

Following the growth of individuals in crowded plant populations

In plants and other sessile organisms with indeterminate growth, the basic demographic processes – birth and death – are very closely linked with the process of growth. For example, the mortality rate is often highest during periods of rapid growth through the process of self-thinning¹ in which the smallest plants tend to die². When plants reproduce, size is correlated with reproductive output^{3–5}. The struggle for existence among plants is, to a large extent, the struggle to grow in the face of competition from neighbours. Plant population biologists are beginning to ask how plant population phenomena, such as density–yield relationships, self-thinning, and patterns of size distribution change, result from the growth of, and interactions among, individual plants. It has become clear that to do this we need to follow the growth of individual plants during competition. Japanese researchers have recently demonstrated the power of this approach in a simple but compelling experiment with crowded populations of the common temperate weed, *Chenopodium album* ('lamb's quarters')⁶.

Focusing on individual growth

Nagashima *et al.*'s experiment⁶ consisted of growing monospecific stands of *C. album* at three densities (400, 800 and 3600 m⁻²), marking many individual plants, and measuring the height of each of these plants nine times, from emergence to fruit maturation. Rather than using the traditional methods of describing the changing distributions as a series of static distributions ('snapshots') over time⁷ or as one or a few relatively large growth intervals that are considered independently^{8,9}, Nagashima *et al.* followed the fate of individual plants and described the development of the stand as a process of individual growth. This simple (but extremely time-consuming) change in approach results in a significant advance in our understanding of the processes that govern the development of crowded plant populations.

Many individuals stopped growing at early stages in stand development and some of these died, whereas other plants continued to grow until fruits matured, attaining large final heights. Individuals that continued to grow were called 'upper' plants, whereas those that ceased height growth were 'lower' plants. The number of 'upper' plants per unit area was around 100 m⁻², irrespective of the initial density, whereas the number of 'lower' plants in-

creased with density. There was also a limit to the number of surviving 'lower' plants. Thus, the shape of the final frequency distributions of height was largely determined by the ratio of the relatively constant number of 'upper' plants to the number of surviving 'lower' plants, which varied with the density. Nagashima *et al.*'s data provide convincing evidence of bimodality in height at 400 plants m⁻², whereas the higher densities showed 'L-shaped' (i.e. highly skewed, unequal) size distributions, with little evidence of bimodality. They conclude that asymmetric competition¹⁰ for light can result in either bimodal or 'L-shaped' distributions, depending on the initial density.

In the study of ecological phenomena from plant population development to community change, it has become clear that dynamic data are needed if we are to understand dynamic processes. Sequential static data, which are much easier to obtain, can only substitute for dynamic data when conditions are highly controlled and sample sizes are very great – rare situations in ecological research. Progress on many ecological questions will be severely limited until we obtain truly dynamic data.

The problem of measuring plant size *in situ*

While Nagashima *et al.*'s results demonstrate the power of the individual growth approach to the study of plant population development, their study does suffer from certain limitations that can be addressed in future studies. First, their analysis was based solely on height growth. While height is an important aspect of plant size, the allometric relationships between height and other measures of plant size that are more closely related to fitness (such as biomass) are altered by competition¹¹, as Nagashima and Terashima show in an accompanying article¹². Thus, it may not be possible to generalize from patterns of height growth to other aspects of plant size, such as biomass. Similar studies with better measures of size will greatly improve our ability to interpret data on individual growth, but such improved measurements present major practical obstacles.

There is a trade-off in practice between following the growth of individuals over time and making good measures of their size. Demographically oriented studies have followed the fate of individuals, but, because measurements need to be non-destructive and non-disruptive, size

has usually been measured in a very crude way, for example, number of leaves, size of the largest leaf, or plant height. Harvesting is traditionally the best way to obtain accurate measures of plant biomass (and therefore energy content), but the ability to follow individuals over time is lost: a plant can be harvested only once. Plant ecology suffers from the lack of an efficient technology for obtaining good measures of plant size non-destructively and non-intrusively. In lieu of such a technology, we can make numerous measures of different aspects of plant size, such as stem diameter, branch lengths, leaf number, and use parallel harvests to develop prediction equations for biomass. The point is not that biomass is necessarily the 'ultimate' measure of plant size, but simply that it does have a clearer biological meaning than most other measures of plant size. Biomass integrates whole plant photosynthesis and respiration. It is highly correlated with reproductive output in herbaceous species, and is also the basis for most of the well-documented population-level phenomena, for example, density–yield^{13,14} and self-thinning^{15–17} relationships.

A new approach using explicit growth models

A second way to further the individual growth approach is through the use of explicit growth models. Foresters¹⁸ and ecologists¹⁹ have started fitting growth curves to individual plants in crowded populations. Although fitting a growth curve with, for example, three parameters to as few as four to six points would (and should) certainly arouse the suspicions of ecologists in a single case, it takes on a very different meaning when we do this for many individual plants. How well the model fits in each case is not the question; the model will usually fit very well indeed with such a large number of parameters relative to the number of points. But if we do this many times we can ask about the distribution of parameter estimates, that is, we can treat the parameter estimates themselves as variables to be analysed. According to this approach, it would be reasonable to fit a model even if the number of points for each growth curve was equal to the number of parameters in the growth equation plus one, such that the model would often fit perfectly. In such a case, we would have a basis for assuming that there is no statistical bias in the fitting of the model. We can then investigate the sensitivity of the results to the specific models used. Adjusted *r*² values, calculated according to Akaike's information measure²⁰, now permit us to compare models with different numbers of parameters.

Scientific explanation is usually reductionist – we explain phenomena from

mechanisms that occur at a lower level of organization. According to this philosophy, the growth of individual plants, as modified by biotic and abiotic factors, provides a basis for understanding plant population and community behaviour.

Jacob Weiner

Dept of Biology, Swarthmore College,
Swarthmore, PA 19081, USA

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Biodiversity and human health

The recent outbreak of Ebola virus in the town of Kikwit in Zaire claimed over a hundred human victims. The current epidemic of HIV/AIDS¹ and the resurgence of tuberculosis (TB) remind us just how susceptible we are to infectious diseases and underline the complacent attitude towards infectious diseases that operates in the health care systems of many developed and developing countries². In our continued assault on natural habitats through population expansion and economic exploitation, humans are not only creating a less healthy environment, but are consequently being exposed to a variety of new pathogens^{3,4,23}. This is occurring at a time when global climate change may lead to expansions in the range of a number of infectious diseases^{5,6} and when resistance is evolving to the antibiotics used to cure many common ailments^{7,8}. A recent meeting at the Dillon Ripley Center of the Smithsonian Institute in Washington on 'Biodiversity and Human Health' highlighted the potential interactions between human health, the destruction of tropical forests, the emergence of new pathogens and the loss of natural products with therapeutic potential that could be used to treat new and existing diseases. The April meeting was organized by the National Institutes of Health, the National Science Foundation and the Smithsonian Institute. The talks at the Conference highlighted the potential dangers to human health of the continued assault on the environment, particularly the destruction of tropical forests.

Just how big is the potential for tropical (and temperate) forests to supply agents with medicinal value that might be used to treat infectious and congenital diseases? Robert McCaleb (Herb Research Foundation, Boulder, CO, USA) gave some important statistics on this. So far, one out of every 125 plant species studied has pro-

duced a major drug. The market value of these drugs in the US is at least \$200 million per year. If we estimate that we lose one tree species a day, then we lose three to four potentially valuable new drugs every year, at a total cost of around \$600 million. If we contrast this with the production of new drugs from synthesized chemicals, the potential for finding major new drugs is in the order of one in 10 000 for each compound tested. The difference in the success rate between screening programs and looking for natural products from plants is patentability. Pharmaceutical companies have a much harder time patenting natural products than ones they have synthesized, and their potential profits are thus diminished when they attempt to market natural compounds over which they have only a limited monopoly. This is in part because of the litigation associated with the potential misuse of drugs in the US, but it is also because of the trade barriers and tariffs that the pharmaceutical industry has lobbied for to prevent the import of drugs based upon plant products. Much of President Bush's reluctance to sign the Rio biodiversity treaty was based on pressure from pharmaceutical companies that felt their 'competitiveness' might be threatened by a treaty that acknowledged the potential use of plant-based drugs with a tropical origin.

Despite significant trade and legislative barriers, the overwhelming majority of prescription drugs used at present in the US are based on natural products. In a fascinating review of the top prescription drugs in the US, Francesca Grifo (American Museum of Natural History, New York, USA)⁹ showed that 118 out of the top 150 prescription drugs, 74% are based on plants, 18% on fungi, 5% on bacteria and 3% on vertebrates (indeed all are from one species of snake *Bothrops asper*). If we look at the top ten prescription drugs in the US, nine

out of the ten are based on natural plant products. The figures are likely to significantly underestimate the use of natural products as drugs in other parts of the world as the US is particularly conservative in terms of its pharmaceutical diversity. The World Health Organization estimates that more than 80% of the world's population relies upon traditional plant medicine for primary health care.

Many drugs and herbal remedies that are widely used in Europe aren't even for sale in the US. For example, a plant derivative based on the leaves of the *Ginkgo* tree is now used by 80% of Europeans older than the age of 45 (Ref. 10). The species escaped extinction in the wild when preserved in monastery gardens where they were tended by Chinese monks for many centuries¹¹. Compounds distilled from leaves of the *Ginkgo* tree increase rates of cerebral blood flow and have major effects in preventing senile dementia. Other compounds that are widely available in Europe, but that are not available in the US, include (1) an extract of mistletoe, which laboratory tests have shown doubles the survival time of women suffering from breast cancer¹⁰; (2) Theokal, a hawthorn extract, which is now widely used as an anti-arrhythmic and is much safer to use than digitalis (itself an extract of foxgloves), having fewer side effects on people with heart problems¹⁰; and (3) Thisilyn, a derivative of milk thistles, that is now kept on hand in all hospitals in Europe and is used widely for liver damage (particularly from alcoholism!) – it can also provide very effective relief for sufferers from hepatitis¹⁰. Garlic-based compounds provide the finest irony. Although Americans can buy as much garlic as they like in their supermarkets, only recently have drugs derived from garlic appeared on the shelves of herbalists and pharmacies in the US. This is despite garlic's proven qualities in reducing cholesterol through its action as an anti-oxidant.

As a mere 1100 of the world's 365 000 known species of plants have been examined