# Relative Growth Rates: A Critique

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**SYNOPSIS**

Forest researchers frequently use mean relative growth rates to compare growth of seedlings that differ in initial size. Reasons for using the technique include: (1) to eliminate any size related growth differences, and (2) to determine which seedlings are inherently more "efficient." Although this technique is based on theory that tree growth occurs as a constant percentage of initial size (the compound interest law), researchers apply this technique even when the percentage increase changes with increasing size (the variable interest law). However, such use may lead to faulty conclusions. Several alternative methods of analysis have been proposed to overcome the problems inherent when comparing mean relative growth rates. One potential alternative is the incremental growth analysis method that changes the basis of comparison from trees of equal age to trees of equal size. This method involves plotting the absolute growth rate (e.g. current annual increment) as a function of tree size at the beginning of the growth interval.

**INTRODUCTION**

Analyzing the mean relative growth rate of seedlings is one method used to compare growth differences that arise from experimental treatments (Evans 1972; Ledig 1974; Causton and Venus 1981; Hunt 1982). This method of growth analysis is popular with many forest researchers and it is believed by some to be one of the most ecologically significant and useful indices of plant growth (Pearcy et al. 1989). The method has been used to examine tree growth as affected by differing levels of fertilisers (Madgwick 1971; van den Driessche 1982), weed control (Byrne and Wentworth 1988; Brand 1991; Harrington and Tappeiner 1991), shading (Kolb and Steiner 1990a), soil moisture (Fredericksen et al. 1993; Margolis and Brand 1990), flooding (Osonubi and Osundina 1987), carbon dioxide (Brown and Higginbotham 1986; Tolley and Strain 1984; Samuelson and Seiler 1993), sulfur dioxide (Jensen 1983) and ozone (Matyssek et al. 1992; Laurence et al. 1993). It is also used to compare differences due to genotype (Sweet and Wells 1974; Kolb and Steiner 1990b) and planting stock size (Britt et al. 1991; van den Driessche 1992; Haase and Rose 1993). This technique is particularly viewed as useful when comparing seedlings that differ in size (Sweet and Wareing 1966; Kramer and Kozlowski 1979; van den Driessche and van den Driessche 1991; Kozlowski et al. 1991). In fact, the main reason for examining relative growth rates is to eliminate growth differences that arise from initial size differences (Wareing 1966). Another reason to examine relative growth rates is to determine which seedlings are more efficient (Causton 1983; Brand 1991). Originally, the relative growth rate was termed the 'efficiency index of dry weight production' (Blackman 1919). Today, many still believe that relative growth rate is the most important index of productivity (Radosevich and Osteryoung 1987).

An assumption necessary for appropriate application of the relative growth rate procedure is that plant growth follows the compound interest law (West et al. 1920; Snedecor and Cochran 1971; Kramer and Kozlowski 1979; Hunt 1990). The analogy with financial investment was first developed by Blackman (1919). One definition of the compound interest law is: the amount of growth made in a unit of time is a constant percentage of the size of the plant at the beginning of the period and the constant percentage *does not change with size* (e.g. is independent of size). In contrast, a variable interest law can be defined as: the amount of growth made in a unit of time is a percentage of the size of the plant at the beginning of the period and this percentage changes as the plant increases in size (often the percentage declines as size increases). Rapidly growing trees (either during the first few months after germination or during the first few years after transplanting) often grow according to the variable interest law. Therefore, one should question if it is appropriate to compare mean relative growth rates when trees are growing according to the variable interest law. This note examines the expected results when applying this technique to three hypothetical seedlings. It also examines two alternative methods of growth analysis.

**RELATIVE GROWTH RATES**

The expression for instantaneous relative growth rate (IRGR) is:

$$\text{IRGR} = \frac{1}{W}\frac{dW}{dt} \tag{1}$$

This is equivalent to the increase in plant biomass (dW) per unit of plant biomass (W) per unit of time (dt). Although simple in concept, it is usually difficult to determine since it represents a value at an instant in time. However, a mean relative growth rate (MRGR) can be calculated by sampling plant size at two points in time. The equation for calculating the MRGR is written as:

$$\text{MRGR} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1} \tag{2}$$

where W1 and W2 are the dry biomass at the beginning (t1) and end (t2) of the sampling period, and ln is the natural logarithm. This is the most common formula used when comparing relative differences between treatments. In some studies, the comparison of MRGR values are made for only one time interval (Kolb and Steiner 1990b; Haase and Rose 1993; Fredericksen et al. 1993). Although Equation 2 can be used to calculate a MRGR for trees growing according to a variable interest law (Fisher 1921; Causton 1983), this does not mean that use of this formula will eliminate any size-related growth differences.

Although terminology and abbreviations for most plant growth analysis indices have been standardized (Hunt 1990), terminology of relative growth rates is sometimes confusing. Some use the same abbreviation (RGR) for both IRGR (Equation 1) and MRGR (Equation 2) even when using annual measurements. Other researchers (Sanders and Sheikh 1985; Matyssek et al. 1992; Laurence et al. 1993) use the following formula to determine RGR over a sampling interval of a week or more.

$$\text{Relative change} = \frac{1}{W_1}\frac{W_2 - W_1}{t_2 - t_1} \tag{3}$$

Multiplying Equation 3 by 100 gives the percentage increase over the sampling period. Equation 3 is analogous to a simple interest rate over the sampling interval while Equation 2 is analogous to a compound interest rate. If a researcher uses Equation 3 to calculate RGR, the values will be higher than the MRGR but the conclusions should be the same. When the equations are not provided, it can be difficult to know if the authors used Equation 2 or Equation 3 when calculating RGR. Some authors use Equation 3 to calculate an annual RGR value and then divide by 365 to obtain a daily RGR value. To add to the confusion, some now define RGR as a function of competition rather than initial size (MacDonald and Weetman 1993).

**EXAMPLE**

Three hypothetical seedlings will be used to illustrate the type of conclusions that can result from using the MRGR technique. All three seedlings grow according to the variable interest law. Seedlings A and B are growing according to the same growth equation:

$$W = 0.005 + 0.00462X^{1.66} \tag{4}$$

where W equals seedling green mass in grams and X is the number of weeks from germination. The third seedling (C) is growing according to a different growth pattern represented by the equation:

$$W = 0.001423 + 0.003577X \tag{5}$$

The three seeds are placed in the growth chamber at the same time. Seed A germinates one week after sowing, seed B germinates on week 3, and seed C germinates on week 4. The green mass of the seedlings are recorded at week five (t1) and again at week six (t2). The researcher wants to correct for the differences in seedling size at week five and wants to determine if the seedlings are growing at inherently different growth rates. In addition, the researcher wants to know which seedling is inherently most "efficient."

When comparing the MRGR values (Table 1), the researcher finds seedling B has a higher MRGR than seedling A and therefore concludes that the two seedlings are growing according to two different growth curves. It is also concluded that although the absolute growth rate of seedling C is much lower than that of seedling B, the main difference in growth rate is due to the initial difference in size (six weeks after sowing). Since both C and B seedlings have the same MRGR, the researcher concludes that both seedlings are growing according to the same inherent growth curve. Although seedling A has the greatest absolute growth rate, seedlings B and C are said to be more efficient. Likewise, it might be concluded that seedling C is not inherently less efficient than seedling B.

All of the above conclusions are wrong. It can be demonstrated from Equation 4 and Figure 1 that seedlings A and B are growing according to the same growth curve. The only difference between the two seedlings is time of germination. Seedling C is growing on a different curve (Equation 5) and, overall, is much less efficient that either seedling A or B. This example illustrates the potential for incorrect conclusions when (1) the relative growth rate technique is applied to seedlings that are growing according to the variable interest law and (2) when the relative growth rates are compared at just one time interval. In this regard, Hunt (1990) concluded that the "efficiency index" is perhaps best reserved for use in the case of populations of unicellular organisms that are reproducing in an unconstrained environment (i.e. where the interest rate is constant).

In the above example (as in many experiments), the researcher does not know the shape of the growth curve and therefore does not know if the seedlings are growing according to the compound interest law. However, it is often the case that seedlings grow according to the variable interest law. Most trees during their first year of growth show an ontogenetic drift in MRGR as their size increases. In fact, many organisms exhibit a declining MRGR over time (Medawar 1941; Causton 1983). In such cases, neither the IRGR nor the MRGR are independent of size. Only in a few special cases will non-transplanted seedlings grow at a constant interest rate. In most of these cases, seedlings have been fertilised at an exponentially increasing rate (Waring et al. 1985; Ingestad and Lund 1986).

## MEAN RELATIVE PRODUCTION RATE

Few researchers have attempted to develop better methods of growth analysis probably because Ledig (1974) stated that "there is no unquestionably better" basis for comparison than MRGR. However, Brand and others (1987) realized that MRGR can become overwhelmingly correlated with tree size, even during the first 5 years of growth. To avoid this problem, they proposed the use of the mean relative production rate (MRPR). Unlike the MRGR, the MRPR is said to be independent of size because accumulated past production is ignored (Brand et al. 1987; Kozlowski et al. 1991). The equation for the MRPR is:

$$MRPR = \frac{\ln (W2\text{-}W1 - \ln (W1\text{-}W0)}{t2 - t1} \qquad (6)$$

This method removes the influence of accumulated biomass and quantifies the growth efficiency of the tree from one time interval to the next. To determine the MRPR, an additional sampling time at week 4 is required. Since three data points are used, the researcher can determine if the absolute growth rate is increasing (a positive MRPR), linear (MRPR = 0), or declining (a negative MRPR). For week 5, the MRPR for the three tree seedlings are 0,17, 0,30, and 0,00 for seedlings A, B and C, respectively.

With regard to comparing seedling B with seedling C, the conclusions from comparing MRPR values are more realistic. Seedling C has a MRPR equal to zero suggesting linear growth over the two week time interval, and it would be correct to conclude that seedling C is less efficient than either seedling A or B. In this respect at least, the MRPR is an improvement.

However, the MRPR for seedling B is still greater than seedling A and therefore the researcher would again conclude that: (1) seedlings A and B are growing according to inherently different growth curves and (2) the growth efficiency of seedling B is greater than seedling A. Since the only difference in the growth of the two seedlings is time of germination, both conclusions are again wrong. When growth is according to the variable interest law, the MRPR is not independent of seedling size (except in the special case of linear growth).

## ALTERNATIVES

In suggesting an alternative, one should consider carefully the primary reason for using mean relative growth rates. If the reason is to determine if the growth curves are basically the same, then procedures need to be followed that will allow the researcher to approximate the form of the growth curves involved. This will necessitate taking numerous samples over time (as opposed to sampling at just two or three points in time). With ten or more points per curve, the researcher should be able to plot the relationship of tree biomass with time and should be able to visually distinguish large differences in growth curves. For the above example, ten weekly measurements would have enabled the researcher to produce Figure 1. A visual assessment of these curves would have easily demonstrated that seedling B is not growing according to the same growth curve as seedling C.

However, deciding if seedlings A and B are growing according to the same growth curve is not easily answered by simply a visual assessment. As the seedlings get larger, the absolute difference between them increases. Are these curves different or basically the same? Plotting the MRGR over time produces two curves (Figure 2A). After germination, the MRGR values are not the same for any time interval. This comparison still suggests an inherent difference in growth curves. The same conclusion is made by plotting the percentage increase for each seedling (Figure 2B).

Plotting the MRPR over time is provided in Figure 2C. Again, the values for the two seedlings are initially different but the difference decreases as the seedlings get larger. Since the MRPR curves are not the same, it would again be concluded that the seedlings are inherently dissimilar in their growth patterns.

Hunt (1982; p. 40) briefly mentioned that to overcome the disadvantage of ontogenetic drift, it may sometimes be useful to plot derived quantities against another index of development. For example, MRGR could be plotted against the total dry biomass. This approach was used by Britt and others (1991) to conclude that seedlings of different initial sizes were growing according to inherently similar curves. In comparison, when the MRGR values were plotted against chronological age, the conclusion was that the MRGR of small-diameter seedlings was greater than that for the large-diameter seedlings.

## INCREMENTAL GROWTH APPROACH

A simpler method of analysis involves analyzing the absolute growth rate (e.g. current weekly increment) as a function of plant size. Although this relationship has been described as a "distribution modifying function" (Cannell et al. 1984; Westoby 1982), some doubt exists on the ability of the function to modify size distributions under field conditions (South and Mason 1991). Therefore, the term "incremental growth" will be used in this note when examining the relationship between absolute growth rate and seedling size.

The incremental growth approach changes the basis of comparison from chronological time to that of equal size. This involves plotting the data with size (W i) on the X-axis and current weekly increment (W i+1 - W i) on the Y-axis. This technique was applied to seedlings A and B and is illustrated in Figure 2D. It is apparent from this graph that seedlings A and B are indeed growing according to the same inherent growth curve. If a more formal method of testing differences is desired, a general regression significance test can be used to compare the parameter estimates for the two growth curves (Draper and Smith 1981).

It is not suggested that analyzing growth with this method will solve all size related problems. It is only suggested that this method is an improvement over the MRGR technique when attempting to separate treatment induced differences from size induced differences. This approach has been successfully used to examine the growth of *Pinus taeda* L. seedlings over a 30-year period (South et al. 1988). The technique was used to conclude that two seedling grades were growing according to the same inherent growth curve. In contrast, if the MRGR method was applied, it could be concluded that the smaller stock size was more efficient than the larger stock size over the entire 30 year period. The incremental growth technique has also been used to compare growth responses due to mycorrhizal inoculation. By examining absolute growth, it was concluded that the growth response from mycorrhizal inoculation lasts for five years (Marx et al. 1988). However, the incremental growth technique was used to conclude that the growth response at age five was due to the initial difference in growth (Mexal and South 1991). Auchmoody (1985) used a similar approach to examine the growth response from fertilization. Even though the technique is simple and relatively easy to use, its use has not been widely adopted. Currently, the MRGR technique is a more popular method of comparing treatments.

## CONCLUSIONS

It is not universally understood that the MRGR method of growth analysis does not eliminate size-related differences for seedlings that are growing according to the variable interest law. Since an ontogenetic drift in MRGR occurs in most tree seedlings, most tree seedlings grow according to the variable interest law. When this occurs, faulty conclusions may be made when using the MRGR method, especially when comparing values for a single time interval. Using the MRGR method as an "efficiency index" should be reserved only in cases where growth is according to the compound interest law.

Hardwick (1984) warns that "there is the ever-present possibility that a method of analysis, because it obscures understanding, or diverts attention or resources from more profitable areas, will prove to have a negative utility." The general belief that a seedling with a higher MRGR is inherently more efficient than one with a lower MRGR has obscured understanding and has caused some confusion. In addition, the general acceptance of the MRGR technique as an appropriate method to remove size-related growth differences has likely diverted attention away from the search for better methods of growth analysis. IGA is one alternative approach and there are other suitable methods as well. Regardless of the method used, the basic relationship of tree biomass with time should be graphed with the objective of reporting the general form of the growth curve in question.

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Table 1. Comparisons of seedling green biomass, mean relative growth rates (from Equation 2) and relative change (from Equation 3) for three hypothetical seedlings.

| Seedling | Biomass at week 5 (g) | Biomass at week 6 (g) | MRGR (per week) | Relative change |
|---|---|---|---|---|
| A | 0.051138 | 0.071824 | 0.34 | 0.40 |
| B | 0.019599 | 0.033619 | 0.54 | 0.72 |
| C | 0.005000 | 0.008577 | 0.54 | 0.72 |

Figure 1. Growth curves for three hypothetical seedlings. Seeds were sown at time = 0 and seedling biomass was recorded at weeks 5 and 6.

Figure 2. Growth curves for two seedlings that germinated two weeks apart but are growing according to the same equation: $y = 0.005 + 0.00426X^{1.66}$ where X= weeks after germination. Mean relative growth rates (A), relative change per week (B) and mean relative production rates (C) are plotted against time. The current weekly increment (D) is plotted against biomass at the beginning of each time interval.