

A STRUCTURALLY BASED ANALYTIC MODEL FOR ESTIMATION OF BIOMASS AND FUEL LOADS OF WOODLAND TREES

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ABSTRACT. Allometric/structural relationships in tree crowns are a consequence of the physical, physiological, and fluid conduction processes of trees, which control the distribution, efficient support, and growth of foliage in the crown. The structural consequences of these processes are used to develop an analytic model based on the concept of branch orders. A set of interrelated equations describe the relationships between structural characteristics, including the distribution of a tree's foliage and the partitioning of the structural components within the crown for the efficient support of that foliage. The foliage biomass distribution in a tree crown and the geometric relationships between the branch orders supporting that distribution are used to define a functional depth that is used to compute an associated functional crown volume. These are computed first for the foliage and then for each of the tree's branch orders. Each functional crown volume is linearly related to its respective biomass component. These consistent linear relationships are demonstrated first with data from pinyon pine and then with data from Utah juniper and Valencia orange trees. The structural changes and associated biomass distribution changes suggest that crown growth is controlled from the outside in, with the resulting structural changes an emergent property of crown adjustment to the annual addition of new foliage. The relationships derived are potentially applicable across a range of additional tree species, in other woody species and applicable over a wide range of locations and conditions.

KEY WORDS: Allometry, tree biomass, crown structure, fuel loads, crown growth patterns, tree form.

1. Introduction. The above-ground biomass characteristics of woodland ecosystems are often not adequately described for many uses (Burgan and Rothermel [1984]), including measuring fuel loads

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for input to fire spread models (Burgan and Rothermel [1984]) and the determination of carbon budgets and carbon sequestration (Jenkins et al. [2003]). Most published biomass equations, usually allometric equations (Jenkins et al. [2003]), were developed using data from single sites, with applicability to a target site sometimes difficult to determine (Jenkins et al. [2003]). Allometry is also used to examine relationships between plant form, function, and growth (Enquist et al. [1999], West et al. [1999], Enquist and Niklas [2002], Niklas [2004]), and to show a common robust, mechanistic basis for multiple levels of biological organization (Enquist [2002]), which provides insight into the nature of these relationships (Strub and Anateis [2008]).

1.1 Crown structural patterns. Allometric/dimensional relationships derived for singleleaf pinyon (*Pinus monophylla* Torr. & Frem.) (Tausch [1980]) were the beginning for model development. Foliage distribution patterns for the model are based on four assumptions (West et al. [1997, 1999, 2000], Enquist et al. [1999], Enquist [2002], Enquist and Niklas [2002])¹: (i) the branching network fills a three-dimensional volume; (ii) both terminal branch units and leaf (needle) and petiole size are invariant with plant size; (iii) biomechanical constraints are uniform; and (iv) energy dissipated in fluid flow is minimized.

Stem branching angle (Honda [1978]), branch length (Honda and Fisher [1979]), and foliage arrangement on a stem (Givnish [1988]) all affect the foliar energy capture efficiency of the whole plant (Givnish [1988]). The branching angle is constant, as is the daughter branch unit length/mother branch unit length ratio for a given plant species (Honda and Fisher [1979]). The constant branching angle (Honda [1978]), fluid transport requirements (West et al. [1997]), and the three-dimensional finite space filling branching network of the plant crown (Enquist [2002]) also limit the number of potential new branches and the number of buds or leaves they contain (Barker et al. [1973]). The branching ratio, consistent within a species, differs among species, species groups, and growth strategies (Oohata and Shidei [1971], Whitney [1976], Horn [2000]). The combination of a constant branching ratio and branching angle, plus size invariant terminal branch units, indicates that tree crowns are structured from the outside in. This model, based on these structural patterns controlling the distribution of foliage biomass in

the crown, quantitatively describes its relationships to the number, diameter, length, and weight of the branches required to support the foliage.

1.2 Foliage biomass distribution patterns. The geometry of a plant's canopy influences the collective photosynthetic rate of its leaves (Horn [1971, 2000], Givnish [1988]). Resource acquisition and allocation are optimized by maximizing the surface area for exchange of resources, while minimizing the transport distances and times in the support structure (West et al. [1999]). The basic seed plant body plan has remained remarkably uniform throughout evolution (Niklas and Enquist [2002]), suggesting that universal principles underlie the organization of tree growth (West and Brown [2005]). Crown geometry, the distribution patterns of foliage in the crown, and whole-tree energy capture optimization are assumed to be relatively consistent from individual to individual within a species.

2. Model development

2.1 Derivation of crown structural patterns. This analytic model uses the concept of branch orders developed by Horton [1945], modified for stream systems by Strahler [1957] and then adapted for woody plant species (Leopold [1971], Whitney [1976]). During sampling, branch orders were assigned to live branches using Order(I), that is, by starting at the outer edge of the crown and then working inward and downward toward the trunk. The smallest branches that are unbranched were labeled as Order(I) = 0 (Figure 1). When two Order(I) = 0 join, the result is an Order(I) = 1 branch. Only when two Order(I) = 1 branches join is the result an Order(I) = 2 branch. The joining of additional Order(I) = 0 or Order(I) = 1 branches to an Order(I) = 2 branch does not change the order. The usual direction for analysis is outward from the trunk (Order(O); West et al. [1997]), where if Z = the total number of branch orders of a plant, the highest order $M = Z - 1$. Thus, Order(O) = $M - \text{Order(I)}$ (Figure 1).

Each branch order is identified in two ways, its basal segment and its full length (Figure 1). The basal part of Order(I) = 2 is labeled 1 (2) in Figure 1. Its full length is from its base to the tip of its furthest

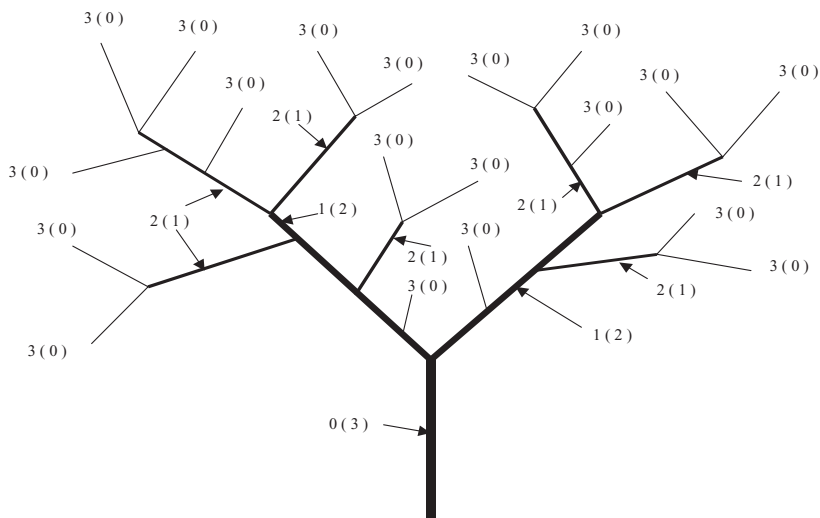


FIGURE 1. A two-dimensional diagram identifying branch order arrangement. Numbers for Order(I) (in parentheses) are counted in from the ends of the branches. Numbers to the left of those in parentheses for Order(O) are counted out from the trunk. The basal segments of each branch order are indicated by different line thicknesses.

Order(I) = 0 segment. Its full weight is the total of its basal segment plus all segments of Order(I) = 1 joined to it (Figure 1). The analysis variables used to describe the branching structure of trees by order include the number of branch segments, their average diameter, average length (both full and basal), average weight (full and basal), total weight (full and basal), and average foliage weight.

2.1.1 Number of branches. The natural log of the number of branch segments ($\ln N_k$) plotted against Order(O) forms a straight line with a positive slope (Leopold [1971], Oohata and Shidei [1971], Whitney [1976]), that is the natural log of the branching ratio (Strahler [1957]) (total number of segments of Order(O) = k , where $0 \leq k \leq M$, divided by the total number of the previous Order(O) = $k - 1$ (i.e., N_k/N_{k-1})). This relationship holds for a wide range of species. Given the average branching ratio β (i.e., $\beta = N_1/N_0 = N_2/N_1 = \dots = N_M/N_{M-1}$),

then $N_1 = \beta$, $N_2 = \beta * \beta$, $N_3 = \beta * \beta * \beta$ and:

$$(1) \quad N_k = \beta^k.$$

The antilog of the regression slope, $(\ln(N_k) = \ln\beta * k)$, is the branching ratio β .

2.1.2 Average branch segment diameter. The cross-sectional area of a branch is related to the foliage biomass it supports (Tausch and Tueller [1988], DeRocher and Tausch [1994]) and to whole-plant xylem transport (Enquist et al. [1999]). Barker et al. [1973] and McMahon [1975] found that $\ln D_k$ is linearly related to branching Order(O), with a slope of about $-1/2\ln\beta$. Assuming total cross-sectional area of any Order(O) = k to equal the total cross-sectional area of the single Order(O) = 0 trunk (Enquist et al. [1999], Horn [2000]), and substituting diameter squared for cross-sectional area, the average cross-sectional area of each order is $\bar{D}_k^2$, $k > 0$, is equal to D_0^2 divided by N_k where D_0^2 represents the single Order(O) = 0 trunk. Substituting from equation (1): $\bar{D}_k^2 \propto D_0^2 \beta^{-k}$. Taking the square root of both sides:

$$(2) \quad \bar{D}_k \propto D_0 \beta^{-k/2}.$$

$$(3) \quad \text{In general form: } \bar{D}_k \propto D_0 \beta^{-kx},$$

where $-x$ = the results from the comparison of regression slopes (slope for $\ln$ average branch segment diameter/slope for $\ln$ number of branches).

2.1.3 Average full branch segment length. The maximum height that can be supported by a tree, limited by its trunk diameter to the $2/3$ power, ($H_0 \propto D_0^{2/3}$) (McMahon [1975], McMahon and Kronauer [1983]) was assumed to hold for all branches (Tausch [1980]). This exponent and β are key parameters in a tree's architecture determining how it responds to mechanical stress (Rodriguez et al. [2008]). For the k th branch order, $\bar{H}_k \propto \bar{D}_k^{2/3}$, where Order(O) = k . Combining with equation (2), and assuming that $H_0 \propto D_0^{2/3}$:

$$(4) \quad \bar{H}_k \propto H_0 \beta^{-k/3}.$$

$$(5) \quad \text{In general form: } \bar{H}_k \propto H_0 \beta^{-kx},$$

where $-x$ = the results from the comparison of regression slopes, as in diameter. Equation (4) predicts a slope of $-1/3\ln\beta$.

2.1.4 Average basal branch segment length. This is $\bar{L}_k$ for each Order(O) = k and is defined as $\bar{L}_k = \bar{H}_k - \bar{H}_{k+1}$ (for Order(I) = 0, $\bar{H}_k = \bar{L}_k$). Representing $\bar{H}_k$ and $\bar{H}_{k+1}$ as in equation (4) $\bar{L}_k \propto H_0 \beta^{-k/3} - H_0 \beta^{-(k+1)/3}$, or

$$(6) \quad \bar{L}_k \propto H_0 \beta^{-k/3} (1 - \beta^{-1/3}).$$

$$(7) \quad \text{In general form: } \bar{L}_k \propto H_0 \beta^{-kx} (1 - \beta^{-x}),$$

where $-x$ = the results from the comparison of regression slopes. Equation (6) is equation (4) times $(1 - \beta^{-1/3})$. Equation (6) predicts a slope of $-1/3\ln\beta$ and the ratio $\bar{L}_k/\bar{H}_k = (1 - \beta^{-1/3})$.

2.1.5 Alternate average full branch segment length. Given equation (6), the sum of the average basal segment lengths for each order from $\bar{L}_k$ to $\bar{L}_M$ should be proportional to $\bar{H}_k$ ($\bar{L}_k + \bar{L}_{k+1} + \dots + \bar{L}_M \propto \bar{H}_k$). Similarly, the sum of the average basal segment lengths for the entire tree should be proportional to its total height: $\sum_{k=0}^M \bar{L}_k \propto H_0$. Modifying equation (4) to $\bar{L}_k + \bar{L}_{k+1} + \dots + \bar{L}_M \propto \beta^{-k/3}$, the general form becomes $\bar{L}_k + \bar{L}_{k+1} + \dots + \bar{L}_M \propto \beta^{-kx}$ where $-x$ = the results from the comparison of regression slopes.

2.1.6 Average full branch segment weight. This is $\bar{W}_k$ for each Order(O) and is the total weight from its base through all higher order segments to its tip at order M (Figure 1). Assuming a constant wood density (see Enquist et al. [1999], Niklas [2004]), branch weight is proportional to branch volume. With total cross-sectional area the same at each branching (West et al. [1999]), $\bar{W}_k \propto \bar{D}_k^2 \bar{H}_k$. Combined with equations (2) and (4):

$$(8) \quad \bar{W}_k \propto D_0^2 \beta^{-k} H_0 \beta^{-k/3} \propto D_0^2 H_0 \beta^{-(4/3)k}.$$

$$(9) \quad \text{In general form: } \bar{W}_k \propto D_0^2 H_0 \beta^{-(1+x)k},$$

where $-(1+x)$ = the comparison of regression slopes. Equation (8) predicts a slope of $-4/3 \ln \beta$.

2.1.7 Total full branch segment weight. This is $W_K = N_K \bar{W}_k$, or equation (8) times equation (1): $W_K \propto D_0^2 H_0 \beta^{-(4/3)k} \beta^k$. Simplifying:

$$(10) \quad W_K \propto D_0^2 H_0 \beta^{-k/3}.$$

$$(11) \quad \text{In general form: } W_K \propto D_0^2 H_0 \beta^{-kx},$$

where $-x$ = the results from comparison of regression slopes. The slope for equation (10) is predicted to be $-1/3 \ln \beta$.

2.1.8 Total basal branch segment weight. This is $B_K = (W_K - W_{K+1}) \propto (D_0^2 H_0 \beta^{-k/3}) - (D_0^2 H_0 \beta^{-1/3(k+1)})$. Simplifying:

$$(12) \quad B_K \propto D_0^2 H_0 \beta^{-k/3} (1 - \beta^{-1/3}).$$

$$(13) \quad \text{In generalized form: } B_K \propto D_0^2 H_0 \beta^{-kx} (1 - \beta^{-1/3}),$$

where $-x$ = the results from comparison of regression slopes. Equation (12) is equation (10) times $(1 - \beta^{-1/3})$ and predicts a slope $-1/3 \ln \beta$. The ratio $B_K/W_K = (1 - \beta^{-1/3})$.

2.1.9 Average basal branch segment weight. This is $\bar{B}_K = B_K/N_K$. Substituting β^k for N_K (equation (1)), $\bar{B}_K = D_0^2 H_0 \beta^{-1/3k} \beta^{-k} (1 - \beta^{-1/3})$. Simplifying:

$$(14) \quad \bar{B}_K = D_0^2 H_0 \beta^{-4/3k} (1 - \beta^{-1/3}).$$

$$(15) \quad \text{In general form: } \bar{B}_K = D_0^2 H_0 \beta^{-(1+x)k} (1 - \beta^{-1/3}),$$

where $-x$ = the results for the comparison of regression slopes. Equation (14) is equation (8) times $(1 - \beta^{-1/3})$ with a predicted slope of $-1.33 \ln \beta$. The ratio $\bar{B}_K/\bar{W}_K = (1 - \beta^{-1/3})$.

2.1.10 *Average branch segment needle (leaf) weight.* Assuming the average size of the leaves of a species is constant (West et al. [2000], Enquist [2002]), that the average terminal branch segment length supporting them is constant, and that the spiral phyllotaxy of foliage arrangement along the branch segments (Charles-Edwards et al. [1986]) by the Fibonacci series (Prusindiewicz and Lindenmayer [1990]) is also constant, then average foliage biomass should be proportional to branch segment length (Barker et al. [1973]): $\bar{F}_M \propto \bar{L}_M$.

2.1.11 *Total number of terminal branches.* For $\text{Order}(\text{O}) = M$, unbranched terminal branches $\bar{D}_M \propto D_0 \beta^{-M/2}$ (equation (2)). Assuming $\bar{D}_M$ is constant, the relationship transposes to $\beta^{M/2} \propto D_0$. Squaring both sides and combining with equation (1) gives:

$$(16) \quad N_M \propto \beta^M \propto D_0^2,$$

or that the total number of $\text{Order}(\text{O}) = M$ branch segments and the number of leaves they contain (Enquist [2002]) are directly proportional to D_0^2 .

2.2 Derivation of foliage biomass crown distribution patterns. Foliage absorbs CO_2 and sunlight, and its distribution and quantity in the crown are controlled by available light. A hierarchical branching support structure terminating in size-invariant foliage units (Barker et al. [1973], West et al. [1999]) has evolved (West et al. [1999]) to efficiently support and distribute the foliage. The structure of a tree crown has an underlying pattern of branching that is consistent within a species (Barthelemy et al. [1991]) and balances photosynthetic efficiency between the branch structure needed to transport fluids and distribute the foliage in space with the energy costs of its construction and maintenance (Givnish [1988], Barthelemy and Caraglio [2007]).

With the foliage biomass on each $\text{Order}(\text{I})$ branch segment proportional to its length (Barker et al. [1973]), there should be a consistency in foliage distribution. These branch and foliage units are self-similar foliated subsets of the tree (Rodriguez et al. [2008]) that represent units of foliated volume. A tree with a branching ratio of three, and with four different sized units of foliated volume, is represented in Figure 2. For $\text{Order}(\text{I}) = 0$, the unit of foliated volume is a single branch segment

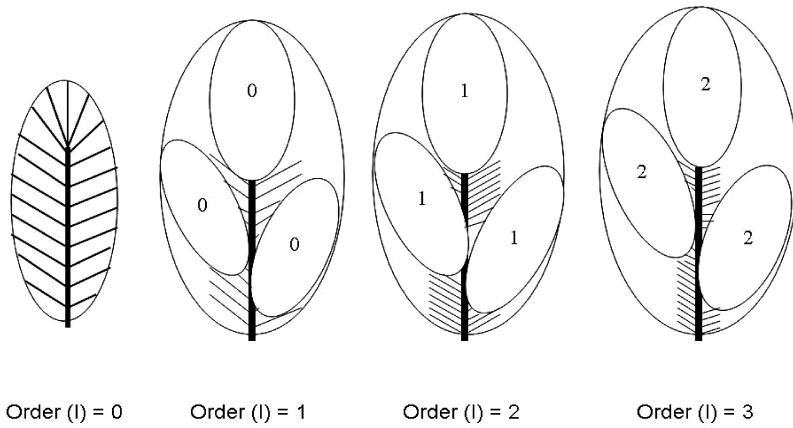


FIGURE 2. A two-dimensional representation of the first four Order(I) foliated volumes for a tree with a branching ratio of three. The Order(I) = 0 branch segment has a single foliated stem. The Order(I) = 1 segment has three Order(I) = 0 units of foliated volume plus its own foliage. This pattern is repeated for the Order(I) = 2 and 3 branch segments.

plus its foliage. Each Order(I) = 1 unit of foliated volume consists of three Order(I) = 0 units plus its own foliage. This pattern repeats for the Order(I) = 2 and Order(I) = 3. The last represents the largest foliated unit for pinyon.

A shaded leaf that is unable to balance its carbon gains and losses has exceeded its ecological light compensation point (Givnish [1988]). In Figure 3 crown size exceeds the ecological light compensation point where the Order(I) = 3 units of foliated volume are distributed around the outer edge of a tree canopy.² The depth of the ecological light compensation point is assumed to be proportional to the average total length of the Order(I) = 3 branch segments. This is the effective functional depth for foliage (F_x , where x = foliage) of the species.³ This foliated volume adds to its outer surface each year through the growth of new stems and foliage (Mitchell [1975]) and sheds foliage from the interior surface as a result of shading. The foliage remains in the crown of Douglas fir for about 5 years (Mitchell [1975]). This defoliated volume increases faster than the foliated volume with growth. Because leaf tissue density is generally constant regardless of plant size (West

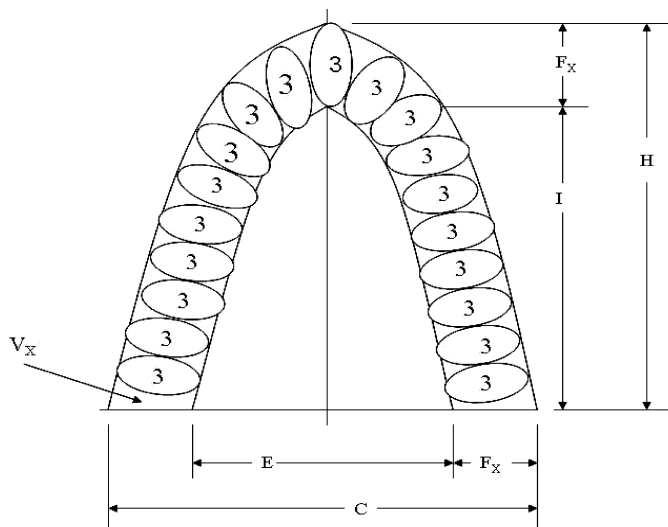


FIGURE 3. A cross section of a plant crown, where H = height and C = diameter for the exterior of the crown. E and I are the diameter and height of the interior defoliated part of the crown. The volume with foliage has a uniform functional depth (F_x) that defines the functional crown volume (V_x) containing the Order(I) = 3 foliated volumes in Figure 2.

et al. [1999], Enquist [2002]), I assumed the spatial branch distribution within the foliated volumes (Figure 2) to maintain an average foliage biomass density (kg needles/m³ foliated volume).

This foliated portion of the crown has been represented by jagged-edged, nested sets of vertically stepped cylinders (MacFarlane et al. [2003]), by a pair of nested cones (Kilmi [1957]), and by nested prolate ellipsoids (Grace [1990]). Similar to Grace [1990], I used a prolate ellipsoid to represent both the upper and lower boundaries of the foliated crown volume (Figure 3). This method closely duplicates the jagged-edged, blocky representation of MacFarlane et al. [2003] but with smoothed contours. It accommodates a wide range of crown shapes, from tall and narrow to short and wide.

Expressed as one-half of a prolate ellipsoid (Tausch [1980]), total crown volume = $\pi/6 C^2 H$, where C = diameter and H = height of

the exterior of the crown. The total crown volume equals the functional volume when $C < 2F_x$ or $H < F_x$. The volume of the crown without foliage, present when both $C > 2F_x$ and $H > F_x$ (Figure 3), is $\pi/6 (C - 2F_x)^2 * (H - F_x)$. The volume with foliage, V_x , is the total volume minus the volume without foliage:

$$(17a) \quad V_x = \pi/6 \left((C^2 H) - ((C - 2F_x)^2 * (H - F_x)) \right),$$

$$(17b) \quad \text{where } C > 2F_x \text{ and } H > F_x, \text{ otherwise } V_x = \pi/6 C^2 H.$$

Assuming a constant biomass density (U_x) of foliage, the foliage biomass (B_x , x = foliage in kg) is directly proportional to V_x . Incorporating U_x , into equation (17) (U_x , x = foliage in kg m⁻³) gives an equation for estimating both functional depth (F_x) and foliage biomass density.

$$(18a) \quad B_x = U_x V_x = U_x \pi/6 \left((C^2 H) - ((C - 2F_x)^2 * (H - F_x)) \right),$$

$$\text{where } C > 2F_x \text{ and } H > F_x,$$

$$(18b) \quad \text{otherwise, } B_x = U_x V_x = U_x \pi/6 C^2 H.$$

These same equations can also be used for analysis of individual branch order biomass.

2.3 Derivation of fuel loads

2.3.1 *Pinyon live fuel loads.* The proportionality of size and weight between branch orders makes it possible to derive similar relationships for the established fuel load classes (Burgan and Rothermel [1984], Pyne et al. [1996]). Fuel load classes are derived by combining the weights of two adjacent branch orders. The derivation for W_k (equation (10)) can be modified by incrementing the order number k by two instead of by one.

$$(Fuel_k) = (W_k - W_{k+2}) \propto (D_0^2 H_0 \beta^{-k/3}) - (D_0^2 H_0 \beta^{-1/3(k+2)}),$$

$$(19) \quad \text{simplifying: } (Fuel_k) \propto D_0^2 H_0 \beta^{-k/3} (1 - \beta^{-2/3}).$$

This differs from equation (10) by the constant $(1 - \beta^{-2/3})$. The functional depth and bulk density can be determined by equation (18) for each fuel load class.

2.3.2 *Juniper live fuel loads.* Because of the relationship between fuel load size classes and individual orders in pinyon, juniper can be directly sampled by fuel load classes and that data used in equation (18) to determine their functional depth and bulk density.

2.3.3 *Dead fuel loads.* Dead branches in pinyon, and dead foliage plus branches in juniper, can be divided into fuel loads the same as live fuels. The dead branches are hypothesized to be related to the defoliated portion of the crown.

3. Methods

3.1 Field data collection. Five data sets for single-leaf pinyon (*Pinus monophylla*) and one for Utah juniper (*Juniperus osteosperma*) were used to test the model. Crown and trunk measurements prior to sampling pinyon and juniper included total tree height, crown height, longest crown diameter, crown diameter perpendicular to the longest diameter, and trunk diameter just above the root crown. Crown measurements were of the portion containing foliage. All collected materials were oven dried before weighing.

Pinyon data set 1, from Tausch [1980], is from one single-leaf pinyon, nearly 2-m-tall, sampled on a low-tree dominance site in the Virginia Range, western Nevada in late summer after tree growth for the year had been completed.

Data set 2 comprised 17 single-leaf pinyon trees from the Pine Grove Hills in western Nevada sampled in the spring before tree growth for that year had started. Two trees each were collected from nine height classes, from 0.5 m to 4.7 m, in 0.5-m steps. One damaged 3.5-m-tall tree was not used. Trees were randomly selected from an area of mid-elevation woodlands with early low-to-mid tree dominance. The maximum length of the branches with needles at the ends of each crown

diameter and at the top of the crown was also measured for each tree. All parts of the above-ground portion of the trees were wrapped in plastic tarps to prevent branch or needle loss and returned to the lab for processing and weighing.

Pinyon data set 3 (Tausch [1980]) comprised 15 trees, 0.5 m to 4.6 m tall, sampled in the Needle Range, southwestern Utah, from mid-elevation woodlands with low-to-mid tree dominance in late summer after tree growth had ended.

Pinyon data set 4 consisted of 16 trees 0.5 m to 7.2 m tall sampled in the Virginia Range in western Nevada (DeRocher and Tausch [1994]) from mid-elevation woodlands with low-to-mid tree dominance in late summer after tree growth had been completed.

Pinyon data set 5 was from six woodland sites on the east side of the Sweetwater Mountains in western Nevada (Tausch and Tueller [1988, 1990]). All collection sites were in mature, fully tree-dominated woodlands and were sampled after tree growth had been completed. Sampling procedures are described in Tausch and Tueller [1990].⁴

Fifteen juniper trees were collected from the same site as data set 2 after tree growth for that year had ended. Nine height classes ranging from 1.0 to 5.2 m in 0.5-m steps were sampled with two trees collected and processed for each height class, except for 4.0-, 4.5-, and 5.2-m where one tree was collected.

3.2 Branch order sampling of pinyon. All branch segments of data set 1 (Tausch [1980]) were labeled in place by order (Figure 1), counted, their total length measured on the straight-line distance from base to tip, and averaged by order. Basal diameters were measured inside and outside the bark, and averaged by order. No biomass data were collected.

Branch segments in data set 2 trees were similarly identified, removed, and bagged by order, as were their needles. Diameters inside and outside the bark were measured on a subset of the trees. Both 0.5-m-tall trees and one randomly selected tree from each remaining size class were sampled, a total of 10 trees. All basal branch segments of the smaller trees, and a random selection of 5% of $\text{Order}(I) = 0$, 10% of $\text{Order}(I) = 1$, and 30% of $\text{Order}(I) = 2$ branch segments of

larger trees were measured. All $\text{Order(I)} = 3$ and higher branches were measured.

3.3 Fuel load sampling of juniper. Juniper foliage is shed in complex units of small branches with adhering foliage, thus identification on the basis of branch order is not possible. Juniper were directly sampled by fuel load class. Live foliage was removed first by cutting the branches where less than half of the foliage was still alive. The remaining live branches were then removed by 1-hour, 10-hour, 100-hour, and larger fuel load classes (Pyne et al. [1996]).

The crowns of both species contained dead branches, and juniper crowns dead foliage. The irregular chunks of branches with appressed foliage shed by juniper can become lodged in the crown. Dead branches were divided into the fuel load classes and dried and weighed.

3.4 Branch analysis methods. Branch segment number data were averaged within and across trees by Order(O) for analysis. Branch segment size averages are expected to be the same by Order(I) regardless of tree size; thus these variables were averaged within and across trees by Order(I) . They were analyzed by Order(O) for consistency with branch number. Branch analysis variable equations were tested with regression utilizing data sets 1 and 2. Results comparing the number of branches with the results for the other branch analysis variables utilized comparisons of semi-log slopes.

3.5 Foliage biomass crown distribution analysis. When the average crown diameter of a tree was less than twice F_x , or height less than F_x , the full crown volume was used for V_x in equation (18). F_x was not allowed to be larger than either the tallest tree or one-half the largest crown radius. A coefficient of determination (Brand and Smith [1985]) was also computed. After utilizing data set 2, data sets 2 through 5 were combined to determine an overall F_x that was used to compute V_x for each tree. These V_x were used in linear regression analyses with three data subsets to predict the foliage biomass values for their trees. These subsets were southwest Utah plus the Virginia Range (sets 3 + 4), Sweetwater Mountains data (set 5), and the Pine Grove Hills data (set 2). The analysis slope is the estimated bulk density.

3.6 Analysis of fuel loads

3.6.1 *Analysis of live fuel loads.* Pinyon branch orders were combined by the pairs of $\text{Order}(I) = 0$ plus $\text{Order}(I) = 1$ for the 1-hour fuels, $\text{Order}(I) = 2$ plus $\text{Order}(I) = 3$ for the 10-hour fuels, $\text{Order}(I) = 4$ plus $\text{Order}(I) = 5$ for the 100-hour fuels, and all branches larger than $\text{Order}(I) = 5$ for the 1,000-hour fuels. Equation (18) was used to determine their respective functional depth and bulk density. Juniper's fuel loads were similarly analyzed.

3.6.2 *Analysis of dead fuel loads.* Dead fuel load size classes and foliage were analyzed in three ways: (i) using equation (18); (ii) by linear regression analysis using V_x for the species; and (iii) by linear regression analysis using the defoliated volume of each species. Analysis results with the highest precision are reported.

4. Results

4.1 **Crown structural patterns.** For data set 1, the slope of $\ln N_k$ against $\text{Order}(O)$ was 1.49 (Tausch [1980]), or a branching ratio ($\beta = \exp(\text{slope})$) of 4.429. For data set 2 the relationship for $\ln N_k$ with branch order has a slope of 1.29 (Figure 4), or the branching ratio = 3.633. This branching ratio is used in the rest of the analyses. For data set 1, the slope of $\ln \bar{D}_k$ outside the bark by $\text{Order}(O)$ was -0.6579 (Tausch [1980]), for a ratio with the slope for $\ln N_k$ of -0.442 , and inside the bark the slope was -0.7661 , for a ratio of -0.514 with the slope for $\ln N_k$. For data set 2 the slope of $\ln \bar{D}_k$ outside the bark with $\text{Order}(O)$ (Figure 4) was -0.5943 , for a ratio with the slope for $\ln N_k$ of -0.461 , and inside the bark, the ratio with the slope for $\ln N_k$ was -0.515 .

For data set 1, the slope of $\ln \bar{H}_k$ against $\text{Order}(O)$ (equation (3)) was -0.526 , for a ratio with the slope for $\ln N_k$ of -0.354 , somewhat larger than the predicted -0.33 . For data set 2, the slope of $\ln \bar{L}_k$ by branch $\text{Order}(O)$ was -0.405 for a ratio with the slope for $\ln N_k$ of -0.314 , somewhat less than the predicted -0.33 . Using $\sum_{k=0-M} \bar{L}_k$ in each tree to predict total height resulted in a significant linear relationship with a slope of 0.953. Thus, this sum can be substituted for actual

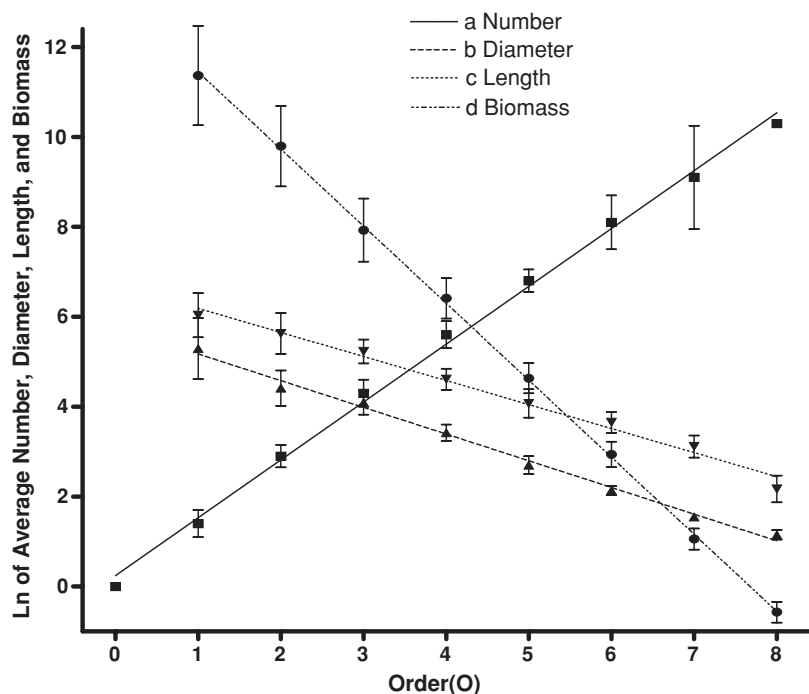


FIGURE 4. Regression analyses for 17 pinyon from data set 2 by Order(O) for (a) the average number of branch segments; (b) the average branch segment diameter outside the bark; (c) the alternate average total branch segment length; and (d) the average full branch segment biomass. Values for (b), (c), and (d) were averaged by Order(I). Bars equal 95% confidence limits.

total height in equation (5). The slope of $\sum_{k=k-M} \bar{L}_k$ by Order(O) was -0.5345 , for a ratio with the slope of $\ln N_k$ of -0.414 (Figure 4).

The slope of $\bar{W}_k$ by Order(O) in data set 2 was -1.714 (Figure 4), for a ratio with the slope for $\ln N_k$ of -1.329 , equivalent to the -1.33 in equation (8). Evaluation of $\ln W_K$ by order (equation (9)) was done by individual tree in data set 2. The slopes of the relationships between average $\ln W_K$ and branch Order(O) were approximately parallel and averaged -0.3959 (average $r^2 = 0.958$). The ratio of this average slope to the slope for $\ln N_k$ is -0.308 , slightly less than the expected value of -0.33 . Analysis results by tree for $\ln B_k$ by order (equation (12))

were similar to those for $\ln W_k$. The average slope of -0.2478 was, however, shallower, and its ratio to the slope for $\ln N_k$ was -0.1926 . There was also greater variability, with average $r^2 = 0.810$. The relationship for $\ln \bar{B}_K$ (equation (14)) for data set 2 had a slope of 1.3801 and a ratio with $\ln N_k$ of -1.07 , less than the expected value of -1.33 (equation (14)).

In data set 2, needles were consistently found only on $\text{Order(I)} = 0$ through 3. The combined length of these basal branch segments I assumed related to the average depth of the ecological light compensation point. Because the average $\text{Order(I)} = 0$ branch segment size is assumed the same regardless of tree size, the average weight of needles on those branch segments is also the same. The same holds for the remaining $\text{Orders(I)} = 1$ to 3. $\bar{F}_M$ also had a significant increasing semi-log linear relationship to branch order.

Analysis results for equation (15) showed an average of about 40 $\text{Order(O)} = \text{M}$ branch segments for each cm^2 of basal area of the $\text{Order(O)} = 0$ trunk ($r^2 = 0.96$) for data set 2. This result is consistent with the sapwood area/foilage biomass relationship (Tausch [1980], Tausch and Tueller [1988], DeRocher and Tausch [1994]) and with the relationships among plant leaf biomass, whole plant transpiration, and whole plant metabolism predicted by the scaling of conductivity (Enquist [2002], Niklas and Enquist [2002]).

4.2 Foliage biomass crown distribution patterns. F_x for foliage from iterative regression analysis of data set 2 was 0.678 m (Table 1), a value not significantly different from 0.634 m, the sum of the $\text{Order(I)} = 0$ through the $\text{Order(I)} = 3$ branch segments (those with needles; $t = -0.57$, $P \leq 0.58$), and less than the average maximum foliage depth of 0.87 m (95% C.L., 0.79 – 0.94 m) measured in the field. Using the calculated values of V_x for foliage (foliated volume) in standard linear regression analysis gave results that were linear over the full range of tree size (Figure 5). Similar results were obtained for each individual branch order.

Data sets 2–5 were combined and analyzed with equation (18) (Table 2). The resulting value of F_x for foliage (0.710 m) was not significantly different from the measured value of 0.634 m. The regression slope of the Sweetwater Mountains data subset (Table 2) was parallel

TABLE 1. Results of applying equation (18) for predicting foliage biomass and branch biomass by order with pinyon data from the Pine Grove Hills.

Biomass component (B_x)	Functional depth (F_x) (dm)	Bulk density (U_x) (g/dm ³)	R^2
Foliage biomass	6.78	1.07	0.992
Order zero total biomass	15.10	0.20	0.980
Order one total biomass	12.93	0.45	0.981
Order two total biomass	12.06	0.67	0.981
Order three total biomass	11.07	1.00	0.959
Order four total biomass	9.91	1.48	0.953
Order five total biomass	12.89	1.83	0.972
Total branch biomass	28.25	2.87	0.994
Total tree biomass	16.44	3.76	0.995

to, slightly below, and not statistically different from the combined Virginia Range and southwest Utah data (Figure 6). The Pine Grove Hills regression slope was about 10% less than, but not significantly different from, the slopes for the other two data sets. This possibly occurred due to over winter needle loss. The results did not differ among years, locations, or elevations, or between high and low tree dominance levels, a consistency indicating that functional depth for foliage is generally constant within a species. Samples collected at different times of the year may reflect different stages of the annual foliage gain or loss.

For data set 2, the relationship between sapwood area and foliage biomass was $R^2 = 0.985$, whereas for that between sapwood area and V_x was $R^2 = 0.983$. The relationship between defoliated crown volume and heartwood area ($R^2 = 0.91$) had a slope of $0.14 \text{ m}^3 \text{ cm}^{-2}$, steeper than the $0.08 \text{ m}^3 \text{ cm}^{-2}$ between sapwood area and V_x as expected.

4.3 Fuel load patterns. Analysis of pinyon with equation (18) for data set 2 resulted in functional depth values for each fuel load class similar to those for the individual orders (Table 3). Biomass determined by sampling a constant set of diameter sizes thus yielded equivalent results to sampling by order. Analysis of the juniper data

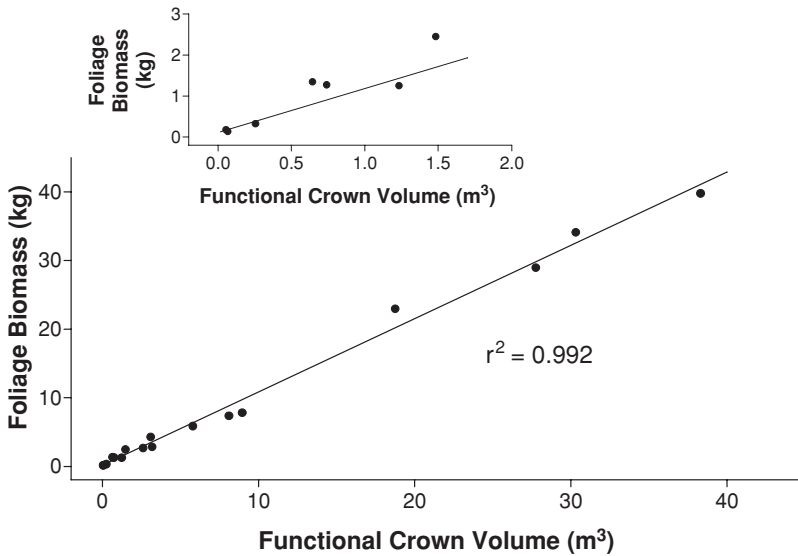


FIGURE 5. Results of regression analysis for foliage biomass by functional crown volume (V_x) for data set 2. Inset is an enlargement of the left 3% of the x-axis and shows the linear fit for the smallest trees.

yielded an F_x for foliage of 4.63 dm that was shallower and a bulk density (U_X) for juniper that was higher (Table 4) than for pinyon (Tables 1 and 3), reflecting the denser foliage of juniper. The other juniper fuel load components yielded similar relationships and precision (Table 4).

The highest analysis precision for dead juniper foliage was with equation (18) (Table 4). This appears related to the retention of dead foliage in the crown. For both the 1-hour and 10-hour dead branch fuel loads, the highest precision was with the defoliated volume in trees large enough to contain it (Table 5). Because dead branches randomly break off, the relationships for dead fuels in both species can be expected to have a lower precision.

4.4 Appendix. An additional test of the model is derived and evaluated, and summary tables are provided in the on-line Appendix.

TABLE 2. Results of applying equation (18) to predict foliage biomass using the combined pinyon data. The functional depth (F_x) from the combined analysis was used to compute the functional crown volume (V_x) for all individual trees. These V_x were then used in linear regression analyses to predict the foliage biomass values for the trees in the three data subsets.

Parameterization analysis			
Data set	Functional depth (F_x) (dm)	Bulk density (U_x) (g/dm ³)	Estimated R^2
Full combined data	7.095	1.176	0.928
Regression analysis of data subsets			
Data set	Intercept	Slope (kg/m ³) (Estimated bulk density)	R^2
Full combined data	0.341	1.170	0.929
Pine Grove Hills	0.169	1.032	0.993
Southwest Utah + Virginia Range	2.680	1.172	0.952
Sweetwater Mountains	−0.313	1.165	0.884

5. Discussion and conclusions

5.1 Crown structural patterns. The number, size, and weight of branch segments, and their relationships by order, were shown to be functions of the branching ratio. These are summarized in the on-line appendix tables.

5.1.1 *Basal diameter.* For data set 1, the computed slope ratios range from 4% greater (inside the bark) to 12% less (outside the bark) than the expected 0.50 (Tausch [1980]). For data set 2, they range from 3% greater to 7% less, respectively. For data set 1, the area inside the bark varied from 84% of the total area of the Order(I) = 5

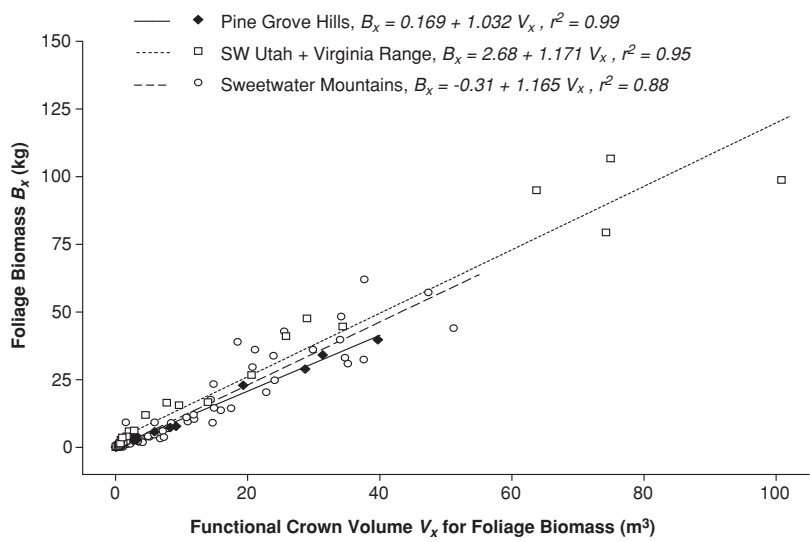


FIGURE 6. Regression results for foliage biomass (B_x) by functional crown volume (V_x) for three data subsets. Functional volumes were computed using the functional depth (F_x) obtained from the analysis of the combined pinyon data (Table 2).

TABLE 3. Results of applying equation (18) for predicting live branch fuel load biomass for pinyon data from the Pine Grove Hills, Nevada.

Biomass (T_x)	Functional depth (F_x) (dm)	Bulk density (U_x) (g/dm ³)	R^2
1-hour fuels	12.93	0.441	0.981
10-hour fuels	9.22	0.579	0.909
100-hour fuels	14.99	0.847	0.980

trunk to an average of only 24% of the total area of the Order(I) = 0 branches. For data set 2, the values were 96% and again 24% respectively. These results are similar to what has been reported for other tree species (Barker et al. [1973], McMahon [1975], McMahon and Kronauer [1976]).

TABLE 4. Results of applying equation (18) for predicting live foliage and branch fuel load biomass for juniper data from the Pine Grove Hills, Nevada.

Biomass (T_x)	Functional depth (F_x) (dm)	Bulk density (U_x) (g/dm ³)	R^2
Foliage biomass	4.63	2.00	0.976
1-hour fuels	3.99	0.39	0.979
10-hour fuels	6.76	0.63	0.977
100-hour fuels	28.48	0.72	0.972
Total branch biomass	28.48	2.90	0.960
Total tree biomass	28.48	3.72	0.992
Dead foliage biomass	2.53	0.23	0.876

TABLE 5. Results of linear regression analyses predicting dead branch fuels (T_x) for pinyon and juniper from the Pine Grove Hills, Nevada. Dead 1-hour and 10-hour branch biomass values are predicted using the defoliated volume (Q_x) from Table 1.

Biomass (B_x)	Intercept	Slope (g/dm ³) (Estimated bulk density)	R^2
Dead 1-hour pinyon stems	0.227	0.274	0.929
Dead 10-hour pinyon stems	0.423	0.357	0.916
Dead 1-hour juniper stems	0.323	0.253	0.940
Dead 10-hour juniper stems	-0.1567	0.144	0.931

5.1.2 *Branch length and weight.* Equation (4) was derived by assuming that height or length would reach the $D^{2/3} \propto H$ limit (i.e., the maximum) that the diameter would support. Tausch [1980] compared this relationship for pinyon between a more mesic site and a drier site. On the mesic site the exponent on diameter was 0.630, and on the drier site 0.753, a value seeming to violate the limits of support. However, over the range of tree sizes present at the drier site, tree height was consistently less for a given basal diameter than at the mesic site. At the same basal area, trees on the drier site also had a higher proportion

of sapwood, suggesting that the cross-sectional area used for fluid conduction exceeds that needed for support at drier sites.

5.2 Foliage biomass distribution patterns. The consistent average length of the branch segments supporting the pinyon needles (Order(I) = 3) is key to how the allometric/structural relationships developed here efficiently distribute the needles in the crown. Results were consistent across several sites and elevations, and across growing conditions ranging from relatively open to crowded stands.

Turrell [1961] weighed and individually measured the surface areas of the leaves on four Valencia orange (*Citrus sinensis*) trees. Analyses using equation (18) yielded for leaf biomass, functional depth = 0.4676 m, bulk density = 2.4070 kg/m², and $R^2 = 0.989$; and for leaf area, functional depth = 0.4528 m, bulk density = 8.516 m²/m³, and $R^2 = 0.984$. The values of functional volume for both leaf biomass and area are essentially the same.⁵

The consistency of the linear relationships with functional volume for all biomass components also indicates that this is a useful way of estimating biomass that does not require data transformation and the bias it can potentially introduce. Analysis results also provide additional input for the interpretation of the monolayer and multi-layer concepts of leaf distribution described by Horn [1971].

5.3 Fuel load patterns. Separating a tree by order is time consuming. Analysis results show that this level of effort is not necessary to determine fuel loads using the concept of functional depth. The fuel load size classes provided analysis results equivalent to those obtained with the individual branch orders, but the effort required to divide the trees into fuel load classes was much less than that needed to sample each tree by branch order.

5.4 Implications for allometric interpretation. Results show that biomass-to-size relationships for many components, although often closely approximated by an allometric analysis, are not truly allometric. The variation results from the three stages of tree growth: (i) the trees are smaller than their functional depth for foliage; (ii) tree size exceeds the functional depth and a defoliated volume occurs;⁶ and

(iii) crown closure and crown lift has occurred, placing additional support requirements on the trunk below the crown. Allometric regression analysis approximates or averages these differences over all tree sizes included.

5.5 Crown growth patterns. The results described here indicate that the primary control on tree crown growth is from the outside in. As new branches and foliage grow, they intercept light, changing foliage distribution throughout the crown as some foliage receives inadequate light (Horn [2000]). Branches retaining foliage continue to grow adding new leaves, whereas branches with too little foliage die, changing the structure of the crown. These changes appear to represent those of a self-organized system (Camazine et al. [2001]), with the evolution of the support structure potentially representing an emergent property. It should be possible to develop similar relationships for a wide range of woody plant species.

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