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An Estimate of Full Density Curves for Branches on Standing Trees: A Case Study of the Evergreen Broadleaf Tree, *Quercus acuta*, in the Tokyo University Forest in Chiba, Japan

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ABSTRACT

The purpose of this study was to determine the full density curves of branches on standing trees. Sixty sample trees of *Quercus acuta* in a single stand were selectively cut in the Tokyo University Forest in Chiba, and then diameters and lengths of those branches with more than 2cm diameter that were at a length between 3.3m and 9.3m above ground were measured at one meter intervals along their stems and branches. To derive the full density curve of branches, the number of branches at a specific length and the maximum average volumes of branches above that length were selected to be independent and dependent variables, respectively in reference to the pipe model theory. The linear relationships between these variables were investigated on a log-log scale. The result showed that the regression estimates were significant for lengths from 4.3m to 8.3m, and that the full density curves for these significant lengths were considered to have a common slope parameter of -0.9801. This implied that the -3/2 power law of self-thinning is effective for branches on standing trees that are similar to the standing trees in forest stands. Further research was required, however, to investigate whether this slope is applicable not only to *Quercus acuta* but also to other species.

Keywords: -3/2 power law, branch, broadleaf tree, full density curve, self-thinning

INTRODUCTION

A full density curve represents the relationship between the mass and number per unit area in overcrowded plant communities (SHIDEI, 1956; KIRA, 1957a, b; TADAKI, 1963). When the average weights of plants among overcrowded communities are plotted against their densities on a log-log scale, the relationship between the two variables will follow a single line. The slope of this line is generally around -3/2 regardless of species, age, initial density and soil fertility level; this has become known as the -3/2 power law of self-thinning (YODA *et al.*, 1963).

The full density curve is expressed as follows:

$$\bar{v}_m = a_0 N^{-a_1} \quad [1]$$

or

$$\log \bar{v}_m = a_2 - a_1 \log N, \quad [2]$$

where $\bar{v}_m$ is the maximum attainable average volume of plants, N is the number or density of plants per unit area, a_0 or a_2 (= $\log a_0$) is the intercept of the line and a_1 is its slope (SMITH and HANN, 1984).

The reason why the slope of the full density curve, a_1 , becomes -3/2 is allometrically explained as follows, referring to WHITE (1981) and ZEIDE (1987). Given that the number of plants in a given space, N , raised to some power is proportional to their average horizontal width, $\bar{w}$, under fully occupied condition, this relation is expressed using the coefficient α by

$$\bar{w} \propto N^{-\frac{1}{\alpha}}. \quad [3]$$

Furthermore, the average width of plants is assumed to be proportional to their average vertical length, $\bar{l}$, on condition that plants of the same species are geometrically similar regardless of age and habitat conditions. Therefore,

$$\bar{l} \propto \bar{w}^\beta. \quad [4]$$

where β is a coefficient. Since the average volume of plants can be assumed to be proportional to the product of length

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and the power of the width, $\bar{v}$ is represented using the coefficient γ by

$$\bar{v} \propto \bar{w}^{\gamma} \bar{l} \propto \bar{w}^{\beta+\gamma} N^{-\frac{\beta+\gamma}{\alpha}}. \quad [5]$$

YODA et al. (1963) considered that if each plant is completely closed, the coefficient α becomes two, and that if the forms of plants are completely similar, the parameters β and γ become one and two, respectively. Thus, the power of N in Eq. 5 becomes -3/2, which is derived from the geometrical manner in which the plants are packed together in a given space.

The slope parameter of the curve, however, is not exactly -3/2 in actual situations, which only exist in the ideal or virtual condition of $(\alpha, \beta, \gamma) = (2, 1, 2)$. For instance, SAKAGUCHI (1961) revealed that the slopes of full density curves on a log-log scale vary with planted tree species such as Japanese cedar, Japanese cypress and red pine in even-aged pure stands. WESTOBY and HOWELL (1986) and WELLER (1987) estimated hundreds of full density curves using both published data and temporal plot data from forest stands and concluded that the slopes were significantly different depending on the species, the site index and the tolerance. NISHIZONO et al. (2002) also supported WESTOBY, HOWELL and WELLER's conclusion, employing thousands of actual plot data from Japanese cedar and Japanese cypress planted stands.

Although the slope parameter of a full density curve is not exactly -3/2, it is a universal law among living creatures that the N - v plot is bounded by a specific curve. For instance, LONSDALE and WATKINSON (1983) showed that this law basically fits well with most plants such as monocotyledonous grass and dicotyledonous herbs. WATANABE (1985) discovered that even bamboo populations follow this law. The law is true not only among plants but also animals such as grasshoppers (BEGON et al., 1986), seashells (HUGHES and GRIFFITHS, 1988) and sea trout (ELLIOT, 1993) if some experimental supports like constant food inputs are given to the target population.

Thus, the previous studies have proved the universality of the law mainly among different species and additionally among different ages, site conditions and so on. Here, from another point of view, since this law is intrinsically derived from the simple geometrical manner as shown in Eqs. 3 - 5, its universality seems to expand on different spatial scales: This law can be effective on an individual scale as well as on a community or population scale that have been reported in previous studies. As for forests, these scale relations are interpreted as standing trees for an individual scale and forest stands for a community scale, namely that the -3/2 power law seems effective for branches on standing trees that are similar to the standing trees in forest stands. Needless to say, there are ecologically, or physiologically, differences between the two scales: The self-thinning in a standing tree deals with new branch production according to height growth and translocation of photosynthates from a stem to branches (SPRUGEL, 2002) while the self-thinning in forest stands generally deals with no ingrowing tree. But at the same time, there are points in common between the two scales like a spatial competition

for survival and resulting mortality according to a lack of sunlight, which make us expect the validity of the law on an individual scale as well. However, this kind of -3/2 power law among overcrowded branches has not been investigated until now.

Thus, in this study we direct our attention to the self-thinning, or to be exact, self-pruning in the following, occurring among branches on a standing tree. The purpose of this study is to determine the full density curve of branches, especially in regard to the relationship between the number of branches on standing trees and their average volume.

MATERIALS AND METHODS

Collection and Measurement of Samples

We collected data on the number of branches and their volumes from 60 samples of *Quercus acuta*, an evergreen broadleaf tree, in a single stand with a mixture of *Quercus acuta* and *Castanopsis sieboldii* in the Tokyo University Forest in Chiba. The university forest is located in the southern Boso peninsular, Kanto region, Japan. *Quercus acuta* is typical of the natural forests in this area. The sample trees were selectively cut to produce fuel woods, which compose the dominant trees in the subject stand. The basic statistics of the sample trees were as follows: The mean and standard deviation of stem diameters at a length (see detail in the following paragraph) of 1.3m were 17.43cm and 3.070cm; the same figures regarding tree length were 12.28m and 1.125m, respectively. Thus, the standard deviations of diameter and length were relatively low because the dominant trees were intentionally selected for fuel woods.

In each sample tree, diameters of those branches with more than 2cm diameter that were at a length between 3.3m to 9.3m above ground were measured at one meter intervals along the stem and branches. Note that the "length" of trees along a stem and branches is employed instead of the vertical "height" of trees in this measurement. The starting length of 3.3m represents the minimum length (or height) at which all sample trees have at least one branch, and the ending length of 9.3m represents the length that does not exceed the minimum sample tree length of 9.9m. In addition, the length of each branch was also measured. Furthermore, the volumes of branches were calculated by summing up the circular truncated cones, as defined by the following equation:

$$v = \frac{l}{3} (g_1 + g_2 + \sqrt{g_1 g_2}), \quad [6]$$

where v is the volume of a circular truncated cone that forms part of a branch, l is the length of the cone (basically one meter except at the top of branch), and g_1 and g_2 are the top and bottom basal areas of the cone, respectively, as calculated from corresponding diameters.

Selection of the Variables of the Density N and Average Volume $\bar{v}$

To derive a full density curve, the number of branches at a specific length per tree and the average volume of branches that are above a specific length per tree are selected as density N and average volume $\bar{v}$, respectively. The variable $\bar{v}$ is expressed by the total volume of branches above a specific length divided by the number of branches at a specific length on a single tree. For instance, let us think of a tree like Fig. 1a, where branches are colored black only to show them clearly. In the case of a 4.3m length (Fig. 1b), where the white lines represent the length along a stem and the branches above ground, the number of branches at that length, $N_{4.3}$, is two, and the corresponding total branch volume is expressed by $(v_{1.4.3} + v_{2.4.3} + v_{3.4.3} + v_{4.4.3})$. Consequently, $\bar{v}_{4.3}$ is $(v_{1.4.3} + v_{2.4.3} + v_{3.4.3} + v_{4.4.3})/2$. Similarly, in the case of a 5.3m length (Fig. 1c), the number of branches at that length, $N_{5.3}$, is four, and the corresponding total branch volume is expressed by $(v_{1.5.3} + v_{2.5.3} + v_{3.5.3} + v_{4.5.3} + v_{5.5.3} + v_{6.5.3})$. Consequently, $\bar{v}_{5.3}$ is $(v_{1.5.3} + v_{2.5.3} + v_{3.5.3} + v_{4.5.3} + v_{5.5.3} + v_{6.5.3})/4$.

Though other variables such as the total number of branches per tree and their average volume may instead be conceivable for N and $\bar{v}$, N_i and $\bar{v}_i$ as defined above seem to represent the full density curve of branches in the most effective way based on the concept of the pipe model theory (SHINOZAKI *et al.*, 1964). The theory expresses the linearly proportional relationship between the total basal area at a specific height and the total biomass above the specific height in a plant body, that can be represented in the case of this study as follows;

$$\frac{\sum_j v_{ji}}{N_i} = \bar{v}_i \propto \frac{\sum_j g_{ji}}{N_i} = \bar{g}_i \quad (\because \sum_j v_{ji} \propto \sum_j g_{ji}) \quad [7]$$

where g_{ji} represents the basal area of the j th branches at length i and $\bar{g}_i$ is their average. Though $\bar{v}_i$ excludes the photosynthetic organ of leaves above the length i while SHINOZAKI *et al.* (1964) includes them, Eq. 7 seems practically valid considering the proportion of leaves is relatively low compared with $\sum_j v_{ji}$. Note that the pipe model theory for branches assumed in Eq. 7 corresponds to the geometrical similarity of plants assumed in Eq. 4. Moreover, if it is assumed that the number of branches in a given space is proportional to their average diameter, so that the number of branches raised to some power is proportional to their average basal area, under fully occupied condition as same as assumed in Eq. 3, then

$$\bar{g}_i \propto N_i^\delta, \quad [8]$$

which indicates that the above-defined $\bar{v}_i$ is proportional to the above-defined N_i raised to some power, δ , on a single tree;

$$\bar{v}_i \propto \bar{g}_i \propto N_i^\delta. \quad [9]$$

The power index, δ , can be analyzed into more specific indices like $(\beta + \gamma)/\alpha$ in Eq. 5.

As shown in the cases of Fig. 1, since the variables N_i and $\bar{v}_i$ change with length i , it is furthermore necessary to investigate what length is appropriate for determining the full density curve between N_i and $\bar{v}_i$; self-pruning does not necessarily work at the height where the density of branches is relatively low.

Thus, N_i s and $\bar{v}_i$ s are calculated at a length of i (=3.3, 4.3, 5.3, 6.3, 7.3, 8.3 and 9.3m) for all 60 sample trees. After this calculation, $\bar{v}_i$ s are arranged in order of corresponding N_i s at each length i , and then the maximum $\bar{v}_{mi}$ s are identified for Eq. 2 among the $\bar{v}_i$ s that have the same value of N_i s for each length i (see details in the next section). Finally, the parameters of a_{i_1} and a_{i_2} in Eq. 2 are estimated by the ordinary least squares method for each length i , and the differences of the parameter

Fig. 1 Illustration of the way to identify the variables for a full density curve: a) A sample tree having branches colored black, b) the identified number of branches and branch volumes at and above a length of 4.3m, and c) similar to b but above a length of 5.3m

values for the lengths are statistically analyzed.

RESULTS AND DISCUSSION

Variable Values

Table 1 shows the variables obtained from 60 sample

Table 1 Variables obtained from 60 sample trees

Tree No.	3.3m		4.3m		5.3m		6.3m		7.3m		8.3m		9.3m	
	$N_{3.3}$	$\Sigma v_{3.3}$	$N_{4.3}$	$\Sigma v_{4.3}$	$N_{5.3}$	$\Sigma v_{5.3}$	$N_{6.3}$	$\Sigma v_{6.3}$	$N_{7.3}$	$\Sigma v_{7.3}$	$N_{8.3}$	$\Sigma v_{8.3}$	$N_{9.3}$	$\Sigma v_{9.3}$
1	1	0.0620	2	0.0494	2	0.0365	2	0.0252	2	0.0154	4	0.0086	2	0.0024
2	1	0.0610	1	0.0490	1	0.0379	2	0.0276	3	0.0188	6	0.0106	2	0.0026
3	1	0.0613	3	0.0495	3	0.0362	6	0.0233	5	0.0109	3	0.0031		
4	1	0.0452	2	0.0350	2	0.0253	2	0.0167	4	0.0088	2	0.0024		
5	3	0.0424	5	0.0297	2	0.0188	5	0.0102	3	0.0039	1	0.0007		
6	2	0.0467	2	0.0349	2	0.0250	5	0.0154	4	0.0063	1	0.0011		
7	1	0.0692	1	0.0559	1	0.0441	1	0.0336	2	0.0241	4	0.0153	3	0.0048
8	2	0.0821	3	0.0634	3	0.0458	5	0.0315	5	0.0180	6	0.0084	3	0.0017
9	1	0.0556	2	0.0444	2	0.0337	3	0.0251	4	0.0169	3	0.0101	3	0.0046
10	1	0.0781	1	0.0643	2	0.0508	2	0.0397	4	0.0280	6	0.0155	5	0.0047
11	1	0.0649	1	0.0513	1	0.0382	3	0.0263	3	0.0162	3	0.0062	2	0.0008
12	1	0.0666	1	0.0536	1	0.0430	1	0.0341	2	0.0242	3	0.0158	4	0.0083
13	1	0.0863	2	0.0701	4	0.0524	6	0.0369	5	0.0229	7	0.0100	2	0.0017
14	1	0.0926	1	0.0769	2	0.0616	2	0.0485	4	0.0349	6	0.0222	3	0.0124
15	1	0.0676	1	0.0540	1	0.0422	1	0.0330	2	0.0244	4	0.0154	3	0.0067
16	1	0.0868	1	0.0732	1	0.0613	1	0.0495	1	0.0394	2	0.0299	4	0.0193
17	1	0.0589	1	0.0481	1	0.0394	2	0.0292	3	0.0209	3	0.0117	3	0.0065
18	1	0.1008	1	0.0877	1	0.0762	2	0.0634	2	0.0506	3	0.0373	5	0.0245
19	1	0.0931	1	0.0774	1	0.0638	2	0.0497	2	0.0367	3	0.0236	4	0.0149
20	1	0.1130	2	0.0942	2	0.0754	2	0.0588	5	0.0400	7	0.0238	5	0.0086
21	1	0.0967	1	0.0811	1	0.0656	1	0.0518	3	0.0394	3	0.0250	4	0.0152
22	1	0.0989	1	0.0851	2	0.0689	2	0.0549	2	0.0422	4	0.0296	3	0.0178
23	1	0.0923	1	0.0783	1	0.0651	2	0.0519	3	0.0385	3	0.0258	5	0.0126
24	1	0.1102	1	0.0947	1	0.0791	2	0.0636	2	0.0498	3	0.0363	3	0.0251
25	1	0.0950	2	0.0770	2	0.0614	3	0.0469	4	0.0336	5	0.0213	3	0.0116
26	1	0.0843	1	0.0685	1	0.0553	2	0.0427	3	0.0293	3	0.0171	3	0.0082
27	3	0.0747	4	0.0558	6	0.0406	4	0.0236	5	0.0124	3	0.0025	1	0.0001
28	1	0.0955	1	0.0801	1	0.0669	2	0.0541	3	0.0405	3	0.0280	4	0.0175
29	1	0.0630	1	0.0499	1	0.0401	2	0.0313	2	0.0206	2	0.0121	3	0.0060
30	3	0.0950	4	0.0713	4	0.0526	5	0.0375	9	0.0228	5	0.0079	3	0.0016
31	1	0.1091	2	0.0912	3	0.0706	6	0.0497	8	0.0287	7	0.0114	3	0.0014
32	1	0.1109	1	0.0929	1	0.0764	1	0.0614	2	0.0475	2	0.0350	4	0.0234
33	1	0.0874	3	0.0717	3	0.0551	3	0.0417	3	0.0311	4	0.0185	3	0.0091
34	1	0.0809	1	0.0662	1	0.0530	1	0.0409	2	0.0291	4	0.0177	3	0.0074
35	1	0.1211	1	0.1022	1	0.0849	3	0.0679	5	0.0468	6	0.0269	7	0.0130
36	2	0.1724	3	0.1504	3	0.1294	4	0.1078	2	0.0896	3	0.0726	5	0.0552
37	1	0.0976	1	0.0800	1	0.0669	1	0.0546	1	0.0438	1	0.0348	2	0.0262
38	1	0.1225	1	0.1061	2	0.0920	2	0.0742	4	0.0582	8	0.0430	7	0.0261
39	2	0.1286	2	0.1056	4	0.0807	6	0.0575	6	0.0379	8	0.0207	6	0.0056
40	2	0.1538	2	0.1257	2	0.1010	2	0.0793	3	0.0594	4	0.0423	4	0.0255
41	2	0.1390	3	0.1164	3	0.0940	5	0.0691	7	0.0455	10	0.0226	4	0.0047
42	1	0.1051	2	0.0832	2	0.0629	3	0.0459	2	0.0304	5	0.0188	7	0.0074
43	1	0.1084	1	0.0891	2	0.0706	4	0.0543	6	0.0375	7	0.0206	3	0.0071
44	1	0.0643	2	0.0425	2	0.0287	3	0.0178	3	0.0095	3	0.0028		
45	1	0.1303	2	0.1088	2	0.0845	3	0.0619	3	0.0438	5	0.0272	7	0.0121
46	1	0.1510	1	0.1272	1	0.1064	2	0.0878	2	0.0667	6	0.0467	8	0.0285
47	3	0.0920	3	0.0707	3	0.0539	6	0.0393	7	0.0230	4	0.0088	3	0.0016
48	2	0.1042	4	0.0821	4	0.0611	4	0.0449	5	0.0288	8	0.0144	6	0.0034
49	1	0.1351	1	0.1153	1	0.0962	1	0.0789	2	0.0623	4	0.0452	7	0.0278
50	1	0.1245	1	0.1039	2	0.0828	3	0.0611	6	0.0419	8	0.0244	5	0.0049
51	2	0.1844	3	0.1493	5	0.1168	6	0.0862	11	0.0582	10	0.0320	8	0.0122
52	1	0.0997	2	0.0775	3	0.0574	6	0.0417	8	0.0258	6	0.0123	1	0.0032
53	1	0.1091	1	0.0908	1	0.0748	1	0.0609	5	0.0448	5	0.0280	7	0.0136
54	1	0.2151	2	0.1874	2	0.1535	4	0.1250	8	0.0957	7	0.0623	8	0.0379
55	5	0.2350	7	0.1824	7	0.1416	10	0.1026	11	0.0671	8	0.0380	7	0.0159
56	3	0.1506	4	0.1079	6	0.0714	9	0.0408	11	0.0150	2	0.0014		
57	3	0.1651	7	0.1297	14	0.0882	12	0.0511	15	0.0206	4	0.0023		
58	3	0.2304	3	0.1792	5	0.1370	10	0.0994	11	0.0622	9	0.0319	9	0.0134
59	2	0.1065	3	0.0796	4	0.0547	3	0.0373	4	0.0219	7	0.0091	3	0.0019
60	2	0.1755	3	0.1367	4	0.1052	5	0.0759	6	0.0511	5	0.0312	8	0.0142

Notes. N_i : the number of branches at the length i ; Σv_i : the cumulative branch volumes above the length i (m^3)

trees; these are the numbers of branches for the length i , N_i s, and the cumulative branch volumes above the length i , $\sum v_i$ s, as calculated by Eq. 6. The sample trees are listed in order of their stem diameter for the 1.3m length, so that the cumulative volumes roughly increase as the sample tree number

increases for each length. The cumulative volume of branches decreases as the length increases for each same sample tree; in several trees there was no countable branch at a length of 9.3m.

Table 2 shows the variables N_i and $\bar{v}_i$. As mentioned

Table 2 The variables of N_i and $\bar{v}_i$ at the length i

3.3m		4.3m		5.3m		6.3m		7.3m		8.3m		9.3m	
$N_{3.3}$	$\bar{v}_{3.3}$	$N_{4.3}$	$\bar{v}_{4.3}$	$N_{5.3}$	$\bar{v}_{5.3}$	$N_{6.3}$	$\bar{v}_{6.3}$	$N_{7.3}$	$\bar{v}_{7.3}$	$N_{8.3}$	$\bar{v}_{8.3}$	$N_{9.3}$	$\bar{v}_{9.3}$
1	0.0452	1	0.0481	1	0.0379	1	0.0330	1	0.0394	1	0.0007	1	0.0001
1	0.0556	1	0.0490	1	0.0382	1	0.0336	1	<u>0.0438</u>	1	0.0011	1	<u>0.0032</u>
1	0.0589	1	0.0499	1	0.0394	1	0.0341	2	0.0077	1	<u>0.0348</u>	2	0.0004
1	0.0610	1	0.0513	1	0.0401	1	0.0409	2	0.0103	2	0.0007	2	0.0009
1	0.0613	1	0.0536	1	0.0422	1	0.0495	2	0.0121	2	0.0012	2	0.0012
1	0.0620	1	0.0540	1	0.0430	1	0.0518	2	0.0121	2	0.0061	2	0.0013
1	0.0630	1	0.0559	1	0.0441	1	0.0546	2	0.0122	2	0.0149	2	<u>0.0131</u>
1	0.0643	1	0.0643	1	0.0530	1	0.0609	2	0.0145	2	<u>0.0175</u>	3	0.0005
1	0.0649	1	0.0662	1	0.0553	1	0.0614	2	0.0152	3	0.0008	3	0.0005
1	0.0666	1	0.0685	1	0.0613	1	<u>0.0789</u>	2	0.0184	3	0.0009	3	0.0005
1	0.0676	1	0.0732	1	0.0638	2	0.0083	2	0.0211	3	0.0010	3	0.0006
1	0.0692	1	0.0769	1	0.0651	2	0.0126	2	0.0238	3	0.0021	3	0.0006
1	0.0781	1	0.0774	1	0.0656	2	0.0138	2	0.0249	3	0.0034	3	0.0015
1	0.0809	1	0.0783	1	0.0669	2	0.0146	2	0.0253	3	0.0039	3	0.0016
1	0.0843	1	0.0800	1	0.0669	2	0.0156	2	0.0312	3	0.0053	3	0.0020
1	0.0863	1	0.0801	1	0.0748	2	0.0198	2	0.0333	3	0.0057	3	0.0022
1	0.0868	1	0.0811	1	0.0762	2	0.0214	2	<u>0.0448</u>	3	0.0079	3	0.0022
1	0.0874	1	0.0851	1	0.0764	2	0.0242	3	0.0013	3	0.0083	3	0.0024
1	0.0923	1	0.0877	1	0.0791	2	0.0248	3	0.0032	3	0.0086	3	0.0025
1	0.0926	1	0.0891	1	0.0849	2	0.0259	3	0.0054	3	0.0093	3	0.0027
1	0.0931	1	0.0908	1	0.0962	2	0.0270	3	0.0063	3	0.0121	3	0.0030
1	0.0950	1	0.0929	1	<u>0.1064</u>	2	0.0275	3	0.0070	3	0.0124	3	0.0039
1	0.0955	1	0.0947	2	0.0094	2	0.0294	3	0.0098	3	<u>0.0242</u>	3	0.0041
1	0.0967	1	0.1022	2	0.0125	2	0.0317	3	0.0104	4	0.0006	3	0.0059
1	0.0976	1	0.1039	2	0.0127	2	0.0318	3	0.0128	4	0.0021	3	<u>0.0084</u>
1	0.0989	1	0.1061	2	0.0144	2	0.0371	3	0.0131	4	0.0022	4	0.0012
1	0.0997	1	0.1153	2	0.0168	2	0.0396	3	0.0135	4	0.0038	4	0.0021
1	0.1008	1	<u>0.1272</u>	2	0.0183	2	<u>0.0439</u>	3	0.0146	4	0.0038	4	0.0037
1	0.1051	2	0.0175	2	0.0254	3	0.0059	3	<u>0.0198</u>	4	0.0044	4	0.0038
1	0.1084	2	0.0175	2	0.0307	3	0.0084	4	0.0016	4	0.0046	4	0.0044
1	0.1091	2	0.0213	2	0.0308	3	0.0088	4	0.0022	4	0.0074	4	0.0048
1	0.1091	2	0.0222	2	0.0315	3	0.0124	4	0.0042	4	0.0106	4	0.0058
1	0.1102	2	0.0247	2	0.0344	3	0.0139	4	0.0055	4	<u>0.0113</u>	4	<u>0.0064</u>
1	0.1109	2	0.0350	2	0.0353	3	0.0153	4	0.0070	5	0.0016	5	0.0009
1	0.1130	2	0.0385	2	0.0377	3	0.0156	4	0.0084	5	0.0038	5	0.0010
1	0.1211	2	0.0387	2	0.0414	3	0.0204	4	0.0087	5	0.0043	5	0.0017
1	0.1225	2	0.0416	2	0.0422	3	0.0206	4	<u>0.0145</u>	5	0.0054	5	0.0025
1	0.1245	2	0.0456	2	0.0460	3	<u>0.0226</u>	5	0.0022	5	0.0056	5	0.0049
1	0.1303	2	0.0471	2	0.0505	4	0.0059	5	0.0025	5	<u>0.0062</u>	5	<u>0.0110</u>
1	0.1351	2	0.0528	2	<u>0.0768</u>	4	0.0112	5	0.0036	6	0.0014	6	0.0006
1	0.1510	2	0.0544	3	0.0121	4	0.0136	5	0.0046	6	0.0018	6	<u>0.0009</u>
1	<u>0.2151</u>	2	0.0628	3	0.0153	4	0.0269	5	0.0058	6	0.0020	7	0.0011
2	<u>0.0233</u>	2	<u>0.0937</u>	3	0.0180	4	<u>0.0312</u>	5	0.0080	6	0.0026	7	0.0017
2	0.0411	3	0.0165	3	0.0184	5	0.0020	5	0.0090	6	0.0037	7	0.0019
2	0.0521	3	0.0211	3	0.0191	5	0.0031	5	<u>0.0094</u>	6	0.0045	7	0.0019
2	0.0533	3	0.0236	3	0.0235	5	0.0063	6	0.0063	6	<u>0.0078</u>	7	0.0023
2	0.0643	3	0.0239	3	0.0313	5	0.0075	6	0.0063	7	0.0013	7	0.0037
2	0.0695	3	0.0265	3	<u>0.0431</u>	5	0.0138	6	0.0070	7	0.0014	7	<u>0.0040</u>
2	0.0769	3	0.0388	4	0.0131	5	<u>0.0152</u>	6	<u>0.0085</u>	7	0.0016	8	0.0015
2	0.0862	3	0.0456	4	0.0132	6	0.0039	7	0.0033	7	0.0029	8	0.0018
2	0.0878	3	0.0498	4	0.0137	6	0.0062	7	<u>0.0065</u>	7	0.0034	8	0.0036
2	<u>0.0922</u>	3	0.0501	4	0.0153	6	0.0065	8	0.0032	7	<u>0.0089</u>	8	<u>0.0047</u>
3	0.0141	3	<u>0.0597</u>	4	0.0202	6	0.0069	8	0.0036	8	0.0018	(9)	(0.0015)
3	0.0249	4	0.0140	4	<u>0.0263</u>	6	0.0083	8	<u>0.0120</u>	8	0.0026		
3	0.0307	4	0.0178	5	0.0234	6	0.0096	(9)	(0.0025)	8	0.0031		
3	0.0317	4	0.0205	5	<u>0.0274</u>	6	<u>0.0144</u>	11	0.0014	8	0.0047		
3	0.0502	4	<u>0.0270</u>	6	0.0068	(9)	(0.0045)	11	0.0053	8	<u>0.0054</u>		
3	0.0550	(5)	(0.0059)	6	<u>0.0119</u>	10	0.0099	11	0.0057	(9)	(0.0035)		
3	<u>0.0768</u>	7	0.0185	(7)	(0.0202)	10	0.0103	11	<u>0.0061</u>	10	0.0023		
(5)	(0.0470)	7	<u>0.0261</u>	(14)	(0.0063)	(12)	(0.0043)	(15)	(0.0014)	10	<u>0.0032</u>		

Notes. The underlined $\bar{v}_i$ s represent the maximum average volume of branches, $\bar{v}_{m_i}$ s (m^3). The $\bar{v}_{m_i}$ s in parentheses represent branches having a single sample for the corresponding N_i s.

Table 3 The variables of N_i and $\bar{v}_{m_i}$ at the length i for the full density curve estimates

3.3m		4.3m		5.3m		6.3m		7.3m		8.3m		9.3m	
$N_{3.3}$	$\bar{v}_{m_{3.3}}$	$N_{4.3}$	$\bar{v}_{m_{4.3}}$	$N_{5.3}$	$\bar{v}_{m_{5.3}}$	$N_{6.3}$	$\bar{v}_{m_{6.3}}$	$N_{7.3}$	$\bar{v}_{m_{7.3}}$	$N_{8.3}$	$\bar{v}_{m_{8.3}}$	$N_{9.3}$	$\bar{v}_{m_{9.3}}$
1	0.2151	1	0.1272	1	0.1064	1	0.0789	1	0.0438	1	0.0348	1	0.0032
2	0.0922	2	0.0937	2	0.0768	2	0.0439	2	0.0448	2	0.0175	2	0.0131
3	0.0768	3	0.0597	3	0.0431	3	0.0226	3	0.0198	3	0.0242	3	0.0084
		4	0.0270	4	0.0263	4	0.0312	4	0.0145	4	0.0113	4	0.0064
		7	0.0261	5	0.0274	5	0.0152	5	0.0094	5	0.0062	5	0.0110
				6	0.0119	6	0.0144	6	0.0085	6	0.0078	6	0.0009
						10	0.0103	7	0.0065	7	0.0089	7	0.0040
								8	0.0120	8	0.0054	8	0.0047
								11	0.0061	10	0.0032		

Table 4 Parameter estimates of full density curves in lengths from 3.3m to 9.3m

Length	Parameter	Estimates ^a	t	p
3.3	$a_{13.3}$	-0.9684 (-3.548, 1.611)	-4.770	0.1316
	$a_{23.3}$	-0.6879 (-1.528, 0.1523)	-10.40	0.0610
4.3	$a_{14.3}$	-0.9208 (-1.535, -0.3064)	-4.769	0.0175 *
	$a_{24.3}$	-0.8504 (-1.175, -0.5258)	-8.339	0.0036 **
5.3	$a_{15.3}$	-1.150 (-1.470, -0.8296)	-9.228	0.0003 **
	$a_{25.3}$	-0.8738 (-1.087, -0.661)	-10.56	0.0001 **
6.3	$a_{16.3}$	-0.9065 (-1.196, -0.6175)	-8.062	0.0005 **
	$a_{26.3}$	-1.109 (-1.291, -0.9273)	-15.67	0.0000 **
7.3	$a_{17.3}$	-0.9270 (-1.262, -0.5916)	-6.535	0.0003 **
	$a_{27.3}$	-1.271 (-1.505, -1.036)	-12.83	0.0000 **
8.3	$a_{18.3}$	-0.9566 (-1.314, -0.5987)	-6.320	0.0004 **
	$a_{28.3}$	-1.394 (-1.641, -1.146)	-13.32	0.0000 **
9.3	$a_{19.3}$	-0.2523 (-1.423, 0.918)	-0.5276	0.6167
	$a_{29.3}$	-2.150 (-2.902, -1.398)	-6.994	0.0004 **

Notes. a) 95% confidence bounds of coefficients are given in parentheses.

α_i : the slope parameter at length i ; $\alpha_{i'}$: the intercept parameter at length i .

above, $\bar{v}_i$ is calculated by $\sum v_i / N_i$ for each length in each sample tree, and then the $\bar{v}_i$ s are sorted depending on their N_i s and arranged in order of volume. Thus, in Table 2 the underlined $\bar{v}_i$ s represent the maximum average volume of branches, $\bar{v}_{m_i}$ s, for the corresponding N_i s for each length i . Note that the N_i s and $\bar{v}_{m_i}$ s in parentheses have only one sample under the corresponding N_i , so that they are excluded from the following full density curve estimate because of their inability to have a maximum attainable value. To summarize, the variable values for the estimate are shown in Table 3.

Full Density Curves

Table 4 shows the parameter estimates for a_{1i} and a_{2i} in Eq. 2 for each length i ; the estimated full density curves are illustrated in Fig. 2 on a log-log scale. The estimates are based on the logarithmic variables of Table 3 using the ordinary least squares method. The result shows that the parameter estimates for lengths of 3.3m and 9.3m are not significant. The reason for their insignificance at 3.3m lies in a lack of data:

There are only three plots for the parameter estimate, which implies that the length of 3.3m is too short to contain an adequate number of branches. The reason for their insignificance at 9.3m lies in an absence of competition: At that length it seems that branches get thinner towards the tips and do not cause self-pruning any longer.

Moreover, the homogeneity of these significant slope parameters, a_{1i} s from 4.3m to 8.3m, is tested based on the concept of the Chow test (CHOW, 1960). The resulting ANOVA table is given in Table 5. In the table, the sum of squares (SS) between- and within-groups are represented by

$$SS_{bg} = \sum_{j=1}^k \sum_{i=1}^{n_j} (Y_{ij} - \bar{Y}_j)^2 - \frac{\left\{ \sum_{j=1}^k \sum_{i=1}^{n_j} (X_{ij} - \bar{X}_j) (Y_{ij} - \bar{Y}_j) \right\}^2}{\sum_{j=1}^k \sum_{i=1}^{n_j} (X_{ij} - \bar{X}_j)^2} - \sum_{j=1}^k \sum_{i=1}^{n_j} \{Y_{ij} - (a_{1j}X_{ij} + a_{2j})\}^2 \quad [10]$$

and

$$SS_{wg} = \sum_{j=1}^k \sum_{i=1}^{n_j} \{Y_{ij} - (a_{1j}X_{ij} + a_{2j})\}^2, \quad [11]$$

Fig. 2 Estimated full density curves at lengths between 3.3m and 9.3m on a log-log scale

The solid lines represent the full density curves, the small circles represent the average volumes of branches, and the small solid circles represent the maximum average volumes of branches, all of which are employed for the full density curve estimates. The figure on the bottom right represents the comparison between the whole estimated curves.

Table 5 ANOVA table for testing the homogeneity of the slope parameters

Sources	SS	df	MS	F	p
Bet. Groups	0.0308	4	0.0077	0.5229	0.7197
Within Groups	0.3979	27	0.0147		
Total	0.4287	31			

where X is the independent variable, Y is the dependent variable, k is the number of groups, n is the sample size, and a_1 and a_2 are the estimates of regression slope and intercept, respectively. For each variable, the subscripts i and j represent the sample number and group index, respectively, e.g., X_{ij} corresponds to the i th sample of N_j at a length of j , and Y_{ij} to the i th sample of $\bar{v}_{mj}$ at a length of j in this study. The degrees of freedom (df) corresponding to SS_{bg} and SS_{wg} are $(k-1)$ and $(n-2k)$, respectively. Thus, the F value is calculated using the mean squares (MS) between- and within-groups under the null hypothesis of equal slopes. The result shows no evidence of violating the equal slopes hypothesis; the F value is 0.5229, with a significance level of 0.7197. In this case, the regression coefficient estimate, $\hat{a}_1$, expresses the common slope among the groups, which is calculated by

$$\hat{a}_1 = \frac{\sum_{j=1}^k \sum_{i=1}^{n_j} (X_{ij} - \bar{X}_j)(Y_{ij} - \bar{Y}_j)}{\sum_{j=1}^k \sum_{i=1}^{n_j} (X_{ij} - \bar{X}_j)^2} \quad [12]$$

As for the sample trees, this estimate is -0.9801. This implies that the full density curves of the branches are represented by lines having a common slope of -0.9801 while having different intercepts corresponding to lengths between 4.3m and 8.3m on a log-log scale. The reason why $\hat{a}_1$ takes -0.9801 is explained as follows: In the stand scale full density curve, the power index of N_i in Eq. 5, $(\beta + \gamma)/\alpha$, takes -3/2 under the ideal condition of $(\alpha, \beta, \gamma) = (2, 1, 2)$. Among these parameters, particularly the numerator of the index, $\beta + \gamma = 3$, means that the average volume of individuals is proportional to the third power of their average width. But in the branch full density curve, the average volume of branches above a specific height is linearly proportional to their average basal area according to Eq. 7, which means the average volume is proportional to the second power of their average diameter. Thus, the parameter value of β is zero in this case with result that the power index of N_i in Eq. 9, δ , takes -1 under the ideal condition of $(\alpha, \beta, \gamma) = (2, 0, 2)$. In the actual situations, however, the index does not take exactly -1, so that $\hat{a}_1$ and corresponding $\hat{a}_1$ s slightly differed from -1.

Unfortunately, we could not investigate the difference in the slopes between species owing to a lack of *Castanopsis sieboldii* sample trees, which were mixed with *Quercus acuta* in the subject stand.

CONCLUSIONS

The purpose of this study was to determine the full density curves of branches on standing trees. The 60 sample trees of *Quercus acuta* in a single stand were selectively cut, and then diameters and lengths of those branches with more than 2cm diameter that were at a height between 3.3m and 9.3m were measured at one meter intervals along their stems and branches. To derive the full density curve of the branches, the number of branches at a specific length and the maximum average volumes of branches above that length were selected to be the independent and dependent variables, respectively based on the pipe model theory. The linear relationships between these variables were investigated on a log-log scale, with the consequence that the regression estimates were significant at lengths between 4.3m and 8.3m. Furthermore, the full density curves for these lengths were considered to have a common slope parameter of -0.9801. Further research is required, however, to investigate whether this slope is applicable not only to *Quercus acuta* but also to other species.

This study discovered that the -3/2 power law of self-thinning is effective for branches on standing trees that are similar to the standing trees in forest stands. In a future study we will examine ways to make good use of the full density curve for branches, such as being able to estimate the obtainable charcoal size for fuel wood production.

ACKNOWLEDGEMENTS

We express our sincere thanks to Dr. Mitsuhiro Minowa for his valuable advice as well as to the professors and staff of the Tokyo University Forest in Chiba for their great help for collecting data. We also would like to thank anonymous reviewers for their helpful comments that led to the improvement of this paper.

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(Received 10 July 2006)

(Accepted 13 November 2006)