Proceedings of the 7th International Conference on Functional-Structural Plant Models, Saariselkä, Finland, 9 - 14 June 2013. Eds. Risto Sievänen, Eero Nikinmaa, Christophe Godin, Anna Lintunen & Pekka Nygren. http://www.metla.fi/fspm2013/proceedings. ISBN 978-951-651-408-9.

Geometrically saturated growth and the pipe model of tree form

Lars Hellström[1], **Linus Carlsson**[1] and **Åke Brännström**[1,2]
[1]*Department of Mathematics and Mathematical Statistics, Umeå University, 90187 Umeå, Sweden*
[2]*Evolution and Ecology Program, International Institute for Applied Systems Analysis, 2361 Laxenburg, Austria*
**correspondence:* lars.hellstrom@residenset.net

Highlights: We combine our self-thinning model of geometrically saturated growth with the pipe model of Shinozaki et al. to yield a composite model that can be used to make predictions about quantities traditionally found in functional models of tree growth.

Keywords: self-thinning, pipe model of tree form, self-similarity, geometric saturation, trunk geometry

Functional-structural plant models traditionally focus on resource production and allocation, which means plant growth is viewed as primarily limited by the amount of available carbon and other nutrients. However, for sufficiently large plants the geometry of space itself may become a more important limitation, in that the resources the plant has available to grow new branches and leaves exceed what it can usefully benefit from growing; at some point, more leaves would only mean higher leaf density and cannot increase the amount of absorbed sunlight enough to raise the net energy production. When this happens, we say that the growth has reached geometric saturation, and one would expect that the surplus production is instead directed towards activities other than growth, such as reproduction.

Previously (not yet in press), we have combined the idea of geometric saturation with (i) the architectural (Barthélémy–Caraglio 2007) view of plant structure and (ii) the self-similarity observation that branches of a given size tend to look pretty much the same regardless of the size of the full plant, to produce the self-thinning model of tree growth: trees discard branches (and a branch may discard subbranches) as they grow, because if they did not then they would quickly exceed the geometric saturation density. This model predicts how the number of metamers of a certain age changes over time, therefore how many must be lost as dead wood, and it also gives many details on what the expected branching structure in a tree should look like. However, to extract from it data on quantities more traditionally considered in functional models, such as total biomass or biomass turnover, one must complement it with a rather extensive table of expected sizes of plant organs of all kinds and ages.

In this follow-up on that earlier work, we combine our self-thinning model with the pipe model of Shinozaki et al. (1964a, 1964b). From a purely mathematical perspective, the two models make a good fit in that there is much overlap regarding the quantities they make claims about, while at the same time approaching them from very different starting points and thus setting up quite independent equations relating these quantities. The net outcome is then that the number of free variables is reduced considerably, and we are therefore able to extract far more functional-style data on the growth of plants from the combined model than from either model by itself, while at the same time reducing the number of parameters to the order of magnitude that would be usual for a functional-structural model.

It should also be pointed out that the model is not primarily a simulation of a process, but rather a system of equalities and inequalities that a plant would have to satisfy. The fastest growth geometrically permitted is then the maximal solution to this system.

LITERATURE CITED

Barthélémy D, Caraglio Y. 2007. Plant Architecture: A Dynamic, Multilevel and Comprehensive Approach to Plant Form, Structure and Ontogeny. *Annals of Botany* **99**: 375–407.

Shinozaki K, Yoda K, Hozumi K, Kira T. 1964a. A quantitative analysis of plant form — the pipe model theory, I: Basic Analyses. *Japanese Journal of Ecology* **14**: 97–105.

Shinozaki K, Yoda K, Hozumi K, Kira T. 1964b. A quantitative analysis of plant form — the pipe model theory, II: Further Evidence of the Theory and its Application in Forest Ecology. *Japanese Journal of Ecology* **14**: 133–139.