A QUANTITATIVE ANALYSIS OF PLANT FORM—THE PIPE MODEL THEORY

II. FURTHER EVIDENCE OF THE THEORY AND ITS APPLICATION IN FOREST ECOLOGY

Kichiro SHINOZAKI*, Kyoji YODA, Kazuo HOZUMI and Tatuo KIRA

Department of Biology, Faculty of Science, Osaka City University, Osaka

Synopsis


To test the applicability of the pipe model theory to actual tree form, the frequency distribution of the thickness of woody organs in a tree was examined in 10 different species. The frequency \( f(D) \) of a certain diameter class \( D \) proved to have a definite pattern of distribution in the root, branch and trunk respectively, with only a little difference between the species. The obtained \( f(D) \sim D \) curves showed that a root system could well be approximated by the assemblage of many pipes of unit thickness, a trunk by a few cones piled up one upon another, and a branch system by a geometric model intermediate between the two. The results were well consistent with the pipe model theory of tree form. As an application of the theory in forest ecology, a new method for estimating the amounts of leaves or branches of trees and stands was also proposed, based on the direct proportionality found between those amounts and the cross-sectional area of the trunk at the height just below the lowest living branch.

In the foregoing paper (SHINOZAKI et al. 1964), the authors proposed the pipe model theory to interpret the form of terrestrial higher plants, in which a plant was considered as the assemblage of unit pipe systems, each composed of a unit amount of leaves and a pipe of unit thickness that serves both as vascular and as supporting tissues. This theory was mainly supported by the fact that the total cross-sectional area of stems and branches at a certain horizon in a plant community was always proportional to the total amount of leaves existing above that horizon.

This proportionality fails to be maintained, however, in the leafless bottom horizons of plant community, especially in those of forest communities where only branchless trunks are present. Instead, the cross-sectional area of the trunks continues to increase toward the base without any further increase of the leaf amount which they support. Analogically speaking, this is most probably due to the accumulation of disused pipes in the trunk which were once connected with the leaves born by the lower branches already shed off years ago. This interpretation was called the pipe model theory of tree form.

The validity of the theory should necessarily be tested by means of quantitative analyses of actual tree form. In this paper, the examination is made based on the frequency distribution of diameter of woody organs constituting a tree.

Frequency distribution of diameter in trunk, branches and roots of a tree

The diameter measurements were made in 1960–63 with ten different species, Abies sachalinensis, Picea jezoensis, P. Glehni, Betula platyphylla japonica, B. Ermanii and B. Maximowiczii in Hokkaido, and Pinus Thunbergii, P. densiflora, Cryptomeria japonica and Camellia japonica in Honshu. A few trees per each species not larger than 35 cm in D. B. H. were carefully dug out from the soil at their natural habitats. Special care was taken not to destroy fine rootlets as far as possible. The diameter of trunk, all branches and all roots was then measured at 10 cm intervals, starting from the trunk base upwards to the top ends of the twigs as well as downwards to the tips of the

Received February 24, 1964

* Present address: Department of Physics, Science Education Institute of Osaka, Karitachō, Sumiyoshiku, Osaka.
rootlets. The obtained figures are grouped into classes at appropriate intervals, and shown as the diameter class—frequency curves on logarithmic coordinates, separately for trunk, branch and root in Figs. 1, 2 and 4.

Before considering the results, some probable patterns of diameter distribution will be postulated in order to obtain the standards to be compared with the actually obtained distributions.

Case 1) The sum of cross-sectional area of woods belonging to a certain diameter class is constant regardless of the diameter range. This case is expected to be realized when the woody parts of a tree represent the simple assemblage of unit-sized pipes as illustrated in Fig. 5-D in the preceding paper. Denoting the diameter of wood and corresponding frequency by \( D \) and \( f(D) \) respectively, it is expected for this case that

\[
f \cdot \pi \cdot \frac{D}{2}^2 = \text{const. or } f \propto D^{-2}. \quad (1)
\]

Case 2) The sum of surface area or circumference of woody organs is constant for any value of \( D \). The expected \( f \sim D \) relation is then given by

\[
f \cdot \pi \cdot D = \text{const. or } f \propto D^{-1}. \quad (2)
\]

Case 3) The shape of a woody organ may also be approximated by a cone. For this case, the following relation is expected.

\[
f = \text{const. independently to } D \quad \text{or } f \propto D^0. \quad (3)
\]

The similarity of the \( \log f \sim \log D \) curves obtained with a variety of species is very striking. As seen in Figs. 1 and 4, the curves for the branches and roots are more or less linear, and the gradient of the lines is approximately equal to \(-2.0\) in roots and to \(-1.5 \sim -2.0\) in branches respectively. The \( \log f \sim \log D \) curves in trunks are not linear, but the specific humpshape of the curves is common in all the species examined (Fig. 2).

The frequency—diameter relations in roots (Fig. 1) fairly well satisfy Eq. (1). This most interesting fact indicates that the form of a root system follows the rule expected from the simple pipe model. Considering the fact that the diameter of woody organs of a tree is the greatest at the trunk base, tapering toward terminal ends with few intermediate maxima, it may be said that a whole root system would make a cylinder of even thickness when packed together, provided a regular system of ramification is assumed. Actually, however, the imagined cylinder is successively split into more and more pipes with increasing distance from the trunk base. This characteristic

---

Fig. 1. Frequency distribution of diameter of roots in a tree measured at 10 cm intervals, \( D \) and \( f \) respectively standing for diameter and frequency

A) Abies sachalinensis  B) Pinus Thunbergii  C) Betula platyphylla japonica  D) Betula Ermani.
habit of root branching suggests a mode of thickening growth quite different from that of the branches or trunk. No such process as the branch-shedding due to light deficiency seems to occur under the ground at least in the main part of root system.

There are a few cases in which the frequency at the smallest diameter class is somewhat smaller than the expected value (Fig. 1-A), but the inadequate way of digging which resulted in the considerable loss of the finest rootlets seems to be responsible for these cases. In cases when ample water was used in the digging to loosen the soil around the root system, no such irregularity was encountered.

As for the main trunk, the pattern of diameter distribution is somewhat complicated. The distribution curves in all of the species examined are characteristically humped on the logarithmic scale (Fig. 2). The trunk is morphologically different from other woody organs in that it is a single continuous bar without branching. The significance of diameter distribution in such a case is easily understood as follows.

When a trunk is divided into many discs of even thickness \( l_0 \) and the discs are numbered 1, 2, 3, \( \cdots \), \( N \), in the order from the top to the base, the distance from the top of the trunk to the \( N \)th disc is given by

\[
x = l_0 N. \tag{4}
\]

The diameter at a distance \( x \) from the top is \( D(x) \). When the discs are grouped according to their diameter, and the number of discs in a class between \( D \) and \( D + dD \) is written as \( f(D) \), it follows that

\[
f(D) dD = dN. \tag{5}
\]

Therefore

\[
f(D) = \frac{dN}{dD} = \frac{1}{l_0} \frac{dx}{dD} = \frac{1}{l_0} \cdot \frac{1}{dD/dx}. \tag{6}
\]

In other words, \( f(D) \) is inversely proportional to the gradient of diameter increase \( dD/dx \).

Fig. 3-A represents a typical cross-section of a trunk, taking a 43-years-old larch tree as the example. Such a form of trunk may be approximated by the combination of three cones as shown by Fig. 3-B. Since the gradient of the diameter increase \( (dD/dx) \) is constant in a cone, the diagrammatic trunk shape of Fig. 3-B is expected to have the \( f(D) \) distribution given in Fig. 3-C. It is easily recognized.
that the actually obtained diameter distributions (Fig. 2) are close to this diagrammatic distribution in their general patterns. The \( f(D) \sim D \) curves in Fig. 2 thus correspond to the trunk shape similar to Fig. 3-B, or more strictly to Fig. 3-A. Among the three cones successively piled one upon another, the central cone is more or less close to a cylinder, with its very high frequency value and narrow diameter range.

Macroscopically speaking, however, it seems possible to approximate the shape of whole trunk by a cone as indicated by dotted lines in Fig. 3. The existence of more disused pipes in the lower parts of the trunk may well account for the conical shape.

In branches, including all aerial shoots other than the main trunk, the \( \log f \sim \log D \) regression is again nearly linear, although the frequency is always less than the value on the regression line at the lowest and the highest classes of the diameter respectively. The deviation at the finest or terminal ends of the branches corresponds to that there is a certain lower limit in the thickness of the branches, while the deviation at the other ends is caused by the rapid thickening of boughs at their bases.

The gradient of \( \log f \sim \log D \) lines in branches of Picea, Abies and Camellia is very near to \(-2.0\), indicating the close resemblance of their branch system to the root in general form (Fig. 4A, B and C). These species, especially spruce and fir, are characterized by the conical tree form specific to conifers, and their shoots each consist of a single, unbranched bole and many slender branches which rarely exceed one-fifth of the trunk thickness (D. B. H.) in their maximum diameter. It is quite probable that the branches in these species fit the simplest case of the pipe model as do the roots.

In ordinary hardwoods, pines, etc., on the other hand, the thickest branch is often as thick as the main trunk at its base, and it is sometimes even difficult to define a trunk. Thicker boughs in trees of this type, from which small branches are shed off as from the trunk, may not differ greatly from the trunk in their morphological characters. Hence the
diameter distribution in such a branch system should have a character intermediate between those of trunk (log $f$ - log $D$ gradient: 0) and root (gradient: -2). The $f(D)$ ~ $D$ curves for Betula, Pinus and Cryptomeria (Fig. 4-D, E and F), in which the log $f$ ~ log $D$ gradient is near -1.5, represent the examples of these cases. Their light-demanding character may also be responsible through vigorous shedding of the lower branches.

These features of diameter distribution in woody organs of trees are well consistent with the expectations based on the pipe model theory.

A method of leaf biomass estimation as an application of the pipe model theory

The establishment of the pipe model theory opens the way to various applications in the field of quantitative ecology. As a case of the application, a reasonable method is here proposed for estimating the foliage biomass of trees or stands.

Since the attempt by Kittredge (1944), the allometric relation between the leaf amount of a tree ($W_L$) and its D.B.H. ($D$),

\[ W_L = A \cdot D^h \] (A, $h$: constants),

has been utilized for the purpose. The equation, once established from several or more sample trees, gives a fairly good estimation of the leaf biomass of other trees as well as of stands in which D.B.H. of all trees are known.

According to Japanese investigators, the value of the allometric constant $h$ ranges between 2.35 and 2.62 in coniferous trees such as Abies and Picea, and between 1.85 and 2.13 in hardwoods (Betula, Fagus, Zelkova and various evergreens), pines, and Cryptomeria and Chamaecyparis (compiled in Hozumi 1963). Differences in the values of $h$ between species are slight within each of the two groups.

Despite its usefulness, some serious difficulties are involved in this way of foliage amount estimation, one of which is illustrated in Fig. 5. The figure shows the log $W_L$ ~ log $D$ regressions in several natural stands of birch, of different ages and growing on different habitats in east-central Hokkaido. The linear relation between log $W_L$ and log $D$ expected from Eq. (7) is recognized for each stand, but the constants $A$ and $h$ in the equation are not equal in all stands. The allometric equation obtained in a certain stand can, therefore, not always be used for the leaf amount estimation in other stands of the same species (Satoo 1962, Hozumi 1963). Similar situations were also found in plantations of larch and Cryptomeria. This makes a rapid survey of many stands almost impossible. Because the exact and rapid estimation of foliage amount is a vital key to the study of organic matter production by forest community, further improvement of the method seems indispensable.

The present theory on tree form provides a reasonable approach. The pipe model suggests that the amount of leaves per tree should be most closely correlated with the sum of cross-sectional areas of living pipes supporting them, which in turn could well be approximated by the cross-sectional area of the trunk at the height just below the lowest living branch.

In Fig. 6, the amount of leaves on a birch

![Fig. 5. Allometric relations between the amount of leaves per tree ($W_L$) and the trunk diameter at breast height ($D$), as shown by the linear regressions between log $W_L$ and log $D$, in birch stands of east-central Hokkaido.](image)

1) Betula platyphylla japonica, 45-years-old stand at Asyoro 2) B. Maximowiczi, 45-years-old stand at Nipesotu 3) B. Ermanii, 18-years-old stand at Simizu 4) B. Maximowiczii, 7-years-old stand.
tree is plotted against its trunk diameter \((D_B)\) measured at the height just below the base of the lowest living branch. The source of data is the same with that of Fig. 5. As expected, a close correlation is found between \(W_L\) and \(D_B\), and it can be approximated by a single log \(W_L\sim\log D_B^2\) line whose gradient nearly equals 1.0. Although the observed values are scattered in a wide zone along the regression line, no systematic trends can be recognized in the distribution of the points belonging to different stands, and the segregation of the stands seen on the log \(W_L\sim\log D\) diagram (Fig. 5) has almost disappeared. The amount of leaves is nearly proportional to \((D_B)^2\) or to the cross-sectional area of the trunk at the joint of the lowest branch (see Fig. 6 in the preceding paper). It is thus proved that \(D_B\) can serve as an overall basis for the foliage amount estimation in any stands regardless of their age or habitat. The error of estimation may be considerably large as Fig. 6 shows, but the estimate for the whole stand is probably more accurate since the errors in individual trees may offset each other.

It should also be noticed that the amount of branches per tree has nearly the same relation to \(D_B\) as found in the leaf amount. Fig. 7 presents a typical example of branch weight \((W_B)\sim D_B\) relations in larch plantations.

There are evidences that the segregation of \(W_L\) (or \(W_B\)) \(\sim D\) relations in different stands is more pronounced in such light-demanding trees as the birch, larch, pine and *Cryptomeria* than in shade-tolerant species. This fact is quite probable because the shedding of branches and the resultant accumulation of disused pipes in the trunk are naturally more pronounced in sun-trees than in shade-trees. In the latter, the \(W_L\sim D\), \(W_B\sim D\) or \(D_B\sim D\) relations do not differ greatly in different stands of the same species. As shown by the case of the fir in Fig. 8, however, the direct proportionality between \(W_L\) and \(D_B^2\) is also apparent in shade-trees. In moderately spaced, mature stands such as Stand A and B, tall canopy trees exhibit a clear-cut \(W_L\sim D_B^2\) proportionality as shown by the solid line, whereas the \(W_L\sim D_B^2\) relation for lower suppressed trees in those stands is somewhat different (dotted line).
Another different relation is also found in Stand C, D and E (dotted line), where small-sized trees are crowded at unusually high density (35,000~170,000 trees per hectare). In latter cases, the trees tend to have less amount of foliage at the same value of \( D_B \) as compared with the dominant trees in mature stands. Delayed response of lower branches to light deficiency seems to be a cause for the phenomenon. Considering, however, that by far the greater part of the leaf amount in a stand is supported by canopy trees, the use of the uppermost regression line in Fig. 8 may be sufficient for estimating the total leaf biomass of stands with fairly high accuracy, except in immature overcrowded stands.

The experiences given in Figs. 5~8 well demonstrate the advantage of \( D_B \) as the basis for the foliage amount estimation in individual trees and stands. If only the proportionality constant or the \( \frac{W_L}{D_B^2} \) ratio were known, the census of \( D_B \) would be the only necessary procedure. In cases where the trees are too tall to permit direct measurement of \( D_B \), the \( D_B \sim D \) relations should firstly be established by means of felling sample trees in the stands to be investigated. The obtained \( D_B \sim D \) curves allow the estimation of \( D_B \) of all trees from the result of D, B, H, census. Even in this case, troublesome weighing of leaves of sample trees could anyway be saved.

Literatures cited

摘 要
樹形に関するバイブ・モデル（第1報）の成立を、さらに別な方面からテストするために、100木の樹木について、非同化部分を幹、枝、根——の各部の直径分布を調べた。各部につき、一定間隔で直径（D）を測定し、あるDをもつ基底数f(D)とDの関係を見る。幹、枝、根はそれぞれほとんど種によらない特有の分布を示す。根では\( f = \frac{D + 2}{D^2} \)（Fig. 1）、これは、同一のDをもつ部分を集めて束にしてみると、その総断面積がDによらず一定であることを示す。すなわち根というものは、一定の太さをもった単位バイブの束が、枝分かれしながら先端まで達していていると考えられる。幹の直径分布はFig. 7のようになる。これはFig. 3のように、幹が3つの円筒の重ね合わせとなることを示す。枝ではFig. 4のように\( f = \frac{D^2}{D^2} \)ないしは\( D^{-1.5} \)に比例する。前者は針葉樹形、後者は広葉樹形に対応し、特に後者は、生長に伴う下枝の省略で説明される。これらの直径分布の結果は、いずれもバイブ・モデルを支持する。

バイブ・モデルは、樹木や森林の葉量の推定に直接応用できる。枝の葉量（\( W_L \)）と胸高直径（D）の関には、一応（7）式の相対生長関係が期待されるが、例えばFig. 5のように樹令、立地条件によって別々の図示直線に分離するのが普通である。枝のバイブ・モデルによれば幹には相当量の残留バイブが存在する、従ってFig. 5のように生育条件で分離することはむしろ当然である。生きた葉を有する一番下の枝、その枝の下における幹の直径——枝下直径（\( D_B \)）——を考えると、\( D \)よりも\( D_B \)の方が直接葉量に対応していることが、バイブ・モデルから期待される。

Figs. 6, 8 is Fig. 5のDを\( D_B \)に置きかえたもので、上の予想がよく成立している。少なくとも同様では、生育条件の差に関係なく\( W_L \sim D_B^2 \)、すなわち葉量は枝下断面積に比例することが結論される。これはバイブ・モデルをさらに支持する。Fig. 6は全体として不正確であった森林の葉量測定が、\( D_B \)の測定によって相当正確に行えることを意味し、森林調査の労力を著しく軽減するであろう。