

The nature of tree growth and the “age-related decline in forest productivity”

Jacob Weiner, Botany Section, Dept of Ecology, Royal Veterinary and Agricultural Univ., Rolighedsvej 21, DK-1958 Frederiksberg, Denmark (jw@kvl.dk). – Sean C. Thomas, Faculty of Forestry, Univ. of Toronto, 33 Willcocks St., Toronto, ON, Canada M5S 3B3.

The decline in the productivity of forests after a period of growth has been much discussed in recent years, with numerous research papers and several review articles on the topic. Most of these articles have focussed on alternative physiological mechanisms to explain this phenomenon (Gower et al. 1996, Ryan and Yoder 1997, Ryan et al. 1997, Smith and Resh 1999, Magnani et al. 2000). Proposed mechanisms include (a) an altered balance between photosynthetic and respiring tissues, (b) decreasing soil nutrient availability, (c) reduced photosynthetic rates due to increasing limitations to water transport, and (d) changes in allocation. At the recent meeting of the Ecological Society of America (5–10 Aug. 2000, Snowbird, Utah), there was a well-attended discussion entitled “What DOES [emphasis theirs] cause age-related decline in forest productivity?” Behind many of the discussions lies the hope that if we can understand what causes the decline in productivity with stand age, perhaps we can do something about it.

We contend that much of this discussion has taken place at the wrong scale, that proximate and ultimate causes have been confused, and that an essential perspective has been ignored. This perspective is simply that trees, like all organisms, exhibit sigmoid growth curves, and that age- and/or size-dependence of growth rates is an expression of this pattern. In this note we present three fundamental and related points which we believe have not been appropriately considered in the discussions to date:

1. The so-called “age-related” decline in forest productivity is primarily a “size-related” decline.
2. This decline is inevitable because growth of any organism will always be constrained eventually by some resource or non-resource factor. Tree growth

must be sigmoidal, and therefore growth rates *must* first increase and then decrease with tree size.

3. Reframing the question of forest productivity decline in terms of growth curves suggests that the proximate causes of this decline can be expected to vary among tree species and forest ecosystems. In this regard, the search of a single physiological basis for “age-related growth declines” is misguided.

Plant population biologists commonly view plants as a population of modules (Harper 1977, White 1984). Similarly, the growth of a plant is analogous in some ways to the growth of a population. Malthus first pointed out that no population could grow exponentially indefinitely. The same is also true of the growth of an individual plant. What would the alternative be? It is true that some plants may show exponential growth until they die due to external factors, such as disturbance or frost, before their growth begins to level off. However, if such external factors do not intervene, the growth rate of any plant will eventually decline. In this general but important sense the decline in forest productivity is inevitable.

The axiom that the growth of all plants, including trees, is sigmoidal has been consistently emphasized in reviews and books on the analysis of plant growth (Evans 1972, Causton and Venus 1981, Hunt 1982). A variety of growth functions, such as the logistic, Gompertz and Richards functions, have been used to model tree growth. All of these functions show the common feature of an initial increase and a later decrease in growth rate with plant size. The point has been made that certain tree size metrics, such as stem diameter, may show “truly indeterminate” growth patterns, with a slow rate of increase even late in tree ontogeny (Thomas 1996a). However, in practice, deviations from

widely-used sigmoidal growth models that assume a size asymptote are small (Hunt 1982, Vanclay 1994). Also, while stand growth patterns may differ from individual growth patterns due to competitive and other interactions among plants, stand growth also always shows a sigmoidal pattern (e.g. Vanclay 1994). In spite of this well-established generalization, none of the recent review articles on stand growth decline discusses forest productivity in terms of the sigmoidal nature of tree and stand growth. Rather, “age-related growth declines” are seen primarily as a physiological phenomenon (“productivity”), rather than as a size-dependent process (“growth”). Most of the recent discussions of growth declines have attempted to “scale up” from sub-organismal physiology to population and community-level phenomena, springing over the organismal/individual level. This kind of “scaling-up” usually fails (Weiner 1996).

A view of size-dependent growth declines as an inevitable outcome of sigmoidal growth curves has implications for current efforts to explain empirical patterns and to generalize results. For example, one well-documented pattern in the “age-related decline” in forest productivity is that the decline occurs sooner on higher fertility sites (Ryan et al. 1997). This pattern may be viewed as a simple outcome of size-dependent growth: under better conditions trees will reach the size at which growth begins to decline sooner. It is possible that enhanced growth conditions could increase the maximal size of the tree, or the size at which the leveling-off begins. This can be analyzed by examining the effects of environmental conditions on the parameters of growth models (e.g. Thomas et al. 1999).

We do not mean to imply that physiological mechanisms for size-related decreases in plant growth are not interesting and important. However, the inevitability of the decline has implications for the search for mechanisms that are its proximate causes. Just as it is of interest to ask if the mechanism of density dependence for a population is resource limitation (and if so, which resource?), territoriality, aggressive behavior or cannibalism, the mechanism of the decline in forest productivity is an important research question. The sigmoidal nature of tree growth suggests that, while it might be possible to postpone the size-related decline by changing the environment or the species, such a decline will inevitably still occur. If we add unlimited food to a growing population, the population’s growth will still level off later due to another limiting factor.

If no other factor intervenes first, tree growth will eventually decline due to increased allocation to reproduction at the expense of allocation to other structures. Trees are the products of natural selection, and producing more trees is, after all, the ultimate reason that trees exist. All organisms allocate more resources to reproduction as adults than they do as juveniles.

Quantitative models of life-history evolution inevitably predict that organisms should show an increasing schedule of reproductive allocation through ontogeny (Cohen 1968, King and Roughgarden 1982), a prediction strongly supported by empirical studies (Thomas 1996b). This increase in allocation to reproduction is expected to result in decreased allocation to growth and therefore a decline in growth rate. While such changes in allocation are certainly not the cause of age-related decline in forest productivity, selective pressures for an increasing schedule of reproductive allocation through ontogeny are likely to ultimately cause such a decline if no other factor constrains growth earlier.

We have argued that the question “What causes the decline in forest productivity?” is similar to the question “Why does the growth of a population slow down?”. The discussion of age-related decline in forest productivity is thus highly reminiscent of the debate among population ecologists in the 1950s about “What limits population size?”. Underlying this discussion was the idea that most populations in nature will be limited by the same thing. This question seems a bit naïve in the year 2001. While it has been shown that population size is often limited by resources, which resource is limiting varies with species and ecosystem, and some populations are limited by non-resource factors such as predation. We suggest the question “What DOES cause age-related decline in forest productivity?” may seem equally naïve in the future. It is possible that there is one predominant proximal cause of this decline across forest ecosystems, but we suggest that there is no reason to expect this to be the case. We believe that putting the issue of forest productivity decline in the context of tree growth curves will help move the discussion forward.

References

- Causton, D. R. and Venus, J. C. 1981. The biometry of plant growth. – Edward Arnold.
- Cohen, D. 1968. A general model of optimal reproduction in a randomly varying environment. – *J. Ecol.* 56: 219–228.
- Evans, G. C. 1972. The quantitative analysis of plant growth. – Blackwell Scientific.
- Gower, S. T., McMurtrie, R. E. and Murty, D. 1996. Above-ground net primary production decline with stand age: potential causes. – *Trends. Ecol. Evol.* 11: 378–382.
- Harper, J. L. 1977. Population biology of plants. – Academic Press.
- Hunt, R. 1982. Plant growth curves. – University Park Press.
- King, D. and Roughgarden, J. 1982. Graded allocation between vegetative and reproductive growth for annual plants in growing season of random length. – *Theor. Popul. Biol.* 22: 1–16.
- Magnani, F., Mencuccini, M. and Grace, J. 2000. Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints. – *Plant Cell Environ.* 23: 251–263.
- Ryan, M. G. and Yoder, B. J. 1997. Hydraulic limits to tree height and tree growth. – *Bioscience* 47: 235–242.

- Ryan, M. G., Binkley, D. and Fownes, J. H. 1997. Age-related decline in forest productivity: patterns and process. – *Adv. Ecol. Res.* 27: 214–252.
- Smith, F. W. and Resh, S. C. 1999. Age-related changes in production and below-ground carbon allocation in *Pinus contorta* forests. – *For. Sci.* 45: 333–341.
- Thomas, S. C. 1996a. Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain forest trees. – *Am. J. Bot.* 83: 556–566.
- Thomas, S. C. 1996b. Reproductive allometry in Malaysian rain forest trees: biomechanics vs. optimal allocation. – *Evol. Ecol.* 10: 517–530.
- Thomas, S. C., Jasienski, M. and Bazzaz, F. A. 1999. Early vs. asymptotic growth responses of herbaceous plants to elevated CO₂. – *Ecology* 80: 1552–1567.
- Vanclay, J. K. 1994. Modelling forest growth and yield. – CAB International.
- Weiner, J. 1996. Problems in predicting the ecological effects of elevated CO₂. – In: Körner, C. and Bazzaz, F. A. (eds), Carbon dioxide, populations and communities. Academic Press, pp. 431–441.
- White, J. 1984. Plant metamerism. – In: Dirzo, R. and Sarukhan, J. (eds), Perspectives on plant population ecology. Sinauer, pp. 141–165.