



Maintenance cost, toppling risk and size of trees in a self-thinning stand

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ABSTRACT

Wind routinely topples trees during storms, and the likelihood that a tree is toppled depends critically on its allometry. Yet none of the existing theories to explain tree allometry consider wind drag on tree canopies. Since leaf area index in crowded, self-thinning stands is independent of stand density, the drag force per unit land can also be assumed to be independent of stand density, with only canopy height influencing the total toppling moment. Tree stem dimensions and the self-thinning biomass can then be computed by further assuming that the risk of toppling over and stem maintenance per unit land area are independent of stand density, and that stem maintenance cost is a linear function of stem surface area and sapwood volume. These assumptions provide a novel way to understand tree allometry and lead to a self-thinning line relating tree biomass and stand density with a power between $-3/2$ and $-2/3$ depending on the ratio of maintenance of sapwood and stem surface.

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1. Introduction

Interest in tree allometry has increased in recent years as forests have been identified as a potential sink for atmospheric carbon. Studies on the proportions of tree organs indicate that much of the biomass in a forest is in stems and that this proportion increases with forest age. Another generalization states that when there are more individuals per unit land area (e.g., per hectare), the total biomass of the individuals decreases (Yoda et al., 1963). This relationship, called the “self-thinning law”, is so consistent that it has been called “the only generalization worthy of the name of a law in plant ecology” (Hutchings, 1983). Numerous empirical papers have shown that for even-aged monocultures, the maximum biomass of an individual is a power function of stand density (individuals per unit land area), with a slope of approximately $-3/2$ when both axes are plotted on logarithmic scales (Osawa and Allen, 1993). Mathematically, this can be described as

$$w_t \propto D^{-3/2}, \quad (1)$$

where w_t is the average total biomass (all symbols listed in Table 1) of a plant and D is stand density and the sign in between stands for proportionality (with equal sign a constant would need to be added). Many theories have been proposed to explain the

self-thinning law (e.g. Adler, 1996; Givnish, 1986), but none has gained wide support.

Schiel and Choat (1980) showed that the self-thinning law does not apply to marine algae, where the size of individuals can even increase with increasing density. This suggests that self-thinning might be related to structural requirements for staying erect on terrestrial environments. Seven years later Weller (1987) demonstrated that many datasets on terrestrial vascular plants published earlier to support the self-thinning law in fact lead to exponents that diverge from $-3/2$ (in Eq. (1)) when the correct statistical approach is applied. His paper (Weller, 1987) led to a decrease in papers on self-thinning even though he concluded that the variable exponent “may provide a valuable measure of the ecological differences among species and stands, and a powerful stimulus for further research”.

The objective of this paper is to present a model to explain self-thinning law from a new perspective, which will probably be the first attempt to explain the self-thinning law based on wind friction in canopies. Because of the novelty of the approach, the presented model is simple in order to introduce the new assumptions and implications, which will hopefully encourage more complex modeling based on the same principles. In the next three sections I present ideas necessary for understanding the thinking behind the assumptions of this new model.

2. Stagnation and self-thinning

A central element of forest management is the use of thinning to manipulate stand structure and maximize growth (Davis and

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Table 1
Symbols in equations.

Symbol	Definition	Possible unit
a	Leaf area of a tree	m^2
D	Stand density	m^{-2}
$const$	Constant (changes from one equation to another)	–
E	Stem maintenance cost per unit land area	W/m^2
e_s	Stem surface maintenance cost of a tree	W
e_w	Wood maintenance cost of a tree	W
h	Height of the tree	m
j	Parameter on maintenance of sapwood	–
k	Parameter on maintenance of stem surface	–
m	Moment that a stem of a tree can resist	Nm
r	Stem radius of a tree	m
w_s	Stem biomass of a tree	kg
w_t	Total biomass of a tree	kg

Johnson, 1987). In a sparse stand, much light penetrates the canopy without being used by the trees and therefore the gross primary production of trees is low. On the other hand, growth in an overly dense stand suffers from high maintenance cost relative to the gross primary production of trees. The maintenance cost is composed of both maintenance respiration and replacement of leaves and fine roots. In extreme cases when the stand is dense and nearly all energy (or carbohydrates) is allocated into maintenance, growth ceases and the stand reaches “stagnative equilibrium”. Theoretically it is obvious that with a given stand density and closed canopy, gross primary production is relatively constant and that larger stems require more energy for maintenance. Therefore, growth ceases at a certain stem size if individuals are identical (or all individuals die).

In practice, stagnative equilibrium has been documented in surprisingly few studies. Ecological papers typically focus on stands with individuals of varying size, age and normally even species and therefore certain individuals start dying (self-thinning occurs) when the most competitive individuals are still growing significantly (e.g. Osawa and Allen, 1993). Forestry literature describes how stand density influences stem growth of often nearly identical individuals but unfortunately the interest has been mainly in wood production and therefore in stand densities leading to high or moderate stem growth and not those close to stagnative equilibrium (Davis and Johnson, 1987). Significant exceptions are the well studied very dense *Pinus contorta* stand that has been naturally regenerated after fire from serotinous cones and which grow very slowly and are close to stagnative equilibrium and can be released from it by thinning (e.g. Farnden and Herring, 2002). At the individual level many understory trees are at a similar situation that nearly all energy produced is required for maintenance and growth is extremely slow. Although at stand level stagnative equilibrium is rare in nature it is ecologically and physiologically nearly identical to self-thinning if the variability between individuals is small and is the simplest basis to understand tree stem dimensions and allometry in general.

3. What determines the stem dimensions of trees?

Several theories have been put forward to explain tree stem dimensions. The “pipe model” assumes that the quantity of leaves above a given level is proportional to stem cross-sectional area at that level (Shinozaki et al., 1964), but does not explain stem height, heartwood and inter-specific variability. The three main approaches to understanding the height-radius ratio are: geometric similitude, elastic buckling and stress similarity (Niklas, 1992). The theory of geometric similitude simply assumes that

ratios of dimensions remain the same when trees grow. However, geometric similitude is not based on understanding of evolutionary drivers of allometry, i.e. survival or reproduction.

It is evident that extra height is beneficial in exposing trees to more light and that the stem radius should be as small as possible in order not to waste energy. The theories of elastic buckling and stress similarity are the main options to explain how small is possible. McMahon (1973) showed that if the fresh biomass of the above-ground parts of a plant is above the limit of “elastic buckling” the stem will bend irreversibly. This theory is based on thinking that crucial in plant allometry is the avoidance of elastic buckling. Interestingly, when only stem biomass (branches and leaves excluded) is taken into account the height leading to elastic buckling scales to stem radius to the power of 2/3 (McMahon, 1973). This mathematically simple relation has been used in dozens of journal articles (e.g. correctly (King et al., 2006) and incorrectly (West et al., 1999) as they do not take into account the influence of subsequent branching). However, empirical data has shown that most plants are far from the maximal height, leading to elastic buckling. For example Niklas (1994a) measured plants belonging to 111 species and concluded that the “safety factor”, which is the ratio of the height leading to elastic buckling and actual height, was very variable but on average approximately 4. Because of non-linear relationships, for a tree with a safety factor of 4, gravity causes just 1.6% of the necessary force needed for elastic buckling. However, it is probable that the safety factor is lower in general in self-thinning stand (King, 1981).

The need for a safety factor has been correctly explained to be necessary as in addition to gravity acting on the fresh biomass of the plants temporary forces such as wind and snow load could potentially cause toppling over and death. However, the approach to understand tree allometry based on elastic buckling is misleading as the additional forces required to cause toppling are very weakly linked and important relative to gravity acting on tree. This causes the wide range of safety factors found in trees. For example swaying in the wind has been shown to decrease the height-radius ratio (Coutand et al., 2008) and therefore increasing the safety factor. In forests in snow-free climates wind is basically the only significant force toppling over trees in addition to their own fresh biomass (with the main exception of trees pulled down by other toppling over trees). I therefore argue that in simple modeling of mature trees when only one toppling over force can be taken into account it is best to focus on wind and the theory of stress similarity that focuses on breaking strengths of stems (Niklas, 1992), as I do in this paper. Plants such as shrubs, which can be bent down to the ground without breaking, need another approach.

The drag caused by wind friction is difficult to model as bending of the branches and leaves and variable wind speeds for each leaf complicate the phenomenon. The moments resisting uprooting are also very difficult to model as they depend on both the roots and the soil. However, beam theory in basic engineering science suggests that stems resist breaking (bending stress of a beam) simply with a moment (m)

$$m \propto r^3, \quad (2)$$

where r is stem radius inside the bark (in this equation at any height but in subsequent equations at any given height relative to stem height), when the wood is homogenous and shear forces are not taken into account (Niklas, 1992). The third power for r comes from the fact that increasing radius not only increases the number of vertical fibers responsible for the strength of the wood, but also increases their average distance from the neutral axis (where neither elongation nor shortening occurs when the stem is bending), thus increasing the average moment of the fibers resisting bending (Larjavaara and Muller-Landau, 2010). The

moment (m) is equal to the product of force and length of the lever arm (e.g. height of a crown). This theory of stress similarity has been successfully used to explain stem tapering (Dean et al., 2002), trunk and branch wood density (Anten and Schieving, 2010) and life-history variation (Sterck et al., 2006).

A strong stem is useless for trees that uproot easily. Therefore evolutionary pressure has strengthened the root system in allometric balance to resist approximately the same moment as the stem in conditions in which the root system would otherwise be weaker (shallow, moist or nutrient-rich soils). This is supported by studies showing that both uprooting and stem breakage occur in many species in a given stand (Niklas, 1992; Peltola et al., 2000; Putz et al., 1983). I therefore argue that Eq. (2) can be used as the basis for theories on tree allometry as is demonstrated in section “Structure of the new model”.

4. How to model wind drag on the canopy?

Eq. (2) has probably never been used in modeling height-radius ratio, presumably because the drag force in canopies is difficult to model at the tree level (Coutts and Grace, 1995) compared to elastic buckling. The self-thinning law has been developed to describe density-size relations in a monocultural even-aged stand. Independent of the stand density, leaves need a certain level of light for a positive energy balance. Therefore the leaf area index (total leaf area per unit area) is independent of the stand density once the stand has recovered from disturbances as in the case of self-thinning stands (Osawa and Allen, 1993). Therefore

$$aD = \text{const}, \quad (3)$$

where a is the leaf area of one tree, D is stand density and “const” refers to a constant. This implies that the drag force caused by the wind on leaves per unit land area is also independent of stand density assuming that the average wind force on an individual leaf is independent of stand density. The moment per unit area caused by this force can then be simply computed from the height of the leaves.

5. Structure of the new model

I now focus on even-aged stands at the self-thinning limit and in stagnative equilibrium to understand the self-thinning law better. I assume that wood density, structure and size of individual roots and branches as well as the total number of roots and branches per unit land area are independent of the stand density. I also assume that the leaf area index is independent of stand density. As growth is very slow, its variation depending on stand density is insignificant and therefore the energy usable for the maintenance per unit land area is also independent of stand density (same assumption justified if growth is significant but the same fraction of energy is always allocated in growth). As the energetic maintenance costs of leaves, branches and roots per unit land area are independent of stand density the energy available for maintenance of stems per unit land area also needs to be independent of stand density at the self-thinning limit. In addition, I assume that gravity does not act on bending trees (see section “What determines the stem dimensions of trees?”).

Wood provides support and transports sap to the canopy. As dead heartwood provides support but does not require maintenance it is justifiable to assume that the sap flow function of the wood causes the total wood maintenance cost and that this cost is proportional to the product of the distance and amount of sap that

needs to be transported. By assuming that the height of branches relative to height of the tree (h) is independent of the stand density in fully stocked stands and that the leaf area of one tree (a) is proportional with the amount of sap transported the wood maintenance cost (e_w) is

$$e_w \propto ah, \quad (4)$$

based on the function of tree stems. Alternatively, based on the tree structure, the same relation can be derived assuming the total wood maintenance (e_w) is proportional to sapwood volume and that the cross-sectional area of sapwood is proportional to the leaf area above it as in the pipe model (Shinozaki et al., 1964).

Empirical studies indicate that the energetic maintenance cost of inner bark is high (Pruyn et al., 2002) and that stem surface area better explains total stem maintenance cost than sapwood biomass or volume (Bosc et al., 2003). This can be caused by both the respiration of the inner bark and increased wood respiration due to closeness of stem surface. The importance of stem surface area in determining stem maintenance cost is not biochemically well understood but could be linked to protection against pathogens, which often enter through the stem surface. It is clear that sapwood of a living tree is actively protected against pathogens as sapwood decays less likely in the living tree but more likely in a dead tree than heartwood (David A. King, unpublished). In the new model the maintenance cost of stem surface (e_s) is proportional to the surface area of the stem, which can be calculated assuming that the stem taper is independent of the stand density as

$$e_s \propto rh. \quad (5)$$

Combining Eqs. (4) and (5) and multiplying by the number of individuals per unit area (D) or stand density leads to the total stem maintenance cost per unit land area (E)

$$E = D(jah + krh), \quad (6)$$

where j and k are parameters dependent on the ratio of maintenance cost of the wood and of the stem surface. These parameters need to be added as the relative importance of these two costs is unknown and probably climate and species specific. According to the assumptions E and the product of D and a are independent of stand density (Eq. (3)) and can be replaced by a constant. Taking this into account when solving h , Eq. (6) converts to

$$h = \frac{\text{const}}{(j \text{const} + kDr)}. \quad (7)$$

Based on another assumption (Eq. (2)), the height of trees leading to breaking at a given wind speed is

$$h \propto \frac{r^3}{a}, \quad (8)$$

as the moment caused by the drag of wind on the base of the stem is proportional to both the height (h) and leaf area (a). Evolutionary pressure forces trees to maximize their height (h), within the constraints of not taking excessive risks of toppling over (Eq. (8)) and not exceeding the highest possible maintenance cost (Eq. (7)) and have dimensions close to the point corresponding to the highest possible value of height (h). Because Eq. (8) is rising (when h is shown in function of r for a given D and therefore a) and Eq. (7) is descending (except when k is zero) the intersection of these two functions reveals the dimensions of tree stems (see Fig. 1). The intersection can be solved by combining Eqs. (7) and (8) as shown in the appendices.

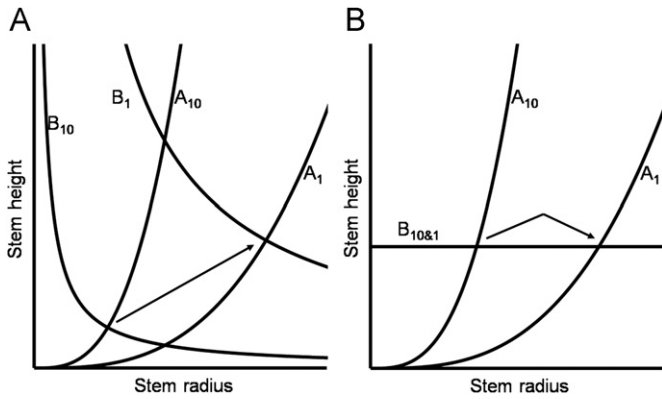


Fig. 1. Functions A_{10} and A_1 show the maximal height without excessively high risk of toppling and functions B_{10} and B_1 the maximal height based on the energetic maintenance cost of the stem for a given stand density in a self-thinning situation. A_{10} and B_{10} are computed from a tenfold stand density compared to A_1 and B_1 . The arrows show how a 90% decrease in stand density changes stem dimensions from the intersection between A_{10} and B_{10} to the intersection between A_1 and B_1 . (A) demonstrates the situation when stem surface and (B) when sapwood is assumed to cause all the maintenance. The functions B_{10} and B_1 form an identical horizontal line in (B). Functions A_{10} and A_1 are based on Eq. (8) (where a is constant for a given function), functions B_{10} and B_1 in (A) on Eq. (A.1) (where D is constant for a given function) and function $B_{10\&1}$ in (B) on Eq. (B.1). The assumption that stem dimensions are determined by the intersection between functions A_{10} or A_1 and $B_{10\&1}$ to give the maximum possible stem height is irrelevant in the theoretical case of (B), as equal heights but larger radii are equally possible, leading to greater strength.

6. Allometry and self-thinning law based on the new model

In the theoretical situation when the value parameter j of Eqs. (6) and (7) is zero and sapwood is assumed to make no contribution to stem maintenance

$$w_s \propto D^{-3/2}, \quad (9)$$

where w_s is biomass of the stem of a tree individual, as shown in Appendix A. This is equal to Eq. (1) with the exception that Eq. (9) is for stem biomass and Eq. (1) for total biomass (or total above-ground biomass). In the reverse theoretical case when the parameter k is zero and sapwood causes all the maintenance of a stem

$$w_s \propto D^{-2/3}, \quad (10)$$

as shown in Appendix B. These two theoretical extremities are shown graphically in Fig. 1A and B. In reality, since both stem surface and sapwood always cause maintenance, both extremities are unrealistic. For example Bosc et al. (2003) showed that for the *Pinus pinaster* that they studied stem surface maintenance cost is approximately half of the total stem maintenance cost.

The classic self-thinning law focuses on the total or above-ground biomass of an individual and not just stem biomass. The new model assumes that the biomass excluding stems per unit land area is independent of stand density and the slope of the self-thinning line excluding stems is therefore -1 . The slopes of self-thinning lines for total tree biomass are intermediate between -1 and the self-thinning line for stem biomass, which depends on the values of j and k . The higher the proportion of stem biomass is, and the higher the proportion of stem surface maintenance of total stem maintenance, the steeper the slope of the self-thinning line is (except when sapwood causes a very large proportion of stem maintenance).

7. Increasing complexity of the new model

The model described in the previous sections is simple and presented in this short article to encourage development of more

realistic and complex models following the same principles. However, most of the dozens of possible adjustments making the model more realistic are species-specific.

Perhaps the most obvious areas in which to make the model more realistic are related to the structure of the trees. Most trees have a main stem as assumed in the new model but they also have varying branch lengths depending on tree size, which is not taken into account in the new model. Furthermore, the model assumes that the biomass and energetic cost per unit land area of roots is independent of stand density.

Ryan et al. (2006) review numerous studies indicating that the assumption of invariable gross primary productivity with invariable leaf area index and variable tree height is incorrect. Increasing height may decrease the efficiency of photosynthesis because of hydraulic limitations (Ryan et al., 2006). This could be taken into account in the model. Also the assumption of equal size of all tree individuals and stagnative equilibrium would not be needed if a game-theoretical approach including realistic ranges of tree radii, heights and growth rates could be chosen.

The drag force created by wind acting on an individual leaf is central to the new model. However, wind also acts on stem and branches, causing an additional drag and the average wind speeds acting on leaves might increase with size as the canopy roughness changes when leaves are arranged more like vertical clusters than a horizontal layer (Coutts and Grace, 1995). As explained earlier, in most falls of healthy trees the force of wind acting on the canopy is probably the most significant single factor. However, gravity acting on the fresh biomass of the tree is always after some bending an additional factor that could be included in the model.

8. Conclusions

Focusing on the allometry of an individual without paying enough attention to its biotic surroundings has been the dominant approach in developing theories on tree structure (Niklas, 1994b). However, understanding the allometry of trees in an overcrowded stand that is stagnating and is at the limit of self-thinning is the simplest and therefore in many ways the best approach to model tree structure. This enables the use of Eq. (3) for modeling the toppling moment caused by wind drag and together with assumptions on stem maintenance not only explains the height–radius ratio as some earlier models (McMahon, 1973) but also explains both the height and radius relative to stand density. Thanks to this it can be applied to self-thinning law and lead to realistic self-thinning line slopes ranging upwards from $-3/2$. Increasing stand density decreases biomass per unit land area (i.e. self-thinning law) as the trees in them need to be shorter for stability and need to avoid a large stem surface area requiring maintenance. Numerous species and site-specific complicating factors influence the precise slope of the self-thinning line. More sophisticated species-specific models including some of the aspects presented in the previous section could be developed and tested with simple self-thinning data. Alternatively ecophysiological data on maintenance or diameter, height and leaf area data for tree individuals in stagnating stands could be used to test some of the assumptions presented in this article. The model could be also applied to non-stagnating stands when growth or leaf area information is available or on estimating biomass based on remote sensing data on tree heights when data on stand density is not available.

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Appendix A

When sapwood is assumed not to make contribution to stem maintenance and the parameter j is therefore zero Eq. (7) simplifies to

$$h = \frac{\text{const}}{Dr}. \quad (\text{A.1})$$

Combining this with Eq. (8) leads to

$$\frac{r^3}{a} = \frac{\text{const}}{Dr}, \quad (\text{A.2})$$

and further to

$$r^4 \propto \frac{a}{D}. \quad (\text{A.3})$$

Combining this with Eq. (3) leads to

$$r^4 = \frac{\text{const}}{D^2}, \quad (\text{A.4})$$

which simplifies to

$$r = \frac{\text{const}}{D^{1/2}}. \quad (\text{A.5})$$

As stem biomass of a tree (w_s) is in general

$$w_s \propto r^2 h, \quad (\text{A.6})$$

it is in this self-thinning situation based on Eq. (A.1)

$$w_s = r^2 \frac{\text{const}}{Dr}. \quad (\text{A.7})$$

Combining this with Eq. (A.5) leads to

$$w_s = \frac{\text{const}}{DD^{1/2}}, \quad (\text{A.8})$$

and to

$$w_s \propto D^{-3/2}. \quad (\text{A.9})$$

Appendix B

When stem surface is assumed not to make contribution to stem maintenance and the parameter k is therefore zero Eq. (7) simplifies to

$$h = \text{const}. \quad (\text{B.1})$$

Combining this with Eq. (8) leads to

$$\frac{r^3}{a} = \text{const}, \quad (\text{B.2})$$

and further to

$$r^3 \propto a. \quad (\text{B.3})$$

Combining this with Eq. (3) leads to

$$r^3 = \frac{\text{const}}{D}, \quad (\text{B.4})$$

which simplifies to

$$r = \frac{\text{const}}{D^{1/3}}. \quad (\text{B.5})$$

As stem biomass of a tree (w_s) is in general

$$w_s \propto r^2 h, \quad (\text{B.6})$$

it is in this self-thinning situation based on Eq. (B.1)

$$w_s \propto r^2. \quad (\text{B.7})$$

Combining this with Eq. (B.5) leads to

$$w_s = \frac{\text{const}}{D^{2/3}}, \quad (\text{B.8})$$

and to

$$w_s \propto D^{-2/3}. \quad (\text{B.9})$$

References

- Adler, F.R., 1996. A model of self-thinning through local competition. *Proceedings of the National Academy of Sciences of the United States of America* 93, 9980–9984.
- Anten, N.P.R., Schieving, F., 2010. The role of wood mass density and mechanical constraints in the economy of tree architecture. *American Naturalist* 175, 250–260.
- Bosc, A., De Grandcourt, A., Loustau, D., 2003. Variability of stem and branch maintenance respiration in a *Pinus pinaster* tree. *Tree Physiology* 23, 227–236.
- Coutand, C., Dupraz, C., Jaouen, G., Ploquin, S., Adam, B., 2008. Mechanical stimuli regulate the allocation of biomass in trees: demonstration with young *Prunus avium* trees. *Annals of Botany* 101, 1421–1432.
- Coutts, M., Grace, J. (Eds.), 1995. *Wind and Trees*. Cambridge University Press, Cambridge.
- Davis, L.S., Johnson, K.N., 1987. *Forest Management*. McGraw-Hill Book Company.
- Dean, T.J., Roberts, S.D., Gilmore, D.W., Maguire, D.A., Long, J.N., O'Hara, K.L., Seymour, R.S., 2002. An evaluation of the uniform stress hypothesis based on stem geometry in selected North American conifers. *Trees—Structure and Function* 16, 559–568.
- Farnden, C., Herring, L., 2002. Severely repressed lodgepole pine responds to thinning and fertilization: 19-year results. *Forestry Chronicle* 78, 404–414.
- Givnish, T.J., 1986. Biomechanical constraints on self-thinning in plant-populations. *Journal of Theoretical Biology* 119, 139–146.
- Hutchings, M., 1983. Ecologys law in search of a theory. *New Scientist* 98, 765–767.
- King, D., 1981. Tree dimensions-maximizing the rate of height growth in dense stands. *Oecologia* 51, 351–356.
- King, D.A., Davies, S.J., Tan, S., Noor, N.S.M., 2006. The role of wood density and stem support costs in the growth and mortality of tropical trees. *Journal of Ecology* 94, 670–680.
- Larjavaara, M., Muller-Landau, H.C., 2010. Rethinking the value of wood density. *Functional Ecology*.
- McMahon, T., 1973. Size and shape in biology. *Science* 179, 1201–1204.
- Niklas, K.J., 1992. *Plant Biomechanics—An Engineering Approach to Plant Form and Function*. The University of Chicago Press, Chicago.
- Niklas, K.J., 1994a. Interspecific allometries of critical buckling height and actual plant height. *American Journal of Botany* 81, 1275–1279.
- Niklas, K.J., 1994b. *Plant Allometry*. The University of Chicago Press, Chicago.
- Osawa, A., Allen, R.B., 1993. Allometric theory explains self-thinning relationships of mountain beech and red pine. *Ecology* 74, 1020–1032.
- Peltola, H., Kellomaki, S., Hassinen, A., Granander, M., 2000. Mechanical stability of Scots pine, Norway spruce and birch: an analysis of tree-pulling experiments in Finland. *Forest Ecology and Management* 135, 143–153.
- Pruyn, M.L., Gartner, B.L., Harmon, M.E., 2002. Respiratory potential in sapwood of old versus young ponderosa pine trees in the Pacific Northwest. *Tree Physiology* 22, 105–116.
- Putz, F.E., Coley, P.D., Lu, K., Montalvo, A., Aiello, A., 1983. Uprooting and snapping of trees—structural determinants and ecological consequences. *Canadian Journal of Forest Research—Revue Canadienne De Recherche Forestiere* 13, 1011–1020.
- Ryan, M.G., Phillips, N., Bond, B.J., 2006. The hydraulic limitation hypothesis revisited. *Plant Cell and Environment* 29, 367–381.
- Schiel, D.R., Choat, J.H., 1980. Effects of density on monospecific stands of marine-algae. *Nature* 285, 324–326.
- Shinozaki, K., Yoda, K., Hozumi, K., Kira, T., 1964. A quantitative analysis on plant form—the pipe model theory. I—Basic analyses. *Japanese Journal of Ecology* 14, 97–105.
- Sterck, F.J., Van Gelder, H.A., Poorter, L., 2006. Mechanical branch constraints contribute to life-history variation across tree species in a Bolivian forest. *Journal of Ecology* 94, 1192–1200.
- Weller, D.E., 1987. A reevaluation of the $-3/2$ power rule of plant self-thinning. *Ecological Monographs* 57, 23–43.
- West, G.B., Brown, J.H., Enquist, B.J., 1999. A general model for the structure and allometry of plant vascular systems. *Nature* 400, 664–667.
- Yoda, K., Kira, T., Ogawa, H., Hozumi, K., 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology, Osaka City University* 14, 107–129.