modeled, and the interactions between foliage elements and light to be characterized by another set of rules. Realistic representations of canopy development can be obtained in this way.

Research Areas

Research on canopies peaked some time ago and resulted in the development of methods and procedures for analyzing canopy structure and function in a wide variety of situations. On the other hand, interest in sustainable farming systems has led to research into canopy management as a means of optimizing input use. However, the exciting prospect of using information about a plant's genome to parameterize an architectural model of crop growth so that yield can be investigated under a wide range of climatic and management scenarios is still a long way off.

List of Technical Nomenclature

Diffuse radiation	The component of solar radiation that is scattered by molecules and particles in the air.
Direct beam	The component of solar radiation that comes directly from the sun.
Eddy flux correlation	A micrometerological method of estimating fluxes of gases from the three-dimensional movement of air parcels and their gaseous composition.
Gap fraction	The proportion of sky not obscured by foliage looking up from below a plant stand.
Heliotropism	The growth of a plant toward the sun, e.g., expressed as solar tracking by leaves of flowers.
Irradiance	The amount of solar energy received per unit time per unit area; expressed as $W m^{-2}$.
Leaf area density	The leaf area of a plant stand divided by the volume of space occupied.
Leaf area index	The ratio of the leaf surface area to the ground area occupied by a plant stand.
Light extinction coefficient	A constant that categorizes the exponential attenuation of light with depth in a homogeneous medium.
Normalized difference vegetation index	An index of ground surface greenness used in remote sensing that makes use of the relative brightness of the surface in the red and near infrared bands.
Phenology	The study of the timing of developmental stages, such as flowering, in organisms.
Sunfleck	A beam of light passing through a gap in the foliage to illuminate a small patch of ground; its position will change with the relative movement of earth and sun.
Sun leaves	Leaves that have developed in full sunlight and can be distinguished anatomically and physiologically from shade leaves, being thicker and with higher rates of photosynthesis at saturating irradiances.

See also: **Growth and Development**: Field Crops; Leaf Development. **Photosynthesis and Partitioning**: Sources and Sinks. **Production Systems and Agronomy**: Plantation Crops and Plantations. **Regulators of Growth**: Phytochromes and other Photoreceptors. **Root Development**: Root Growth and Development. **Weeds**: Weed Competition.

Further Reading

Hallé F, Oldemann RAA, and Tomlinson PB (1978) *Tropical Trees and Forests*. Berlin: Springer Verlag.

Lindenmeyer A and Prusinkiewicz (1988) Developmental models of multicellular organisms: a computer graphics perspective. In: Langton CG (ed.) *Artificial Life*, pp. 221–249. Redwood City: Addison Wesley.

Marshall B and Roberts JA (2000) *Leaf Development and Canopy Growth*. Sheffield: Sheffield Academic Press.

Moffett MW (2000) What's "up"? A critical look at the basic terms of canopy biology. *Biotropica* 32: 569–596.

Russell G, Marshall B, and Jarvis PG (1989) *Plant Canopies: Their Growth Form and Function*. Society for Experimental Biology Seminar Series, vol. 31. Cambridge: Cambridge University Press.

Growth Analysis, Individual Plants

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Introduction

The term plant growth analysis refers to a useful set of quantitative methods that describe and interpret the performance of whole plant systems grown under natural, seminatural, or controlled conditions. Plant growth analysis provides an explanatory, holistic, and integrative approach to interpreting plant form and function. It uses simple primary data such as weights, areas, volumes, and contents of plants or plant components to investigate processes within and involving the whole plant or crops. Originating at the

FROM: **Thomas, B., Murphy, D. J. and Murray, D. (eds.) 2003**. *Encyclopaedia of applied plant sciences, 588-596*. Academic Press, London.

end of the nineteenth century, plant growth analysis first illuminated plant physiology, then agronomy and, most recently, physiological and evolutionary plant ecology.

In plant growth analysis, there is an historical and practical distinction between the organism (and below) and the population (and above). These two areas demand different approaches, though each is similar in concept and consistent in application. The two are treated separately elsewhere (*see* **Growth and Development:** Growth Analysis, Crops), so this article deals only with the analysis of whole plants grown as spaced individuals.

"Growth" in the context of the individual plant means an irreversible change with time. Such changes are mainly in size (however measured), often in form, and occasionally in number. For example, classical experiments have shown that in both annual and perennial plants raised under productive conditions, growth initially follows the same typical course (**Figure 1**). Because the changes in total dry weight over these periods vary many-fold, very little of the earliest phases of development can be seen. When the data are transformed to logarithms, however, several benefits are gained (**Figure 2**). A visual benefit of the logarithmic transformation is that all the successive phases of growth series become equally clear; a statistical benefit is that variability between replicates is homogenized across the whole series, and a mathematical benefit is that a first step is taken toward calculations of rates of growth or efficiency of function, many of which require logarithmic transformation of primary data in order to be practical.

In the logarithmic plots, a zero or negative initial phase of growth is followed by a "grand period" of near-exponential (log-linear) increase and then by an approach to a plateau in the plant's maturity, with senescence and decay following. This pattern is quite general to annual plants grown in a productive environment, though there is great variation in the magnitude of the dry weights attained, in the symmetry of the curve, and in the time-scale covered. In perennial plants, the pattern is similar at first, but later, at least in a temperate climate, dry weight increase proceeds in a series of annual steps, which may be separated by periods of negative growth. Environmental conditions affect the magnitude of growth at all stages.

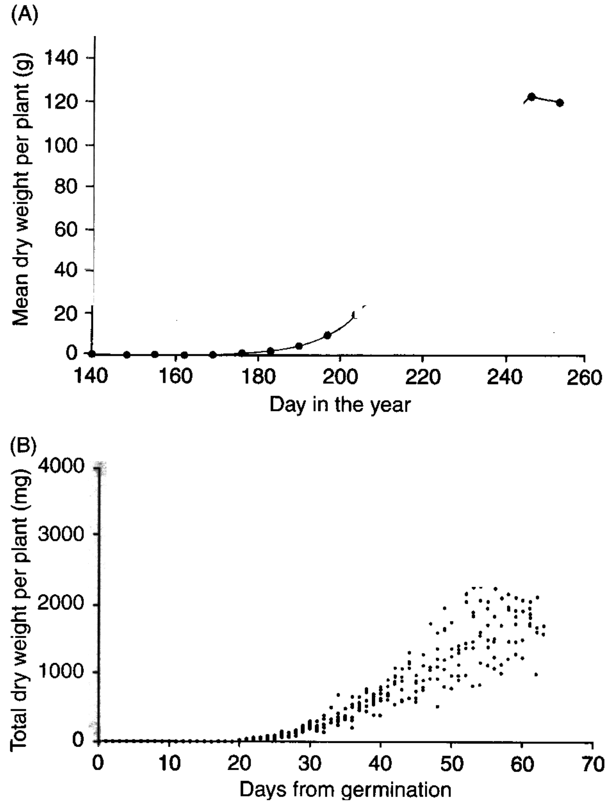

Figure 1 The accumulation with time of total dry weight per plant: (A) in corn, showing mean values each derived from 40 to 120 individuals harvested weekly from an outdoor environment. Reproduced from Kreusler U, Prehn A, and Hornberger R (1879) Beobachtungen über das Wachsthum der Maispflanze (Bericht über die Versuche vom Jahre 1878). *Landwirtschaftliche Jahrbücher* 8: 617. (B) in the grass *Holcus lanatus*, showing individual plants harvested daily from a productive, controlled environment.

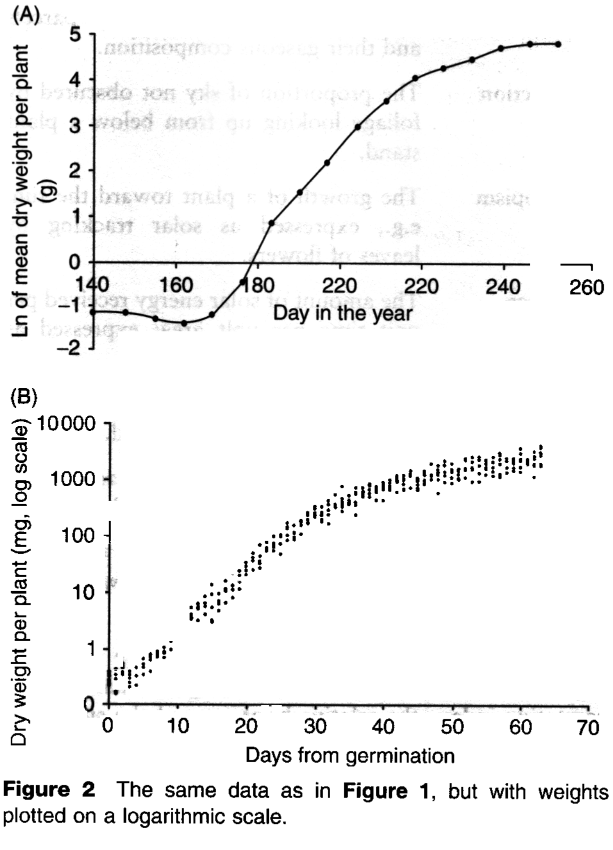

Figure 2 The same data as in **Figure 1**, but with weights plotted on a logarithmic scale.

Plant growth analysis addresses data such as these by means of powerful comparative tools. These aim to negate, as far as possible, the inherent differences in scale that can exist between different organisms or phases of growth. For example, rates of growth in the near-exponential phase can be below 10% per day in tree seedlings, even under very favorable conditions, but values rise much higher as we move in turn through herbaceous plants, algae, fungi, and microorganisms, to as much as 20 000% per day in an anti-*Escherichia coli* phage. The larger, older, or more complex the organism, the lower the maximum rate of dry weight increase that is normally possible. Plant growth analysis aims to compare such performance like for like.

Basic Technical Concepts

Classical and Functional Approaches

Two distinct approaches to the growth analysis of individual plants have evolved. In the so-called "classical" approach, events are followed through a series of relatively infrequent, large, often destructive, harvests (with much replication of measurements). In the so-called "functional" approach, the individual harvests supply data for curve-fitting, but they are each smaller (having less replication of measurements) and often much more frequent. The two approaches are not mutually exclusive if time and space are no object (harvests may be large and frequent), but in most cases, the experimenter is forced to choose one or other in advance, as this influences the design of the experiment.

Where to Start?

The stock in trade of plant growth analysis is a collection of simple primary data, the measured quantities upon which the subsequent analyses depend. These data may be determined either for the whole plant or for different components such as roots, stems, and leaves, as required. Naturally, all of the analytical and statistical techniques should be chosen before practical work is begun. In the growth analysis of individual plants, the primary data are used to calculate values of one or more of four distinct types of derivate.

Absolute Growth Rates

These are simple rates of change involving only one plant variate and time, examples being the whole plant's rate of dry weight increase, or the rate of increase in number of roots per plant.

Relative Growth Rates

These are more complex rates of change, but still involving only one plant variate and time, an example being the whole plant's rate of dry weight increase per unit of dry weight (for example, the percentage rate of growth mentioned above).

Simple Ratios

These involve ratios between two quantities, and may either be ratios (or more strictly quotients) between two like quantities, such as total leaf dry weight and whole plant dry weight, or ratios between two unlike quantities, such as total leaf area and whole plant dry weight.

Compounded Growth Rates

These are rates of change involving more than one plant variate, such as the whole plant's rate of dry weight increase per unit of its leaf area.

Basis of Calculation

It is usual to define all of the derived quantities and their interrelationships instantaneously: that is, as they stand at a single point in time. Though this provides a mathematically precise specification, it was for many years necessary to base the estimates upon mean values over a stated time interval, using the "classical" approach. (To appreciate the difference between the two, note that in the context of a car journey, the instantaneous and mean velocities are obtained from momentary speedometer readings, on the one hand, and from whole-journey calculations involving total times and distances, on the other.) Most of the instantaneous values can be determined only as mathematical derivatives from curves fitted in a "functional" approach, a method that was not generally practical until the 1960s.

Only instantaneous values may properly be represented as single points on a progression plotted against time; mean values should appear as a histogram with one column for each harvest interval. **Table 1** provides a synopsis of instantaneous and mean (harvest-interval) definitions of the four principal types of derivate.

Absolute Growth Rates

Absolute Growth Rate in Size

This is the simplest index of plant growth: a rate of change in size, which is an increment in size per unit of time. Most commonly if W is the total dry weight of the plant, then G is its absolute growth rate in total dry weight. The dimensions and units of G are

Table 1 Formulae defining instantaneous and mean values of each type of derivate (the formula for the mean value is approximate except in the case of absolute growth rate)

Type of derivate	*Instantaneous definition*	*Formula for mean value over the time interval t_1 to t_2*
Absolute growth rate	dY/dt	$(Y_2 - Y_1)/(t_2 - t_1)$
Relative growth rate	$(1/Y)(dY/dt)$	$(\ln Y_2 - \ln Y_1)/(t_2 - t_1)$
Simple ratio	Y/Z	$((Y_1/Z_1) + (Y_2/Z_2))/2$
Compounded growth rate	$(1/Z)(dY/dt)$	$((Y_2 - Y_1)/(t_2 - t_1)) \times ((\ln Z_2 - \ln Z_1)/(Z_2 - Z_1))$

mass per time, e.g., g day^{-1}. Instantaneously, $G = dW/dt$, and its mean value over the interval t_1 to t_2 is $(W_2 - W_1)/(t_2 - t_1)$. The instantaneous G can be derived from functions fitted to W versus t; thus if $W = f_W(t)$, then $G = f_W'(t)$. Mean values are obtained from the separate destructive estimates W_1 and W_2 made at times t_1 and t_2, respectively.

The mean values of absolute growth rate in the corn (*Zea mays*; maize) series (**Figure 1**) are shown in **Figure 3**; the greatest weekly increases occur relatively late in the series.

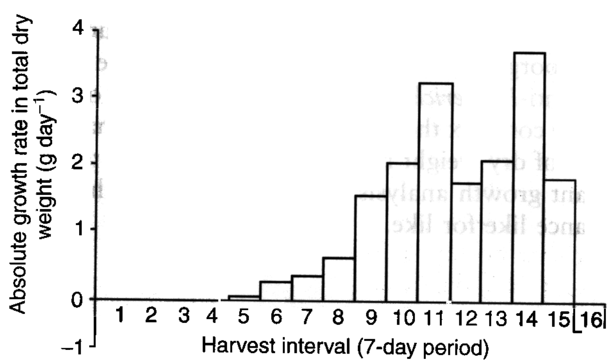

Figure 3 The progress of mean absolute growth rate in total dry weight in outdoor grown corn (see **Figures 1A** and **2A**).

Absolute Growth Rate in Number

This is the simplest index of growth in number; a rate of change in number, which is an increment in number per unit time. In individual plants, its use is confined to describing growth in numbers of discrete organs, such as leaves or roots. The definitions and calculations are the same as above, but the primary data differ, with the number of plant organs N being used in place of W.

Figure 4 illustrates growth in flower number in cotton (*Gossypium* spp.) crops; varietal and seasonal differences are discernible.

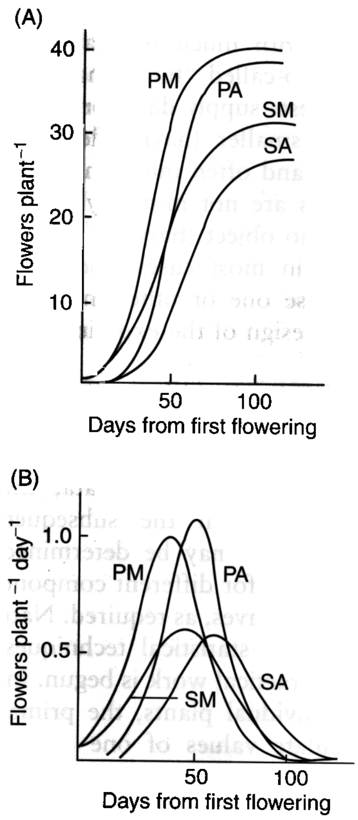

Figure 4 Flowering in Egyptian cotton: (A) logistic growth curves fitted to flower number per plant in varieties P (Pilion) and S (Sakellaridis) sown in M (March) or A (April); (B) instantaneous absolute growth rates in flower number, the slopes of the curves shown in (A). Reproduced with permission from Prescott JA (1922) The flowering curve of the Egyptian cotton plant. *Annals of Botany* 36: 121–130.

Relevance

The absolute growth rates are the simplest possible measures of plant growth rate. They can be valuable comparative tools when they are used within like bodies of data (as in **Figure 4**). When used to compare unlike systems, however, their usefulness declines. To compare the overall performance in such circumstances requires other approaches. For example, if two different species are grown for equal periods of time and both put on equal amounts of dry weight, they will both exhibit the same absolute growth rate even if the species differed in initial dry weight. Some measure of growth is needed that also takes into account this original difference in size. That measure is relative growth rate.

Relative Growth Rate

Explanations and Examples

This was originally termed an "efficiency index" because it expresses growth in terms of a rate of increase in size per unit of size. As such, it permits more equitable comparisons between organisms than does absolute growth rate. Normally, relative growth rate deals with total dry weight per plant, though other measures of size have also been used. In the financial world, relative growth rate is analogous to the rate of compound interest earned on capital. Negative relative growth rates are called relative decay rates.

The relative growth rate, R, is the rate of increase of total dry weight per plant, W, expressed per unit of W. Its dimensions are mass per mass per time, typically in units of $g\,g^{-1}\,day^{-1}$ or $g\,g^{-1}\,week^{-1}$ (if both weights appear in identical units they can be cancelled out); per cent per time may also be used. Instantaneously, $R = (1/W)(dW/dt)$. In calculus notation, this is the same as $d(\ln W)/dt$. The mean value over the interval t_1 to t_2 is $(\ln W_2 - \ln W_1)/(t_2 - t_1)$. The instantaneous R is derived from functions fitted to $\ln W$ versus t; thus, if $\ln W = f_W(t)$, then $R = f_W'(t)$. Mean values are obtained from the separate destructive estimates W_1 and W_2 made at times t_1 and t_2, respectively.

Figure 5 shows the drift in mean relative growth rate in a classical analysis of the corn series and, from the functional approach, the drift in instantaneous relative growth rate in the *Holcus* series. In each case, maximum relative growth rate occurs sooner rather than later.

Screening experiments have shown that maximum mean relative growth rate varies approximately tenfold between different temperate herbaceous species, but only twofold between different geographical populations of the same species, or between different genotypes within one population ("genets"), or between different clones within one genotype ("ramets").

Relevance

Relative growth rate is useful wherever current size realistically controls current increase in size. It provides a convenient integration of the many component processes that contribute to the performance of the whole plant, but it depends upon the assumption that all parts of the relevant "size" are equally capable of producing further amounts of the same quantity (in the same way that invested capital grows through the accrual of compound interest). However, as most plants grow, the proportion of their mass that is largely supporting material (i.e., not directly productive) increases, for much the same reason that larger animals develop proportionally more bulky bones than smaller ones. So, relative growth rate soon declines with time (**Figure 5**), and the interest then passes to the components of relative growth rate in the hope of explaining how this decline comes about.

Simple Ratios

Leaf Area Ratio

This is a morphological index describing the leafiness of the plant. A measure of the "balance of payments" between income and expenditure, it deals with the potentially photosynthesizing and the potentially respiring components of the plant. It is the ratio, F, between total leaf area per plant, L_A, and total dry weight per plant, W. Its dimensions are area per mass; typical units are $mm^2\,mg^{-1}$ or $m^2\,g^{-1}$. Instantaneously, $F = L_A/W$ and its mean value over the interval t_1 to t_2 is $((L_{A1}/W_1) + (L_{A2}/W_2))/2$, which is, of course, $(F_1 + F_2)/2$. The instantaneous values can be derived from functions fitted to $\ln L_A$ and $\ln W$ versus t; thus, if $\ln L_A = f_L(t)$ and $\ln W = f_W(t)$, then $F = L_A/W = \exp(f_L(t) - f_W(t))$. Unsmoothed instantaneous values are also available directly from the defining formula.

Mean leaf area ratio in Kreusler's corn series is shown in **Figure 6**. The relatively early position of the maximum in these values is common among herbaceous species.

Specific Leaf Area

This is an index of the "leafiness of the leaf": a measure of density or of relative thinness, which involves an assessment of the leaf's area in relation to its dry weight. No particular symbol is in general use. Leaf area ratio is the ratio between total leaf area per plant L_A and total leaf dry weight per plant L_W. (The term "specific" means divided by weight.) The dimensions are area per mass, typically $mm^2\,mg^{-1}$ or $m^2\,g^{-1}$. Instantaneously defined as L_A/L_W, the mean value over the interval t_1 to t_2 is $((L_{A1}/L_{W1}) + (L_{A2}/L_{W2}))/2$. From functions fitted to $\ln L_A$ and $\ln L_W$ versus t, $f_A(t)$ and $f_W(t)$, the instantaneous L_A/L_W is derived as $\exp(f_A(t) - f_W(t))$. Unsmoothed instantaneous values are also available directly from the defining formula.

Specific leaf areas in three successive crops of glasshouse-grown winter lettuce (*Lactuca sativa*) are shown in **Figure 7**. The differences between the three curves are environmentally driven, principally by the level of photosynthetically active radiation.

Leaf Weight Ratio

This is an index of leafiness of the plant on a dry weight basis: a measure of the "productive

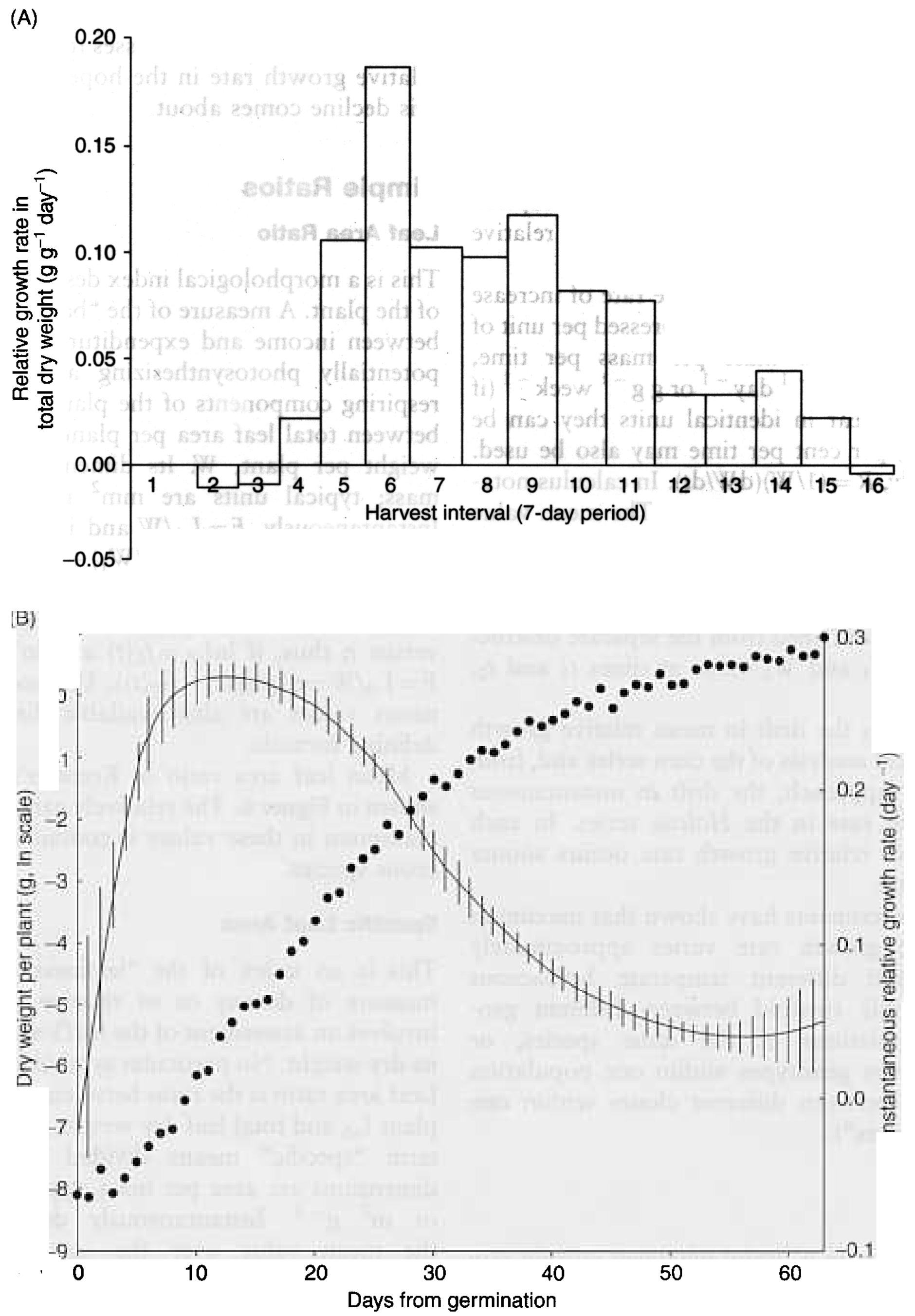

Figure 5 Relative growth rates in total dry weight: (A) mean values for outdoor grown corn (see **Figures 1A** and **2A**); (B) instantaneous values, with 95% confidence limits and harvest means of total dry weight, for *Holcus lanatus* in a productive, controlled environment (see **Figures 1B** and **2B**).

investment" of the plant, dealing with the relative expenditure on potentially photosynthesizing organs. No particular symbol is in general use. The leaf weight ratio is the ratio between total leaf dry weight per plant, L_W, and total dry weight per plant, W. It is more strictly a leaf weight fraction, but the term "ratio" is widely used. Its dimensions are mass per mass, which is effectively dimensionless. Numerically, the values are $0<x<1$. Instantaneously, L_W/W, the mean value over the interval t_1 to t_2 is given by $((L_{W1}/W_1)+(L_{W2}/W_2))/2$. The instantaneous values can be derived from functions fitted to $\ln L_W$ and $\ln W$, $f_L(t)$ and $f_W(t)$, so that $L_W/W=\exp(f_L(t)-f_W(t))$. Unsmoothed instantaneous values are also available directly from the defining formula.

Table 2 shows that species and varietal differences play an important part in determining leaf weight ratio.

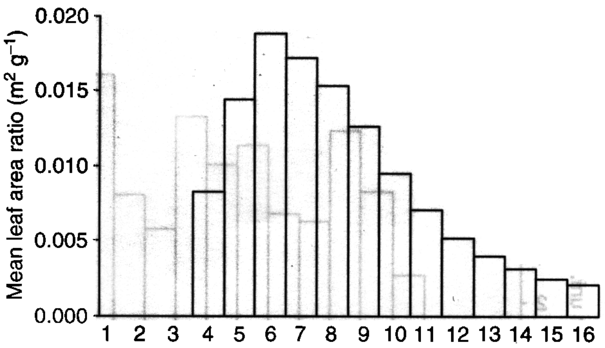

Figure 6 The progress of mean leaf area ratio in outdoor grown corn (see **Figures 1A** and **2A**).

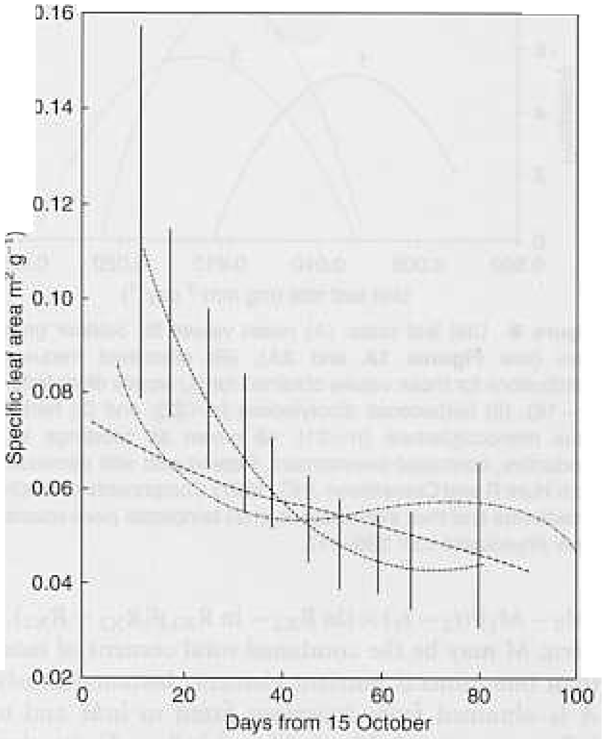

Figure 7 The progress of instantaneous specific leaf area in winter lettuce grown in a glasshouse in three successive seasons (95% confidence limits are added to the curve for the earliest year). Reproduced with permission from Hunt R, Warren Wilson J, Hand DW, and Sweeney DG (1984) Integrated analysis of growth and light interception in winter lettuce. I. Analytical methods and environmental influences. *Annals of Botany* 54: 743–757.

Root–Shoot Allometric Coefficient

This is an index of the balance of growth between root and shoot components of the plant integrated over a period of time. Effectively, a ratio between root and shoot mean relative growth rates (q.v.). The usual symbol is K; and the allometric relationship is defined as $R_W = bS_W{}^K$, where b is a constant. The allometric coefficient is dimensionless within the range $0 < K < \infty$. Equally balanced growth above and below ground gives a K value of unity. In "shooty" growth $K < 1$ and in "rooty" growth $K > 1$. Because $R_W = bS_W{}^K$, then $\log R_W = \log b + K \log S_W$ and $K = (\log R_W - \log b)/\log S_W$. Which base of logarithms is used is not important.

In practice, the coefficient K is derived from a series of paired measurements of R_W and S_W. The function $\log R_W = f(\log S_W)$ is fitted. Usually this is a linear regression of the form $\log R_W = \log b + K \log S_W$, but a bivariate principal axis should be used wherever possible because the x-variate (S_W) cannot be determined without error.

The allometric coefficient is highly sensitive to environmental conditions and generally exhibits a partitioning of material toward the more resource-deficient part of the plant (Table 3).

Table 2 Leaf weight ratio in ryegrass (*Lolium* spp.) and clover (*Trifolium* spp.): 16 cultivars examined over a 3-week period (95% confidence intervals in parentheses)

Species	*Cultivar*	*Leaf weight ratio*
Lolium multiflorum		
Lolium perenne × *Lolium multiflorum*		
Trifolium repens	S100	0.452 (0.036)
	Hiua	0.458 (0.011)
	S184	0.483 (0.018)
	Blanca	0.471 (0.019)
	Kersey	0.444 (0.032)
	Pajbjerg	0.457 (0.039)
Trifolium pratense	Tetri	0.467 (0.016)
Trifolium hybridum	"British"	0.467 (0.015)

Source: Elias CO and Chadwick MJ (1979) Growth characteristics of grass and legume cultivars and their potential for land reclamation. *Journal of Applied Ecology* 16: 534–537.

Table 3 Root–shoot allometry in perennial ryegrass (*Lolium* spp.): values of K, the allometric coefficient, for the vegetative growth of perennial ryegrass under different conditions (95% confidence intervals in parentheses)

	Full light	*Shade*
Full nutrients		
Low nitrogen		

Source: Hunt R (1975) Further observations on root–shoot equilibria in perennial ryegrass. *Annals of Botany* 39: 744–757.

Relevance

Mathematically, these ratios are alone capable of instantaneous evaluation without recourse to fitted growth curves. However, if the functional approach is followed, the component ratio Z/Y should always be evaluated from the separate functions $\ln Z = f_Z(t)$ and $\ln Y = f_Y(t)$, rather than directly from $Z/Y = f_{Z/Y}(t)$, which can have difficult statistical properties. Where Z and Y are like quantities, their ratio is simply an index of allocation; where they are unlike quantities, the ratio is a "snapshot" of the functional balance between two related or antagonistic components. In the case of the allometric coefficient, there is the added advantage that it often remains approximately constant across substantial intervals of time, which increases its value as a comparative tool.

Compounded Growth Rates

Unit Leaf Rate

This is an index of the productive efficiency of plants calculated in relation to total leaf area. It is synonymous with the term net assimilation rate. The usual symbol is E: the rate of dry weight production expressed per unit of total leaf area, L_A. Its dimensions are mass per area per time, typically mg mm^{-2} day^{-1} or g m^{-2} day^{-1}. Instantaneously, $E = (1/L_A)(dW/dt)$. The mean value over the interval t_1 to t_2 is approximately $(W_2 - W_1)/(t_2 - t_1) \times (\ln L_{A2} - \ln L_{A1})/(L_{A2} - L_{A1})$. The unit leaf rate can be obtained instantaneously from functions fitted to $\ln W$ and $\ln L_A$ versus t, $f_W(t)$, and $f_L(t)$, such that $E = (1/L_A)(dW/dt) = f_W'(t) \times \exp(f_W(t) - f_L(t))$. Mean values are obtained from the formula given above, using the separate estimates (W_1, L_{A1}) and (W_2, L_{A2}) from harvests at t_1 and t_2, respectively.

Mean unit leaf rate in the corn series (**Figure 8A**) exhibits a relatively constant general level modified by fluctuations in the weather during the growing season. In the seedling phases of herbaceous and woody species grown in a productive, controlled environment (**Figure 8B**), there are two- to threefold variations between species within a functional group and also moderate overall differences between the groups themselves.

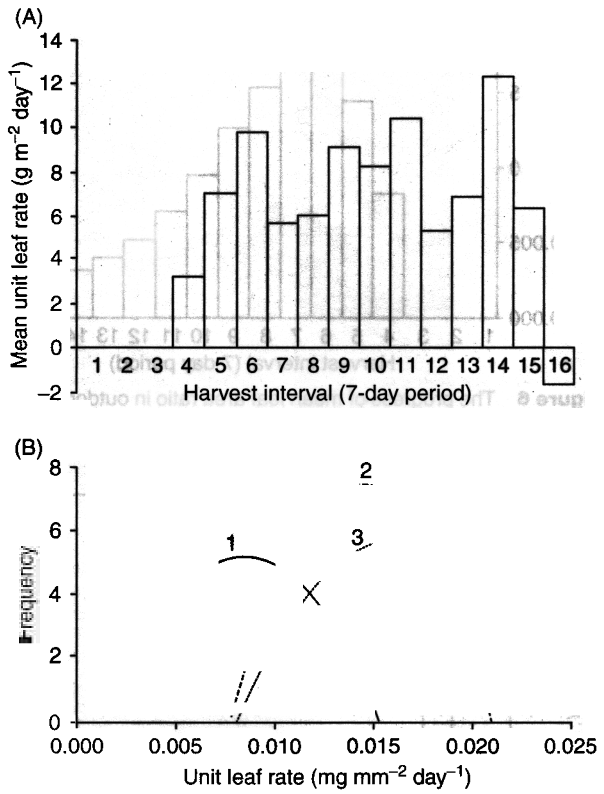

Figure 8 Unit leaf rates: (A) mean values for outdoor grown corn (see **Figures 1A** and **2A**); (B) smoothed frequency distributions for mean values obtained for (1) woody dicotyledons ($n = 16$), (2) herbaceous dicotyledons ($n = 22$), and (3) herbaceous monocotyledons ($n = 21$), all grown as seedlings in a productive, controlled environment. Reproduced with permission from Hunt R and Cornelissen JHC (1997) Components of relative growth rate and their interrelations in 59 temperate plant species. *New Phytologist* 135: 395–417.

Specific Absorption Rate

This is an index of the uptake efficiency of roots, calculated in relation to some measure of root size. The usual symbol is A, defined as the rate of uptake of mineral nutrient, M, expressed per unit of total root size, which may be root dry weight, R_W, or, alternatively, root length, area, volume, or number. The dimensions are mass per mass per time and typical units are μg mg^{-1} day^{-1} or mg g^{-1} day^{-1}. Instantaneously, $A = (1/R_X)(dM/dt)$, where R_X is some measure of root size. The mean value over the interval t_1 to t_2 is approximately $(M_2 - M_1)/(t_2 - t_1) \times (\ln R_{X2} - \ln R_{X1})/(R_{X2} - R_{X1})$. Term M may be the combined total content of more than one mineral nutrient element. Instantaneously, A is obtained from functions fitted to $\ln M$ and to $\ln R_X$ versus t; if $\ln M = f_M(t)$ and $\ln R_X = f_{RX}(t)$, then $A = (1/R_X)(dM/dt) = f_M'(t) \times \exp(f_M(t) - f_{RX}(t))$.

Mean values are obtained from the formula given above, using the separate estimates (M_1, R_{X1}) and (M_2, R_{X2}) from times t_1 and t_2, respectively.

Figure 9 shows curves for specific absorption rate in cultivated cranberry (*Vaccinium macrocarpon*); mycorrhizal infection increases nitrogen uptake but soil irradiation does not.

Relevance

These are rates of production of something per unit of something else. In plant growth analysis, provided that the "something" Y is of interest to the experimenter and that the "something else" Z may reasonably be held responsible for its production, then $(1/Z)(dY/dt)$ is an analytical tool of fundamental

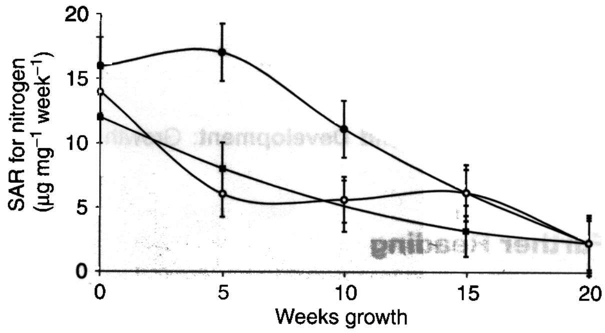

Figure 9 The progress of instantaneous specific absorption rate (SAR) for nitrogen in cultivated cranberry grown in a controlled environment: ■, mycorrhizal plants grown on poor soil; •, mycorrhizal plants grown on the irradiated soil; ○, nonmycorrhizal plants grown on the irradiated soil (95% confidence limits are added). Reproduced with permission from Stribley DP, Read OJ, and Hunt R (1975) The biology of mycorrhiza in the Ericaceae. V. The effects of mycorrhizal infection, soil type and partial soil-sterilization (by gamma-irradiation) on growth of cranberry (*Vaccinium macrocarpon* Ait.). *New Phytologist* 75: 119–130.

importance. As such, it has been used to describe plant processes from the molecular level, through organs, and whole herbaceous plants up to perennial woody crops. There is no reason why such applications should not flourish still further.

Interrelations

In General

Although the terms involved in plant growth analysis have the individual meanings described above, their strength as analytical tools owes much to their interrelations with one another, or the ways in which an individual term may be decomposed into others. Various types of interrelation can occur, but they all have the status of mathematical identities, not conditional equations. (A mathematical identity states a logical truth, not an hypothesis that is open to disproof.)

Simple

Where both parts of a simple ratio or fraction bear the same units, they provide an index of the importance of one component of the plant in relation to another. All such components can be linked into a single scheme. As a simple example, in young grasses if R_W/W is the root weight ratio (where R_W is the total root dry weight of the plant), S_W/W is the stem weight ratio (where S_W is the total stem dry weight of the plant), and L_W/W is the leaf weight ratio (where L_W is the total leaf dry weight of the plant), then the three are related by the expression $R_W/W + S_W/W + L_W/W = 1$.

Interrelations between more heterogeneous quantities can also occur. For example, a subdivision of leaf area ratio is $L_A/W = L_A/L_W \times L_W/W$, where L_A/L_W is the specific leaf area and L_W/W is the leaf weight ratio. By looking simultaneously at all three of these terms it is possible, for example, to establish that the much less leafy nature of Scots pine (*Pinus sylvestris*), in comparison with sunflower (*Helianthus* spp.), is due almost entirely to the relatively greater density of the pine needles and hardly at all to variation in leaf weight ratio (the productive investment of the plant), which, in fact, shows a small difference in favor of pine.

More Complex

It is often useful to subdivide an index of overall performance, such as relative growth rate, into indices that represent the individual performances of components of the system. In fact, unit leaf rate and leaf area ratio originally evolved as subdivisions of relative growth rate. So, it is by definition that $(1/W)(dW/dt) = (1/L_A)(dW/dt) \times L_A/W$. Simply expressed, the growth rate of the plant depends simultaneously upon the efficiency of its leaves as producers of new material and upon the leafiness of the plant itself. (Except in very special circumstances, this relation holds only approximately for the three mean values of these quantities; instantaneous values are needed for the interrelation to be exact.) Also, as $L_A/W = L_A/L_W \times L_W/W$, these subdivisions of leaf area ratio may be inserted into the equation for relative growth rate to give $(1/W)(dW/dt) = (1/L_A)(dW/dt) \times L_A/L_W \times L_W/W$ otherwise, relative growth rate expressed as the product of unit leaf rate, specific leaf area, and leaf weight ratio.

Tools for Performing the Calculations

Classical Approach

The instantaneous mathematical definitions of the various terms are usually not amenable to direct substitution of experimental data. That is why the harvest interval mean formulae were developed. When using these formulae, however, if there has been any replication of the measurements that require logarithmic transformation and it is wished to work with harvest mean values of these variables, it is important to calculate these as (for example) mean(ln W) and not ln(mean W).

The statistical properties of the harvest interval means are important and often neglected. It is incorrect simply to calculate, say, the variance of a group of several unit leaf rates spanning the same harvest interval. Not only does this involve difficult decisions as to how to "pair" the primary data across the harvest interval, but it also ignores the fact that the statistical properties of a derived term depend upon those of its primary data and not upon those of its sibling values. Spreadsheet tools are available within the growth analytical literature that will perform these calculations correctly.

Functional Approach

This involves curve fitting. The great advantages are that the instantaneously defined terms can be obtained directly from the fitted curves, seen in their exact interrelation to one another, and provided with statistics derived only from the primary data. The disadvantage is that an appropriate type of fitted curve has to be selected and applied, without under-fitting (forcing the data into too simple a strait-jacket) or over-fitting (chasing off after outliers, which should really be eliminated or smoothed). The growth analytical literature contains tools for fitting low-order polynomials, nonlinear asymptotic functions with up to four parameters, and splined curves (smoothly joined polynomials) which offer almost unlimited flexibility.

List of Technical Nomenclature

A	Specific absorption rate.
b	Intercept coefficient in allometry.
E	Unit leaf rate (net assimilation rate).
F	Leaf area ratio.
f	Suitable mathematical function.
f'	Slope of function *f*.
G	Absolute growth rate.
K	Allometric coefficient.
L_A	Total leaf area per plant.
L_W	Total leaf dry weight per plant.
M	Total mineral nutrient content per plant.
N	Integer number of individual organs.
R	Relative growth rate.
R_W	Total root dry weight per plant.
R_X	Root size, generalized.
S_W	Total shoot dry weight per plant or total stem dry weight per plant (according to context).
t	Time.
W	Total dry weight per plant.
	Generalized real number.
Y	Generalized plant variate.
Z	Generalized plant variate.

See also: **Growth and Development**: Growth Analysis, Crops.

Further Reading

Causton DR (1983) *A Biologist's Basic Mathematics.* Edward Arnold: London.

Causton DR and Venus JC (1981) *The Biometry of Plant Growth.* London: Edward Arnold.

Evans GC (1972) *The Quantitative Analysis of Plant Growth.* Oxford: Blackwell Scientific Publications.

Hunt R (1978) *Plant Growth Analysis.* London: Edward Arnold.

Hunt R (1982) *Plant Growth Analysis: Statistical Checklist No 4.* Cambridge: Institute of Terrestrial Ecology.

Hunt R (1982) *Plant Growth Curves: the Functional Approach to Plant Growth Analysis.* London: Edward Arnold.

Hunt R (1990) *Basic Growth Analysis: Plant Growth Analysis for Beginners.* London: Unwin Hyman.

Hunt R and Cornelissen JHC (1997) Components of relative growth rate and their interrelations in 59 temperate plant species. *New Phytologist* 135: 395–417.

Hunt R and Evans GC (1980) Classical data on the growth of maize: curve-fitting with statistical analysis. *New Phytologist* 86: 155–180.

Hunt R and Lloyd PS (1987) Growth and Partitioning. In: Rorison IH, Grime JP, Hunt R, Hendry GAF, and Lewis DH (eds) *Frontiers of Comparative Plant Ecology,* pp. 235–249. London: Academic Press.

Hunt R, Causton DR, Shipley B, and Askew AP (2002) A modern tool for classical plant growth analysis. *Annals of Botany* 90: 485–488.

Mead R and Curnow RN (1983) *Statistical Methods in Agriculture and Experimental Biology.* London: Chapman and Hall.

Sattler R (1986) *Biophilosophy: Analytic and Holistic Perspectives.* Berlin: Springer-Verlag.

Growth Analysis, Crops

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Introduction

The cardinal concepts of plant growth analysis (*see* **Growth and Development**: Growth Analysis, Individual Plants) are those of:

- rates of growth (such as absolute or relative growth rate);