

Toward a metabolic scaling theory of crop systems

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Stable and secure food production is essential to civilization. Any methods that improve our understanding of crop yields have the potential to reduce human suffering and help provide the caloric needs of an expanding world population. Similar hopes apply to commodity crops such as cotton and those used to meet energy needs. Given the vast amount of agricultural research and experience, it might be expected that we have a thorough understanding of the major crops upon which our civilization depends. As is evident from all-too-frequent crop failures, we clearly do not have a very effective means to predict yields accurately. The assumption is that year-to-year yield variability in crop yields arises from factors outside our control such as varying weather conditions. Although weather-impacted yield variability may not be feasibly and economically constrained by management practice, the expectation is that increased knowledge of crop systems will enhance the efficacy of management. Deng et al. (1) point out how to obtain relatively simple macrodescriptors of crop growth that are applicable across diverse species, and provide the surprising result that the single variable of maximal size at maturity can be used to project major crop properties such as maximal yield.

Many of the key questions driving plant science arise from agriculture (2), and it is therefore appropriate to consider a panoply of approaches to enhance knowledge of crop systems. As with much of the life sciences, the tendency in recent decades has been to delve further and further into details of the genetics and cell physiology of important crops, providing a much greater understanding of biological processes at the molecular and cellular level. This reductionist approach has created opportunities, and concerns in some quarters, for genetically modified crops to significantly reduce the impacts of disease and weather on crop yield.

Models of Crop Systems

Coincident with the growth in data and mechanistic understanding of processes at the cellular level has been the expansion of process-oriented models for whole-plant growth. Early crop models used few details of plant architecture, physiological responses of photosynthesis and respiration, below-ground processes, or developmental

pathways. Instrumentation now provides the capacity to obtain real-time data on many physiological processes and stand-level information on CO₂ uptake and transpiration losses. Although analysis at the whole-plant level has languished as the research focus shifted to the cell level and below, there have been extensive ongoing efforts to derive detailed whole-plant models that are consistent with observations. These models have explicit environmental drivers, incorporate diurnal responses, account for soil moisture and nutrients, consider interactions between individual plants, and have been used to project climate change impacts on crop yields and guide breeding programs (3). Compendia of plant models built on modular components have readily allowed them to be applied to diverse crops and varieties (4).

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Plant growth modeling has built upon the use of relatively simple growth functions tied to observation (5) and models based on the main physiological mechanisms affecting growth (6) to produce more detailed systems models, as pioneered by de Wit and colleagues (Wageningen University, The Netherlands). The range of systems models varies from those that include a small number of compartments mimicking aggregated components of crops such as root, stem, leaves, and seeds to those that track physiological details and differences among large numbers of individual plants. Although there can be rational disagreement concerning which details to include and exclude—for example, whether to incorporate details of above- and below-ground architecture (7) or how to account for lack of data on below-ground processes involving soil microbiota and their interactions with plant

root systems—elaborated systems models have been a main approach driving the study of whole-plant physiology.

An alternative theme in the development of plant models has been derived from mainly empirical perspectives focused on general rules for allometric growth, concerned with the capacity for relatively simple power-law relations to provide a reasonably accurate descriptor of various characteristics of plants. There is a long history of application of allometry in plant science, with an example being so-called self-thinning laws. These assert that changes in individual plant size and overall plant density (i.e., stems per unit area) vary through time in a local plant population or community, presumably because of competition for resources. The classic model indicated that average individual plant mass was proportional to plant density raised to a power of $-3/2$, but there is considerable empirical and theoretical evidence that such a relationship is not typical (8). The existence of general empirical scaling patterns, and prediction of these patterns from models based on metabolic assumptions for allocation of matter between plant parts, have been found for an array of vascular species (9), but there has not been concordance on a general theory (10).

Scaling and Crop Models

Plant allometry is directly aligned with efforts to discern general scaling patterns in biological systems (11). For animals and plants, a theory of metabolic scaling has arisen, with a goal of predicting macro-scale patterns at population and community level from the metabolic properties of individuals (12). Energetics is the main currency in this theory, as extensions of the observations of Kleiber concerning metabolic rates of mammals scaling as body mass to a power of $3/4$. Temperature is a critical component through its effects on energetics within organisms, and energy exchange links individuals to other levels of biological organization.

Building upon allometry and scaling, Deng et al. (1) present an approach to

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creating a simple but general model for annual crop growth. Observations on seeding planting density illustrates self-thinning, with there being an intermediate seeding density at which maximal stand growth occurs. High seed planting densities cause competition for resources at initial growth stages that reduces individual growth, whereas low seed planting densities do not fully use available resources. Starting with the assumption of logistic growth, Deng et al. (1) account for the impacts of seeding density, and their model predicts a seeding density at which a switch occurs in growth response. This is an optimum seeding density below which all plants reach their maximum potential size at maturity and above which the maximum size at maturity is proportional to seeding density to the $-4/3$ power. Nine years of empirical data on multiple crop species show that, when corrected for alternative potential maximum sizes at maturity for the different species, there is concordance with the predicted relationships and a sharp threshold in growth response [i.e., their figure 3 (1)].

Under reasonable simplifying assumptions, the allometric theory predicts that many aspects of crop growth can be calculated as a function only of maximum potential individual plant size at maturity. This can be used to calculate optimal seed planting density, maximum yield (assuming yield is directly correlated with biomass), and maximum energy use per unit area. There is remarkable concordance with the predicted results from a very large number of experiments at alternative seeding densities for numerous crop species [figure 4 (1)]. The result that a single variable can be used to effectively char-

acterize many aspects of crop growth is surprising and should foster new observations or analysis of existing data to determine if the generality goes beyond the extensive data sets of Deng et al. (1). This is an illustration of how theory can mesh with data-intensive science to more effectively explicate patterns in nature than could be done with only theory or statistical analysis of data. Their results also provide a means to evaluate crop systems models (4) by conducting in-silico experiments similar to the field experiments of Deng et al. (1) with differing seeding densities. If results from diverse crop system models reproduce figure 4 of Deng et al. (1), this provides strong evidence for the predictive capabilities of these models.

Although the results of Deng et al. (1) are quite effective at providing accurate mean predictions, what is missing is a mechanism to directly incorporate key aspects of plant growth to explain the variance structure of the results. This includes the impacts of phenotypic plasticity and other sources of individual variability that may not be effectively averaged out in the empirical analyses. Relaxing the model assumptions of optimum water and nutrient resource availability, with only competition for light limiting growth, leads to the longstanding issues of how to account for multiple limitations on plant growth. This initial development of a metabolic theory for crop growth is a step toward the development of a capacity to better predict variability of yields, but is not a panacea. Crop systems are highly constrained, as they are constructed the way an engineer might build a biological system—as repeated units that are as identical as can

be. If we can better understand how these constructed systems respond to individual differences and the vagaries of interacting factors affecting growth and yield, and build a general theory to do so, we might just find this to be feasibly extended to natural plant systems.

In the panoply of modeling approaches used in agriculture, the approach of Deng et al. (1) is at the end of the spectrum with the fewest parameters. However, through careful combination with extensive data—used not in a statistical analysis sense, but in a manner to evaluate their general theory—they have produced powerful, testable hypotheses. Although elaborate systems approaches that account for more of the complex of biotic and abiotic interactions within crops may be helpful in capturing finer details to account for variance in the observations, there is a cost to this in terms of loss of intuition. In an argument concerning the limitations of systems models, Thompson (13) notes that, although they may be informative, they should not be relied upon too heavily in informing policy for issues such as agricultural sustainability. As Deng et al. (1) clearly illustrate, there is much to be gained from the melding of theory based upon basic metabolic principles with the data sets we are readily able to obtain from crop systems.

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- Deng J, et al. (2012) Models and tests of optimal density and maximal yield for crop plants. *Proc Natl Acad Sci USA*, 10.1073/pnas.1210955109.
- Grierson CS, et al. (2011) One hundred important questions facing plant science research. *New Phytol* 192: 6–12.
- Heuvelink E, Marcelis LFM, Bakker MJ, Van Der Ploeg A (2007) Use of crop growth models to evaluate physiological traits in genotypes of horticultural crops. *Scale and Complexity in Plant Systems Research: Gene-Plant-Crop Relations*, eds Spiertz JHH, Struijk PC, van Laar HH (Springer, Heidelberg), pp 223–233.
- Jones JW, et al. (2003) DSSAT cropping system model. *Eur J Agron* 18:235–265.
- Hunt R, Causton DR, Shipley B, Askew AP (2002) A modern tool for classical plant growth analysis. *Ann Bot (Lond)* 90:485–488.
- Thornley JHM (1976) *Mathematical Models in Plant Physiology* (Academic, London).
- Fourcaud T, Zhang X, Stokes A, Lambers H, Körner C (2008) Plant growth modelling and applications: The increasing importance of plant architecture in growth models. *Ann Bot (Lond)* 101:1053–1063.
- Ford ED (2012) Plant competition and canopy interactions. *The Encyclopedia of Theoretical Ecology*, eds Hastings A, Gross LJ (Univ California, Berkeley), pp 565–571.
- Enquist BJ, Niklas KJ (2002) Global allocation rules for patterns of biomass partitioning in seed plants. *Science* 295:1517–1520.
- Niklas KJ (2004) Plant allometry: Is there a grand unifying theory? *Biol Rev Camb Philos Soc* 79:871–889.
- Levin SA (1992) The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.
- Thompson PB (2010) *The Agrarian Vision: Sustainability and Environmental Ethics* (Univ Kentucky, Lexington, KY).