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2 **Maintenance Cost, Toppling Risk and Size of Trees in a Self-thinning Stand**

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14

1 **Abstract**

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

14

15 **Keywords**

16 allometric, allometry, biomass, self-thinning law, wind drag

17

1 Introduction

2

3 Interest in tree allometry has increased in recent years as forests have been identified as a
4 potential sink for atmospheric carbon. Studies on the proportions of tree organs indicate
5 that much of the biomass in a forest is in stems and that this proportion increases with
6 forest age. Another generalization states that when there are more individuals per unit
7 land area (e.g., per hectare), the total biomass of the individuals decreases (Yoda et al.,
8 1963). This relationship, called the “self-thinning law”, is so consistent that it has been
9 called “the only generalization worthy of the name of a law in plant ecology” (Hutchings,
10 1983). Numerous empirical papers have shown that for even-aged monocultures, the
11 maximum biomass of an individual is a power function of stand density (individuals per
12 unit land area), with a slope of approximately $-3/2$ when both axes are plotted on
13 logarithmic scales (Osawa and Allen, 1993). Mathematically, this can be described as

14

$$15 \quad w_i \propto D^{-3/2}, \quad \text{Equation 1}$$

16

17 where w_i is the average total biomass (all symbols listed in Table 1) of a plant and D is
18 stand density and the sign in between stands for proportionality (with equal sign a
19 constant would need to be added). Many theories have been proposed to explain the self-
20 thinning law (e.g. (Adler, 1996; Givnish, 1986)), but none has gained wide support.

21

22 Schiel and Choat (1980) showed that the self-thinning law does not apply to marine
23 algae, where the size of individuals can even increase with increasing density. This

1 suggests that self-thinning might be related to structural requirements for staying erect on
2 terrestrial environments. Seven years later Weller (1987) demonstrated that many
3 datasets on terrestrial vascular plants published earlier to support the self-thinning law in
4 fact lead to exponents that diverge from $-3/2$ (in Equation 1) when the correct statistical
5 approach is applied. His paper (Weller, 1987) led to a decrease in papers on self-
6 thinning even though he concluded that the variable exponent “may provide a valuable
7 measure of the ecological differences among species and stands, and a powerful stimulus
8 for further research”.

9

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

17

18

19 **Stagnation and self-thinning**

20

21 A central element of forest management is the use of thinning to manipulate stand
22 structure and maximise growth (Davis and Johnson, 1987). In a sparse stand, much light
23 penetrates the canopy without being used by the trees and therefore the gross primary

1 production of trees is low. On the other hand, growth in an overly dense stand suffers
2 from high maintenance cost relative to the gross primary production of trees. The
3 maintenance cost is composed of both maintenance respiration and replacement of leaves
4 and fine roots. In extreme cases when the stand is dense and nearly all energy (or
5 carbohydrates) is allocated into maintenance, growth ceases and the stand reaches
6 “stagnative equilibrium”. Theoretically it is obvious that with a given stand density and
7 closed canopy, gross primary production is relatively constant and that larger stems
8 require more energy for maintenance. Therefore, growth ceases at a certain stem size if
9 individuals are identical (or all individuals die).

10

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

1 Although at stand level stagnative equilibrium is rare in nature it is ecologically and
2 physiologically nearly identical to self-thinning if the variability between individuals is
3 small and is the simplest basis to understand tree stem dimensions and allometry in
4 general.

5

6

7 **What determines the stem dimensions of trees?**

8

9 Several theories have been put forward to explain tree stem dimensions. The “pipe
10 model” assumes that the quantity of leaves above a given level is proportional with stem
11 cross-sectional area at that level (Shinozaki et al., 1964), but does not explain stem
12 height, heart wood and inter-specific variability. The three main approaches to
13 understand the height-radius ratio are: geometric similitude, elastic buckling and stress
14 similarity (Niklas, 1992). The theory of geometric similitude simply assumes that ratios
15 of dimensions remain the same when trees grow. However, geometric similitude is not
16 based on understanding of evolutionary drivers of allometry, i.e. survival or reproduction.

17

18 It is evident that extra height is beneficial in exposing trees to more light and that the
19 stem radius should be as small as possible in order not to waste energy. The theories of
20 elastic buckling and stress similarity are the main options to explain how small is
21 possible. McMahon (1973) showed that if the fresh biomass of the above-ground parts of
22 a plant are above the limit of “elastic buckling” the stem will bend irreversibly. This
23 theory is based on thinking that crucial in plant allometry is the avoidance of elastic

1 bucking. Interestingly, when only stem biomass (branches and leaves excluded) is taken
2 into account the height leading to elastic buckling scales to stem radius to the power of
3 $2/3$ (McMahon, 1973). This mathematically simple relation has been used in dozens of
4 journal articles (e.g. correctly (King et al., 2006) and incorrectly (West et al., 1999) as
5 they do not take into account the influence of subsequent branching). However, empirical
6 data has shown that most plants are far from the maximal height leading to elastic
7 buckling. For example Niklas (1994a) measured plants belonging to 111 species and
8 concluded that the “safety factor”, which is the ratio of the height leading to elastic
9 buckling and actual height was very variable but on average approximately 4. Because of
10 non-linear relationships, for a tree with a safety factor of 4, gravity causes just 1.6 % of
11 the necessary force needed for elastic buckling. However, it is probable that the safety
12 factor is lower in general in self-thinning stand (King, 1981).

13
14 The need for a safety factor has been correctly explained to be necessary as in addition to
15 gravity acting on the fresh biomass of the plants temporary forces such as wind and snow
16 load could potentially cause toppling over and death. However, the approach to
17 understand tree allometry based on elastic buckling is misleading as the additional forces
18 required to cause toppling are so weakly linked and important relative to gravity acting
19 on tree. This causes the wide range of safety factors found in trees. For example swaying
20 in the wind has been shown to decrease the height-radius ratio (Coutand et al., 2008) and
21 therefore increasing the safety factor. In forests in snow free climates wind is basically
22 the only significant force toppling over trees in addition to their own fresh biomass (with
23 the main exception of trees pulled down by other toppling over trees). I therefore argue

1 that in simple modelling of mature trees when only one toppling over force can be taken
2 into account it is best to focus on wind and the theory of stress similarity that focuses on
3 breaking strengths of stems (Niklas, 1992) , as I do in this paper. Plants such as shrubs
4 which can be bent down to the ground without breaking need another approach.

5

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

11

$$12 \quad m \propto r^3, \quad \text{Equation 2}$$

13

14 where r is stem radius inside the bark (in this equation at any height but in subsequent
15 equations at any given height relative to stem height), when the wood is homogenous and
16 shear forces are not taken into account (Niklas, 1992). The third power for r comes from
17 the fact that increasing radius not only increases the number of vertical fibres responsible
18 for the strength of the wood, but also increases their average distance from the neutral
19 axis (where neither elongation or shortening occurs when the stem is bending), thus
20 increasing the average moment of the fibres resisting bending (Larjavaara and Muller-
21 Landau, 2010). The moment (m) is equal to the product of force and length of the lever
22 arm (e.g. height of a crown). This theory of stress similarity has been successfully used to

1 explain stem tapering (Dean et al., 2002), trunk and branch wood density (Anten and
2 Schieving, 2010) and life-history variation (Sterck et al., 2006).

3

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

12

13

14 **How to model wind drag on the canopy?**

15

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

1

2 $aD = \text{const}$,

Equation 3

3

4 where a is the leaf area of one tree and D is stand density and “const” refers to a constant.

5 This implies that the drag force caused by the wind on leaves per unit land area is also

6 independent of stand density assuming that the average wind force on an individual leaf

7 is independent of stand density. The moment per unit area caused by this force can then

8 be simply computed from the height of the leaves.

9

10

11 **Structure of the new model**

12

13 I now focus on even-aged stands at the self-thinning limit and in stagnative equilibrium to

14 understand the self-thinning law better. I assume that wood density, structure and size of

15 individual roots and branches as well as the total number of roots and branches per unit

16 land area are independent of the stand density. I also assume that the leaf area index is

17 independent of stand density. As growth is very slow, its variation depending on stand

18 density is insignificant and therefore the energy usable for the maintenance per unit land

19 area is also independent of stand density (same assumption justified if growth is

20 significant but the same fraction of energy is always allocated in growth). As the

21 energetic maintenance cost of leaves, branches and roots per unit land area are

22 independent of stand density the energy available for maintenance of stems per unit land

23 area also needs to be independent of stand density at the self-thinning limit. In addition, I

1 assume that gravity does not act on bending trees (see section “What determines the stem
2 dimensions of trees?”).

3

4 Wood provides support and transports sap to the canopy. As dead heartwood provides
5 support but does not require maintenance it is justifiable to assume that the sap flow
6 function of the wood causes the total wood maintenance cost and that this cost is
7 proportional with the product of the distance and amount of sap that needs to be
8 transported. By assuming that the height of branches relative to height of the tree (h) is
9 independent of the stand density in fully stocked stands and that the leaf area of one tree
10 (a) is proportional with the amount of sap transported the wood maintenance cost (e_w) is

11

$$12 \quad e_w \propto ah, \quad \text{Equation 4}$$

13

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

18

19 Empirical studies indicate that the energetic maintenance cost of inner bark is high
20 (Pruyn et al., 2002) and that stem surface area better explains total stem maintenance cost
21 than sapwood biomass or volume (Bosc et al., 2003). This can be caused by both the
22 respiration of the inner bark and increased wood respiration due to closeness of stem
23 surface. The importance of stem surface area in determining stem maintenance cost is not

1 biochemically well understood but could be linked to protection against pathogens which
 2 often enter through the stem surface. It is clear that sapwood of a living tree is actively
 3 protected against pathogens as sapwood decays less likely in the living tree but more
 4 likely in a dead tree than heart wood (David A. King, unpublished). In the new model the
 5 maintenance cost of stem surface (e_s) is proportional with the surface area of the stem,
 6 which can be calculated assuming that the stem taper is independent of the stand density
 7 as

$$8 \quad e_s \propto rh. \quad \text{Equation 5}$$

10
 11 Combining Equations 4 and 5 and multiplying by the number of individuals per unit area
 12 (D) or stand density leads to the total stem maintenance cost per unit land area (E)

$$13 \quad E = D(jah + krh), \quad \text{Equation 6}$$

15
 16 where j and k are parameters dependent on the ratio of maintenance cost of the wood and
 17 of the stem surface. These parameters need to be added as the relatively importance of
 18 these two costs is unknown and probably climate and species specific. According to the
 19 assumptions E and the product of D and a are independent of stand density (Equation 3)
 20 and can be replaced by a constant. Taking this into account when solving h , Equation 6
 21 converts to

$$22 \quad h = \frac{const}{(j \cdot const + kDr)}. \quad \text{Equation 7}$$

1

2 Based on another assumptions (Equation 2), the height of trees leading to breaking at a
3 given wind speed is

4

$$5 \quad h \propto \frac{r^3}{a}, \quad \text{Equation 8}$$

6

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

16

17

18 **Allometry and self-thinning law based on the new model**

19

20 In the theoretical situation when the value parameter j of Equations 6 and 7 is zero and
21 sapwood is assumed to make no contribution to stem maintenance

22

$$23 \quad w_s \propto D^{-3/2} \quad \text{Equation 9}$$

1

2 where w_s is biomass of the stem of a tree individual, as shown in Appendix A. This is
 3 equal to Equation 1 with the exception that Equation 9 is for stem biomass and Equation
 4 1 for total biomass (or total above ground biomass). In the reverse theoretical case when
 5 the parameter k is zero and sapwood causes all the maintenance of a stem

6

$$7 \quad w_s \propto D^{-2/3} \quad \text{Equation 10}$$

8

9 as shown in Appendix B. These two theoretical extremities are shown graphically in Fig
 10 1A and Fig 1B. In reality, since both stem surface and sapwood always cause
 11 maintenance, both extremities are unrealistic. For example Bosc et al. (2003) showed that
 12 for the *Pinus pinaster* that they studied stem surface maintenance cost is approximately
 13 half of the total stem maintenance cost.

14

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

1

2

3 Increasing complexity of the new model

4

5 The model described in the previous sections is simple and presented in this short article
6 to encourage development of more realistic and complex models following the same
7 principles. However, most of the dozens of possible adjustments making the model more
8 realistic are species-specific.

9

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

15

16 Ryan et al. (2006) review numerous studies indicating that the assumption of invariable
17 gross primary productivity with invariable leaf area index and variable tree height is
18 incorrect. Increasing height may decrease the efficiency of photosynthesis because of
19 hydraulic limitations (Ryan et al., 2006). This could be taken into account in the model.

20 Also the assumption of equal size of all tree individuals and stagenative equilibrium would
21 not be needed if a game-theoretical approach including realistic ranges of tree radii,
22 heights and growth rates could be chosen.

23

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

11 **Conclusions**

12
13 Focusing on the allometry of an individual without paying enough attention to its biotic
14 surroundings has been the dominant approach in developing theories on tree structure
15 (Niklas, 1994b). However, understanding the allometry of trees in an overcrowded stand
16 that is stagnating and is at the limit of self-thinning is the simplest and therefore in many
17 ways the best approach to model tree structure. This enables the use of Equation 3 for
18 modelling the toppling moment caused by wind drag and together with assumptions on
19 stem maintenance not only explains the height-radius ratio as some earlier models
20 (McMahon, 1973) but explains both the height and radius relative to stand density.
21 Thanks to this it can be applied to self-thinning law and lead to realistic self-thinning line
22 slopes ranging upwards from $-3/2$. Increasing stand density decreases biomass per unit
23 land area (i.e. self-thinning law) as the trees in them need to be shorter for stability and

1 need to avoid a large stem surface area requiring maintenance. Numerous species and
2 site-specific complicating factors influence the precise slope of the self-thinning line.
3 More sophisticated species-specific models including some of the aspects presented in
4 the previous section could be developed and tested with simple self-thinning data.
5 Alternatively ecophysiological data on maintenance or diameter, height and leaf area data
6 for tree individuals in stagnating stands could be used to test some of the assumptions
7 presented in this article. The model could be also applied to non-stagnating stands when
8 growth or leaf area information is available or on estimating biomass based on remote
9 sensing data on tree heights when data on stand density is not available.

10

11

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17

1 **Figure caption**

2

3 Figure 1. Functions A_{10} and A_1 show the maximal height without excessively high risk of

4 toppling and functions B_{10} and B_1 the maximal height based on the energetic

5 maintenance cost of the stem for a given stand density in a self-thinning situation.

6 A_{10} and B_{10} are computed from a tenfold stand density compared to A_1 and B_1 .

7 The arrows show how a 90% decrease in stand density changes stem dimensions

8 from the intersection between A_{10} and B_{10} to the intersection between A_1 and B_1 .

9 Fig. 1A demonstrates the situation when stem surface and Fig. 1B when sapwood

10 is assumed to cause all the maintenance. The functions B_{10} and B_1 form an

11 identical horizontal line in Fig. 1B. Functions A_{10} and A_1 are based on Equation 8

12 (where a is constant for a given function), functions B_{10} and B_1 in Fig. 1A on

13 Equation A.1 (where D is constant for a given function) and function $B_{10\&1}$ in Fig.

14 1B on Equation B.1. The assumption that stem dimensions are determined by the

15 intersection between functions A_{10} or A_1 and $B_{10\&1}$ to give the maximum possible

16 stem height is irrelevant in the theoretical case of Fig. 1B, as equal heights but

17 larger radii are equally possible, leading to greater strength.

18

19

1 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

2

1 **References**

2

- 3 Adler, F.R., 1996. A model of self-thinning through local competition. *Proceedings of the*
4 *National Academy of Sciences of the United States of America* 93, 9980-9984.
- 5 Anten, N.P.R., and Schieving, F., 2010. The Role of Wood Mass Density and Mechanical
6 Constraints in the Economy of Tree Architecture. *American Naturalist* 175, 250-
7 260.
- 8 Bosc, A., De Grandcourt, A., and Loustau, D., 2003. Variability of stem and branch
9 maintenance respiration in a *Pinus pinaster* tree. *Tree Physiology* 23, 227-236.
- 10 Coutand, C., Dupraz, C., Jaouen, G., Ploquin, S., and Adam, B., 2008. Mechanical
11 stimuli regulate the allocation of biomass in trees: Demonstration with young
12 *Prunus avium* trees. *Annals of Botany* 101, 1421-1432.
- 13 Coutts, M., and Grace, J. Eds.), 1995. *Wind and Trees*. Cambridge University Press,
14 Cambridge.
- 15 Davis, L.S., and Johnson, K.N., 1987. *Forest Management*. McGraw-Hill Book
16 Company.
- 17 Dean, T.J., Roberts, S.D., Gilmore, D.W., Maguire, D.A., Long, J.N., O'Hara, K.L., and
18 Seymour, R.S., 2002. An evaluation of the uniform stress hypothesis based on
19 stem geometry in selected North American conifers. *Trees-Structure and Function*
20 16, 559-568.
- 21 Farnden, C., and Herring, L., 2002. Severely repressed lodgepole pine responds to
22 thinning and fertilization: 19-year results. *Forestry Chronicle* 78, 404-414.
- 23 Givnish, T.J., 1986. BIOMECHANICAL CONSTRAINTS ON SELF-THINNING IN
24 PLANT-POPULATIONS. *Journal of Theoretical Biology* 119, 139-146.
- 25 Hutchings, M., 1983. ECOLOGYS LAW IN SEARCH OF A THEORY. *New Scientist*
26 98, 765-767.
- 27 King, D., 1981. TREE DIMENSIONS - MAXIMIZING THE RATE OF HEIGHT
28 GROWTH IN DENSE STANDS. *Oecologia* 51, 351-356.
- 29 King, D.A., Davies, S.J., Tan, S., and Noor, N.S.M., 2006. The role of wood density and
30 stem support costs in the growth and mortality of tropical trees. *Journal of*
31 *Ecology* 94, 670-680.
- 32 Larjavaara, M., and Muller-Landau, H.C., 2010. Rethinking the value of wood density.
33 *Functional Ecology*.
- 34 McMahon, T., 1973. SIZE AND SHAPE IN BIOLOGY. *Science* 179, 1201-1204.
- 35 Niklas, K.J., 1992. *Plant Biomechanics - An Engineering Approach to Plant Form and*
36 *Function*. The University of Chicago Press, Chicago.
- 37 Niklas, K.J., 1994a. INTERSPECIFIC ALLOMETRIES OF CRITICAL BUCKLING
38 HEIGHT AND ACTUAL PLANT HEIGHT. *American Journal of Botany* 81,
39 1275-1279.
- 40 Niklas, K.J., 1994b. *Plant Allometry*. The University of Chicago Press, Chigago.
- 41 Osawa, A., and Allen, R.B., 1993. ALLOMETRIC THEORY EXPLAINS SELF-
42 THINNING RELATIONSHIPS OF MOUNTAIN BEECH AND RED PINE.
43 *Ecology* 74, 1020-1032.

- 1 Peltola, H., Kellomaki, S., Hassinen, A., and Granander, M., 2000. Mechanical stability
2 of Scots pine, Norway spruce and birch: an analysis of tree-pulling experiments in
3 Finland. *Forest Ecology And Management* 135, 143-153.
- 4 Pruyn, M.L., Gartner, B.L., and Harmon, M.E., 2002. Respiratory potential in sapwood
5 of old versus young ponderosa pine trees in the Pacific Northwest. *Tree*
6 *Physiology* 22, 105-116.
- 7 Putz, F.E., Coley, P.D., Lu, K., Montalvo, A., and Aiello, A., 1983. UPROOTING AND
8 SNAPPING OF TREES - STRUCTURAL DETERMINANTS AND
9 ECOLOGICAL CONSEQUENCES. *Canadian Journal Of Forest Research-Revue*
10 *Canadienne De Recherche Forestiere* 13, 1011-1020.
- 11 Ryan, M.G., Phillips, N., and Bond, B.J., 2006. The hydraulic limitation hypothesis
12 revisited. *Plant Cell and Environment* 29, 367-381.
- 13 Schiel, D.R., and Choat, J.H., 1980. EFFECTS OF DENSITY ON MONOSPECIFIC
14 STANDS OF MARINE-ALGAE. *Nature* 285, 324-326.
- 15 Shinozaki, K., Yoda, K., Hozumi, K., and Kira, T., 1964. A quantitative analysis on plant
16 form - The pipe model theory. I - Basic analyses. *Japanese Journal of Ecology* 14,
17 97-105.
- 18 Sterck, F.J., Van Gelder, H.A., and Poorter, L., 2006. Mechanical branch constraints
19 contribute to life-history variation across tree species in a Bolivian forest. *Journal*
20 *of Ecology* 94, 1192-1200.
- 21 Weller, D.E., 1987. A REEVALUATION OF THE $-3/2$ POWER RULE OF PLANT
22 SELF-THINNING. *Ecological Monographs* 57, 23-43.
- 23 West, G.B., Brown, J.H., and Enquist, B.J., 1999. A general model for the structure and
24 allometry of plant vascular systems. *Nature* 400, 664-667.
- 25 Yoda, K., Kira, T., Ogawa, H., and Hozumi, K., 1963. Self-thinning in overcrowded pure
26 stands under cultivated and natural conditions. *Journal of Biology, Osaka City*
27 *University* 14, 107-129.
- 28
29

1 **Appendix A**

2
3 When sapwood is assumed not to make contribution to stem maintenance and the
4 parameter j is therefore zero Equation 7 simplifies to

5
6
$$h = \frac{const}{Dr} .$$
 Equation A.1

7
8 Combining this with Equation 8 leads to

9
10
$$\frac{r^3}{a} = \frac{const}{Dr}$$
 Equation A.2

11
12 and further to

13
14
$$r^4 \propto \frac{a}{D} .$$
 Equation A.3

15
16 Combining this with Equation 3 leads to

17
18
$$r^4 = \frac{const}{D^2} ,$$
 Equation A.4

19
20 which simplifies to

21
22
$$r = \frac{const}{D^{1/2}} .$$
 Equation A.5

23
24 As stem biomass of a tree (w_s) is in general

25
26
$$w_s \propto r^2 h ,$$
 Equation A.6

27
28 it is in this self-thinning situation based on Equation A.1

29
30
$$w_s = r^2 \frac{const}{Dr}$$
 Equation A.7

31
32 Combining this with Equation A.5 leads to

33
34
$$w_s = \frac{const}{DD^{1/2}}$$
 Equation A.8

35
36 and to

37

1 $w_s \propto D^{-3/2}$.

Equation A.9

2

3

4

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1 **Appendix B**

2
3 When stem surface is assumed not to make contribution to stem maintenance and the
4 parameter k is therefore zero Equation 7 simplifies to

5
6 $h = \text{const} .$ Equation B.1

7
8 Combining this with Equation 8 leads to

9
10 $\frac{r^3}{a} = \text{const}$ Equation B.2

11 and further to

12
13
14 $r^3 \propto a .$ Equation B.3

15
16 Combining this with Equation 3 leads to

17
18 $r^3 = \frac{\text{const}}{D} ,$ Equation B.4

19 which simplifies to

20
21
22 $r = \frac{\text{const}}{D^{1/3}} .$ Equation B.5

23
24 As stem biomass of a tree (w_s) is in general

25
26 $w_s \propto r^2 h ,$ Equation B.6

27
28 it is in this self-thinning situation based on Equation B.1

29
30 $w_s \propto r^2 .$ Equation B.7

31
32 Combining this with Equation B.5 leads to

33
34 $w_s = \frac{\text{const}}{D^{2/3}}$ Equation B.8

35 and to

36
37
38 $w_s \propto D^{-2/3} .$ Equation B.9

39

