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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.

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.

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

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