by a slow decrease towards senescence (see Fig. 1). Shortly before death, RGR is close to zero, which makes this characteristic interesting for mortality studies. For causing this decrease a combination of factors have been suggested, including an accumulation of non-photosynthetic biomass in the form of stems and roots, self-shading of leaves and decreases in local concentrations of soil nutrients (Paine et al., 2012; Philipson et al., 2012).

In the context of production biology such as forestry, it is important to note that $p(t)$ multiplied by age is equal to 1, when the mean

annual increment (MAI) culminates. MAI is the temporal mean of a growth function, i.e., $y(t)/t$. In the point where $p(t)$ multiplied by t (where t is age) is equal to 1, $y'(t)$ (CAI) is equal to MAI. If $p(t) < 1/t$ then *MAI* has already culminated, if $p(t) > 1/t$ MAI has not yet culminated (Prodan, 1965, p. 434f.).

Hunt (1982, p. 16) motivates relative growth by an example of two plants that achieved the same absolute increment but had different initial sizes. In this example, he concluded that a measure of growth is needed, which takes this original difference in size into account. In a similar way, Murphy and Pommerening (2010) explain that modelling relative increment is an analysis where the influence of the growth variable is excluded. Wenk et al. (1990, p. 78) also state that relative growth is an expression of "growth energy" or "plant vigour" and Causton (1977, p. 197) asserts that relative growth rate is a measure of the efficiency of plant material to produce new material and that it is a very important physiological characteristic. Since RGR varies widely between species, Houghton et al. (2013) conclude that relative growth rate is a useful metric for separating species into functional groups. As such RGR has become a central parameter determining a species' growth strategy (Grime, 1977). The authors also provided a meta-analysis on the common finding that herbaceous plants have higher relative growth rates than woody plants.

We can continue the analogy to mechanics by defining *growth acceleration*, i.e. the rate of change of the rate of change, as the second derivative of the growth function $F(t)$ (Schnute, 1981; Shimojo et al., 2002).

$$y''(t) = f'(t) = \frac{d^2y}{dt^2} \tag{4}$$

Similar to mechanics, growth acceleration is the change in growth velocity or growth rate divided by time taken. The concept of *relative growth acceleration* can then be defined as in Eq. (5), see also Schnute (1981) and Zeide (1993).

$$z(t) = \frac{y''(t)}{y'(t)} = \frac{d^2y}{dt^2}\frac{1}{y'(t)} \tag{5}$$

Shimojo et al. (2002) could also show that the following relations hold linking relative growth acceleration, $z(t)$, relative growth rate (RGR), $f(t)/F(t)$, absolute growth rate (AGR), $f(t)$ and absolute growth, $F(t)$.

$$\frac{f(t)}{F(t)} = \frac{z(t)}{f(t)} = p(t) \tag{6}$$

However, according to our calculations Eq. (6) is only satisfied if $F(t)$ is an exponential function, see Appendix 2. In later work, Shimojo (2006) even went a step further and defined the concept of *growth jerk*, i.e., the derivative of growth acceleration with respect to time.

Growth velocity and growth acceleration are of theoretical importance and not measurable. In a practical research context, plants are measured at discrete points in time. In this context, Hunt (1982, p. 10f.; 1990, p. 8) distinguishes between *functional* and *classical* approaches of plant growth analysis drawing on previous work by Causton. In the analysis based on growth functions, time-series or any kind of repeated surveys provide data for curve fitting; characteristics like instantaneous growth rates are then calculated from the fitted functions and not directly from the observed data (Hunt, 1982, p. 15). In the classical approach, time-series data including a number of survey periods are analysed using *mean growth rates* (or *periodic increments* in forestry) as introduced in the next section. Differences in sample size between the two analysis approaches may apply but otherwise they are not mutually exclusive.

2.2. Absolute growth rate

As instantaneous growth rates cannot be measured in practice, the difference between growth characteristics of interest is usually studied at discrete points in time, $t_1, t_2, \ldots, t_n$, which, for example, are scheduled survey years. In this context, the period between two discrete points in time is denoted $\Delta t = t_k - t_{k-1}$ with $k = 2, \ldots, n$. For ease of notation in the remainder of this section we set $y(t_k) = y_k$ and $p(t_k) = p_k$ etc., and assume equidistant time periods. However, the notation can also be modified to accommodate unequal time periods.

Periodic increment or *mean absolute growth rate*, in the context of discrete growth data, is the difference in the value of a particular plant characteristic y at different times t_k and t_{k-1} divided by Δt. This can be written as

$$\bar{i}_k = \frac{y_k - y_{k-1}}{t_k - t_{k-1}} = \left(\frac{\Delta y}{\Delta t} \right)_k. \tag{7}$$

Since growth function F is differentiable, this difference quotient is proportional to derivative F'. Indeed, $\bar{i}_k = F'(s)$, where s denotes a point in time located somewhere between times t_k and t_{k-1}. The exact location of s is unknown, but as the difference in time, Δt, grows smaller, point s will be close to t_k and the continuity of F' implies that $F'(s)$ will be close to $F'(t_k)$. Thus considering a short time period, the mean absolute growth rate, $\bar{i}_k$, is approximately equal to the instantaneous growth rate $F'(t_k)$.

When the mean absolute growth rate is positive, this indicates that during the short time period Δt the plant size characteristic grows. When $\bar{i}_k = 0$, this is an indication that the plant size characteristic does not change during the short time period. Also, when $\bar{i}_k < 0$ the plant size characteristic appears to shrink or even decays in that period.

In the remainder of this paper, for ease of reading and understanding equations we consider absolute growth rate with reference to the time elapsed since the last sampling or measurement rather than mean absolute growth rate. Thus, absolute growth rate, i_k, simplifies to

$$i_k = y_k - y_{k-1}. \tag{8}$$

2.3. Relative growth rate

According to Blackman (1919), Fisher (1921), Whitehead and Myerscough (1962) and Hunt (1982, 1990) *periodic relative increment* or *mean relative growth rate*, $\bar{p}_k$, is the difference of the logarithms of y_k and y_{k-1} divided by Δt, see also Causton (1977, p. 213).

$$\bar{p}_k = \frac{\log y_k - \log y_{k-1}}{t_k - t_{k-1}} = \frac{\log(y_k / y_{k-1})}{\Delta t} \tag{9}$$

Fisher (1921) defines mean relative growth rate as amount of change per unit area of material per unit area of time. Blackman (1919) originally referred to Eq. (9) as "efficiency index" and "specific growth rate", see also Causton and Venus (1981, p. 37). From the last term we can see that Eq. (9) can be interpreted as the logarithm of the ratio of successive size measurements divided by the corresponding time interval. Mean growth rate is thought to reflect systematic variation in physiology, allocation and leaf construction (Houghton et al., 2013). $\bar{p}_k$ is the most common RGR characteristic used in the literature.

Fig. 2 gives a comparison between absolute growth rate (AGR) and relative growth rate (RGR) applied to the data from a mixed-species woodland in North Wales. This is a very common and traditional application of the concept of relative plant growth. The growth rates in this example are based on surveys in 2002 and 2007. Scots pine (*Pinus sylvestris* L.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) are dominant species that form the main forest

canopy, whilst rowan (*Sorbus aucuparia* L.) and silver birch (*Betula pendula* Roth.) are species of understorey regeneration. The non-native Scots pine and Sitka spruce trees were originally planted in 1931 on the site and the two native broadleaved species colonised naturally. A growth analysis is interesting here for anticipating the future species composition in this woodland.

Over- and under-storey species understandably show very different tree sizes, which suggest the use of RGR for better comparison. The two main-canopy species Scots pine and Sitka spruce have markedly higher absolute growth rates than the understorey species (Fig. 2, left). This confirms Causton's and Venus' (1981, p. 17) statement that absolute growth rate is often roughly proportional to plant size. Relative growth rate, however, gives a different impression and reveals that Sitka spruce has the highest mean relative growth rate of all species followed by rowan and silver birch. Scots pine – although a dominant main-canopy species – apparently has the lowest relative growth rate.

It is also interesting to note that the variation of species-specific growth rates is quite different for AGR and RGR. Growth rate variation is much more variable with RGR and more homogeneous for AGR.

Larocque and Marshall (1993) reviewed and investigated the relationship between RGR and competition in red pine (*Pinus resinosa* Ait.) stands in Canada. In this study, RGR decreased with increasing tree size before the onset of competition and when competition was not severe. Under severe competitive stress RGR increased with tree size. They concluded that small trees were more efficient than large trees at producing new biomass before the onset of competition. Competition reduced the efficiency of small trees relative to large trees.

Again, for ease of reading and understanding equations we consider growth rates only with reference to the time elapsed since the last sampling or measurement in the remainder of this section. Thus, relative growth rate, p_k, simplifies to

$$p_k = \log y_k - \log y_{k-1} = \log(y_k / y_{k-1}). \tag{10}$$

Independently of Blackman and Hunt, Wenk (1978) and other forestry authors defined relative growth rate more directly and intuitively as absolute growth rate divided by the plant size characteristic. Apparently this approach has a long tradition in forest science, going back to authors like Hartig, Koenig, Schneider, Pressler and Breymann in the 18th and 19th centuries (Prodan, 1965, p. 433). Since we consider discrete points in time, the plant size characteristic in the denominator can now refer to the end, y_k, or to the beginning, y_{k-1}, of the survey period leading to lower $(-)$ and upper $(+)$ bounds. Eq. (9) avoids this problem and relates to an unknown point in time between k and $k - 1$. This unknown point in time is near the centre between k and $k - 1$, as a comparison with Pressler's increment formula reveals (see Fig. 3). In forestry, Pressler (1865) simply assuming a linear increase of y suggested the formula

$$p_k^0 = 2 \frac{y_k - y_{k-1}}{y_k + y_{k-1}}, \tag{11}$$

thus dividing absolute growth rate by the mean of y_k and y_{k-1}, which was also proposed by Fisher (1921) without reference to Pressler (1865). Müller (1915) also mentioned the use of the geometric mean in the denominator and there are even more variants of calculating relative growth rates, however, all of them differ from p_k. Using upper and lower bounds leads to equations

$$p_k^+ = \frac{y_k - y_{k-1}}{y_{k-1}} \tag{12}$$

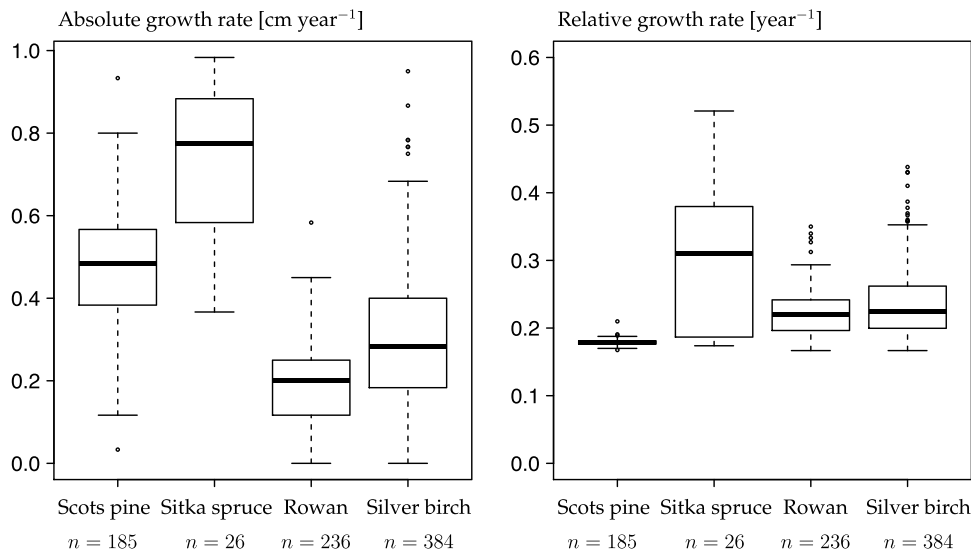and

$$p_k^- = \frac{y_k - y_{k-1}}{y_k} \tag{13}$$

Fig. 2. A comparison of absolute and relative growth rates of four species in a mixed-species woodland at Pen yr Allt Ganol in Gwydyr Forest (North Wales, UK).

Wenk et al. (1990, p. 78) argue for the use of Eq. (13), as y_{k-1} can take very small values near zero. Also, experimentally only past growth can be measured and the current size characteristic y_k is naturally always related to the end of that growth period. Other authors prefer Eq. (12) and in fact p_k, p_k^+ and p_k^- can be easily converted to one another according to Eq. (14).

$$p_k^+ = \frac{p_k^-}{1 - p_k^-}; \quad p_k^- = \frac{p_k^+}{1 + p_k^+}; \quad p_k^+ = e^{p_k} - 1; \quad p_k^- = 1 - \frac{1}{e^{p_k}} \quad (14)$$

Fig. 3 illustrates the relationships between p_k, p_k^0, p_k^+ and p_k^- using stem analysis data. For small values of relative growth rate all three definitions lead to almost the same results whilst increasingly larger deviations from p_k can be observed with increasing relative growth rate, whereby p_k^+ and p_k^- form the upper and lower bounds as expected. Since the underlying growth function F is increasing, $y_{k-1} < 0.5\,(y_k + y_{k-1}) < y_k$ implies $p_k^- < p_k < p_k^+$, which is confirmed in Fig. 3. Pressler's relative growth rate apparently is very similar to p_k, however, both characteristics are not exactly identical.
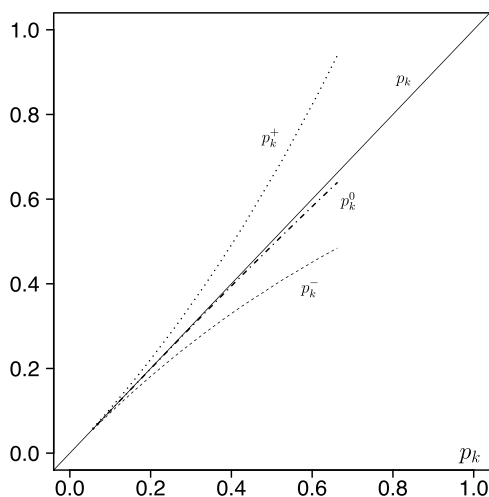

Fig. 3. A comparison of the relative growth rates p_k, p_k^0, p_k^+ and p_k^- using the annual stem analysis data of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) tree # 4000 from Cefn Du (plot 1), Clocaenog Forest (North Wales, UK).

Absolute growth rate can be calculated from relative growth rate as the product of plant characteristic and relative increment:

$$i_k = y_{k-1}p_k^+ = y_k p_k^- = y_{k-1}e^{p_k} - y_{k-1} \quad (15)$$

However, for projecting growth the concept of the *growth multiplier* or *growth coefficient* has proved useful (Wenk, 1972; Kangas, 1968, p. 50; Evans, 1972, p. 197; Hunt, 1982, p. 17). The idea of the growth multiplier is to calculate a current size characteristic from a past size characteristic in a multiplicative way:

$$y_k = y_{k-1}\frac{y_k}{y_{k-1}} = y_{k-1}M_k, \quad (16)$$

where, factor M_k is the growth multiplier or growth coefficient. The growth multiplier is a function of relative growth rate and defined as the ratio of a particular plant size characteristic at different times. The use of M_k leads to an integrated form of the relative growth rate (West et al., 1920; Wenk, 1978). Growth multipliers therefore offer an alternative to integrating functions of relative growth rate (Wenk, 1972). Eq. (16) also implies that a size characteristic in the past, y_{k-1}, can be calculated by dividing the current size characteristic, y_k, by the growth multiplier.

Circumstances where $M_k > 1$ indicate growth, the condition $M_k = 1$ occurs where there is no growth and with $M_k > 1$ the corresponding plant size characteristic shrinks or even decays.

Depending on how relative growth rate is defined, M_k can be expressed in one of the following ways:

$$M_k = p_k^+ + 1 = \frac{1}{1 - p_k^-} = e^{p_k} \quad (17)$$

Evans (1972, p. 197) and Hunt (1982, p. 17) refer to the growth multiplier as Backman's efficiency index, which is supposed "to represent the efficiency of the plant as a producer of new material, and to give a measure of the plant's economy in working". Obviously, growth multipliers as functions of relative growth rate offer another possibility of relating different approaches to quantifying relative growth to one another.

Average relative growth rates and average growth multipliers calculated from empirical time series data over a number of growth periods can be obtained by applying the geometric mean rather than the arithmetic mean (Wenk et al., 1990, p. 98ff.; Fahrmeier et al., 2011, p. 61ff.).

Interestingly Blackman (1919), entitling his paper "The compound interest law and plant growth", drew analogies to financial

investment projection, which are also obvious in Gadow (2005, p. 146), who used the well-known formula for *asset growth with compound interest* (see Clutter et al., 1983, p. 144ff.), also referred to as *constant relative growth*, for predicting the standing volume of forest stands. Using the notation of this paper we can write this formula as

$$y_k = y_{k-1}\left(1 + p_k^-\right)^c. \tag{18}$$

From Eq. (16) it follows immediately that $M_k = \left(1 + p_k^-\right)^c$. By taking the logarithm of this we obtain $c = \log(M_k)/\log\left(1 + p_k^-\right)$. From Eq. (17) follows $\log(M_k) = -\log\left(1 - p_k^-\right)$, finally resulting in $c = -\log\left(1 - p_k^-\right)/\log\left(1 + p_k^-\right)$. This highlights that the concept of relative growth is mathematically related to the financial concept of projecting investments based on compound interest rates and vice versa. This is not surprising, as growth is a universal, mathematical-statistical problem. Also Kangas (1968, p. 49f.), Prodan (1961, p. 337f.; 1965, p. 431ff.) drew analogies to financial investments. Incidentally, Eq. (12) corresponds to the simple interest rate.

Finally, in analogy to relative growth rate, *growth acceleration* can be calculated from empirical data in the following ways:

$$z_k^+ = \frac{\Delta p}{p_{k-1}^{\cdot\cdot}}; \quad z_k^- = \frac{\Delta p}{p_k^{\cdot\cdot}}; \quad z_k = \log p_k^{\cdot\cdot} - \log p_{k-1}^{\cdot\cdot}, \tag{19}$$

where, the upper index ".." can denote either "+", "−" or "".

2.4. Allometry

Allometry studies the statistical association between size and shape (Mosimann, 1970). As a biological concept, allometry is part of the field of relative growth (Gayon, 2000). In any organism, there are relationships between different size characteristics of an organism and also between one of these dimensional elements and the whole organism. According to Huxley (1932) and Teissier (1934) an allometric relationship between two plant size characteristics, say $x(t)$ and $y(t)$, can be expressed in the form.

$$\frac{dy}{dt}\frac{1}{y(t)} = \left(\frac{dx}{dt}\frac{1}{x(t)}\right)m(t). \tag{20}$$

This equation relates changes in $\log y(t)$ to changes in $\log x(t)$. Specifically, it states that $\log y(t)$ changes proportionally with $\log x(t)$ over short time periods, assuming that $m(t)$ is constant. The function $m(t)$ mediating the changes is often referred to as the allometric coefficient (or exponent). Allometric coefficients are key biological characteristics that describe the way in which resources are allocated to different parts of a plant (Gayon, 2000): an increase of $x(t)$ by 1% corresponds to an increase by $m(t)$ percent in $y(t)$. Allometric coefficients can be interpreted as *compounded growth rates*, i.e., as rates of change involving more than one plant size characteristic (Hunt, 1990, p. 15). The better known integrated representation of the allometric equation is

$$y(t) = bx(t)^{m(t)}, \tag{21}$$

where, b is a model parameter. Note that Eq. (21) is only correct if the allometric coefficient is constant for all times t. Empirical research has provided evidence that $m(t)$, however, is rarely constant. In that case the model parameter b turns into a complicated function $b(t)$. Gayon (2000) provides an extensive discussion of the biological meaning of model parameter b.

The condition $m(t) = 1$ indicates *isometric* growth, i.e., both tree characteristics change at the same rate and as a consequence the original properties between two size characteristics $x(t)$ and $y(t)$ remain unchanged. If $m(t) > 1$, there is a *positive* allometric relationship implying that $y(t)$ changes faster than $x(t)$, which leads to a change of proportions between $x(t)$ and $y(t)$. If $m(t) < 1$, there is a *negative* allometric relationship, i.e., $x(t)$ changes faster than $y(t)$.

Using the concept of relative growth rates, Wenk (1978) could show that in the case of discrete points in time the relative growth rates $p_{x,k}^{\cdot\cdot}$ and $p_{y,k}^{\cdot\cdot}$ of size characteristics x and y are related as

$$p_{x,k}^{\cdot\cdot} = 1 - \left(1 - p_{y,k}^{\cdot\cdot}\right)^{\frac{1}{m_k}}, \tag{22}$$

where, the upper index "." can denote either "+", "−" or "".

2.5. Functions of relative growth rate

In the analysis of functions, as previously mentioned, observed data are not directly analysed but used for model fitting. Summary characteristics are then calculated from the models. Mean absolute growth rate can for example be simply calculated from a growth function as

$$\frac{F(t) - F(t - \Delta t)}{\Delta t}. \tag{23}$$

In analogy, mean relative growth rate in an analysis using growth functions is given by the ratio

$$\frac{F(t) - F(t - \Delta t)}{F(t)\ \Delta t}. \tag{24}$$

Hunt (1982) has dedicated a whole book to this research strategy and explains that it is a branch of mathematical modelling. The rationale is that a mathematical expression or group of expressions behaves in some way like a real system and can then be referred to as a mathematical model of that system (Hunt, 1982, p. 47). In the same way, Wenk's research school as documented in his book (Wenk et al., 1990) modelled relative plant growth not only for predicting future yields from stands of trees, but also for interpreting the model parameters like statistical characteristics. This is considered as a model-based plant growth analysis.

Attempts to directly analyse growth observations often result in a scattered and distorted picture of reality. A mathematical function fitted to those observations may regain much of the clarity with which the reality is perceived by the experimenter (Hunt, 1982, p. 53). The fitted function can often be of more value to the experimenter than the data from which it was derived. Also functional methods give relative growth rates having smaller variances than those yielded by the classical method (Causton and Venus, 1981, p. 59). On the other hand, every mathematical model comes with underlying assumptions, which need to be verified when applying the model.

It is always good advice to use mechanistic or semi-mechanistic growth functions where possible. This is particularly important when temporal extrapolations are intended. Polynomials are for example generally a poor choice and lack theoretical foundation (Vanclay, 1994, p. 9f.). Growth functions with few model parameters that have a biological meaning and thus can be interpreted are also useful for making quick plausibility checks.

Hunt (1982), Wenk et al. (1990, p. 79), Zeide (1993) and Burkhart and Tomé (2012, p. 111ff.) give a number of plant growth functions and provide detailed discussions. They are often combinations of power functions and exponential functions (Zeide, 1989) and are special cases of a general form, which can be written as

$$F(t) = ae^{-bg(t)}\left\{1 + c_1 e^{-bh(t)}\right\}^{c_2} \text{ with } t \in [0, \infty) \text{ and } c_1 \neq 0,\ c_2 \in \mathbf{R}. \tag{25}$$

The individual growth functions are then determined by two auxiliary functions (g, h) and two model parameters (c_1, c_2) as specified in Table 1.

Table 1
Specification of how individual growth functions relate to the generic model proposed in Eq. (25).

Function name	$g(t)$	$h(t)$	c_1	c_2
Chapman-Richards	0	t	-1	c
Gompertz	e^{-ct}	–	–	0
Korf	t^{-c}	–	–	0
Logistic	0	t	c	-1
Monomolecular	0	t	$-c$	1
Weibull	0	t^c	-1	1

Table 2
Functions of relative growth rate and asymptotic relative growth rate based on Eq. (26).

Function name	Relative growth rate	Asymptotic relative growth rate
Chapman-Richards	$bc\left(1 - e^{-bt}\right)^{-1}$	bce^{-bt}
Gompertz	bce^{-ct}	bce^{-ct}
Korf	$bct^{-(1+c)}$	$bct^{-(1+c)}$
Logistic	$bc\left(c + e^{bt}\right)^{-1}$	bce^{-bt}
Monomolecular	$bc\left(e^{bt} - c\right)^{-1}$	bce^{-bt}
Weibull	$bct^{c-1}\left(e^{bt^c} - 1\right)^{-1}$	bct^{c-1}

The derivative of Eq. (25) and function of absolute growth rate is given by the expression

$$f(t) = -bF(t)g'(t) - bF(t)\frac{c_2 h'(t)}{1 + \frac{1}{c_1}e^{bh(t)}} \text{ with } t \in [0, \infty) . \quad (26)$$

If the non-negative function h is unbounded and increasing as $t \to \infty$, a condition satisfied by all growth functions discussed here except for the Weibull function, then the long-term behaviour of the relative growth rate is determined by auxiliary function g alone. This allows the definition of asymptotic functions of relative growth rate. The corresponding functions of relative growth rate and of asymptotic relative growth rate are given in Table 2.

The Chapman-Richards function is a very flexible and accurate growth function published by Richards (1959). It can be interpreted as a generalisation of Bertalanffy's (1957) growth function for animal growth and has frequently been used to model tree and tree population growth (Pienaar and Turnbull, 1973).

Gompertz (1825) originally proposed his function for describing age distribution in human populations. Only a century later, it was applied as a growth model by Winsor (1932). Interestingly, the corresponding function of relative growth rate is an elementary function of age. It has, therefore, also been referred to as function of exponential decay (Laird et al., 1965). The Gompertz function is often used in biological studies.

Korf proposed his growth function in 1939 and it has been rediscovered by Lundqvist (1957). The Korf function has been applied to the growth of various tree characteristics (Zeide, 1993, 1989) refers to this function as a power decline function because asymptotic relative growth can be presented as an elementary power function.

The logistic growth function (Verhulst, 1838), according to Causton (1977, p. 198) and Hunt (1982, p. 126) also known as autocatalytic function, has been a famous model in ecology. Unfortunately, it lacks both theoretical foundation and accuracy (Zeide, 1993), but still is often in use.

Originally developed in physical chemistry, the monomolecular growth function is also known as Mitscherlich function after a German agronomist who used it at the beginning of last century. Zeide (1993) also refers to an early use by Weber (1891). The monomolecular function is one of the simplest of asymptotic functions and has no inflection point; hence its biological plausibility is rather limited.
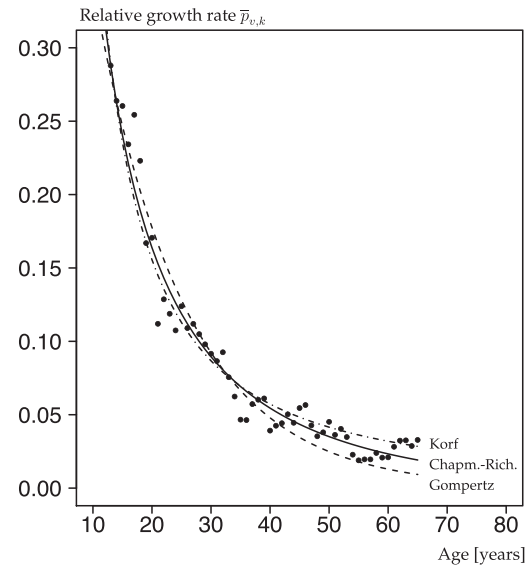

Fig. 4. The three best functions of Table 2 fitted to the mean relative volume growth rate, $\bar{p}_{v,k}$, of Sitka spruce tree # 486 in Gwydyr Forest (Pen yr Allt Ganol, North Wales, UK). For model statistics see Table 3.

Although originally intended to describe a probability distribution, the Weibull function has turned out to be a very reliable empirical model for tree growth (Zeide, 1993).

Similar to Zeide (1993) we have pointed out that all growth functions in Table 2 have a common element. It is interesting to note that the functions of relative growth rate share even more similarities than the growth functions. The functions of relative growth rate have also fewer model parameters than the growth functions and the functions of absolute growth. The relative growth rate function terms are also simpler and it is, therefore, possible to argue that using the concept of relative growth rate helps to standardise growth functions. The reduction of model parameters is another desirable property.

Fig. 4 and Table 3 give an impression of how the functions of relative growth rate can be fitted to observed relative tree volume data. Naturally stem diameter, biomass or leaf-area-index growth data can alternatively be used. Judging by the statistics in Table 3 the Chapman-Richards function is the best choice in this case. The fitted function can now be used to carry out plant growth analyses based on relative growth.

Whilst most growth projection models in forestry and ecology are based on AGR (Larocque and Marshall, 1993), the fitted function of relative growth can be inserted in Eq. (17) to obtain a growth multiplier, so that $y_{k+1} = y_k M_{k+1}$. The growth multiplier thus acts as a wrapper of any growth function. Depending on environmental factors and competition, the model parameters may even change over time for one individual or population and produce different relative growth rates. The relative growth rates of other characteristics of the same plant are estimated through allometric relationships and simultaneous regression techniques. Wenk et al. (1990) and Wenk (1994) show how population growth models can thus be based on

Table 3
The model parameters, *bias* and *RMSE* relating to the Chapman-Richards, the Gompertz and the Korf model of relative growth rate (Table 2) applied to the data of the Sitka spruce tree no. 486 in Gwydyr Forest (Pen yr Allt Ganol, North Wales, UK). See also Fig. 4.

Function name	b	c	Bias	RMSE
Chapman-Richards	-0.03479	4.73352	0.00018	0.01451
Gompertz	10.05581	0.06555	0.00341	0.01653
Korf	26.45393	0.44151	-0.00161	0.01634

the concept of relative growth. Pommerening and Muszta (2015) explored this further by demonstrating that individual plant and population models using RGR are based on similar principles. Also Dyer (1997, p. 102ff.) developed a basal area growth disaggregation model for loblolly pine (*Pinus taeda* L.) plantations in the southern US based on growth multipliers.

In this context, it is worth noting that the algebraic difference form of growth functions (see Burkhart and Tomé, 2012, p. 145ff.) as originally suggested by Bailey and Clutter (1974) is also a way of modelling growth multipliers. Eq. (27) for example shows the algebraic difference form of the Chapman-Richards growth function:

$$y(t) = y(t - \Delta t) \left[\frac{1 - e^{-bt}}{1 - e^{-b(t-\Delta t)}} \right]^c \tag{27}$$

In Eq. (27), the second term essentially constitutes the growth multiplier as defined in Eq. (16). The current value of y, $y(t)$, is calculated from the previous value at time $t - \Delta t$ (Wenk et al., 1990, p. 204f.). Any function of Table 1 can be expressed in the algebraic difference form. The advantage of this approach is that it is possible to use the original AGR versions of growth functions directly.

2.6. Sampling, growth rate combinations and size standardisations

The possibilities for applying growth rates and functions discussed in the previous sections to arbitrary growth characteristics to $y(t)$ are unlimited. The applications can range from dry weight, biomass to leaf area, stem volume, basal area and stem diameters. Often measurements are destructive, e.g., for biomass and dry weight, and such destructive measurements are then referred to as "harvests" in the plant science literature, see for example Evans (1972, p. 44f.). This often implies that for establishing growth rates, the measurements of different plants or the averages of several plants have to be used (Evans, 1972, p. 247).

If, however, many non-destructive measures are made on the same individuals, as this is common practice in long-term monitoring in forestry (longitudinal studies), then the error structure of the model fit must take this into account and mixed-effect models for repeated-measures data can be used (Paine et al., 2012; Philipson et al., 2012; Zhao et al., 2014).

Naturally, it is possible to study the growth of individual plants, of groups of plants and of whole plant populations. Evidently RGR is the result of complex processes determined by physiology, morphology and biomass (Shipley, 2006). This characteristic is also simultaneously affected by genetic, ontogenetic and environmental factors (Grime and Hunt, 1975). Therefore, much effort has been put into partitioning relative growth rates (e.g., Hunt, 1982; Hunt and Cornelissen, 1997; Shipley, 2006; Rees et al., 2010). An example of a widely quoted partitioning approach is

$$\text{RGR} = \text{NAR} \times \text{SLA} \times \text{LMR}, \tag{28}$$

where, NAR = net assimilation rate, SLA = specific leaf area and LMR = leaf mass ratio. In a meta-analysis, Shipley (2006) found that NAR generally was the best predictor of RGR, but that as light intensity decreased the importance of SLA increased on the expense of NAR. The relationship between LMR and RGR is apparently inconsistent (Houghton et al., 2013). There are many such interrelations and Hunt (1990, p. 83ff.) provides a good summary. In addition, Ingestad (1982) summarised studies proving that nutrient uptake rates are closely related to relative growth rates.

Combinations of growth rates are referred to as *compounded growth rates* by Hunt (1990, p. 15). They involve more than one plant characteristic, such as the whole plant's rate of dry weight

increase per unit of its leaf area. One of the characteristics may not be a plant characteristic, as in the rate of dry matter production per unit area of land or in the unit leaf rate (Hughes and Freeman, 1967).

As relative growth rate continuously decreases with increasing time and size, criticism has frequently been noted when, for example, comparisons between species with different initial sizes were carried out. Through self-shading and tissue aging, plants become increasingly inefficient as they get larger leading to systematic changes in physiology, morphology and allocation (Rees et al., 2010). This rationale is often put forward to explain the decline of RGR with size and is referred to as *ontogenetic drift* (see Evans, 1972, p. 16). The size dependency of RGR implies that mean RGR as defined in the literature and in this paper is, at least partly, an artefact of initial size and could potentially mask important relationships (South, 1995; Turnbull et al., 2008; Paul-Victor et al., 2010; Paine et al., 2012; Philipson et al., 2012). When comparing individuals at a given point in time, RGR cannot distinguish between individuals that grow slowly because they are large, and individuals that grow slowly because they are pursuing a slow growth strategy (Rose et al., 2009). Using methods of *size correction* or *size standardisation* Turnbull et al. (2008) could, for example, demonstrate that small-seeded species are not necessarily physiologically better adapted for rapid growth than large-seeded species. Since relative growth rate is already a standardised measure, discussions are still ongoing in which context size correction/standardisation is required. A common method of size standardisation is to fit a suitable growth curve to RGR data from multiple sampling (as shown in the next section) and then to calculate RGR for all species at a common reference size, see for example, Rees et al. (2010). This method essentially means replacing time-dependent RGR by size-dependent RGR. Already Larocque and Marshall (1993) and Dyer (1997) report relationships between RGR and tree size.

To account for the continuous accumulation of non-productive tissues in perennial plants, Brand et al. (1987) suggested the relative production rate, i.e. the logarithmic ratio of current AGR to the AGR of the previous year or period. A related measure was introduced in dendrochronological research by Nowacki and Abrams (1997) as the percentage or relative growth change.

3. Conclusions

This study has clearly shown that the various approaches to quantifying and modelling relative growth in plant science and beyond are all related. Using a rigid and consistent mathematical notation has facilitated the integration of all scattered methods in one theoretical body, ranging from absolute and relative growth rates to allometry and growth acceleration. This now provides a common basis for new methodological work and applications. The study of the concept of relative growth has also highlighted the similarity of growth and mechanical processes.

As part of this synthesis, the review has demonstrated the mathematical equivalence of relative growth rate and logarithmic absolute growth rate, which is particularly important for allometric relationships. We could also show that different definitions of RGR can easily be harmonised and how they relate.

Similar to the attempt by Zeide (1993) we have been able to standardise growth functions and to present the corresponding absolute and relative growth rate functions (Table 2). A comparison of the latter has revealed that the functions of relative growth rate are even more similar than the basic growth functions and that functions of relative growth rate are usually simpler and have fewer model parameters than functions of absolute growth rate. These findings suggest that modelling relative growth has substantially more advantages over absolute growth than just removing

the influence of size. This can be important for traditional as well as for comparatively new branches of plant science such as dendrochronology, where functions can help to reconstruct past plant growth patterns.

Combining models of relative growth and allometrics is a natural, alternative choice for modelling plant growth, as these two concepts are closely related. This was clearly in Huxley's (1932) mind when he entitled his book about allometry "Problems of relative growth". Following this tradition Wenk et al. (1990) and Wenk (1994) have shown how several characteristics of individual plants and of plant populations can simultaneously be modelled by a combination of relative growth function and allometric coefficients. Expanding on this, Pommerening and Muszta (2015) demonstrated how this tradition of the Tharandt school can easily be combined with that of the British school of plant growth analysis to create new powerful options for modelling relative growth rates.

Studying relative growth rates has found many applications in ecology. Schnute (1981), for example, used the concept for modelling the growth of fish. Bentil et al. (2007) used RGRs for modelling the growth of invasive species and Grime and Hunt (1975) for explaining the adaptivity of local flora. Larocque and Marshall (1993) studied competition effects in trees using relative growth rates. Interestingly, recent evidence has shown that RGR continuously dropping below a certain threshold is a good indicator of imminent death (Bigler and Bugmann, 2003; Gillner et al., 2013). These findings make the concept of relative growth even more interesting and suggest its use in diagnosing and modelling plant death processes. To this end more systematic research is needed to study the relative growth rates of plants at the brink of dying. Brand et al. (1987) therefore emphasize that growth analysis based on relative growth rates connects strictly mechanistic studies of plant physiology with strictly empirical studies of growth and yield.

Having reviewed the concept of relative growth it is obvious that its methods were more frequently used for growth analysis in general plant science whilst forestry put more emphasis on using them for modelling. This suggests an ideal synergy and more emphasis should in the future be placed on modelling and on identifying dependencies of relative growth across a wide range of different fields of plant science. Modelling relative growth is ideal for growth reconstruction as required in dendrochronology, climate change and forest decline research.

As growth is a fundamental phenomenon of life beyond the realms of plants and animals, we trust that the concept of relative growth continues to have a considerable potential in quantitative biological and ecological research and that this synthesis provides a common basis for interdisciplinary research activities.

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Appendices 1 and 2. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2015.10.015.

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