

1990

Demographic Growth Analysis

James B. McGraw

Keith Garbutt

Follow this and additional works at: https://researchrepository.wvu.edu/faculty_publications

Digital Commons Citation

McGraw, James B. and Garbutt, Keith, "Demographic Growth Analysis" (1990). *Faculty Scholarship*. 116.
https://researchrepository.wvu.edu/faculty_publications/116

This Article is brought to you for free and open access by The Research Repository @ WVU. It has been accepted for inclusion in Faculty Scholarship by an authorized administrator of The Research Repository @ WVU. For more information, please contact ian.harmon@mail.wvu.edu.



Demographic Growth Analysis

James B. McGraw; Keith Garbutt

Ecology, Vol. 71, No. 3. (Jun., 1990), pp. 1199-1204.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28199006%2971%3A3%3C1199%3ADGA%3E2.0.CO%3B2-I>

Ecology is currently published by Ecological Society of America.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

The JSTOR Archive is a trusted digital repository providing for long-term preservation and access to leading academic journals and scholarly literature from around the world. The Archive is supported by libraries, scholarly societies, publishers, and foundations. It is an initiative of JSTOR, a not-for-profit organization with a mission to help the scholarly community take advantage of advances in technology. For more information regarding JSTOR, please contact support@jstor.org.

Ecology, 71(3), 1990, pp. 1199–2004
 © 1990 by the Ecological Society of America

DEMOGRAPHIC GROWTH ANALYSIS

James B. McGraw and Keith Garbutt¹

Conventional plant growth analysis (Blackman 1919) and recent advances in it (Causton and Venus 1981, Kauffman 1981, Parsons and Hunt 1981, Hunt 1982) have provided useful tools for describing plant growth in terms of biomass accumulation. However, for certain kinds of studies, growth analysis has serious drawbacks. These include: (1) Growth analysis is difficult to implement in field studies. Roots are difficult, or often impossible, to isolate from natural soils, and thus total plant biomass often cannot be obtained. Even where complete destructive harvests can be carried out, environmental heterogeneity increases the sample size required to obtain firm estimates of growth parameters. (2) Using the conventional harvest methodology of growth analysis, growth rate cannot be determined for individual plants, making it difficult to estimate variance in growth parameters among individuals. (3) Conventional growth analysis is labor-intensive; this places limits on the sample size that can be achieved per harvest, which in turn (a) limits the ability to determine growth rates over short intervals, (b) restricts the number of treatments for which growth parameters can be calculated, and (c) decreases the power of statistical tests for treatment differences. (4) Unless plants are rearranged at every harvest, densities change through the course of an experiment. This change in density is a particularly serious problem in the field, where density change cannot be readily accommodated by moving plants.

Bazzaz and Harper (1977) pioneered a new approach to analyzing growth that recognized the modular, population-like structure of an individual plant. By marking and censusing parts of the plant, it was possible to measure births and deaths of those parts, calculate turnover, population growth rates, etc., giving a great deal of information about the dynamics of growth within an individual plant. Demographic models could now be applied to the "metapopulation" as a completely different way of assessing plant growth. Many researchers followed the lead of Bazzaz and Harper (1977), applying modular, demographic approaches to a variety of species in natural environments (e.g., Abul-Fatih and Bazzaz 1980, Shaver 1981, Maillette 1982, Chester and McGraw 1983, Fetcher and Shaver 1983,

Garbutt and Bazzaz 1983, McGraw and Antonovics 1983, McGraw 1989). With this method, some disadvantages of classical growth analysis are overcome, including the problems of variance estimation and application of the method in field studies. Despite its many good features, modular demography has drawbacks. One problem is that links of modular growth rate to photosynthesis, and hence to other physiological processes, are less clear. For example, a modular analysis yields no equivalent of unit leaf rate (the rate of biomass increase per unit leaf area), which is proportional to a time-integrated measure of photosynthesis on a whole-plant basis. A second problem is that performing detailed censuses to parameterize demographic models can be labor-intensive; hence estimates of modular population growth rate on a large number of individuals may be impractical.

In the present paper we present demographic growth analysis, a hybrid approach that retains the formal mathematical structure of growth analysis, while incorporating the advantages of modular demography. The essence of demographic growth analysis is that a proper surrogate is chosen for plant dry mass, utilizing the concept that a plant is constructed of a population of parts, and that this metapopulation size (η) can effectively substitute for destructive measures of plant dry mass in growth analysis. The particular plant parts chosen—e.g., leaves, stems, buds, shoots—can vary from species to species, depending on what is appropriate. Below, we illustrate the new method with a study of ten seed families of *Abutilon theophrasti*, a common weed of agricultural fields. A parallel comparison of demographic and conventional growth analysis illustrates the effectiveness of the new approach.

Methods

Demographic growth analysis. Seeds of ten half-sib families of *A. theophrasti* were collected from plants growing in a corn field at the University of Illinois field station (Philips Tract) near Urbana, Illinois, in fall, 1983. On 7 March 1988, after breaking dormancy by boiling the seeds for 15 s, 2–4 seeds from each family were sown in each of ten plastic pots ($n = 100$ pots; 10 pots per family) containing 250 mL of surface (chipped montmorillonite clay; Applied Industrial Mineral Corporation). Pots were assigned completely randomly to positions on a greenhouse bench where they were kept for the duration of the experiment. Within one week most seedlings had emerged, and pots were thinned to a density of one plant per pot. Pots were watered twice daily for the first 10 d and once daily thereafter. Fifty mL of Miracle Gro nutrient solution were added to each pot at weekly intervals. Censuses were carried out 10 d after sowing, then weekly there-

¹ Department of Biology, P.O. Box 6057, West Virginia University, Morgantown, West Virginia 26506-6057 USA.

TABLE 1. Formulations for conventional growth analysis and demographic growth analysis. \bar{W} = total plant biomass, \bar{w} = mean plant biomass for a group of harvested plants, \bar{A} = leaf area, \bar{a} = mean leaf area, t = time, and η = number of modules. To differentiate between conventional growth analysis (GA) and demographic growth analysis (DGA) we write the acronym for the demographic quantity with a "D" at the beginning (e.g., RGR → DRGR).

Derived quantity	Acronym	GA instantaneous value	GA interval formula	DGA analog instantaneous value	DGA analog interval formula
Absolute growth rate	DAGR	$\frac{d\bar{W}}{dt}$	$\frac{\bar{W}_2 - \bar{W}_1}{t_2 - t_1}$	$\frac{d\eta}{dt}$	$\frac{\eta_2 - \eta_1}{t_2 - t_1}$
Absolute growth rate in leaf area	DAGR _A	$\frac{d\bar{A}}{dt}$	$\frac{\bar{A}_2 - \bar{A}_1}{t_2 - t_1}$	$\frac{dA}{dt}$	$\frac{A_2 - A_1}{t_2 - t_1}$
Relative growth rate	DRGR	$\frac{1}{\bar{W}} \frac{d\bar{W}}{dt}$	$\frac{\ln \bar{W}_2 - \ln \bar{W}_1}{t_2 - t_1}$	$\frac{1}{\eta} \frac{d\eta}{dt}$	$\frac{\ln \eta_2 - \ln \eta_1}{t_2 - t_1}$
Relative growth rate on an area basis	DRGR _A	$\frac{1}{\bar{A}} \frac{d\bar{A}}{dt}$	$\frac{\ln \bar{A}_2 - \ln \bar{A}_1}{t_2 - t_1}$	$\frac{1}{A} \frac{dA}{dt}$	$\frac{\ln A_2 - \ln A_1}{t_2 - t_1}$
Unit leaf rate (=net assimilation rate)	DULR (=DNAR)	$\frac{1}{\bar{A}} \frac{d\bar{W}}{dt}$	$\left(\frac{\bar{W}_2 - \bar{W}_1}{t_2 - t_1}\right) \cdot \left(\frac{\ln \bar{A}_2 - \ln \bar{A}_1}{\bar{A}_2 - \bar{A}_1}\right)$	$\frac{1}{A} \frac{d\eta}{dt}$	$\left(\frac{\eta_2 - \eta_1}{t_2 - t_1}\right) \cdot \left(\frac{\ln A_2 - \ln A_1}{A_2 - A_1}\right)$
Unit module rate	DUMR†	$\frac{1}{\bar{W}} \frac{d\bar{A}}{dt}$	$\left(\frac{\bar{A}_2 - \bar{A}_1}{t_2 - t_1}\right) \cdot \left(\frac{\ln \bar{W}_2 - \ln \bar{W}_1}{\bar{W}_2 - \bar{W}_1}\right)$	$\frac{1}{\eta} \frac{dA}{dt}$	$\left(\frac{A_2 - A_1}{t_2 - t_1}\right) \cdot \left(\frac{\ln \eta_2 - \ln \eta_1}{\eta_2 - \eta_1}\right)$
Leaf area ratio	DLAR	$\frac{\bar{A}}{\bar{W}}$	$\frac{(\bar{A}_2/\bar{W}_2) + (\bar{A}_1/\bar{W}_1)}{2}$	$\frac{A}{\eta}$	$\frac{(A_2/\eta_2) + (A_1/\eta_1)}{2}$
Leaf area duration	DLAD	Does not exist	$\frac{(\bar{A}_1 + \bar{A}_2)(t_2 - t_1)}{2}$	Does not exist	$\frac{(A_1 + A_2)(t_2 - t_1)}{2}$
Module number duration	DMND†	Does not exist	$\frac{(\bar{W}_1 + \bar{W}_2)(t_2 - t_1)}{2}$	Does not exist	$\frac{(\eta_1 + \eta_2)(t_2 - t_1)}{2}$

* \bar{W} and \bar{w} have been used, rather than M and \bar{M} , for mass in order to conform with the established conventions of the growth-analysis literature.

† Not standard for conventional growth analysis, but can be computed from the data.

after for 12 wk, by which time most plants had ceased growth and become reproductive. Each census involved counting and marking leaves on each plant. At the first census, leaf area was measured on each plant directly and nondestructively using a video camera-based area meter (Delta-T Devices, Cambridge, England). In subsequent censuses, leaf length was measured on each leaf to determine leaf area by polynomial regression, using an equation derived by harvesting a few additional plants at each census ($r^2 > 0.97$ for all equations used). Destructive harvesting was not necessary for this procedure. However, since conventional growth analysis was being carried out at the same time, it was convenient in this instance.

To differentiate between conventional growth analysis (GA) and demographic growth analysis (DGA), we propose that the acronym for the demographic quantity be written with a "D" at the beginning; thus "RGR" would become "DRGR," etc. Absolute growth rates (DAGR and DAGR_A), relative growth rates (DRGR and DRGR_A), unit rates (DULR and DUMR), demographic leaf area ratios (DLAR), leaf area duration (DLAD), and module number duration (DMND) were

determined for each individual plant in each census interval in the experiment according to the formulas in Table 1. Most of these measures have a direct analog with conventional growth analysis, which allows a direct comparison of the two parameters (although units will differ). Demographic relative growth rate (DRGR) is equivalent to the natural log of λ in modular demography for module populations in a stable stage/age distribution.

Since growth parameters could be determined for each individual plant, one-way analysis of variance could be used to determine whether there were significant differences among families. This analysis was carried out using PROC GLM (SAS 1985).

Conventional growth analysis. At the same time and in the same manner as for the demographic growth analysis experiment, seeds were sown for conventional growth analysis in 500 pots randomly placed and intermingled on the same greenhouse bench. Fifty plants from each of the same ten half-sib families were planted, to permit 10 harvests of 5 plants per family at each harvest. Plants were treated in the same manner upon emergence as those used for demographic growth anal-

ysis. Harvests were carried out at the same times as for demographic growth analysis, although after harvest 7, they were carried out bi-weekly to extend the analysis into the flowering phase. At harvest the growth medium was washed from the roots, plants were divided into root, stem, leaf, and reproductive tissue, and dried at 65°C for at least 48 h.

Conventional growth analysis parameters were determined by family for all plants, using the formulas in Table 1. Means and variances of growth parameters across all families were calculated, but these were not determined for each family separately since the growth parameters are not measured on each individual within a family in conventional growth analysis. Three of the growth parameters (RGR_A , AGR_A , and LAD) could be compared directly with those obtained from demographic growth analysis, since the formulas are the same. This allowed an evaluation of whether procedural differences between methods influenced the measured growth parameters. The remaining six growth parameters differed in units for the two procedures, and therefore could not be compared directly. However, the patterns of change in these parameters were compared by superimposing the values on the same graph.

Results

Using demographic growth analysis, we detected significant differences in several growth parameters among half-sib families of *A. theophrasti*. Early allocation differences were evident in the variation in $DLAR$ and $DLAD$ ($P < .05$). Early differences in $DULR$ (census intervals 2–5) were followed by differences in both absolute and relative growth rates ($DAGR$, $DRGR$, and $DRGR_A$; $P < .05$). Family means for $DRGR$ and $DULR$ during census interval 5 were positively correlated with mean final leaf area achieved by that family ($r^2 = 0.53$, $P < .05$ for $DRGR$; $r^2 = 0.677$, $P < .05$ for $DULR$). Differences among families generally decreased past census interval 5. The analyses described above were performed separately for each census interval. However, the experimental design also lends itself to one of a number of repeated-measures analyses (e.g., repeated-measures ANOVA).

In *A. theophrasti*, because of the sharp changes in the size of successive leaves, many of the demographic growth parameters do not parallel their counterparts in conventional growth analysis, i.e., leaf number is not a good surrogate for mass in this species. Therefore, strictly area-based measures of growth rate ($DAGR_A$, $DRGR_A$) and pattern ($DLAD$) best approximated conventional measures (Fig. 1). As expected, the curves for these parameters were parallel for growth analysis (GA) and demographic growth analysis (DGA). Small differences in a few censuses may be due to differences

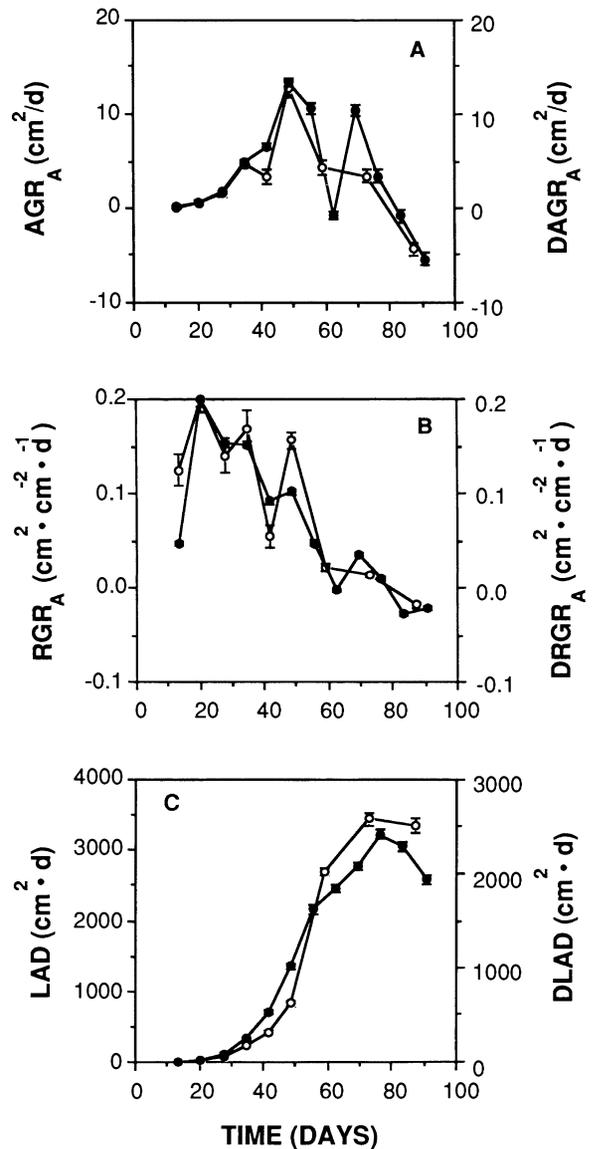


FIG. 1. Comparison of growth analysis parameters and their demographic growth analysis analogs that have common units. Acronyms are defined in Table 1. ● values derived from demographic growth analysis; ○ values derived from conventional growth analysis.

in the methods of estimating area for GA and DGA. The GA method clearly missed fluctuations in $DAGR_A$ and $DRGR_A$ due to the 2-wk census interval near the end of the experiment (vs. 1 wk for DGA; Fig. 1A, B).

Some DGA and GA parameters showed similar patterns over the course of the study, but were displaced to the right or left for DGA (Fig. 2A–C). This is explained by the fact that leaf numbers reached a plateau early, while mass continued to increase until the end of the experiment. Other parameters differed between

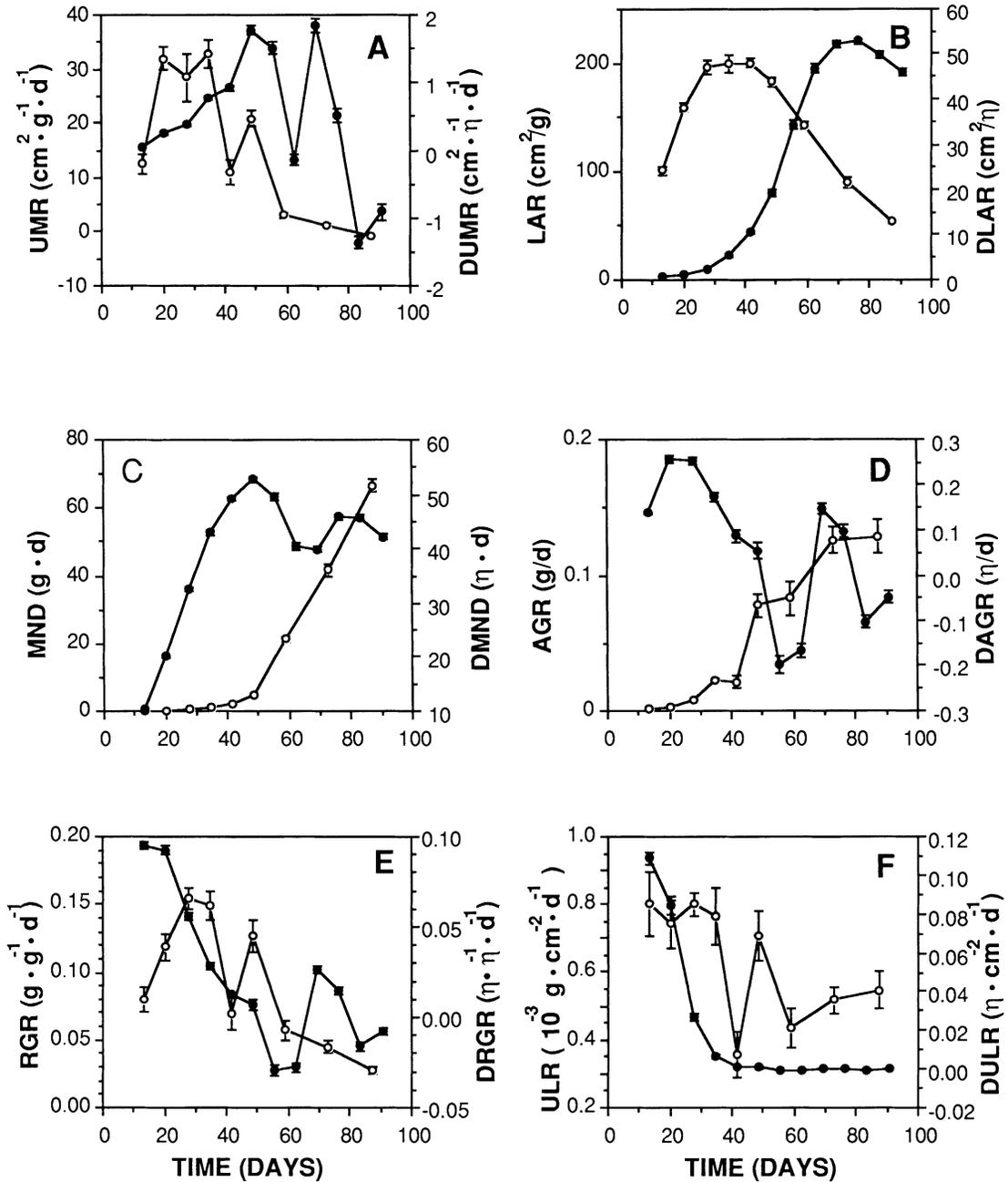


FIG. 2. Comparison of growth analysis parameters and their demographic growth analysis analogs that are measured in different units. Acronyms are defined in Table 1. ● values derived from demographic growth analysis; ○ values derived from conventional growth analysis.

the two methods, and DGA revealed aspects of growth that were not evident from GA. For example, DAGR (Fig. 2D) dropped below zero during the 2 wk corresponding to flower bud formation, increased while flowers were open, and decreased again during capsule formation, suggesting that leaf birth, senescence, and

abscission were strongly tied to the reproductive activity of the plant.

In general, parameters estimated by DGA had smaller standard errors than their counterparts estimated by GA. This was most likely due to the larger sample size possible with DGA than GA.

Discussion

The advantages of the composite demographic growth analysis approach are: (1) Measurements are made on the individual, and thus legitimate estimates of variances of DRGR and DULR can be determined (as well as of the other parameters), allowing comparisons of genotypes, species, and treatment effects in a rigorous, statistically sound manner. In addition, growth is being measured on the same units as physiological measurements (the individual, and leaves or shoots within the individual), and thus physiological variation can be related directly to growth-rate variation. (2) Retaining the mathematical structure of classical growth analysis maintains the links with physiological variation. (3) Measurements are readily carried out in the field. (4) For a given amount of effort, the sample size can be approximately two- to three-fold greater for demographic than for conventional growth analysis. This lowers the standard error of the measurements, and increases the power to detect statistical differences among groups of plants. (5) Densities can be kept constant or allowed to change naturally, since plants are not removed by destructive harvesting.

The disadvantages of demographic growth analysis are those inherent in most demographic approaches: The entire plant is not measured, and thus a complete biomass budget and allocation pattern cannot be estimated. Roots, especially, are ignored, and while demography of roots is theoretically possible, root biomass is easier to measure than root numbers. This problem can be reduced by destructively harvesting a few plants at each census to obtain allometric relationships that can allow whole-plant dry mass to be estimated from the non-destructive measures (example in Schmitt et al. [1987]). Knowing the ratio of biomass to module number from harvested plants, biomass could then be derived for censused plants from module number. A second problem is that number of modules, unlike plant biomass, is a discrete value, so that a somewhat arbitrary decision must be made concerning when a module can be counted. This, too, can be accommodated, particularly in modules where size can be calculated as a proportion of final size achieved on expansion. For example, if a leaf is half-expanded (has half of its final area), it could be counted as 0.5 leaves at that census. This procedure could smooth growth curves plotted for individual plants and reduce the variance in module number at each census. A third problem is that for some plants it may be difficult to find an appropriate demographic surrogate for biomass. Indeed, this was illustrated by the present study; in *A. theophrasti*, leaf number is not highly correlated with leaf area or total biomass. Therefore, this annual plant is not an ideal species for demographic growth

analysis. The fact that the demographic analysis was successfully applied to it suggests that the technique will work very well for other species with a modular architecture. For plants in which modules are highly variable in size (as for leaves in *A. theophrasti*), leaf area can be used. However, most species possess a variety of easily counted modules (leaves, buds, nodes, shoots, etc.) that can be used for demographic growth analysis. As our analysis also showed, even where these measures do not parallel biomass changes, useful interpretations can be made. The technique could be readily adapted to studies in perennial plants by lengthening the interval between censuses; an annual census at a prescribed date or phenostage might be most appropriate in long-lived plants. With large perennials such as shrubs, trees, or clonal plants, subsampling the module population would permit manageable censuses for demographic growth analysis.

Ours is not the first attempt at hybridizing conventional and alternative techniques for analyzing plant growth (Hunt 1978, Hunt and Bazzaz 1980, Porter 1983a, b). Hunt (1978) proposed, and later tested (Hunt and Bazzaz 1980), a method that scales down growth analysis to operate at the modular level. This approach was shown to be useful in interpreting the details of the modular response to fertilizer of *Ambrosia trifida*. Demographic growth analysis takes precisely the opposite tack, scaling up modular analysis to the level of the individual. This is essentially an extension of indirect growth analysis (Chiariello 1989). Typically, indirect growth analysis has involved making estimates of total biomass and area, using allometry determined by parallel harvests, for the purpose of performing classical growth analysis on the derived biomass values (Ondok 1971). Although this procedure could be followed with DGA (not shown in this study), we would argue (as others have for strictly demographic analysis—e.g., Harper 1980) that module number may in many cases be *more* relevant to ecological performance (effect on neighbors, flower production, survival, resistance to herbivores, etc.) than biomass. Thus demographic growth analysis goes beyond emulating conventional growth analysis, permitting experiments, results, and conclusions not possible with other techniques.

Literature Cited

- Abul-Fatih, H. A., and F. A. Bazzaz. 1980. The biology of *Ambrosia trifida* L. IV. Demography of plants and leaves. *New Phytologist* **84**:107–111.
- Bazzaz, F. A., and J. L. Harper. 1977. Demographic analysis of the growth of *Linum usitatissimum*. *New Phytologist* **78**:193–208.
- Blackman, V. H. 1919. The compound interest law and plant growth. *Annals of Botany* **33**:353–360.

- Causton, D. R., and J. C. Venus. 1981. The biometry of plant growth. Edward Arnold, London, England.
- Chester, A. L., and J. B. McGraw. 1983. Effects of nitrogen addition on the growth of *Vaccinium uliginosum* and *Vaccinium vitis-idaea*. Canadian Journal of Botany **61**:2316–2322.
- Chiariello, N. R. 1989. Plant populations and ecophysiology. Bulletin of the Ecological Society of America **70**:62–63.
- Fetcher, N., and G. R. Shaver. 1983. Life histories of tillers of *Eriophorum vaginatum* in relation to disturbance. Journal of Ecology **71**:131–148.
- Garbutt, K., and F. A. Bazzaz. 1983. Leaf demography, flower production and biomass of diploid and tetraploid populations of *Phlox drummondii* Hook. on a soil moisture gradient. New Phytologist **93**:129–141.
- Harper, J. L. 1980. Plant demography and ecological theory. Oikos **35**:244–253.
- Hunt, R. 1978. Demography versus plant growth analysis. New Phytologist **80**:269–272.
- . 1982. Plant growth curves: an introduction to the functional approach to plant growth analysis. Edward Arnold, London, England.
- Hunt, R., and F. A. Bazzaz. 1980. The Biology of *Ambrosia trifida* L. V. Response to fertilizer with growth analysis at the organismal and sub-organismal levels. New Phytologist **84**:113–121.
- Kauffman, K. W. 1981. Fitting and using growth curves. Oecologia (Berlin) **49**:293–299.
- Maillette, L. 1982. Structural dynamics of silver birch. II. A matrix model of the bud population. Journal of Applied Ecology **19**:219–238.
- McGraw, J. B. 1989. Effects of age and size on life histories and population growth of *Rhododendron maximum* shoots. American Journal of Botany **76**:113–123.
- McGraw, J. B., and J. Antonovics. 1983. Experimental ecology of *Dryas octopetala* ecotypes. II. A demographic model of growth, branching and fecundity. Journal of Ecology **71**:899–912.
- Ondok, J. P. 1971. Indirect estimation of primary values used in growth analysis. Pages 343–391 in Z. Sestak, J. Catsky, and P. G. Jarvis, editors. Plant photosynthetic production. Manual of methods. Dr. W. Junk, The Hague, The Netherlands.
- Parsons, I. T., and R. Hunt. 1981. Plant growth analysis: a curve-fitting program using the method of B-splines. Annals of Botany **48**:341–352.
- Porter, J. K. 1983a. A modular approach to analysis of plant growth. I. Theory and principles. New Phytologist **94**:183–190.
- . 1983b. A modular approach to analysis of plant growth. II. Methods and results. New Phytologist **94**:183–190.
- SAS (Statistical Analysis Systems). 1985. SAS user's guide: statistics. SAS Institute, Cary, North Carolina, USA.
- Schmitt, J., J. Eccleston, and D. W. Ehrhardt. 1987. Dominance and suppression, size-dependent growth and self-thinning in a natural *Impatiens capensis* population. Journal of Ecology **75**:651–666.
- Shaver, G. R. 1981. Mineral nutrition and leaf longevity in an evergreen shrub, *Ledum palustre* ssp. *decumbens*. Oecologia (Berlin) **49**:362–365.

Manuscript received 5 May 1989;
revised 21 September 1989; accepted 25 September 1989;
final version received 18 October 1989.

Ecology, 71(3), 1990, pp. 2004–2007
© 1990 by the Ecological Society of America

WILL THE REAL SELF-THINNING RULE PLEASE STAND UP?—A REPLY TO OSAWA AND SUGITA

Donald E. Weller¹

In their recent comment on my reevaluation of the self-thinning rule for even-aged plant populations (Weller 1987a), Osawa and Sugita (1989) raise three questions that require further discussion. What is the self-thinning rule? What kind of data and analyses are relevant to testing the rule? Do recent analyses support or refute the thinning rule as a quantitative law? I would like to address these questions, compare our approaches to the thinning rule, and clarify some misconceptions about my monograph (1987a).

¹ Smithsonian Environmental Research Center, P.O. Box 28, Edgewater, Maryland 21037-0028 USA.

The classic thinning rule states that measurements of crowded, even-aged plant populations form a thinning line of slope $-1/2$ when the logarithm of stand biomass (in mass per unit area) is plotted against the logarithm of plant density (in plants per unit area); or equivalently, a line of slope $-3/2$ when average plant biomass is plotted in place of total stand biomass (see review in Westoby 1984). At its zenith (see White 1981, Hutchings 1983, Westoby 1984), the rule united several size–density relationships that were all considered facets of a single quantitative law. More recently, the rule has been divided into two concepts that should be tested and explained independently: the interspecific size–density relationship and the single-species thinning line (Zeide 1985, 1987, Weller 1987a, 1989, Norberg 1988, Lonsdale 1990).

Osawa and Sugita (1989) advocate a different definition of the single-species thinning rule than the one I tested. They define the thinning line strictly as an upper boundary of possible yield–density combinations for a species, and fit the thinning line using data from the most extreme of several hundred stands. I refer to this line as the *species boundary line*. In contrast, I focused on the straight line that is approached and

LINKED CITATIONS

- Page 1 of 3 -



You have printed the following article:

Demographic Growth Analysis

James B. McGraw; Keith Garbutt

Ecology, Vol. 71, No. 3. (Jun., 1990), pp. 1199-1204.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28199006%2971%3A3%3C1199%3ADGA%3E2.0.CO%3B2-I>

This article references the following linked citations. If you are trying to access articles from an off-campus location, you may be required to first logon via your library web site to access JSTOR. Please visit your library's website or contact a librarian to learn about options for remote access to JSTOR.

Literature Cited

The Biology of *Ambrosia trifida* L. IV. Demography of Plants and Leaves

H. A. Abul-Fatih; F. A. Bazzaz

New Phytologist, Vol. 84, No. 1. (Jan., 1980), pp. 107-111.

Stable URL:

<http://links.jstor.org/sici?sici=0028-646X%28198001%2984%3A1%3C107%3ATBOATL%3E2.0.CO%3B2-G>

Demographic Analysis of the Growth of *Linum usitatissimum*

F. A. Bazzaz; John L. Harper

New Phytologist, Vol. 78, No. 1. (Jan., 1977), pp. 193-208.

Stable URL:

<http://links.jstor.org/sici?sici=0028-646X%28197701%2978%3A1%3C193%3ADAOTGO%3E2.0.CO%3B2-C>

Life Histories of Tillers of *Eriophorum Vaginatum* in Relation to Tundra Disturbance

Ned Fetcher; G. R. Shaver

The Journal of Ecology, Vol. 71, No. 1. (Mar., 1983), pp. 131-147.

Stable URL:

<http://links.jstor.org/sici?sici=0022-0477%28198303%2971%3A1%3C131%3ALHOTOE%3E2.0.CO%3B2-M>

Leaf Demography, Flower Production and Biomass of Diploid and Tetraploid Populations of *Phlox drummondii* Hook. On a Soil Moisture Gradient

K. Garbutt; F. A. Bazzaz

New Phytologist, Vol. 93, No. 1. (Jan., 1983), pp. 129-141.

Stable URL:

<http://links.jstor.org/sici?sici=0028-646X%28198301%2993%3A1%3C129%3ALDFPAB%3E2.0.CO%3B2-C>

LINKED CITATIONS

- Page 2 of 3 -



Demography Versus Plant Growth Analysis

Roderick Hunt

New Phytologist, Vol. 80, No. 1. (Jan., 1978), pp. 269-272.

Stable URL:

<http://links.jstor.org/sici?sici=0028-646X%28197801%2980%3A1%3C269%3ADVPGA%3E2.0.CO%3B2-C>

The Biology of *Ambrosia trifida* L. V. Response to Fertilizer, with Growth Analysis at the Organismal and Sub-Organismal Levels

Roderick Hunt; F. A. Bazzaz

New Phytologist, Vol. 84, No. 1. (Jan., 1980), pp. 113-121.

Stable URL:

<http://links.jstor.org/sici?sici=0028-646X%28198001%2984%3A1%3C113%3ATBOATL%3E2.0.CO%3B2-H>

Structural Dynamics of Silver Birch. II. A Matrix Model of the Bud Population

Lucie Maillette

The Journal of Applied Ecology, Vol. 19, No. 1. (Apr., 1982), pp. 219-238.

Stable URL:

<http://links.jstor.org/sici?sici=0021-8901%28198204%2919%3A1%3C219%3ASDOSBI%3E2.0.CO%3B2-2>

Effects of Age and Size on Life Histories and Population Growth of *Rhododendron maximum* Shoots

James B. McGraw

American Journal of Botany, Vol. 76, No. 1. (Jan., 1989), pp. 113-123.

Stable URL:

<http://links.jstor.org/sici?sici=0002-9122%28198901%2976%3A1%3C113%3AEQAASO%3E2.0.CO%3B2-U>

Experimental Ecology of *Dryas Octopetala* Ecotypes: II. A Demographic Model of Growth, Branching and Fecundity

J. B. McGraw; J. Antonovics

The Journal of Ecology, Vol. 71, No. 3. (Nov., 1983), pp. 899-912.

Stable URL:

<http://links.jstor.org/sici?sici=0022-0477%28198311%2971%3A3%3C899%3AEEOEOE%3E2.0.CO%3B2-J>

A Modular Approach to Analysis of Plant Growth. I. Theory and Principles

J. R. Porter

New Phytologist, Vol. 94, No. 2. (Jun., 1983), pp. 183-190.

Stable URL:

<http://links.jstor.org/sici?sici=0028-646X%28198306%2994%3A2%3C183%3AAMATAO%3E2.0.CO%3B2-W>

LINKED CITATIONS

- Page 3 of 3 -



A Modular Approach to Analysis of Plant Growth. I. Theory and Principles

J. R. Porter

New Phytologist, Vol. 94, No. 2. (Jun., 1983), pp. 183-190.

Stable URL:

<http://links.jstor.org/sici?sici=0028-646X%28198306%2994%3A2%3C183%3AAMATAO%3E2.0.CO%3B2-W>

Dominance and Suppression, Size-Dependent Growth and Self-Thinning in a Natural *Impatiens Capensis* Population

Johanna Schmitt; Jill Eccleston; D. W. Ehrhardt

The Journal of Ecology, Vol. 75, No. 3. (Sep., 1987), pp. 651-665.

Stable URL:

<http://links.jstor.org/sici?sici=0022-0477%28198709%2975%3A3%3C651%3ADASSGA%3E2.0.CO%3B2-N>