

ALLOMETRIC SCALING THEORY APPLIED TO FIA BIOMASS ESTIMATION

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ABSTRACT.—Tree biomass estimates in the Forest Inventory and Analysis (FIA) database are derived from numerous methodologies whose abundance and complexity raise questions about consistent results throughout the U.S. A new model based on allometric scaling theory (“WBE”) offers simplified methodology and a theoretically sound basis for improving the reliability and usefulness of biomass estimation for all tree species. Although a complete test of the WBE theory is beyond the scope of this paper, implications of the theory are explored from results of another study consistent with WBE theory. Two interesting results were found: (1) a simplified approach using 10 generalized equations is within 10 to 40 percent of FIA county-scale biomass estimates, and (2) of the two methods, FIA’s methodology appears more inconsistent from State to State.

The largest application of current biomass methodology in the U.S. is found in the Forest Inventory and Analysis (FIA) database. FIA biomass estimates are calculated either from conversion functions of merchantable volume to total tree biomass or from species-specific biomass equations. Because so many different equations and techniques are used, there is concern about equation bias confounding FIA biomass results. For example, Hansen (this volume, table 5) compared 67 tree species common to four eastern FIA regions and found that biomass estimates differed by an average of 25 to 30 percent among regions for trees of the same size and species. The test did not include a control for “known” biomass, but methodology differences among FIA regions seem a likely explanation for the observed differences among equations for the same species.

Improving FIA biomass estimates by constructing new equations would be a huge and costly undertaking because there is no theory to guide the process other than statistically subsampling for new biomass data, which would need to represent all tree species in all locations throughout the entire U.S. However, allometric scaling theory offers a possible area of research to simplify the process.

Allometric scaling is an old idea in biology—linking an organism’s size to its energy balances and structural dimensions (Niklas 1994, Peters 1983, Schmidt-Nielsen 1984)—that is being revisited with new theoretical explanation (Enquist and Niklas 2001; Enquist and others 1998, 1999, 2000; West and others 1997, 1999a, 1999b). The logarithmic model currently used for many tree biomass and volume equations (Schumacher and Hall 1933, Whittaker and Woodell 1968) is related to allometric scaling theory. However, the widespread use of the logarithmic model is generally based on empirical evidence resulting from the fitting of regression data rather than on any firm theoretical basis. The objective of this paper is to explore devising new biomass estimators through greater use of the allometric scaling theory.

First, tree biomass estimation is discussed based on recent work (Jenkins and others 2003), in which we surveyed the literature of all published biomass equations for U.S. tree species and summarized results into 10 equations based on diameter at breast height (d.b.h.). The synthesis into so few equations is consistent with allometric scaling theory or what we call the “WBE allometric-scaling model,” where WBE stands for the developers—West, Brown, and Enquist. Next, to hypothesize about the usefulness of the WBE model for FIA biomass estimation, the 10 equations were compared to FIA biomass in the Eastern U.S. (Hansen and others 1992). Because neither the 10 equations nor the FIA biomass estimates offer a satisfying measure for “true” biomass, the paper concludes with a fuller discussion of the WBE model that might be tested for improved biomass estimators.

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BIOMASS EQUATIONS

The literature contains more than 2,300 biomass equations for various wood, bark, foliage, branch, and root components for more than 100 species. However, use of these equations for consistent forest biomass estimation for all species is messy because there are many gaps among species, tree sizes, and geographic areas not covered by the equations. Furthermore, developers of these equations often caution against extrapolation beyond their study area.

As an interim solution to this problem, Jenkins and others (2003) synthesized all the published equations in a modified meta-analysis to develop new equations that could be used for similar species groups covering all U.S. species. The idea was to “average” the variation among existing equations as a way to extend the data pool for filling all the gaps. From our database of component equations, we were able to compile 315 species-specific equations to estimate total aboveground biomass from d.b.h. only, which eliminated all equations requiring more variables than d.b.h. From the species-specific equations, we generated what we called “pseudodata” within the d.b.h. ranges of the original data (fig. 1). Published equations were most numerous for hardwood and conifer species up to 70 cm d.b.h. Large-tree equations up to 150 cm d.b.h. were available only for western conifer species.

The pseudodata were used to construct 10 new total biomass equations as a summary of the literature. The 10 equations—fit to a simple log model form—included 5 equations for conifer species, 4 for hardwoods, and 1 for a woodland group including both conifer and hardwood dryland forest species (table 1). The objective of the meta-analysis was to develop an easy-to-use set of biomass equations for using FIA data to measure the amount of carbon sequestered in U.S. forests. Because the equations predicted total biomass only, we also developed generalized hardwood and conifer ratio equations to partition estimates into foliage, bark, stem wood, and coarse root components (see Jenkins and others 2003, for details).

A secondary observation from this work was a surprising similarity of pseudodata among species. Graphs of combined pseudodata showed much overlap for many species from diverse geographic areas. For example, loblolly, pinyon, and lodgepole pine species—which grow in warm/humid Southeast, hot/arid Southwest, and cool/montane northern Rocky Mountains, respectively—overlapped each other and all other pine species (fig. 2). This seems a remarkable coincidence, suggesting some underlying explanation such as the WBE model.

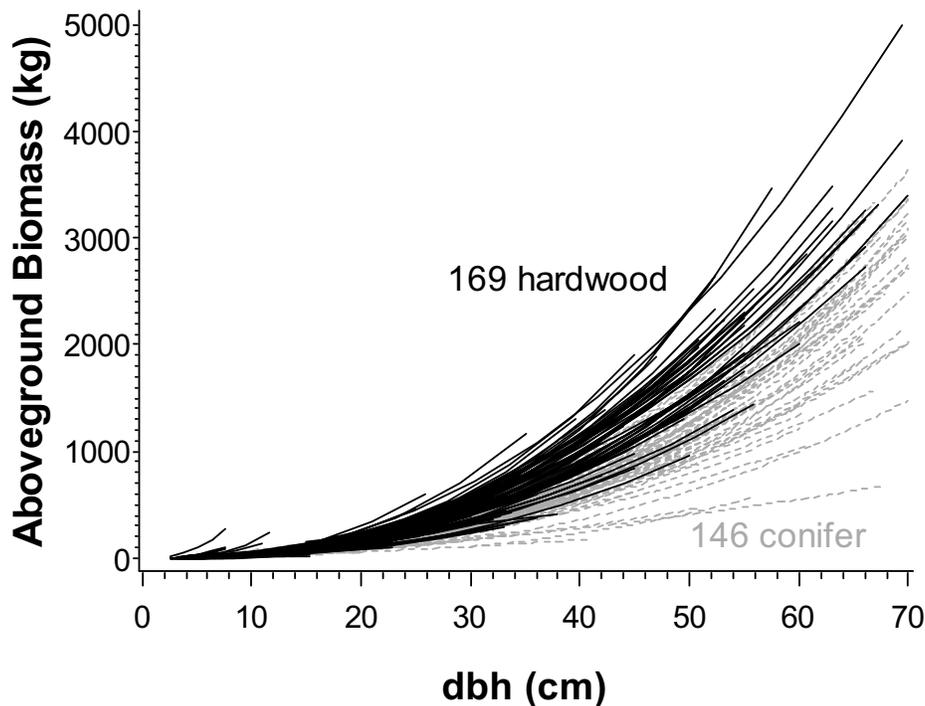


Figure 1.—Pseudodata were generated within d.b.h. ranges of the original data from 315 species-specific equations for hardwoods and conifers throughout the U.S.

Table 1. —Parameters and equations¹ for estimating total aboveground biomass for all hardwood and conifer species in the U.S. (from Jenkins and others 2003)

	Species group ²	Parameters		Data points ³	Max ⁴ d.b.h. cm	RMSE ⁵ - - - log units - - -	R ²
		β_0	β_1				
Hardwood	Aspen/alder/cottonwood/willow	-2.2094	2.3867	230	70	0.507441	0.953
	Soft maple/birch	-1.9123	2.3651	316	66	0.491685	0.958
	Mixed hardwood	-2.4800	2.4835	289	56	0.360458	0.980
	Hard maple/oak/hickory/beech	-2.0127	2.4342	485	73	0.236483	0.988
Softwood	Cedar/larch	-2.0336	2.2592	196	250	0.294574	0.981
	Douglas-fir	-2.2304	2.4435	165	210	0.218712	0.992
	True fir/hemlock	-2.5384	2.4814	395	230	0.182329	0.992
	Pine	-2.5356	2.4349	331	180	0.253781	0.987
	Spruce	-2.0773	2.3323	212	250	0.250424	0.988
Woodland ⁶	Juniper/oak/mesquite	-0.7152	1.7029	61	78	0.384331	0.938

¹ Biomass equation:

$$bm = \text{Exp}(\beta_0 + \beta_1 \ln d.b.h.)$$

where

- bm = total aboveground biomass (kg) for trees 2.5-cm $d.b.h.$ and larger
- $d.b.h.$ = diameter at breast height (cm)
- Exp = exponential function
- ln = natural log base "e" (2.718282)

² See Jenkins and others (2003) for definition of species groups and a suggested match to the FIA species list.

³ Number of data points generated from published equations (generally at 5-cm $d.b.h.$ intervals) for parameter estimation.

⁴ Maximum $d.b.h.$ of trees measured in published equations.

⁵ Root mean squared error or estimate of the standard deviation of the regression error term in natural log units.

⁶ Woodland group includes both hardwood and softwood species from dryland forests.

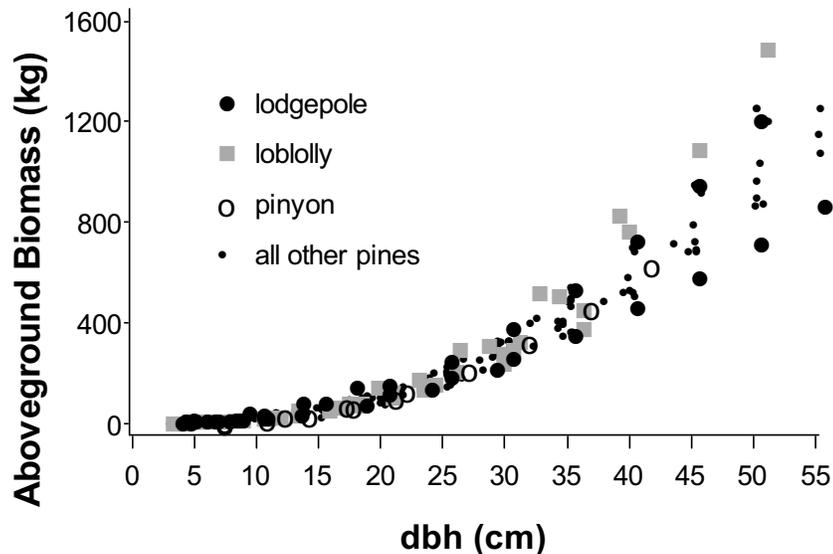


Figure 2.—There is little pattern within pseudodata generated from published biomass equations for several diverse pine species throughout the U.S. Loblolly grows in warm/humid Southeast, pinyon in hot/arid Southwest, and lodgepole in cool/montane northern Rocky Mountains.

FIA BIOMASS COMPARISON

The new 10 equations (hereafter called Jenkins estimates or Jenkins equations) were compared to the biomass estimators in the FIA database. Differences of up to 40 percent or more were revealed between FIA estimates and the new equations for a county-scale compilation (fig. 3). In each case, tree-level data were compiled for each county by the two methods; comparison was made by subtracting FIA biomass from the Jenkins estimate, then dividing by Jenkins and multiplying by 100 to express as a percentage. Except for Georgia, the FIA estimates for most of the Southern States were within 10 percent of the Jenkins estimates, but the differences between the two methods increased to 40 percent or more when moving north and west.

Since the Jenkins equations are constant for all States, abrupt changes at State boundaries (such as for Georgia, New York, and Indiana) cause special concern because they create the impression that FIA methods change abruptly at State or FIA unit boundaries. A more speckled map showing county-to-county variation within States, depending on species composition, would have been expected if the FIA equations had simply been more precise. It is difficult to say which equations are better, but the FIA estimates do seem to include some State-to-State variation due to methodology, whereas the Jenkins equations are at least consistent in methodology throughout.

Although the comparison lacks a control for “true” biomass, it does show that: (1) there is inconsistency in FIA biomass estimates, and (2) the Jenkins equations seem close enough to the FIA biomass estimates to warrant further study of simplified methods. Furthermore, a “repair task” to fix inconsistencies in the FIA database or construct new species-specific equations to fill gaps seems daunting with the current empirical framework that allows different equation parameters for every possible species and site difference. Perhaps it is time to seek a general theoretical framework to make the task more manageable. Allometric scaling theory might help in this regard.

ALLOMETRIC SCALING THEORY

Whether used with plants or animals, the WBE model applies to naturally occurring networks that carry sustaining fluids in organisms, in which each small part of the network is a self-similar replicate of the whole (fig. 4). Two key tenets

of the theory are (1) individual cells are of similar size in all organisms, and (2) no matter what the size of the organism, the ends of the fractal network are the same size. Tree leaves are an example of the second tenet; leaves are at the end of the fractal branching network in trees, and leaves for a given species are roughly the same size no matter the tree age. The WBE model offers many proportionalities relating components of structure and function, and it is these proportionalities that appeal to applied modelers.

The WBE framework describes biomass with the following equation:

$$B_{TA} = C(p \text{ d.b.h.}^{8/3}) \quad (1)$$

where

B_{TA} = total aboveground dry weight biomass

C = proportionality constant

p = specific gravity of aboveground material

$8/3$ = scaling exponent, derived from earlier studies where d.b.h. scales as volume to the $3/8$ power (Enquist and others 1998)

d.b.h. = stem diameter at breast height.

The WBE framework is not too unlike what is normally used for biomass estimation, except for two key differences: (1) the exponent on d.b.h. is fixed to $8/3$, and (2) specific gravity is included in the model. By specific gravity we mean total tree specific gravity (an average of wood, bark, branches, and leaves), which is not often measured. Generally in an allometric equation, both the proportionality constant (C) and the scaling ($8/3$) exponent would be estimated from accurately measured biomass data. In this case, we need only estimate C and use an appropriate specific gravity.

Applying the WBE biomass framework (equation 1) to the Jenkins equations (table 1) does make the WBE model seem plausible. In 9 of the 10 equations, the scaling parameter estimated from pseudodata is remarkably close to the theoretical $8/3$ or 2.67. However, all of the scaling exponents are lower than the theoretical 2.67, which warrants further testing before drawing conclusions. A more formal test, involving confidence intervals around the scaling exponents to test for inclusion of 2.67, does not seem useful because of the complexity of the modified meta-data analysis used to estimate the coefficients. The pseudodata have their own biases and other problems that limit usefulness for an objective test. Instead, a test of the WBE model with carefully measured tree biomass and specific gravity data seems more worthwhile.

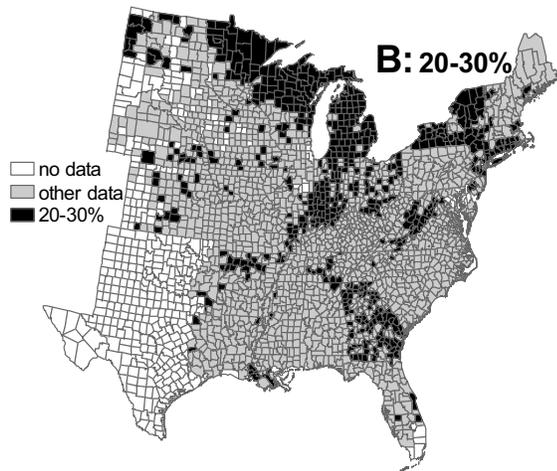
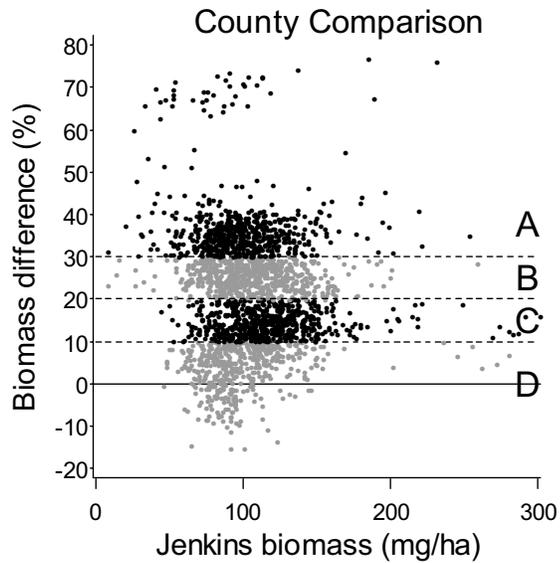
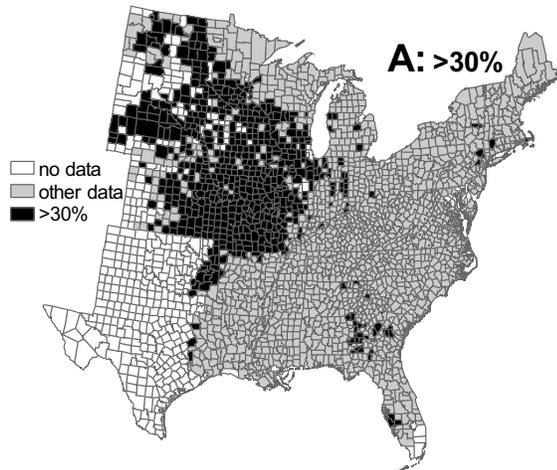
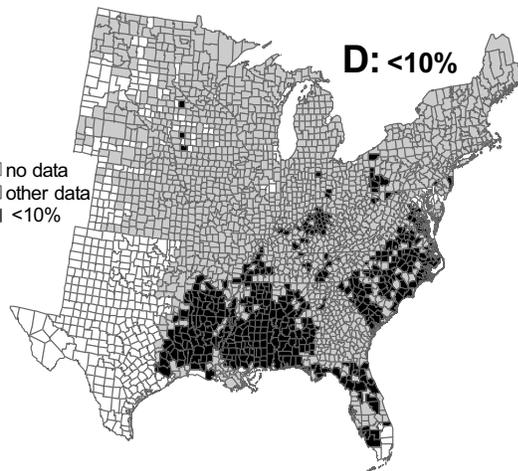
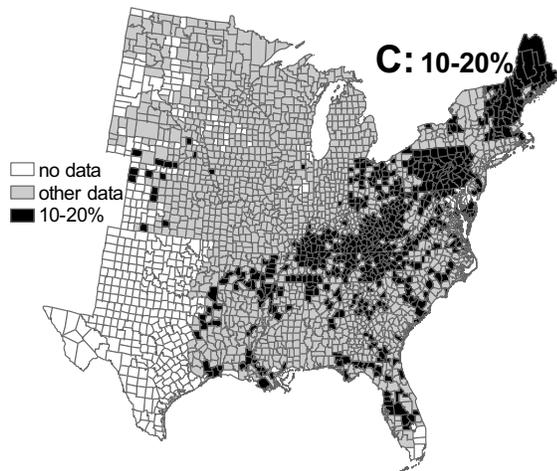


Figure 3.—County-level comparison between Jenkins and FIA volume equations (applied to same tree-level data) reveals differences in methodology that range from <10 to 80 percent depending on geographical area. The largest differences (A) are found in the Midwest, and the smallest differences (D) appear in the Southeast. Because the Jenkins equations are constant for every State, the difference pattern suggests that FIA volume methodology varies greatly from State to State. Comparison was made by subtracting FIA from Jenkins, then dividing by Jenkins and multiplying by 100 to express as a percentage.

*-37% for Cherokee County, Iowa, omitted from graph





Lung circulatory system is a self-similar fractal.



Likewise, tree branching follows a similar pattern.

Figure 4.—*The scientists who developed the scaling theory took clues from naturally occurring networks that carry sustaining fluids in both plants and animals. Each small part of the network is a self-similar replicate of the whole.*

CONCLUSION

Although thousands of equations have been published for components of tree biomass, consistent application for all species across the U.S. is difficult because most equations were developed from small local populations. However, the FIA database pieces together existing biomass methodology for nationwide estimates. The FIA approach offers a “bottom up” strategy in which each FIA unit uses the best equations or methodology for a particular State or region. Jenkins and others (in press) offer an alternative by first summarizing existing literature into 10 equations in a consistent fashion for hardwood and conifer species groups. This is a “top down” strategy, which averages equation differences within species and across similar species, and which groups species broadly enough to logically cover gaps. Comparison of the two strategies showed the most similarity in the Southern States but differences up to 40 percent or more elsewhere.

Although neither the FIA database nor the Jenkins equations offer a satisfying “true” biomass estimator, the Jenkins equations seem close enough to the FIA estimates to warrant

further study of a simplified method. Furthermore, the Jenkins equations are consistent with the notion of a generalized WBE allometric scaling model. Allometric scaling theory offers the WBE model for improved biomass estimation. Although similar to previous logarithmic models, the WBE model has one less parameter to estimate and includes a total tree specific gravity variable, which is an appealing concept for grouping large numbers of species into similar specific gravity classes.

Needed to test the WBE model is a designed experiment of field data strategically sampled at a few sites throughout the U.S. For example, biomass data might be collected with either destructive or non-destructive sampling methods (such as discussed in Gregoire and others 1995) from about 10 species of several sizes each, spanning specific gravity ranges from 0.3 to 0.8 for at least four sites in the Southeastern, Northeastern, Southwestern, and Northwestern U.S. The replications of tree size and site conditions would provide a total sample of about 120 trees. Each tree would also require subsampling for specific gravity throughout its wood, bark, branches, and foliage. If successful, results would provide biologically consistent methodology for all species, and specific gravity parameters would be used to group species.

The WBE model also offers linkage to volume estimation. Tree boles (trunks) have been characterized in geometric terms as stacked frustums of neiloids, paraboloids, and cones since the middle of the 19th century (Grey 1943). A vascular pipe model of a tree (Shinozaki and others 1964) is consistent with the middle and upper geometric models (the paraboloid and the cone) and is consistent with the WBE model of biomass. The WBE model thus should be consistent with a stem taper model. Therefore, it might be possible to develop the mathematical details of a connection between the WBE model and stem taper, and then fit the resultant joint model to data. Estimates of bole volume could then be obtained from the integral of the taper model, a standard mensurational procedure. Promising results in this endeavor may result in a major research thrust to fit the joint models regionwide or nationwide.

Lastly, if the WBE model could successfully separate bole from total biomass, there seems further opportunity for separating biomass components. Even if rough ratios for bark, branch, and foliage components are used, the WBE model would offer vast improvement over what is currently available because the largest biomass component—the bole—would be estimated quite precisely, which would limit errors to bark, branches, and foliage.

The WBE model might vastly improve the reliability, consistency, and usefulness of biomass and perhaps volume estimation across the Nation. The FIA database and all users of biomass data would benefit greatly.

LITERATURE CITED

- Enquist, B.J.; Niklas, K.J. 2001. Invariant scaling relations across tree-dominated communities. *Nature*. 410: 655–660.
- Enquist, B.J.; Brown, J.H.; West, G.B. 1998. Allometric scaling of plant energetics and population density. *Nature*. 395: 163–166.
- Enquist, B.J.; West, G.B.; Brown, J.H. 2000. The origin and ecological consequences of quarter-power allometric scaling in vascular plants. In: Brown, J.H.; West, G.B., eds. *Scaling in biology*. London, UK: Oxford University Press: 167–198.
- Enquist, B.J.; West, G.B.; Charnov, E.L.; Brown, J.H. 1999. Allometric scaling of production and life history variation in vascular plants. *Nature*. 401: 907–911.
- Gregoire, T.G.; Valentine, H.T.; Furnival, G.M. 1995. Sampling methods to estimate foliage and other characteristics of individual trees. *Ecology*. 76(4): 1181–1194.
- Grey, H.R. 1943. Volume measurement of forest crops. *Aust. Forestry*. 7: 48–74.
- Hansen, M.H. [In press.] Volume and biomass estimation in FIA, national consistency –vs.- regional accuracy. In: *Proceedings: 2001 Midwest forest mensurationists' annual meeting and the 3rd annual forest inventory and analysis science symposium; 2001 October 17–19; Traverse City, MI*.
- Hansen, M.H.; Frieswyk, T.; Glover, J.F.; Kelly, J.F. 1992. The eastside forest inventory database: users manual. Gen. Tech. Rep. NC-151. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 48 p.
- Jenkins, J.C.; Chojnacky, D.C.; Heath, L.S.; Birdsey, R.A. 2003. National-scale biomass estimation for United States tree species. *Forest Science*. 49(1): 12–35.
- Niklas, K.J. 1994. *Plant allometry: the scaling of form and process*. Chicago, IL: University of Chicago Press. 395 p.
- Peters, R.H. 1983. *The ecological implications of body size*. Cambridge, UK: Cambridge University Press. 345 p.
- Schmidt-Nielsen, K. 1984. *Scaling: why is animal size so important?* Cambridge, UK: Cambridge University Press. 241 p.
- Schumacher, F.X.; Hall, F.S. 1933. Logarithmic expression of timber-tree volume. *Journal of Agriculture Research*. 47: 719–734.
- Shinozaki, K.; Yoda, K.; Hozumi, K.; Kira, T. 1964. A quantitative analysis of plant form: the pipe model theory. I. Basic analysis. *Japan Journal of Ecology*. 14: 97–105.
- West, G.B.; Brown, J.H.; Enquist, B.J. 1997. A general model for the origin of allometric scaling laws in biology. *Science*. 276: 122–126.
- West, G.B.; Brown, J.H.; Enquist, B.J. 1999a. The fourth dimension of life: fractal geometry and allometric scaling of organisms. *Science*. 284: 1677–1679.
- West, G.B.; Brown, J.H.; Enquist, B.J. 1999b. A general model for the structure and allometry of plant vascular systems. *Nature*. 400: 664–667.
- Whittaker, R.H.; Woodell, G.M. 1968. Dimension and production relations of trees and shrubs in the Brookhaven forest, New York. *Journal of Ecology*. 56: 1–25.