TESTING THE HYPOTHESIS THAT MEAN RELATIVE GROWTH RATES ELIMINATE SIZE-RELATED GROWTH DIFFERENCES IN TREE SEEDLINGS

DAVID B. SOUTH

Forest Regeneration Center, School of Forestry and Alabama Agricultural Experiment Station,
Auburn University, Alabama 36849-5418, United States

(Received for publication 31 March 1992; revision 10 September 1992)

ABSTRACT

Various hypothetical growth curves were used to evaluate the suitability of using mean relative growth rate ($\overline{\text{RGR}}$) to compare growth when tree seedlings differ in initial size. Two seedlings were said to be growing according to the same basic growth curve if the only difference between the two growth curves was due to time (i.e., the larger seedling was always 2 weeks ahead of the smaller seedling). The $\overline{\text{RGR}}$ technique eliminated such size-related growth differences when growth exhibited an exponential pattern: $y = k + e^{b+ct}$ (where $k = 0$, t = time, and b and c are constants). The $\overline{\text{RGR}}$ technique did not eliminate size-related growth differences under conditions where k was not equal to zero or when the growth curve was not exponential. Various examples are given to show that $\overline{\text{RGR}}$ usually declines as seedling size increases during the first 5 months after germination. Where the $\overline{\text{RGR}}$ value is a function of size, the $\overline{\text{RGR}}$ method of analysis is not suitable for eliminating growth differences related to seedling size.

Keywords: growth analysis; relative growth rate; growth curves; seedling size.

INTRODUCTION

Researchers in forestry often use mathematical models to help provide insight into the biological principles behind empirical studies. When a new model of tree growth is proposed, it should be thoroughly tested before being widely accepted as useful. It is important to fully understand the underlying assumptions necessary for correct use of the model. Understanding the assumptions is especially helpful when mathematical equations are used to test the validity of the model. One hypothetical growth equation may indicate the model is valid and useful but, in order to be universally applicable, the model must withstand testing by numerous examples. A model which is correct in only a few specialised cases will have limited utility.

One method used to analyse tree growth is the comparison of mean relative growth rates ($\overline{\text{RGR}}$) (Evans 1972; Hunt 1982). Although the technique was proposed in the early part of this century (Blackman 1919), it was several decades before this method was used to analyse growth of tree seedlings (Rutter 1957). The popularity of this technique in forestry grew after a meeting of tree physiologists in Edinburgh, Scotland. At this meeting, Wareing (1966) stated that "mean relative growth rates eliminated the differences in growth rates due to differences in tree size". His statement was supported by a hypothetical example (Sweet & Wareing 1966) in which $\overline{RGR}$ declined with time but the relative size difference between two seedlings remained the same (proportional growth*). Later, Sweet & Wells (1974) used another hypothetical example of two seedlings that exhibited a "constant" $\overline{RGR}$ for a 3-year period. However, in both studies (Sweet & Wareing 1966; Sweet & Wells 1974) the experimental data did not support the hypothetical examples. Thus far, the only hypothetical cases used to justify the use of $\overline{RGR}$ have involved either proportional growth or exponential growth†. The $\overline{RGR}$ method has not been tested for other types of growth curves.

The $\overline{RGR}$ technique is often viewed as useful in comparing the growth of seedlings of different sizes (Causton & Venus 1981; Brand 1991; van den Driessche & van den Driessche 1991). As a result, this technique is used by researchers when initial size differences exist owing to species (Sweet & Wareing 1968a; Kolb & Steiner 1990a), genotypes (Sweet & Wareing 1968b; Kolb & Steiner 1990b), stock types (van den Driessche 1992), mycorrhizal inoculations (Mexal 1980), and fertiliser treatment (van den Driessche 1982). Regarding plant growth analysis, Causton (1983) has said we need concern ourselves no longer with absolute growth rates. Therefore, some papers have published $\overline{RGR}$ values without reporting absolute growth rates (Kolb & Steiner 1990b; Margolis & Brand 1990).

Although the $\overline{RGR}$ technique is applied regardless of the shape of the growth curve, few researchers understand the outcome when growth is non-exponential. This paper examines the expected results of applying the $\overline{RGR}$ technique when using various types of growth curves. These curves were used to test the hypothesis that the use of $\overline{RGR}$ eliminates the size-related growth differences.

THEORY

The Relative Growth Rate (RGR) of a plant at an instant in time (t) is defined as "the increase of plant material per unit of material present per unit of time". The equation is written as:

$$RGR = \frac{1}{W} \frac{dw}{dt} = \frac{d}{dt} (\ln W) \qquad (1)$$

where ln is the natural logarithm and W is a measure of the plant material present. The total dry weight of the seedling is often used but other measures of W include above-ground weight (Britt *et al.* 1991), fresh weight (Sweet & Wareing 1968a; Ingestad & Lund 1986),

---

* The term "proportional growth" as used in this paper is defined as existing when two trees that differ in size have equivalent mean relative growth rates for any given time interval.

† The definition of exponential growth is usually restricted to population growth of animals or unicellular organisms (Collocott & Dobson 1974; Martin 1977; Parker 1989). Most dictionaries do not define exponential growth in terms of the growth of an individual organism. However, since tree seedlings grown under conditions of increasing fertiliser can exhibit exponential growth for a short period of time, the term "exponential growth" as used in this paper is defined as the growth of an individual plant that can be modelled with a function that includes the value "e" raised to some exponent and the function will predict the final weight to within 10% of the measured weight.

diameter (Perry 1985), basal area (Harrington & Tappeiner 1991), height (Sweet & Wells 1974; Roberts & Wareing 1975; Burdon & Sweet 1976; van den Driessche 1982; Cannell *et al.* 1984), stem volume (Byrne & Wentworth 1988; Thomas & Weiner 1989), and canopy volume (Shainsky & Radosevich 1986).

Since it is not practical to make a continuous record of the changes of W with time, it is customary to make measurements at a number of isolated times and then calculate the RGR over the period between two measurements.

The $\overline{\text{RGR}}$ over a period of t_1 to t_2 is given in Equation 2.

$$\overline{RGR} = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} \frac{1}{W} \frac{dW}{dt}\, dt \qquad (2)$$

Integration of Equation 2 yields the following.

$$\overline{RGR} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1} \qquad (3)$$

Although this formula can be used to correctly calculate a $\overline{\text{RGR}}$ even for non-exponential growth (Fisher 1921; Causton 1983), it does not follow that use of Formula 3 will eliminate size-related growth differences when growth does not follow a constant exponential pattern. The failure to appreciate this distinction has caused many researchers to misuse this technique to eliminate size-related growth differences when growth is not exponential.

METHODS

When working with actual data, determining the portion of growth that is purely size-related is not an easy task. This is because under natural conditions, growth is a function of size as well as differences in temperature, nutrient uptake, moisture availability, photoperiod, light intensity, and genetics. It therefore is much easier to illustrate the theory behind a technique by using hypothetical examples which do not confound size-related growth differences with growth differences due to genetics or a changing environment. Therefore, a series of hypothetical growth curves were selected to test whether the $\overline{\text{RGR}}$ method will remove growth differences that are related to size. The growth curves examined involved exponential, curvilinear, sigmoid, and linear models.

Size-related growth differences can be modelled either with a "proportional growth" model or with a "time gain" model. The "proportional growth" model (used by Sweet & Waring 1966) was rejected as an appropriate way to model size-related growth. If the only difference between two plants is in initial size, then a biological reason for use of proportional growth would be difficult to explain. For example, why would two genetically identical clones of different initial sizes grow according to two different growth curves in a competition-free growth chamber environment? When comparing the growth rate at a given weight (e.g., 1 g), chronological age would be the only variable to explain why the smaller clone would grow proportionally less. In the absence of exponential growth, there is a lack of dry weight data to support the existence of proportional growth in young seedlings.

A "time gain" model was selected since it appears to be the most biologically appropriate way to model growth differences due to initial size. For each growth curve examined, size-related differences were modelled by determining the initial plant weight that would be required to be equivalent to a 2-week gain in growth. Therefore, expressions of the form W=f(t) and W=f(t+2) were chosen where W is the plant weight and t is the number of weeks from germination. Two growth curves were considered to be the "same basic growth curve" if they exactly overlapped when the curve of the small seedling was shifted along the x-axis to the left. If they did not overlap after the shift, then the two growth curves were said to be different.

The null hypothesis (H_0) in this study can be stated: seedling size does not affect $\overline{RGR}$ when seedlings are growing according to the same growth curve. The null hypothesis was accepted where there were no size-related differences in $\overline{RGR}$ for all weekly time intervals examined. The null hypothesis was rejected when differences in $\overline{RGR}$ were observed.

In addition to examining the effectiveness of the $\overline{RGR}$ technique in eliminating size-related differences with hypothetical data, studies involving real data were summarised. $\overline{RGR}$ values were examined to determine if exponential growth is typically observed during the first 5 months after seed germination.

RESULTS

Exponential Model

Although there can be several types of exponential growth curves, the type used in this study was of the following form:

$$W = k + e^{(b+ct)} \qquad (4)$$

where W equals seedling weight in grams; seed weight is equal to $k + e^b$, and c is a constant; and t is the number of weeks from germination. The c term equals the $\overline{RGR}$ only when k equals zero. When $k = 0$, $b = -3.7886$, and $c = 0.31572$, the equation fits the hypothetical data provided by van den Driessche & van den Driessche (1991). The initial difference between the two plants at germination is 0.0199 g (Table 1 Equation 4A). However, the difference in size after 20 weeks is increased to 11.0 g (Fig. 1a). Use of this exponential curve does not allow us to reject the null hypothesis because the two plants have the same $\overline{RGR}$ for all time intervals (Fig. 1b).

Regardless of either the size of the organism, or the time interval examined, the $\overline{RGR}$ of the small seedling always equals the $\overline{RGR}$ of the large seedling. A mathematical proof of this equality follows:

$$\textit{large plant } \overline{RGR} = \frac{\ln e^{\,b+c(t_2+2)} - \ln e^{\,b+c(t_1+2)}}{t_2 - t_1} = c$$

$$\textit{small plant } \overline{RGR} = \frac{\ln e^{\,b+ct_2} - \ln e^{\,b+ct_1}}{t_2 - t_1} = c$$

The constant k in Equation 4 is useful when e^b does not accurately reflect the initial seed weight. Without k, some exponential models may produce a high r^2 but over-estimate or under-estimate seed weight. The effect of k on the pattern of $\overline{RGR}$ was examined with Equation 4B (Table 1). In this example, $k = -0.02$ (i.e., 0.02 g is subtracted from each of the weights in the previous example). Again, at germination there is only a 0.0199-g difference

TABLE 1–Equation parameters and predicted seedling weight at various times after germination.

Growth curve	Equation designation	Equation parameters				Seedling size	Weeks after germination—plant weight (g)				
		k	a	b	c		0	2	4	12	20
Exponential	4A	0.0	–	–3.7886	0.31572	small	0.0226	0.0425	0.0800	1.0000	12.5000
						large	0.0425	0.0800	0.1504	1.8803	23.5056
	4B	–0.02	–	–3.7886	0.31572	small	0.0026	0.0225	0.0600	0.9800	12.4800
						large	0.0225	0.0600	0.1304	1.8603	23.4856
Curvilinear	5A	0.005	1.66	0.00462	–	small	0.0050	0.0196	0.0511	0.2908	0.6723
						large	0.0196	0.0511	0.0954	0.3741	0.7867
Sigmoid	6A	0	0.69	1000	12	small	0.0119	0.0475	0.1866	9.5729	11.9878
						large	0.0475	0.1866	0.7091	11.2804	11.9969
	6B	0.02	0.69	1000	12	small	0.0319	0.0675	0.2066	9.5929	12.0078
						large	0.0675	0.2066	0.7291	11.3004	12.0169
Linear	7A	1	0.2	0.6	–	small	0.2	1.4	2.6	7.4	12.2
						large	1.4	2.6	3.8	8.6	13.4
	7B	1	0.1	0.1	–	small	0.1	0.3	0.5	1.3	2.1
	7C	9	0.1	0.1	–	large	0.9	2.7	4.5	11.7	18.9

Note: Exponential = $k + e^{(b + ct)}$
Curvilinear = $k + bt^{a}$
Sigmoid = $k + c(1 + be^{(-at)})^{-1}$
Linear = $k\,(a + bt)$

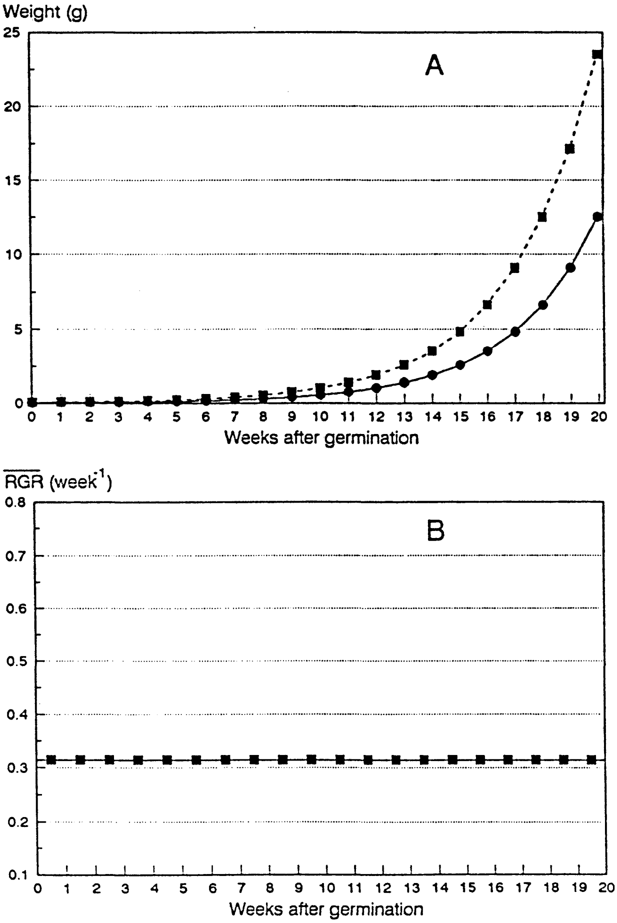

FIG. 1–Growth curves (A) and mean relative growth rates (B) for two seedlings that are growing according to the following exponential equation: $Y = 0 + e^{(-3.7886 + 0.31572\, t)}$

For the larger seedling (■) t = 2 + weeks after germination.

For the smaller seedling (●) t = weeks after germination.

in weight and after 20 weeks the difference is 11 g (Fig. 2a). In this example, the $\overline{\mathrm{RGR}}$ values decline as the seedling increases in size (Fig. 2b). Since the $\overline{\mathrm{RGR}}$ varies with tree size, c in Equation 4 is no longer equal to the $\overline{\mathrm{RGR}}$. Initially, the difference in $\overline{\mathrm{RGR}}$ is rather large, but at the end the values are almost the same (difference was at the fourth decimal place). Since the $\overline{\mathrm{RGR}}$ values for the two seedlings are not the same, the null hypothesis is rejected.

As long as k does not equal zero, the $\overline{\mathrm{RGR}}$ of the large seedling will always be different from the small seedling. Where k is less than zero (but greater than $-e^{b}$), the large seedling will always have a smaller $\overline{\mathrm{RGR}}$ than the small seedling:

$$\frac{\ln\left(k + e^{\,b+c(t_2+2)}\right) - \ln\left(k + e^{\,b+c(t_1+2)}\right)}{t_2 - t_1} < \frac{\ln\left(k + e^{\,b+ct_2}\right) - \ln\left(k + e^{\,b+ct_1}\right)}{t_2 - t_1}$$

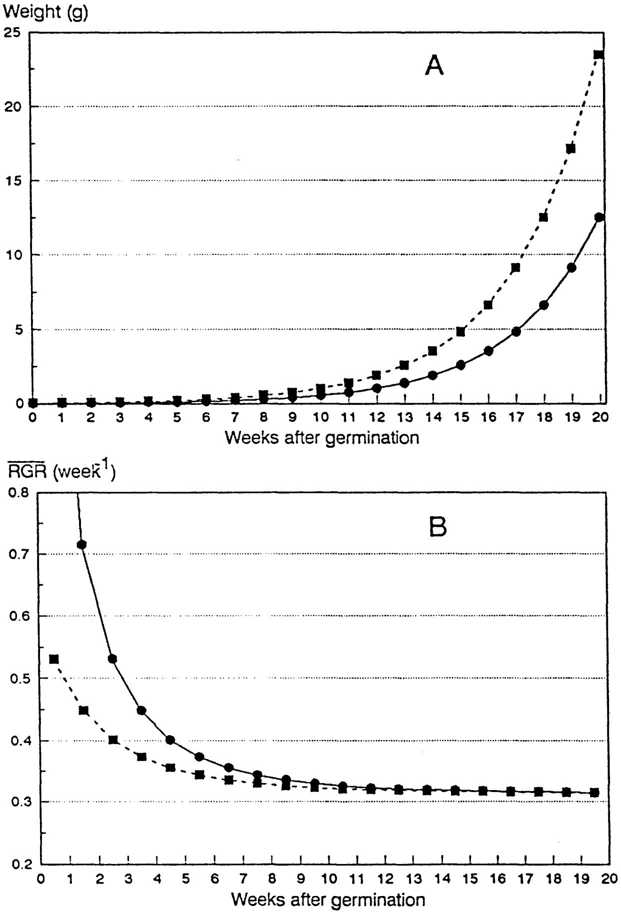

FIG. 2–Growth curves (A) and mean relative growth rates (B) for two seedlings that are growing according to the following exponential equation:
$Y = -0.02 + e^{(-3.7886 + 0.31572\,t)}$
For the larger seedling (■) t = 2 + weeks after germination.
For the smaller seedling (●) t = weeks after germination.

Even though the $\overline{RGR}$ of both seedlings will approach c when t is large, the $\overline{RGR}$ for the larger seedling will still be marginally smaller. However, when k is greater than zero the large seedling will always have a larger $\overline{RGR}$ than the small seedling.

Curvilinear Model

The following curve was selected to test the null hypothesis.

$$W = k + bt^a \tag{5}$$

When k = 0.005, a = 1.66, and b = 0.00462, this curve is similar to the data for *Picea mariana* (Mill.) B.S.P. seedlings grown in containers (Timmer 1991). Initially, there is less than a 15-mg difference in seedling weight at the beginning of the 20-week period (Table 1 Equation 5A). The two seedlings grow according to the same growth curve and after 20 weeks a 0.114-g difference in weight is observed (Fig. 3a). However, despite the fact that the seedlings are growing on the same growth curve, there are differences in the $\overline{\text{RGR}}$ (Fig. 3b). The initial increase in $\overline{\text{RGR}}$ for the small seedling occurs because k is positive. For this example, one might consider k to be the seed weight since when t = 0, there must be some weight present. However, even if k was equal to zero, the two seedlings would not have the same $\overline{\text{RGR}}$ and the null-hypothesis would still be rejected.

When k = 0 the large seedling will always have a smaller $\overline{\text{RGR}}$ than the small seedling:

$$\frac{\ln(b(t_2+2)^a) - \ln(b(t_1+2)^a)}{t_2 - t_1} < \frac{\ln(bt_2^a) - \ln(bt_1^a)}{t_2 - t_1}$$

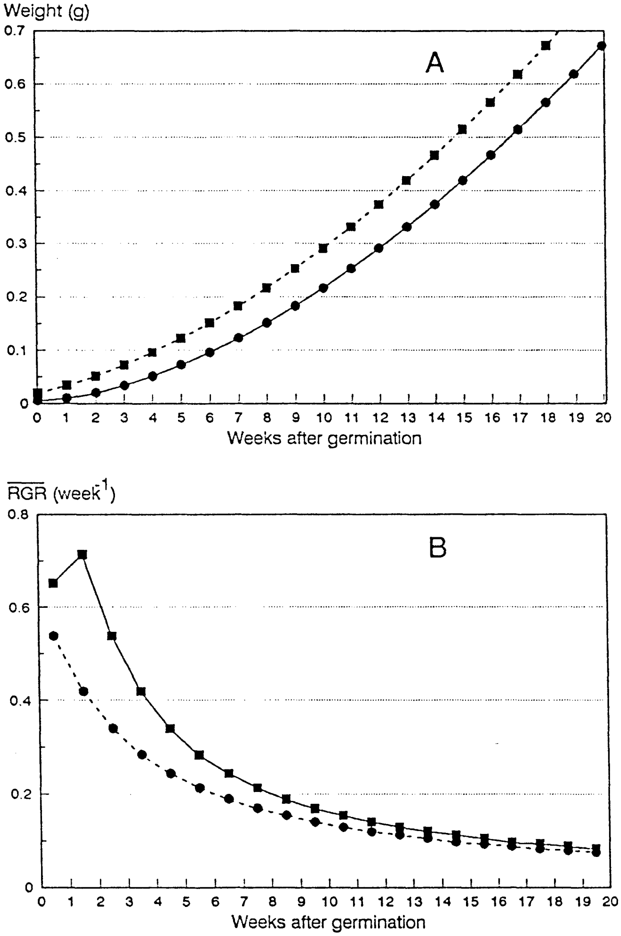

FIG. 3–Growth curves (A) and mean relative growth rates (B) for two seedlings that are growing according to the following quadratic equation: $Y = 0.005 + 0.00426t^{(1.66)}$

For the larger seedling (■) t = 2 + weeks after germination.

For the smaller seedling (●) t = weeks after germination.

Sigmoid Model

A logistic function of the type used by Ledig & Perry (1969) is provided as an example of a symmetric sigmoid curve.

$$W = k + c(1 + be^{-at})^{-1} \qquad (6)$$

The difference in initial seed weight in this example is less than 0.036 g (Table 1 Equation 6A). Since the upper limit (c) is equal to 12.0 g when k = 0, the difference in weight at the tenth week is greater than at the end of 20 weeks (Fig. 4a). The $\overline{\text{RGR}}$ of the two curves is about the same at the beginning and end, but during the linear phase of growth, the smaller seedling exhibits a higher $\overline{\text{RGR}}$ (Fig. 4b). This growth curve also rejects the null hypothesis. In this example, the large seedling will always have a smaller $\overline{\text{RGR}}$ than the small seedling:

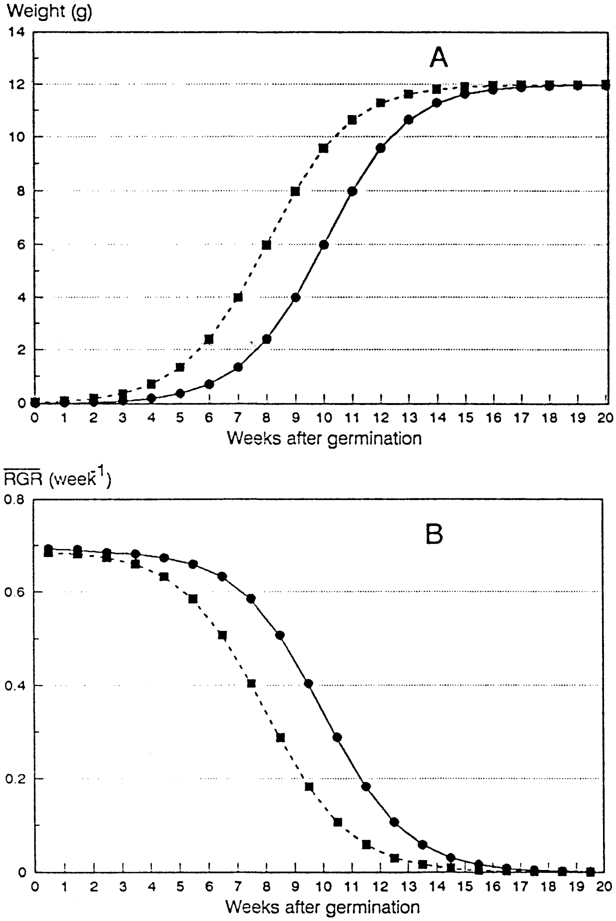

FIG. 4—Growth curves (A) and mean relative growth rates (B) for two seedlings that are growing according to the following sigmoidal equation:

$Y = 0 + 12(1 + 1000e^{(-0.69t)})^{-1}$

For the larger seedling (■) t = 2 + weeks after germination.

For the smaller seedling (●) t = weeks after germination.

$$\frac{\ln(c(1+be^{-a(t_2+2)})^{-1} - \ln(c(1+be^{-a(t_1+2)})^{-1}}{t_2-t_1} < \frac{\ln(c(1+be^{-at_2})^{-1} - \ln(c(1+be^{-at_1})^{-1}}{t_2-t_1}$$

To demonstrate the effect that a small difference in initial seed weight can have on the $\overline{\text{RGR}}$ curve, another sigmoid curve with k = 0.02 g was constructed (Table 1 Equation 6B). The difference in the growth curves (Fig. 4a *v*. Fig. 5a) appears imperceptible, but the small difference in seed weight during the early phases of growth results in a substantial difference in $\overline{\text{RGR}}$ (Fig. 5b). The $\overline{\text{RGR}}$ values are now different during the early as well as middle stages of growth. Soon after germination, the $\overline{\text{RGR}}$ rises and peaks after 5 to 10 days and then steadily declines. This pattern in $\overline{\text{RGR}}$ is typical of many annual plants (Hunt & Lloyd 1987).

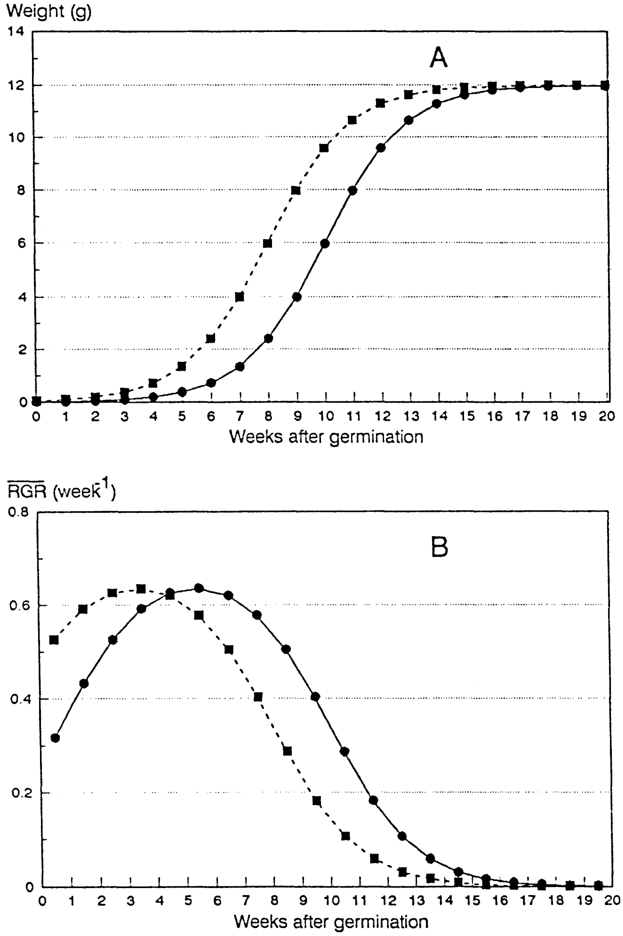

FIG. 5–Growth curves (A) and mean relative growth rates (B) for two seedlings that are growing according to the following sigmoidal equation:
$Y = 0.02 + 12(1 + 1000e^{(-0.69t)})^{-1}$
For the larger seedling (■) t = 2 + weeks after germination.
For the smaller seedling (●) t = weeks after germination.

Linear Model

Two sets of linear functions were examined. In both, the model was of the following form.

$$W = k\,[a + bt] \qquad (7)$$

In the first example (Table 1 Equation 7A), as with all previous ones, the difference in the initial weight of the plant results in a 2-week difference in tree weight. Since the absolute growth rate (0.6 g/week) is the same for both seedlings, the initial difference in weight (1.2 g) is maintained throughout the study (Fig. 6a). Even though there is no difference in absolute growth rates, there are large initial differences in $\overline{RGR}$. As the seedlings get larger, the $\overline{RGR}$ values get closer together and differ only at the third decimal place after 20 weeks (Fig. 6b). This type of linear growth curve rejects the null hypothesis. In this example, the large seedling will always have a smaller $\overline{RGR}$ than the small seedling:

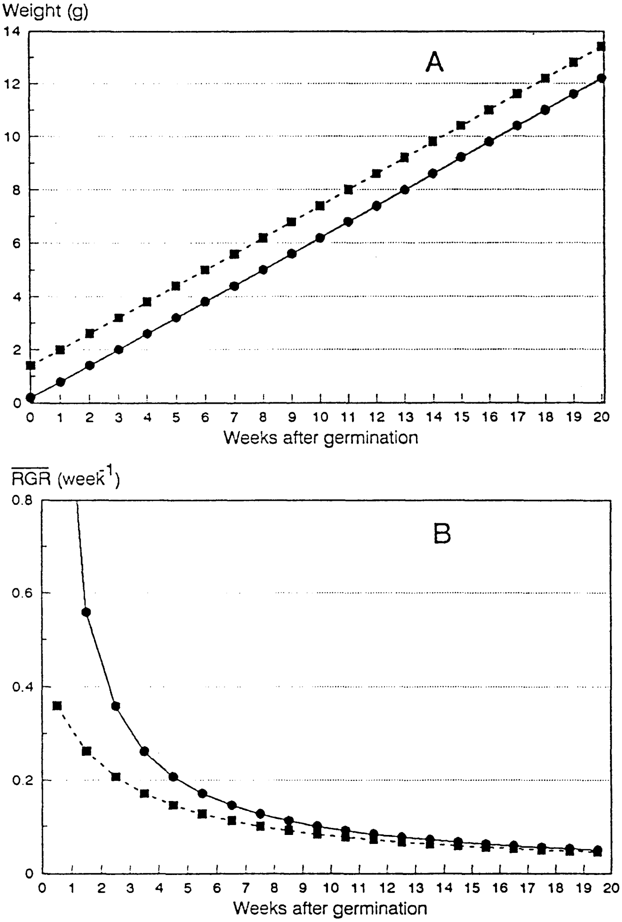

FIG. 6—Growth curves (A) and mean relative growth rates (B) for two seedlings that are growing according to the following linear equation: $Y = 1(0.2 + 0.6t)$
For the larger seedling (■) t = 2 + weeks after germination.
For the smaller seedling (●) t = weeks after germination.

$$\frac{\ln[a + b(t_2 + 2)] - \ln[a + b(t_1 + 2)]}{t_2 - t_1} < \frac{\ln[a + bt_2] - \ln[a + bt_1]}{t_2 - t_1}$$

For each of the previous examples, both the small and the large seedlings were growing according to the same growth curve. The observed difference in growth could be explained by just a 2-week difference in development. Therefore, if the curve for the small tree was shifted along the x-axis to the left by 2 weeks, the two curves would exactly overlap.

The last example (Table 1 Equations 7B and 7C) deals with two seedlings that exhibit proportional growth (Fig. 7a) but have different growth curves. Even though the growth curves can not be overlapped (by shifting one along the x-axis), the $\overline{RGR}$ values (Fig. 7b) are the same. The equations within the brackets are the same but, because of different k values, the weight values for Equation 7C are always nine times that for Equation 7B. Although this

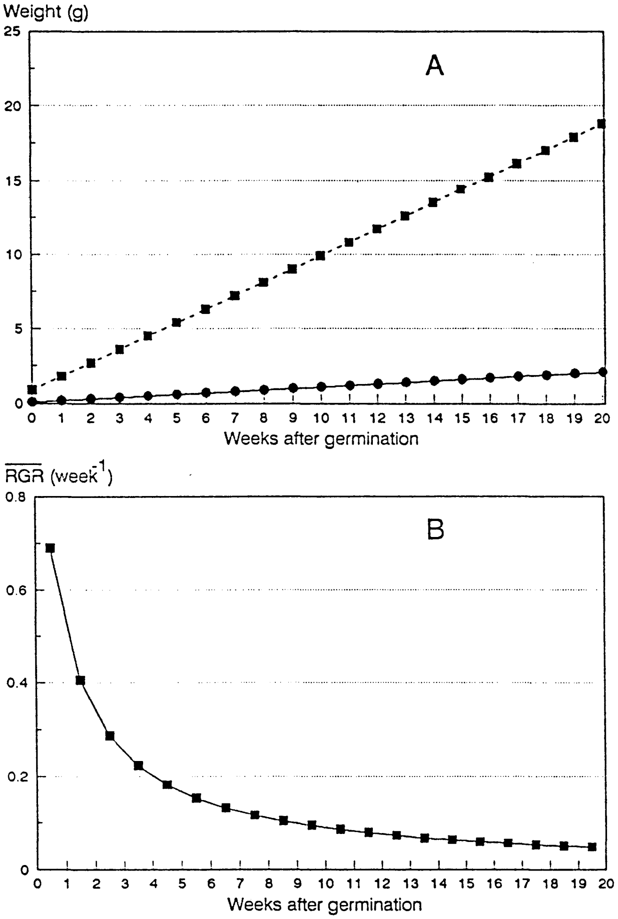

FIG. 7–Growth curves (A) and mean relative growth rates (B) for two seedlings that are growing according to two different linear equations.
The line for the larger seedling (■) is: $Y = 9(0.1 + 0.1t)$
The line for the smaller seedling (●) is: $Y = 1(0.1 + 0.1t)$

particular example is for linear growth, it really does not matter what shape of curve is represented by the function within the brackets of Equation 7. For example, the hypothetical case of proportional growth used by Sweet & Wareing (1966) was not linear but the k value for the larger seedling was three times that of the small seedling. As long as the function within the brackets is the same, the $\overline{\text{RGR}}$ will be the same for any given point in time, regardless of the difference in absolute growth rates (and regardless of differences in the constant of proportionality, k). The following two equations are equal regardless of the time interval examined.

$$\frac{\ln(k[a + bt_2]) - \ln(k[a + bt_1])}{t_2 - t_1} = \frac{\ln[a + bt_2] - \ln[a + bt_1]}{t_2 - t_1}$$

REAL DATA

If tree seedlings normally grow at a constant exponential rate (with $k = 0$) during the first 5 months after germination, then the $\overline{\text{RGR}}$ would be the same throughout the 5-month period (Causton 1983). However, if the growth curve is (1) exponential with a $k < 0$, (2) curvilinear, (3) sigmoid, or (4) linear then the $\overline{\text{RGR}}$ will decline as the plant gets larger in weight. A number of studies that document tree weight during the first 5 months of growth were reviewed (Table 2). In each study, the $\overline{\text{RGR}}$ decreased as the seedlings gained weight. Therefore, in general, it appears that tree growth during the first year of growth is not exponential (with $k = 0$).

Although a constant exponential growth of trees (with $k = 0$) does not usually occur in nature, it can be achieved artificially in hydroponics for a short period of time with small seedlings (Ingestad & Lund 1986). A constant $\overline{\text{RGR}}$ (constant exponential growth with $k = 0$) was achieved by treating small *Betula pendula* Roth. seedlings (10 mg seedlings fresh weight) with an exponentially increasing rate of nutrients (Fig. 8). Although there was some fluctuation in $\overline{\text{RGR}}$, the rate appeared relatively constant from week 5 till week 13. However, Ingestad & Lund (1986) have stated that this period of constant $\overline{\text{RGR}}$ can be obtained only before self-shading begins. When the trees get larger and self-shading begins, $\overline{\text{RGR}}$ will begin to decline.

Many, or perhaps most, organisms exhibit a declining $\overline{\text{RGR}}$ over time (Caloin & Yu 1982; Causton 1983). Therefore, reports of seedlings exhibiting a "constant" exponential growth (with a $k = 0$) and a weight greater than 1 g are difficult to find in the literature. Donald & Young (1982) reported possible examples for pine seedlings growing in bare-root nurseries in South Africa (Table 3). Fertiliser was applied to seedlings three times at 6- to 8-week intervals (the first top-dressing was applied 6–8 weeks after germination). It was concluded that a high level of nutrition was essential to maintain a high $\overline{\text{RGR}}$. However, even though r^2 values were high, the exponential equations over-predicted the final weight by 37–54% (Table 3). Apparently, the observed $\overline{\text{RGR}}$ had declined since seedlings last received fertiliser about 2 months prior to harvest.

Determining whether the examples provided by Donald & Young (1982) represent "constant" exponential growth rate is somewhat subjective. Although the growth curve appears rather smooth for *Pinus taeda* L. (Fig. 9a), there was a great deal of fluctuation in $\overline{\text{RGR}}$ between harvest periods (Fig. 9b). This fluctuation likely occurs as a result of episodic growth, periodic fertiliser application, and sampling error. In fact, the variation in $\overline{\text{RGR}}$

TABLE 2–The $\overline{RGR}$ and weight of seedlings from studies during the first 5 months of growth.

Species	Initial values			3–15 weeks later			Reference
	Age (weeks)	Weight (g)	$\overline{RGR}$ (per week)	Age (weeks)	Weight (g)	$\overline{RGR}$ (per week)	
Betula pendula	3	0.004	0.37	14	0.063	0.24	Ingestad & Lund (1986)
Citrus jambhiri	2	0.43	0.34	13	3.91	0.07	Dixon *et al.* (1988)
Gmelina arborea	8	0.35	0.68	11	2.10	0.34	Osonubi & Osundina (1987)
Larix leptolepis	12	2.9	0.26	20	23.4	0.17	Sweet & Wareing (1966)
Liquidambar styraciflua	1	0.011	0.58	16	3.748	0.23	Tolley & Strain (1984)
Picea glauca	7	0.015	0.69	17	0.962	0.26	Brown & Higginbotham (1986)
Pinus cortina	8	0.03	0.45	14	0.34	0.31	van den Driessche & Wareing (1966)
Pinus radiata	8	0.12	0.51	14	1.23	0.30	van den Driessche & Wareing (1966)
Pinus sylvestris	8	0.08	0.40	14	0.58	0.25	van den Driessche & Wareing (1966)
Pinus sylvestris	10	0.54	0.37	17	4.0	0.22	Roberts & Wareing (1975)
Pinus taeda	1	0.019	0.53	12	0.949	0.32	Tolley & Strain (1984)
Populus tremuloides	7	0.107	0.82	17	5.83	0.13	Brown & Higginbotham (1986)

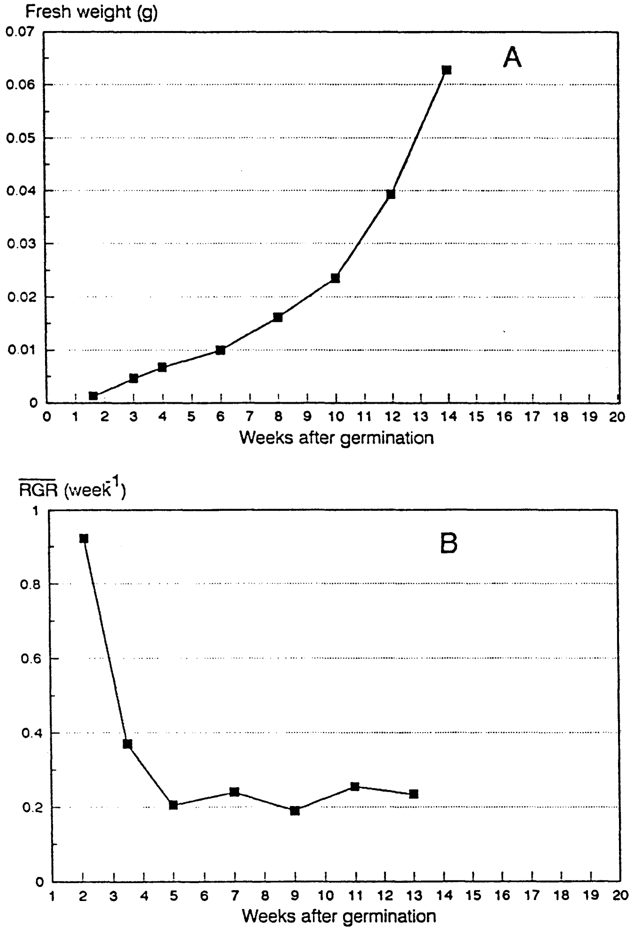

FIG. 8–Growth curve (A) and mean relative growth rates (B) for *Betula pendula* seedlings growing in hydroponics and fertilised at an exponentially increasing rate beginning approximately 6 weeks after germination (Ingestad & Lund 1986).

values for *Pinus elliottii* Engelm. is so wide that the 95% confidence interval for the $\overline{\text{RGR}}$ (per week) ranges from 0.15 to 0.26 (standard error of the mean = 0.0261). Although the exponential equation implies a "constant" exponential growth rate, the observed $\overline{\text{RGR}}$ values were not "constant" from one harvest to the next.

DISCUSSION

It is concluded from the above examples that the $\overline{\text{RGR}}$ technique will "eliminate" size-related growth differences when growth can be represented by a "constant" exponential equation that has $k = 0$. When an exponential curve has a k value less than zero, the technique will initially show that smaller seedlings have larger $\overline{\text{RGR}}$ values. The $\overline{\text{RGR}}$ technique does not "eliminate" size-related growth differences for all types of exponential curves (Fig. 2b).

TABLE 3–Regression equations for growth of *Pinus* for days after sowing (t) with predicted final dry weight (W) and observed final dry weight (Donald & Young 1982)

Species	Nursery	N	Regression equation	r^2	Last harvest day (t)	Final dry weight		Last observed $\overline{\text{RGR}}$ (per day)
						Observed (g)	Predicted (g)	
Pinus patula	Grootgeluk	15	$W = e^{(-4.5562 + 0.023538t)}$	0.98	266	3.801	5.501	0.008
Pinus patula	Mtubatuba	17	$W = e^{(-5.7071 + 0.031594t)}$	0.98	256	7.000	10.815	0.033
Pinus elliottii	Mtubatuba	14	$W = e^{(-4.3592 + 0.030049t)}$	0.97	212	5.437	7.472	0.028
Pinus taeda	Mtubatuba	14	$W = e^{(-4.4412 + 0.031691t)}$	0.99	212	7.110	9.750	0.013
Pinus radiata	Steenbras	12	$W = e^{(-4.2284 + 0.030881t)}$	0.97	194	4.110	5.827	0.028

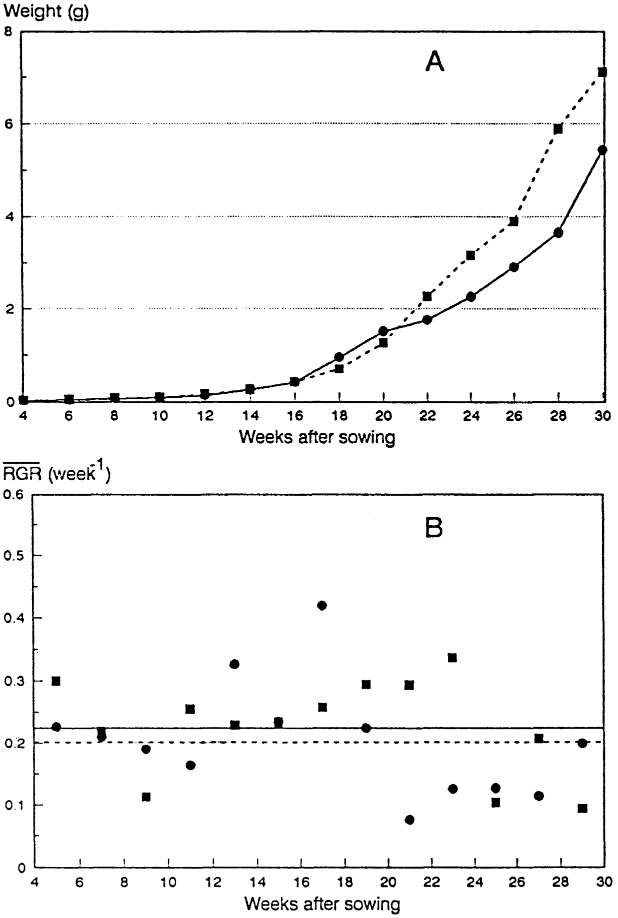

FIG. 9–Growth curve (A) and mean relative growth rates (B) for *Pinus taeda* seedlings (■) and *Pinus elliottii* seedlings (●) growing in a bare-root nursery in South Africa (Donald & Young 1982).

When the growth curve is not exponential, the use of $\overline{\text{RGR}}$ does not "eliminate" size-related growth differences. Even though correct calculations of $\overline{\text{RGR}}$ can be made for non-exponential curves, the $\overline{\text{RGR}}$ of two trees that are different in size but growing according to the same growth curve will not be the same. For some types of curves, the difference in $\overline{\text{RGR}}$ values will be greatest during the initial stages of growth (e.g., first 10 weeks). In other types of curves (i.e., sigmoid), the difference may be greater during the rapidly increasing linear phase of growth.

Although the above examples focus on growth soon after germination, exponential growth curves (with k = 0) are less likely to occur when growth is measured over several years. It has previously been pointed out that the $\overline{\text{RGR}}$ technique does not adequately correct for size differences from years 1 to 6 (Burdon & Sweet 1976; Britt *et al.* 1991) or from years 5 to 30 (Brand *et al.* 1987; South *et al.* 1988).

Van den Driessche & van den Driessche (1991) have suggested that the $\overline{RGR}$ technique is useful for comparing seedlings of different sizes "even though larger seedlings may show smaller values of relative growth rate than smaller seedlings". They suggested that in many situations, size differences between seedlings are not so large that the estimation of relative growth rate is seriously biased. However, it is not the "estimation" that is in danger of being biased since the $\overline{RGR}$ is correctly calculated as defined by Equation 3 (van den Driessche & van den Driessche 1991). What is in question is the degree of bias in interpretation of the experimental data that can result from a lack of removing the confounding of size. Can an unbiased comparison of $\overline{RGR}$ values be made without considering the size of the tree for which it was derived? If size differences are ignored when they are not "large," how much bias is acceptable before an alternative method of analysis is required?

For example, let us consider the growth of *Picea mariana* seedlings (Fig. 3). Since the initial size difference is less than 0.015 g, would it be acceptable to use the $\overline{RGR}$ method to conclude that the two seedlings were not growing according to the same growth curve during the first 14-week period? If so, the researcher would make a Type I error (the hypothesis that there is no difference in growth curves is true but the decision to reject the hypothesis is wrong). In fact, when the difference in size between seedlings becomes larger (i.e., after week 14), the chance of making a Type I error actually decreases instead of increases.

In contrast, when dealing with seedlings that are growing according to two different growth curves (e.g., Fig. 7a), it is likely that the $\overline{RGR}$ technique results in a high percentage of Type II errors (the hypothesis that the two seedlings are growing according to the same growth curve is false but the statistical test causes the researcher to accept the null hypothesis). In addition, because of a large variation in $\overline{RGR}$ from harvest to harvest, statistical tests will often lead to the conclusion that there is no statistical difference in $\overline{RGR}$ among different genotypes (e.g., Sweet & Wareing 1968b). For example, Donald & Young (1982) reported no statistical difference in $\overline{RGR}$ for *Pinus taeda* and *P. elliottii* growing in a bare-root nursery (Table 3). Indeed, the trees were approximately the same weight between weeks 4 and 22 (Fig. 9a). However, there was a final weight difference of 30% by the thirtieth week. Although it was concluded that the growth of *P. taeda* and *P. elliottii* might be safely predicted from the same exponential equation, there was no explanation as to why the growth was less for *P. elliottii* during the final 8 weeks of growth.

Tall genotypes usually exhibit smaller $\overline{RGR}$ than shorter genotypes (Burdon & Sweet 1976) and seedlings from large seed usually exhibit smaller $\overline{RGR}$ than those from small seed (Taylor 1972; Fenner 1983; Barclay & Crawford 1984; Pathak & Patil 1985; Hunt & Lloyd 1987). Despite these findings, the $\overline{RGR}$ technique continues to be used to compare the growth of different genotypes. However, when testing the statistical difference of $\overline{RGR}$ for different species, it is possible to conclude that there is no "genetic" effect on early growth by making Type II errors. By accepting the hypothesis that there is no difference in $\overline{RGR}$ due to species, it follows that the only difference in early seedling growth is due to initial differences in seed size (van den Driessche & Wareing 1966). If this were indeed true, the conclusion could easily be tested by sowing seed of equal size and comparing seedlings that germinate on the same date. However, instead of taking this approach (which would eliminate the need for use of the $\overline{RGR}$ technique since the plants would be starting out at an equal weight), many researchers are satisfied that the conclusions made with the $\overline{RGR}$ technique are valid and do not require verification.

CONCLUSIONS

Although it has been more than 15 years since Burdon & Sweet (1976) realised that $\overline{RGR}$ "... appears to be unsatisfactory as a means of eliminating initial size effects", this method of growth analysis continues to be used in forestry. Apparently, it is not well understood that although the $\overline{RGR}$ can be correctly calculated for growth curves that do not exhibit a constant exponential growth with $k = 0$, the technique does not "eliminate" size-related differences. A decline in $\overline{RGR}$ over time occurs when trees do not grow in a "constant" exponential fashion with $k = 0$.

Hardwick (1984) warned 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". Using the $\overline{RGR}$ technique to remove size-related growth differences can obscure the understanding of tree growth by producing different values when the trees are growing according to the same growth curve (Fig. 2–6). The general belief that $\overline{RGR}$ is a measure of growth efficiency (Causton 1983; Brand 1991) has caused some confusion since it implies a seedling with a higher $\overline{RGR}$ is somehow better than one with a lower $\overline{RGR}$. With regard to improving our understanding of how trees grow, this technique has had negative utility when used to "eliminate" size-related growth differences. The method tends to divert attention away from the basic data and as a result, in some studies, absolute growth data are not even reported. It is clear that, if progress is to be made, researchers must avoid assuming tree growth is of a "constant" exponential form with $k = 0$. When presenting data, the basic relationship of tree biomass with time should be graphed with the objective of reporting the true form of the growth curve (Radford 1967).

ACKNOWLEDGMENTS

The author would like to thank Dr. Torsten Ingestad for discussions regarding the lack of exponential tree growth in many controlled environment studies. Alabama Agricultural Experiment Station Journal Series No. 9-912988P. Research supported in part by the Auburn University Southern Forest Nursery Management Cooperative.

REFERENCES

BARCLAY, A.M.; CRAWFORD, R.M.M. 1984: Seedling emergence in the rowan (*Sorbus aucuparia*) from an altitudinal gradient. *Journal of Ecology 72*: 627–36.

BLACKMAN, V. H. 1919: The compound interest law and plant growth. *Annals of Botany 33*: 353–60.

BRAND, D.G. 1991: The establishment of boreal and sub-boreal conifer plantations: An integrated analysis of environmental conditions and seedling growth. *Forest Science 37*: 68–100.

BRAND, D.G.; WEETMAN, G.F.; REHSLER, P. 1987: Growth analysis of perennial plants: The relative production rate and its yield components. *Annals of Botany 59*: 45–53.

BRITT, J.R.; MITCHELL, R.J.; ZUTTER, B.R.; SOUTH, D.B.; GJERSTAD, D.H.; DICKSON, J.F. 1991: The influence of herbaceous weed control and seedling diameter on six years of loblolly pine growth—A classical growth analysis approach. *Forest Science 37*: 655–68.

BROWN, K.; HIGGINBOTHAM, K.O. 1986: Effects of carbon dioxide enrichment and nitrogen supply on growth of boreal tree seedlings. *Tree Physiology 2*: 223–32.

BURDON, R.D.; SWEET, G.B. 1976: The problem of interpreting inherent differences in tree growth shortly after planting. Pp. 483–502 *in* Cannell, M.G.R. (Ed.) "Tree Physiology and Yield Improvement". Academic Press, London.

BYRNE, S.V.; WENTWORTH, T.R. 1988: Relationship between volume and biomass of early successional vegetation and the prediction of loblolly pine seedling growth. *Forest Science 34*: 939–47.

CALOIN, M.; YU, O. 1982: An extension of the logistic model of plant growth. *Annals of Botany 49*: 599–607.

CANNELL, M.G.R.; ROTHERY, P.; FORD, E.D. 1984: Competition within stands of *Picea sitchensis* and *Pinus contorta*. *Annals of Botany 53*: 349–62.

CAUSTON, D.R. 1983: "A Biologist's Basic Mathematics". Edward Arnold. 216 p.

CAUSTON, D.R.; VENUS, J.C. 1981: "The Biometry of Plant Growth". Edward Arnold. 307 p.

COLLOCOTT, T.C.; DOBSON, A.B. 1974: "Dictionary of Science and Technology". W. & R. Chambers. 1328 p.

DIXON, R.K.; GARRETT, H.E.; COX, G.S. 1988: Cytokinins in the root pressure exudate of *Citrus jambhiri* Lush. colonized by vesicular-arbuscular mycorrhizae. *Tree Physiology 4*: 9–18.

DONALD, D.G.M.; YOUNG, I. 1982: The growth of pine seedlings in South African forest nurseries. *South African Forestry Journal 123*: 36–50.

EVANS, G.C. 1972: "The Quantitative Analysis of Plant Growth". Blackwell Scientific, Oxford. 734 p.

FENNER, M. 1983: Relationships between seed weight, ash content and seedling growth in twenty-four species of Compositae. *New-Phytologist 95*: 697–706.

FISHER, R.A. 1921: Some remarks on the methods formulated in a recent article on 'The quantitative analysis of plant growth'. *Annals of Applied Biology 7*: 367–372.

HARDWICK, R.C. 1984: Some recent developments in growth analysis—A review. *Annals of Botany 54*: 807–12.

HARRINGTON, T.B.; TAPPEINER, J.C.II 1991: Competition affects shoot morphology, growth duration, and relative growth rates of Douglas-fir saplings. *Canadian Journal of Forest Research 21*: 474–81.

HUNT, R. 1982: "Plant Growth Curves: The Functional Approach to Plant Growth Analysis". Edward Arnold Ltd, London. 248 p.

HUNT, R.; LLOYD, P.S. 1987: Growth and partitioning. *New Phytologist 106(Suppl.)*: 235–49.

INGESTAD, T.; LUND, B.B. 1986: Theory and techniques for steady state mineral nutrition and growth of plants. *Scandinavian Journal of Forest Research 1*: 439–53.

KOLB, T.E.; STEINER, K.C. 1990a: Growth and biomass partitioning of northern red oak and yellow-poplar seedlings: Effects of shading and grass root competition. *Forest Science 36*: 34–44.

———1990b: Growth and biomass partitioning response of northern red oak genotypes to shading and grass root competition. *Forest Science 36*: 293–303.

LEDIG, F.T.; PERRY, T.O. 1969: Net assimilation rate and growth in loblolly pine seedlings. *Forest Science 15*: 431–38.

MARTIN, E.A. 1977: "A Dictionary of Life Sciences". Pica Press, New York. 374 p.

MARGOLIS, H.A.; BRAND, D.G. 1990: An ecophysiological basis for understanding plantation establishment. *Canadian Journal of Forest Research 20*: 375–90.

MEXAL, J.G. 1980: Aspects of mycorrhizal inoculation in relations to reforestation. *New Zealand Journal of Forestry Science 10*: 208–17.

OSONUBI, O.; OSUNDINA, M.A. 1987: Comparison of the responses to flooding of seedlings and cuttings of *Gmelina*. *Tree Physiology 3*: 147–56.

PARKER, S.P. 1989: "Dictionary of Scientific and Technical Terms". McGraw-Hill, New York. 2088 p.

PATHAK, P.S.; PATIL, B.D. 1985: Seed weight affecting early seedling growth of *Butea monosperma* (Lam.) Taub. *Nitrogen-Fixing Tree Research Reports 3*: 23–4.

PERRY, D.A. 1985: The competition process in forest stands. Pp. 481–506 *in* Cannell, M.G.R.; Jackson, J.E. (Ed.) "Attributes of Trees as Crop Plants". Institute of Terrestrial Ecology, Huntingdon, England. 592 p.

RADFORD, P.J. 1967: Growth analysis formulae—Their use and abuse. *Crop Science 7*: 171–5.

ROBERTS, J.; WAREING, P.F. 1975: An examination of the differences in dry matter production shown by some progenies of *Pinus sylvestris* L. *Annals of Botany 39*: 311–24.

RUTTER, A.J. 1957: Studies in the growth of young plants of *Pinus sylvestris* L. I: The annual cycle of assimilation and growth. *Annals of Botany 21*: 399–426.

SHAINSKY, L.J.; RADOSEVICH, S.R. 1986: Growth and water relations of *Pinus ponderosa* seedlings in competitive regimes with *Arctostaphylos patula* seedlings. *Journal of Applied Ecology 23*: 957–66.

SOUTH, D.B.; MEXAL, J.G.; van BUIJTENEN, J.P. 1988: The relationship between seedling diameter at planting and long term volume growth of loblolly pine seedlings in east Texas. Pp. 192–9 *in* Worrall, J.; Loo-Dinkins, J.; Lester, D.P. (Ed.) "North American Forest Biology Workshop". University of British Columbia, Vancouver. 364 p.

SWEET, G.B.; WAREING, P.F. 1966: The relative growth rates of large and small seedlings in forest tree species. *Forestry Supplement*: 110–7.

———1968a: A comparison of the seasonal rates of dry matter production of three coniferous species with contrasting patterns of growth. *Annals of Botany 32*: 721–34.

———1968b: Comparison of the rates of growth and photosynthesis in first-year seedlings of four provenances of *Pinus contorta* Dougl. *Annals of Botany 32*: 735–51.

SWEET, G.B.; WELLS, L.G. 1974: Comparison of the growth of vegetative propagules and seedlings of *Pinus radiata*. *New Zealand Journal of Forestry Science 4*: 399–409.

TAYLOR, G.B. 1972: The effect of seed size on seedling growth in subterranean clover (*Trifolium subterraneum* L.) *Australian Journal of Agricultural Science 23*: 595–603.

THOMAS, S.C., WEINER, J. 1989: Including competitive asymmetry in measures of local interference in plant populations. *Oecologia 80*: 349–55.

TIMMER, V.R. 1991: Interpretation of seedling analysis and visual symptoms. Pp. 113–34 *in* van den Driessche, R. (Ed.) "Mineral Nutrition of Conifer Seedlings". CRC Press, Boca Raton, Florida. 274 p.

TOLLEY, L.C.; STRAIN, B.R. 1984: Effects of CO_2 enrichment on growth of *Liquidambar styraciflua* and *Pinus taeda* seedlings under different irradiance levels. *Canadian Journal of Forest Research 14*: 343–50.

van den DRIESSCHE, R. 1982: Relationship between spacing and nitrogen fertilization of seedlings in the nursery, seedling size, and outplanting performance. *Canadian Journal of Forest Research 12*: 865–75.

———1992: Absolute and relative growth of Douglas-fir seedlings of different sizes. *Tree Physiology 10*: 141–52.

van den DRIESSCHE, P.; van den DRIESSCHE, R. 1991: Growth analysis. Pp. 61–84 *in* van den Driessche, R. (Ed.) "Mineral Nutrition of Conifer Seedlings". CRC Press, Boca Raton, Florida. 274 p.

van den DRIESSCHE, R.; WAREING, P.F. 1966: Dry matter production and photosynthesis in pine seedlings. *Annals of Botany 30*: 673–82.

WAREING, P.F. 1966: The physiologist's approach to tree growth. *Forestry Supplement*: 7–18.