Foliage distribution in old-growth coniferous tree canopies

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The vertical distribution of foliage for several old-growth trees is discussed and modeled. The data include the foliage distribution of nine Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) crowns, the foliage distribution of a sugar pine (*Pinus lambertiana* Dougl.) crown, and the foliage distribution of a composite of the nine Douglas-fir trees which represents the stand canopy. The data show that the foliage is distributed asymmetrically in the crown with the maximum amount often located at a height approximately equal to 80% of the tree height. The data further show that the crown base is 9–30 m above the ground. Five different mathematical models of the foliage distribution (a normal distribution, a chi-square distribution, a beta distribution, a difference of exponentials, and a chi-square-like distribution) are fitted to the data and compared. The beta distribution and the chi-square distribution appear to fit the data slightly better than the others; but the differences in r^2 between all the models are often small. The normal distribution has the advantage that it shows the least variability from one tree to the next; however, it also has the disadvantage that it is significantly different from zero at the top of all the tree crowns modeled here.

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Le déploiement vertical du feuillage de plusieurs arbres matures est discuté et modélisé. Les données portent sur les cimes de neuf Douglas taxifolié (*Pseudotsuga menziesii* (Mirb.) Franco) et sur une cime de *Pinus lambertiana* Dougl. et sur le feuillage d'un groupe de neuf Douglas taxifolié représentant le couvert forestier. Les données révèlent un déploiement asymétrique du feuillage de la cime où le gros du feuillage se trouve souvent à environ 80% de la hauteur de l'arbre et dont la base se situe entre 9 et 30 m du sol. Cinq modèles mathématiques différents du déploiement foliaire (les distributions normale, de chi carré, bêta, de différence d'exponentielles et de chi carré modifié) sont ajustés aux données et comparés. Les distributions bêta et de chi carré semblent s'ajuster mieux que les autres aux données; cependant, les différences dans les coefficients de détermination entre tous les modèles sont souvent faibles. La distribution normale présente l'avantage d'être la plus stable d'un arbre à l'autre mais l'inconvénient de s'éloigner significativement de zéro à la flèche terminale de toutes les cimes modélisées dans cette étude.

[Traduit par le journal]

Introduction

Knowledge of the vertical distribution of foliage in a canopy is fundamental to the study of basic exchange processes within the canopy. The extinction of light, the allocation of energy for photosynthesis and transpiration, the microclimate within and beneath the canopy, the dispersion of particles in the canopy, and the cycling of nutrients within the canopy are all affected by the foliage distribution.

Foliage distribution as a function of height is termed the foliage surface area density (FSAD) or needle surface area density (NSAD) for conifers, and is the foliage surface area per unit volume of space at a given height above the ground. FSAD is measured in square metres foliage surface area per cubic metre volume and hence has dimensions metre^{-1}. The FSAD has been described for many different canopies with many different models. Harrington (1965, 1979) used a chi-square distribution for a midlatitude deciduous forest as has Perrier (1970) for a number of different plant canopies. Stephens (1969) found that the NSAD was well approximated by a normal distribution in red pine (*Pinus resinosa*, AIT). Kinerson and Fritschen (1971) modeled the NSAD for a naturally regenerated Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stand as the sum of several triangular functions. Allen (1974) used a parabolic curve for sorghum (*Sorghum bicolor* (L.) Moench); and Hsia (1979) matched two separate parabolic curves for a young-growth Douglas-fir.

The purpose of this paper is to present data on the NSAD of nine old-growth Douglas-fir crowns and one old-growth sugar pine (*Pinus Lambertiana* Dougl.) crown and to compare how well several different models fit the data.

Materials and methods

The 10 trees used in this work were climbed, sampled, and reconstructed in a manner similar to that outlined by Pike et al. (1977). The first stage of sampling consisted of four steps. First, all the branch systems (one or more stems which radiate from an area of a few square decimetres on the trunk) within the crown were numbered. Second, the number of axes (stems larger than 4 cm in diameter) within each branch system were counted. Third, the total needle biomass for each branch system was estimated from existing correlation between nee-

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TABLE 1. General characteristics of old-growth trees

Tree name	Total needle biomass, kg	Total needle surface area, m^2	Tree height, m	Tree height at crown base	Needle surface area index	No. of strata
'Slim'	115	1430	52	14	8.3	8
1137	160	2230	47	14	11.7	7
98	196	2730	57	9	14.3	10
'Galadriel'	197	2700	70	30	35.1	8
286	198	2820	70	14	14.8	11
'El Capitan'	210	2700	77	15	16.1	13
'Minerva'	238	3310	70	30	19.2	8
174	249	3470	57	10	18.2	10
'Neptune'	280	3900	74	24	23.3	10
Douglas-fir composite	204	2850	77	9	14.9	14
705[a]	132	—	55	9	—	9

[a]Sugar pine not included in the composite tree.

dle biomass and axis diameter. Fourth, the total needle biomass for all branch systems within a stratum,[2] 5 m in depth as measured along the trunk, were summed. These estimations were then used to produce a vertical distribution of relative needle biomass. For the second stage of sampling the total needle biomass for the entire crown was reestimted, although the relative distribution was unchanged from the first stage. Except for tree 'Minerva,' all trees had a second round of sampling.

For this study the vertical distributions of needle biomass of the nine Douglas-firs were converted into the NSAD in the following manner:

$$f_i = [w/(A\ \Delta Z_i)]N_i$$

where f_i is the NSAD of the ith stratum and is a constant for any given stratum; w is the ratio of surface area of freshly cut needles to the dry mass of those needles; A is the projected ground surface area of the tree crown; ΔZ_i is the depth of the ith stratum; and N_i is the needle biomass of the ith stratum. The surface area to dry mass ratio, w, is known for only four trees and has a mean value of 13.9 m^2/kg. This mean value was assumed for those trees where it is not known and is probably within 10% of the true value. The projected ground surface area, A, was estimated in the field for five of the Douglas-fir trees, and for the remaining four firs, which were felled several years ago, a value of 191 m^2 was assumed. This assumed value was derived from the original tree descriptions and comparisons between it and those estimated in the field suggest that it may overestimate the true area by 10–15%.

Because the sugar pine was also felled several years ago, the ratio w is unknown.Therefore, instead of converting the needle biomass distribution data into a NSAD, a needle biomass density was used instead. The needle biomass density is the needle biomass of any given stratum divided by the depth of the stratum, and hence is measured in kilograms per metre.

Table 1 summarizes the general features of the 10 trees. The total needle biomass and needle surface area may be slightly underestimated because the tops of the trees could not be climbed and sampled. However, this error is expected to be small. For two trees, sight observation yielded estimates of the needle biomass in the treetop, and it was less than 1% of the total foliage in one case and less than 5% in the other. Likewise, the tree height may also be underestimated. The tree heights shown in this table vary between 47 and 77 m and are usually very nearly equal to the actual tree height. However, in a few cases, such as tree 286, the height is several metres less than the actual tree height (Pike et al. 1977). Finally, the unusually high value for the needle surface area index of tree 'Galadriel' is due to its unusually small projected ground surface area.

Table 1 also includes a composite tree which represents the stand canopy as an average of the individual crowns. The composite tree was derived from the nine Douglas-fir trees only.

The NSAD values of each of the 10 trees and the composite tree are shown in Figs. 1–11. The vertical axis on these figures is normalized height which is the absolute height above the ground, z, divided by the height of the tree, H. In deriving the composite tree (Fig. 10) the NSAD was computed on the basis of absolute heights rather than the normalized heights. These figures also show three of the five models which are discussed in the next section.

Results and discussions

Because the foliage distribution is often different from one tree to the next, generalizations are not always true when applied to an individual tree. However, three general characteristics can be seen from the NSAD value. First, the foliage is not distributed symmetrically within the crown, but skewed upward toward the crown top. The maximum foliage density often occurs at a height approximately equal to 80% of tree height. Second, the crown base is 9–30 m above the ground. Third, the foliage distribution is often irregular. To fit all these trees perfectly with one model is, of course, impossible. However, there are simple functions using

[2]For this study the top stratum of eight of the trees was not 5 m, but either 4 or 6 m.

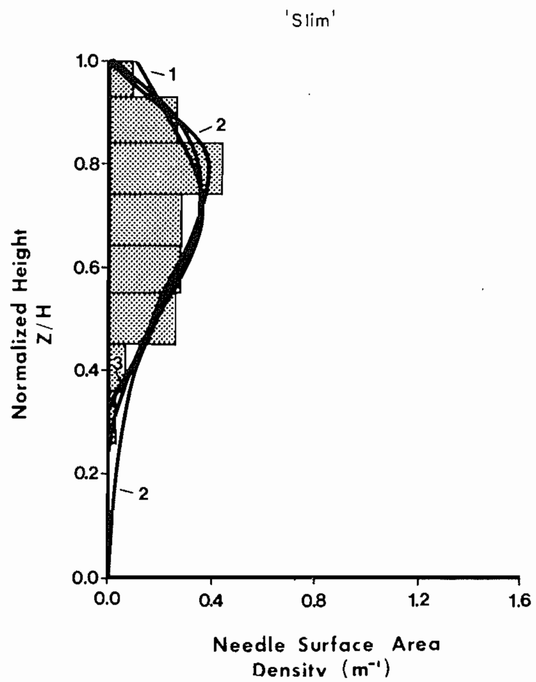

FIG. 1. Needle surface area density and three model curves for an old-growth Douglas-fir, tree 'Slim.' The height above the ground is shown on the vertical axis and has been normalized by the tree height. For this tree height (H) is 52 m.

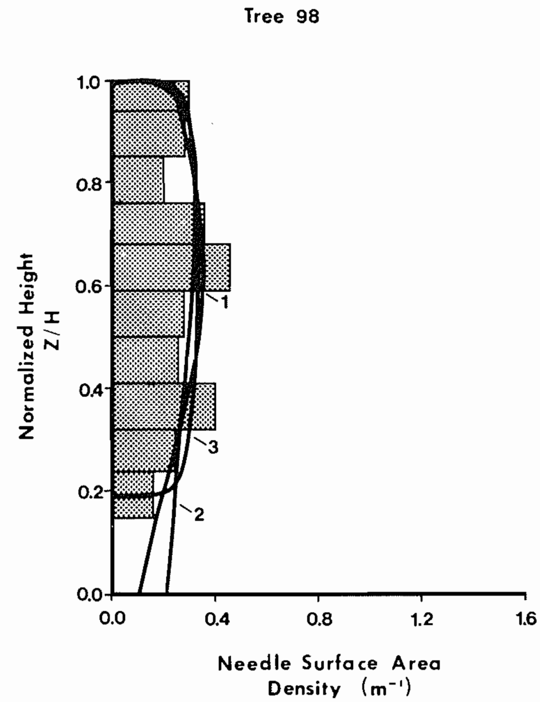

FIG. 3. Needle surface area density and three model curves for an old-growth Douglas-fir, tree 98. The vertical axis is the same as in Fig. 1. The tree height (H) is 57 m.

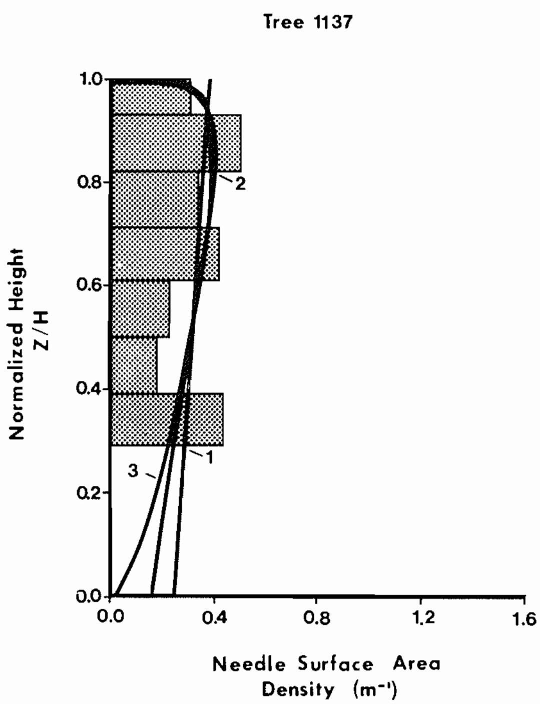

FIG. 2. Needle surface area density and three model curves for an old-growth Douglas-fir, tree 1137. The vertical axis is the same as in Fig. 1. The tree height (H) is 47 m.

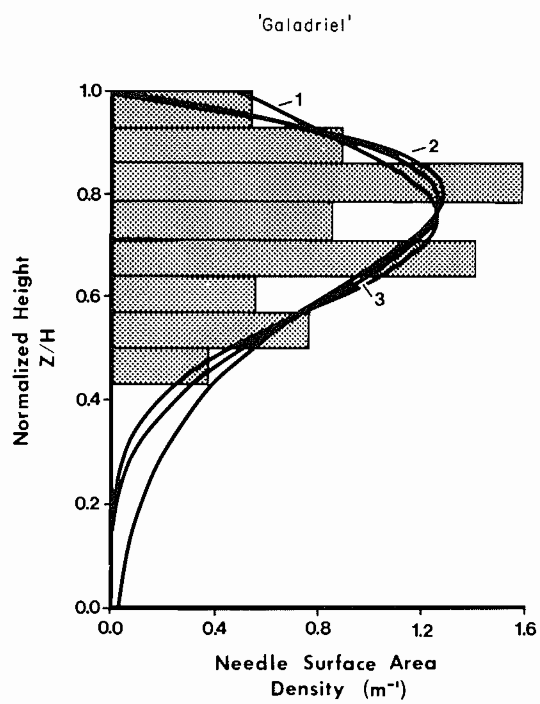

FIG. 4. Needle surface area density and three model curves for an old-growth Douglas-fir, tree 'Galadriel.' The vertical axis is the same as in Fig. 1. The tree height (H) is 70 m.

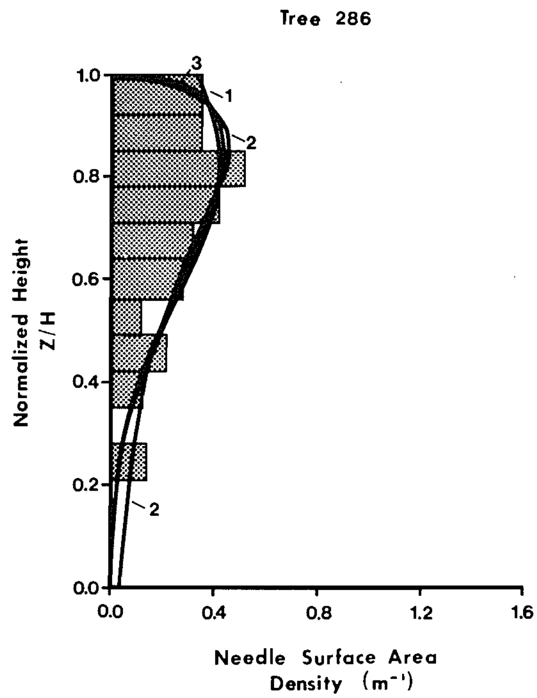

FIG. 5. Needle surface area density and three model curves for an old-growth Douglas-fir, tree 286. The vertical axis is the same as in Fig. 1. The tree height (H) is 70 m.

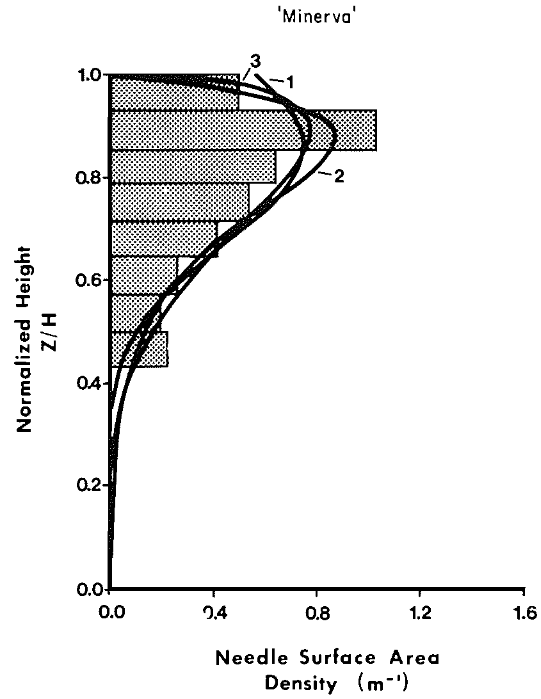

FIG. 7. Needle surface area density and three model curves for an old-growth Douglas-fir, tree 'Minerva.' The vertical axis is the same as in Fig. 1. The tree height (H) is 70 m.

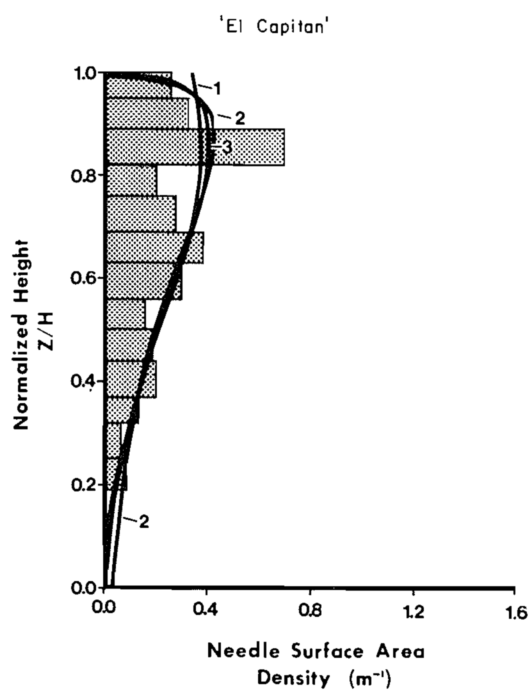

FIG. 6. Needle surface area density and three model curves for an old-growth Douglas-fir, tree 'El Capitan.' The vertical axis is the same as in Fig. 1. The tree height (H) is 77 m.

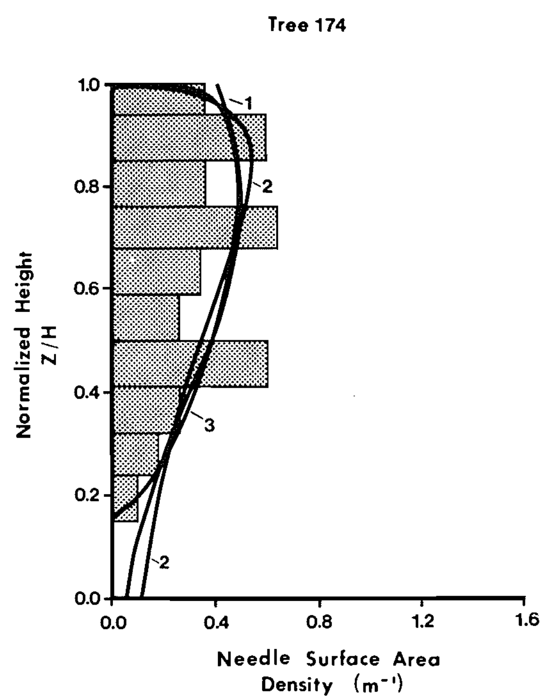

FIG. 8. Needle surface area density and three model curves for an old-growth Douglas-fir, tree 174. The vertical axis is the same as in Fig. 1. The tree height (H) is 57 m.

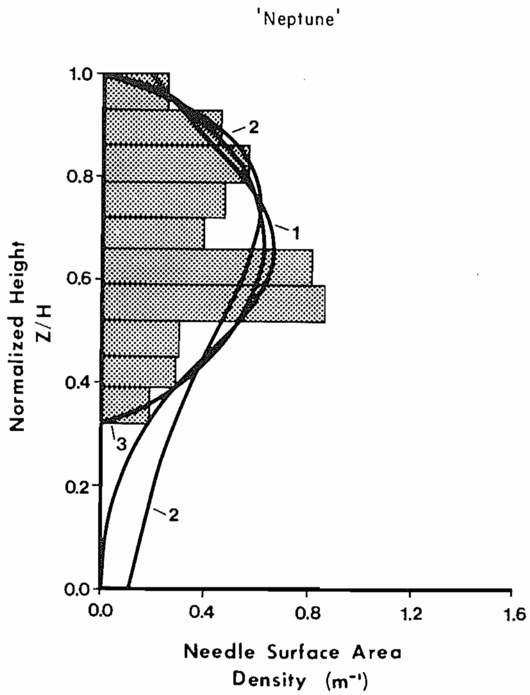

FIG. 9. Needle surface area and three model curves for an old-growth Douglas-fir, tree 'Neptune.' The vertical axis is the same as in Fig. 1. The tree height (H) is 74 m.

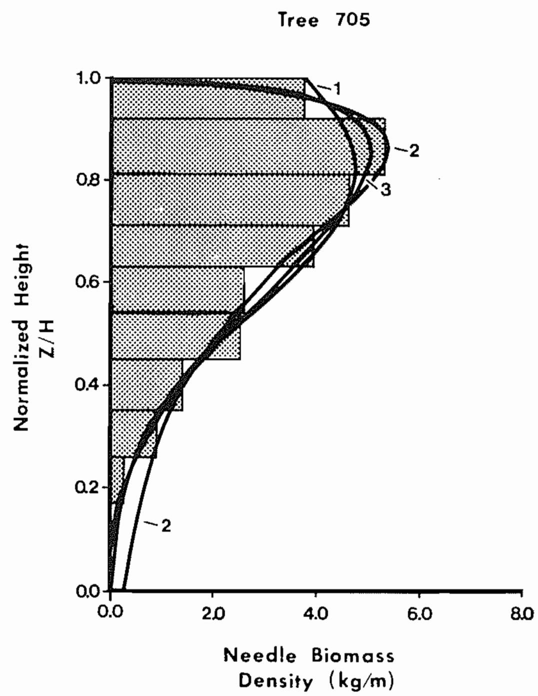

FIG. 11. Needle biomass density and the three model curves for the old-growth sugar pine, tree 705. The vertical axis is the same as in Fig. 1. The tree height (H) is 55 m.

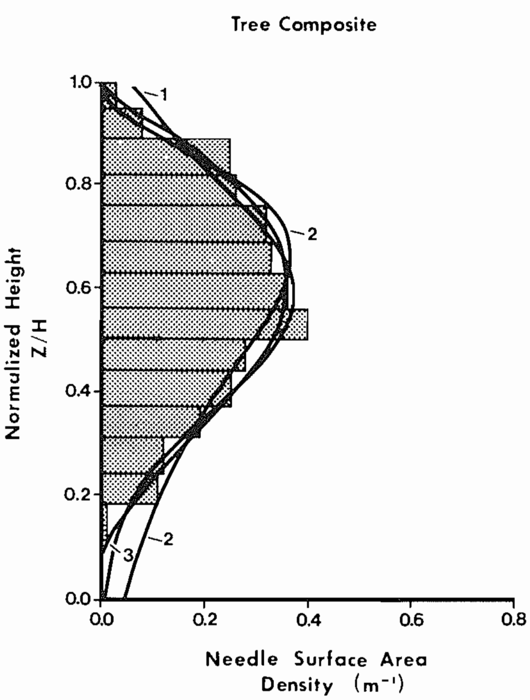

FIG. 10. Needle surface area density and the three model curves for the composite old-growth Douglas-fir. The vertical axis is the same as in Fig. 1. The tree height (H) is 77 m.

only a few parameters which can be used to fit the NSAD value of most of these trees.

Each NSAD was fit with five different models using a nonlinear least-square optimization technique. Each model, listed below, fits the data as functions of the normalized height (ξ).

A normal distribution:

[1] $a_1 e^{-a_2^2(\xi - a_3)^2}$

A chi-square distribution:

[2] $a_1(1 - \xi)^{a_2} e^{a_3 \xi}$

A beta distribution:

[3] $a_1(1 - \xi)^{a_2}(\xi - a_3)^{a_4}$

A difference of exponentials:

[4] $a_1(e^{-a_2(1 - \xi)} - e^{-a_3(1 - \xi)})$

A chi-square-like distribution:

[5] $a_1(1 - \xi)(\xi - a_2)e^{-a_3(1 - \xi)}$

The parameters a_1, a_2, . . ., etc., are the model parameters which were determined for each model separately by the nonlinear least-squares optimization technique. Model 2 is Harrington's (1965, 1979) model and is slightly more general than Perrier's (1970) model. Perrier chose $a_2 = 2$ for his model and he optimized on a_1 and a_3 only. Harrington (1965) did not use an optimization scheme, but rather he derived mathematical relationships between the parameters and the general tree characteristics.

Model 2 is a chi-square distribution; however, it has been written in a slightly different form than the usual chi-square distribution. The usual form for a chi-square distribution is $a'_1 (1 - \xi)^{a'_2} e^{-a'_3(1 - \xi)}$ which is related to model 2 by simply redefining the model 2 parameter a_1 as $a'_1 e^{-a'_3}$. The normal distribution, model 1, has also been rewritten from the usual form; this was done only to simplify the computations and it does not affect the results.

The optimal fit of each of the first three models is shown in each figure with the corresponding NSAD. The last two models are not shown because they are very similar to models 2 and 3 and they confuse the figures unnecessarily without adding much information. These figures highlight the basic differences between all models. The normal distribution is always significantly different from zero at the top of all trees. This is due primarily to the NSAD values themselves and hence due to the nature of the trees. To optimally fit these data, the normal distribution must be different from zero at the top. The ideal fit for the normal distribution would show a negligibly small amount of foliage at the top and bottom of the crown and would be symmetric about the point of maximum foliage density. However, the trees in general show that the NSAD is not symmetric about the region of maximum foliage density but skewed upward toward the top. The model 1 fit could be slightly improved at the top if there were more information about the treetop; but this would not remove the problem entirely. Hence, the normal distribution may not be suitable for some applications, because it does not go to zero at the top. The other four models, on the other hand, are zero at the top; and they are also asymmetric and skewed upward toward the top.

Another basic difference between all models can be seen in the region below the crown base. Model 2 and model 4 (not shown) are not always zero near the bottom of the crown. In fact, they are not always zero at the ground either; but this is really not too serious. In many numerical applications the region of interest is just the crown and any excess model NSAD predicted below the crown is simply ignored. In other applications it may be desirable that a model not be zero at the ground. For instance, the understory foliage or the tree trunk itself might also be included in a model.

Model 1, the normal distribution, generally is negligibly small somewhere in the region below the crown and above the ground. However, this is not true in every case, e.g., trees 1137 and 98. For these two trees the NSAD is best fit by a normal distribution with a very large standard deviation. In fact, for tree 1137 the optimal standard deviation was over six times the tree height. As will be discussed later tree 1137 was difficult to fit with any model, because its NSAD is very nearly a constant.

The remaining two models, 3 and 5 (also not shown), are zero either at the crown base or at the ground. In those cases where model 3 or 5 shows a finite amount of foliage beneath the crown base it is always much less than what the other three models show.

While the foregoing qualitative discussion suggests that models 3 and 5 are best for reproducing the general features of the NSAD values, the best choice of models is often dependent upon the application. To quantitatively test how well each model reproduced the NSAD values, an r^2 was computed for each fit and the results were tabulated in Table 2.

The relative performance of these five models was tested by a Friedman test (Hollander and Wolfe 1973). Excluding the composite tree, the models were ranked according to their r^2 and it was found that the null hypothesis (no difference between models) could not be supported.[3] Subsequent distribution-free multiple comparisons based on the Friedman test (Hollander and Wolfe 1973) suggested the following: (*i*) model 3 performed significantly better than model 5 at the 94% confidence level; (*ii*) model 3 performed significantly better than model 4 at the 89% confidence level; (*iii*) model 2 performed significantly better than model 5 at the 89% confidence level; and (*iv*) all other comparisons were significant at or below the 80% confidence interval. However, the differences in r^2 from one model to the next are usually small. The most difficult tree to fit was tree 1137 which had the lowest r^2 of all the trees. The foliage of this tree is distributed almost uniformly throughout its crown; hence its NSAD is nearly constant. Because the models are all curvilinear they cannot fit a constant NSAD very well; thus all models produce a very low r^2 for tree 1137.

So far the discussion of model performance has centered on how well, either qualitatively or quantitatively, each model has reproduced the general features of the NSAD value. There is yet another consideration when comparing the performance of the models. An important feature for any model is that its parameter values differ very little from one tree to the next. Such a feature is extremely useful in cases where there is no data available on which to build or choose a model. Of the five models, only model 1, the normal distribution, comes closest to achieving this feature. The parameter values for model 1 are tabulated in Table 3. For this table the model parameter a_2 has been converted into a standard deviation which is shown in the third column.

[3] P value of the null hypothesis was less than 0.02.

TABLE 2. The r^2 (correlation coefficient) of the fit for five models

	Model type				
Tree name	Normal distribution	Chi-square distribution	Beta distribution	Difference of exponentials[a]	Chi-square-like distribution[b]
'Slim'	0.81	0.84	0.88	0.78	0.88
1137	0.08	0.15	0.06	0.0[c]	0.0[c]
98	0.33	0.13	0.35	0.05	0.0[c]
'Galadriel'	0.55	0.60	0.60	0.57	0.60
286	0.81	0.82	0.82	0.79	0.76
'El Capitan'	0.50	0.57	0.54	0.56	0.43
'Minerva'	0.73	0.88	0.80	0.88	0.87
174	0.49	0.48	0.53	0.47	0.23
'Neptune'	0.51	0.36	0.51	0.36	0.48
Douglas-fir composite	0.93	0.89	0.95	0.74	0.94
705[d]	0.96	0.98	0.98	0.96	0.75

[a]The functional form for this model is $a_1(e^{-a_2(1-\xi)} - e^{-a_3(1-\xi)})$ where ξ is the height above the ground normalized by the tree height and a_1, a_2, and a_3 are model parameters.

[b]The functional form for this model is $a_1(1 - \xi)(\xi - a_2)e^{-a_3(1-\xi)}$.

[c]In these cases the residual sum of squares of the optimized fit was actually larger than the original variance of the data. Hence, the r^2 is set to 0.0 and the fit is ignored.

[d]Sugar pine not included in the composite tree.

TABLE 3. General characteristics of model 1, the normal distribution, for each tree

Tree name	a_1	Mean[a]	Standard deviation*	% overestimate of NSA index using total area under normal curve
'Slim'	0.37	0.72	0.18	6
1137	15.1	17.6	6.15	99
98	0.35	0.63	0.40	29
'Galadriel'	1.26	0.75	0.18	12
286	0.42	0.82	0.26	23
'El Capitan'	0.38	0.85	0.33	33
'Minerva'	0.76	0.86	0.18	22
174	0.49	0.77	0.36	29
'Neptune'	0.66	0.66	0.21	10
Douglas-fir composite	0.38	0.60	0.22	6
705†	4.78	0.82	0.26	24

*The functional form for this model is $a_1e^{-a_2^2(\xi-a_3)^2}$ where ξ is the height above the ground normalized by the tree height and a_1, a_2, and a_3 are model parameters. The mean is given by a_3 and the standard deviation is given by $\sqrt{2}/(2a_2)$.

†Sugar pine not included in the composite tree.

The second column is the parameter a_3 which is the mean of the distribution. The parameter values for tree 1137 are quite eccentric because its NSAD is too uniform to fit with a normal distribution. In the following discussion of Table 3, tree 1137 will be disregarded.

The average mean of the remaining eight Douglas-fir trees was 0.76 and the average standard deviation for the same trees was 0.26. The sugar pine had similar values for its mean and standard deviation. The composite tree had a mean of 0.60 and a standard deviation of 0.22. For red pine, Stephens (1969) found an average mean of 0.5 and an average standard deviation of 0.2; which are different values than suggested here for old-growth trees. He also found that his average applied to the stand as well as to individual trees. This does not occur here.

Generally all the trees had the upper portion of the normal distribution missing as has been discussed. Therefore, the needle surface area index is always overestimated by the total area under the normal curve. This amount of overestimate is given in the last column of Table 3. Again disregarding tree 1137, the average overestimate of the eight remaining Douglas-fir trees was 21%. For the sugar pine the overestimate was 24% and for the composite tree it was 6%. The first column of Table 3 shows the variation in the model 1 parameter

a_1. Aside from trees 1137 and 705 this parameter varies between 0.35 and 1.26 with an average of 0.59. For tree 705, the sugar pine, this parameter is different because the data being fit is the needle biomass distribution, rather than the NSAD.

Although there are disadvantages in using the normal distribution (model 1) to describe the NSAD of these old-growth trees, it does have the advantage that the parameter values show far less variability from one tree to the next than do the parameters of the other models. The parameter values for the other models generally show a 10-fold to 30-fold variation, whereas for the normal distribution they show only a 2-fold to 4-fold variation.

In summary, model 3, the beta distribution, is probably best for fitting the old-growth tree crowns of this study. It is zero at the top of the tree and zero at either the bottom of the crown or the ground and it fits the data as well as, and often slightly better than, the other models. The chi-square distribution, model 2, is probably a close second. The normal distribution, model 1, had the advantage of less variability in its parameter values, but it also had the disadvantage of always being significantly different from zero at the treetop. For any given application, there may be advantages for choosing one model over another; thus it may be worthwhile to compare several models before choosing a specific one. This study compares five models. They are not the only ones which could have been used. However, they are fairly general and represent a broad selection of simple functions.

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