ALLOMETRY OF WOODY BIOMASS AND LEAF AREA IN FIVE TROPICAL MULTIPURPOSE TREES

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FOWNES, J.H. & HARRINGTON, R.A. 1992. Allometry of woody biomass and leaf area in five tropical multipurpose trees. To derive allometric equations for leaf area and woody biomass, and to test for differences due to tree age and planting density and geometry, two field experiments were conducted on the island of Maui using *Acacia auriculiformis, Acacia mangium, Eucalyptus camaldulensis, Gliricidia sepium* and *Leucaena diversifolia*. In the first experiment, harvest at 6, 12, 18 and 24 months of a 2 × 1 *m* spacing showed that woody biomass allometrics did not differ for any of the species over time. Leaf area equations differed among harvests for *G. sepium* due to seasonal leaf shedding, and for *L. diversifolia*, due to episodic psyllid attack, but did not differ for the other species. A second series of plots containing *A. auriculiformis* only were started six months later and harvested at 6, 12 and 18 months; there was no difference attributable to season as opposed to tree age. In the second experiment, *A. auriculiformis* and *L. diversifolia* were grown in four spacing treatments: 1 × 1, 2 × 1, 2 × 2, and 4 × 0.5 *m*. Harvest at 24 months showed no differences in leaf area or woody biomass allometric equations among spacings for either of these species. Combined across both experiments, the exponents of the leaf area allometric equations did not differ from 2.0, supporting the "pipe model" theory of physiological regulation of leaf area. The exponents of the biomass allometrics were significantly different from 2.0 (generally near 3.0), implying that sampling and mensuration methods based on diameter squared are biased.

Key words: Allometry - leaf area - woody biomaass - multipurpose trees - spacing trial - *Acacia auriculiformis* - *Acacia mangium* - *Eucalyptus camaldulensis* - *Gliricidia sepium* - *Leucaena diversifolia*

Introduction

The demand for fuelwood and other tree products in tropical countries has increased the use of fast-growing "multipurpose" trees which may provide fuel, fodder, green manure, soil conservation and income. It is often desirable to estimate wood and leaf biomass or leaf area non-destructively through the use of allometric equations relating these quantities to tree height or stem diameter. Such equations must be created from destructive harvests, and the question arises of how far results can be extended from harvest of one age or tree spacing to other conditions. The purpose of this paper is to describe our field research showing that woody biomass allometric equations are relatively stable across the experimental spacings and ages of multipurpose tree plantings, and that leaf area allometric equations are stable for some species but not for others.

In practical terms, allometric equations are needed to monitor biomass growth, and particularly to determine when stands attain maximum mean annual increment, one criterion for optimal management (Evans 1982). Allometric analyses are also prerequisite to the creation of stand yield tables, which can then be used by people who do not have access to computers and calculators. Furthermore, allometric equations are needed by scientists in analyzing experimental growth trials or in creating physiologically-based models of tree growth as a function of leaf area index (Fownes & Harrington 1990) or absorbed radiation (Linder *et al.* 1985, Cannell *et al.* 1987, 1988).

Equations relating biomass or leaf area to tree diameter or height have been developed for many species (Whittaker & Marks 1975, Parde 1980), including some fast-growing tropical tree species (Kanazawa et al. 1982, Lim 1988, Whitesell *et al.* 1988, Schubert *et al.* 1988, Fownes & Harrington 1990). The allometric equation generally used is:

$$Y = aD^b$$

where Y is biomass (*kg*) or leaf area (m^2) and D is diameter (*cm*), and a and b are determined by linear regression of log-transformed Y and D. There are several advantages to this procedure, including homogenizing variance (which almost always increases with increasing tree size), allowing a continuous range in exponents (rather than presupposed transformations), and ease of constructing simple tests of hypotheses on the values of a and b. Furthermore, because tree height (H) is also proportional to some power of diameter, models containing D^2H are essentially equivalent to aD^b (Snowdon 1985), and the independent contribution of H can easily be tested by multiple regression methods (Schubert *et al.* 1988, Whitesell *et al.* 1988).

Allometric equations relating woody biomass and D usually have exponents between 2 and 3 (White 1981, Schubert *et al.* 1988, Whitesell *et al.* 1988) and generally do not differ much by site, provided that tree diameters fall within similar ranges among sites (Pastor *et al.* 1984). Mensuration procedures for multipurpose trees sometimes treat multi-stemmed trees as if they were single-stemmed trees having basal areas equal to the sum of the basal areas of the multiple stems (MacDicken & Brewbaker 1988, Stewart 1989, Briscoe 1990). However, if woody biomass exponents differ significantly from 2.0, these procedures are biased. We therefore tested the hypothesis that $b = 2.0$ to assess the significance and likely import of this bias.

Leaf area is typically correlated with cross-sectional area of sapwood (Shinozaki *et al.* 1964, Gholz *et al.* 1976, Snell & Brown 1978, Rogers & Hinckley 1979, Kaufmann & Troendle 1981, Waring *et al.* 1977, 1982, Marshall & Waring 1986). The "pipe model" theory (Shinozaki *et al.* 1964) explains this correlation as a homeostatic relation between transpiration rate and water movement through the sapwood. We therefore hypothesized that the exponent in the leaf area allometric would not differ from 2.0 because in young trees sapwood area is virtually equal to cross-sectional area, and thus proportional to D^2. Leaf area:sapwood ratios did not differ with stand density in some cases (Hungerford 1987, Thompson 1989), but we felt it important to test this relationship for tropical multipurpose trees. The allometry of leaf biomass has been found to vary with site or fertilisation even when wood biomass allometry did not change (Cromer & Williams 1982, Snowdon 1985, Adams & Lockaby 1988, Canadell *et al.* 1988).

To assess the generality of woody biomass and leaf area allometric equations we chose five well-known tropical multipurpose tree species spanning a range in leaf morphology and stem form. *Acacia auriculiformis* is phyllodinous and has a tendency for stems to fork. When branching occurs near the ground, the tree is considered to have multiple stems. *Acacia mangium* is also phyllodinous, but usually has a single straight trunk. *Leucaena diversifolia* has bipinnate foliage and has a straight stem. When this species is grown at low densities, it often produces multiple stems, all with the same straight growth form. *Eucalyptus camaldulensis* has a single straight stem and has simple entire leaves. *Gliricidia sepium* produces many straight stems and has pinnately compound leaves.

Our first objective was to generate usable leaf area and woody biomass equations for the five species and to test for the significance of height in the logarithmic regressions. Our second objective was to test whether equations differed among harvests at different ages and seasons. The third objective was to separate the seasonal effect from that of tree age, which we attempted only for *A. auriculiformis.* Our fourth objective was to test the hypothesis that allometric equations did not differ among planting densities and geometries. Finally, we tested whether the values of the exponents of the woody biomass and leaf area allometric equations differed from 2.0.

Methods

Study site

This study was conducted at the Hamakuapoko Experimental Site located at 99 *m* elevation on the island of Maui, Hawaii. The dry season from May through October receives only one third of the mean annual rainfall of 1200 *mm.* The soil was the Paia series, a silty clay classified as an Oxic Haplustoll, with surface (0-15 *cm*) soil pH of 5.2 (water), 2.4% organic C, and 0.18% total N.

Seedling establishment

Seedlings of *A. auriculiformis* (CSIRO seedlot 15648, from Papua New Guinea), *A. mangium* (CSIRO seedlot 15642, from Papua New Guinea), *L. diversifolia* (NFTA accession K-156, from Veracruz, Mexico), *G. sepium* (NFTA seedlot #14/84, from Cuyotenango, Guatamala), and *E. camaldulensis* (BioEnergy Development Corporation seedlot 182-6, from Northern Queensland) were grown for five months in the greenhouse before planting in the field. Seeds of the leguminous species were inoculated with specific rhizobia produced by the University of Hawaii's NifTAL (Nitrogen Fixation in Tropical Agricultural Legumes) Project.

Experimental design

In the first experiment, to compare allometric equations across species, age, or planting date, we used two planting dates and harvest ages ranging from 6 to 24 months (Table 1). The experiment was installed in a split plot design within each of two blocks, with species as the main plots and harvest ages of 6, 12, 18 and 24 months as sub-plots. Only three plots of *A. mangium* were planted due to high seedling mortality in the greenhouse. Sub-plot size was 9 × 9 *m*, with trees at a 2 × 1 *m* spacing. Nine trees in the center of each sub-plot were measured, with the remaining trees as border, but sometimes fewer than nine measurement trees per plot survived until the harvest date.

Table 1. Planting date and harvest ages for *Acacia auriculiformis, Acacia mangium, Eucalyptus camaldulensis, Gliricidia sepium* and *Leuceana diversifolia*

Species	Planting	Harvest age (months)			
A. auriculiformis	20 May	6	12	18	24
A. auriculiformis	20 December	6	12	18	-
A. mangium	20 May	-	12	18	24
E. camaldulensis	20 December	6	12	18	-
G. sepium	20 May	6	12	18	24
L. diversifolia	20 May	6	12	18	24

In the second experiment, to compare allometry across planting density and geometry *A. auriculiformis* and *L. diversifolia* were planted at 1× 1, 2 × 1, 2 × 2, and 4 × 0.5 *m* spacings in sub-plots of 9 × 9 *m*. The experiment was installed in a split plot design within each of two blocks, with species as main plots and spacing treatments as sub-plots. All sub-plots were harvested at the end of two years to test the hypothesis that allometry is independent of planting density or geometry.

Measurements and sampling

Basal diameter and height were measured for each stem; in the case of multiple-stemmed trees, each stem originating below 15 *cm* was treated as an individual observation. At harvest, each stem was separated into wood (>1 *cm* diameter) and a combined twig (<1 *cm* diameter) and leaf component, and weighed in the field. Sub-samples of the combined twig and leaf fraction were separated into twigs and leaves and the ratio used to estimate twig and leaf biomass per tree. Twig biomass was added to stem biomass for total woody biomass. Leaf area was measured with a LiCor 3100 leaf area meter on fresh leaves from the sub-sample. However, because *Leucaena* leaves tended to fold up rapidly, a second sub-sample of these was immediately pressed flat onto paper and stored inside plastic folders until area measurement. The leaf and twig sub-samples and three stem sections per tree were dried at 70°*C* for wet:dry conversion.

Statistical analysis

Although allometric equations describe the relation between diameter and biomass of individual trees, treatments such as age, season and spacing are applied at the level of sub-plots. Therefore, the traditional method for testing for differences among regression equations (testing homogeneity of slopes first, then coincidence of intercepts) would be misleading, because individual trees were not the "experimental unit". For each sub-plot a slope and intercept were calculated for the model $\ln(Y) = a' + b \ln(D)$, where Y is woody biomass (*kg*) or leaf area (m^2) and D is basal diameter (*cm*). Within each species we used a randomized block analysis of variance to test for age (first experiment) and spacing effects (second experiment) on slope and intercept, with blocks as the replication factor. To separate the effects of age versus season for *A. auriculiformis*, we used a "split-plot" analysis where planting date was the main effect and age was the subfactor. We did not test for differences between species.

For each species, a single summary allometric equation was created from all biomass harvests combined. To test for the effect of height, the model $\ln(Y) = a' + b \ln(D) + c \ln(H)$ and a t-test on c were used. For the simple allometric equation $Y = aD^b$, we used the model $\ln(Y) = a' + b \ln(D)$, and tested the null hypothesis that $b = 2.0$ using a t-test. Although a is nominally the antilog of a', a correction factor is needed to counteract bias from fitting the model to log-transformed data (Baskerville 1972, Sprugel 1983). The correction factor is $\exp(S_{y.x}^2/2)$, where $S_{y.x}$ is the standard error of estimate of the regression; therefore $a = \exp(a' + S_{y.x}^2/2)$.

Results

Allometry of woody biomass did not differ between harvests of different ages for any of the species, as shown by the pattern of field data(Figure 1) and the analysis of variance for slope and intercept for *A. auriculiformis, E. camaldulensis, G. sepium* and *L. diversifolia* ($P>0.05$). *A. mangium* could not be tested, due to lack of replicate plots, but appeared not to differ (Figure 1).

Allometry of leaf area did not differ between harvests of different ages for *A. auriculiformis* and *E. camaldulensis* ($P>0.05$, Figure 2), but the intercepts differed with age for *L. diversifolia* ($P = 0.009$) and *G. sepium* ($P = 0.038$). *L. diversifolia* was attacked episodically by the Leucaena psyllid (*Heteropsylla cubana*), reducing its leaf area, although the effect was relatively small (Figure 2). *G. sepium* had the highest intercept at six months and lowest at 18 months, apparently due to partial defoliation at 18 months (Figure 2). It is not clear what caused these differences, but similar patterns are observed elsewhere in Hawaii. *A. mangium* could not be tested, but appeared not to differ among harvest ages (Figure 2). The effect of planting time and the planting time by age interaction on wood biomass or leaf area allometry for *A. auriculiformis* were not significant ($P > 0.05$).

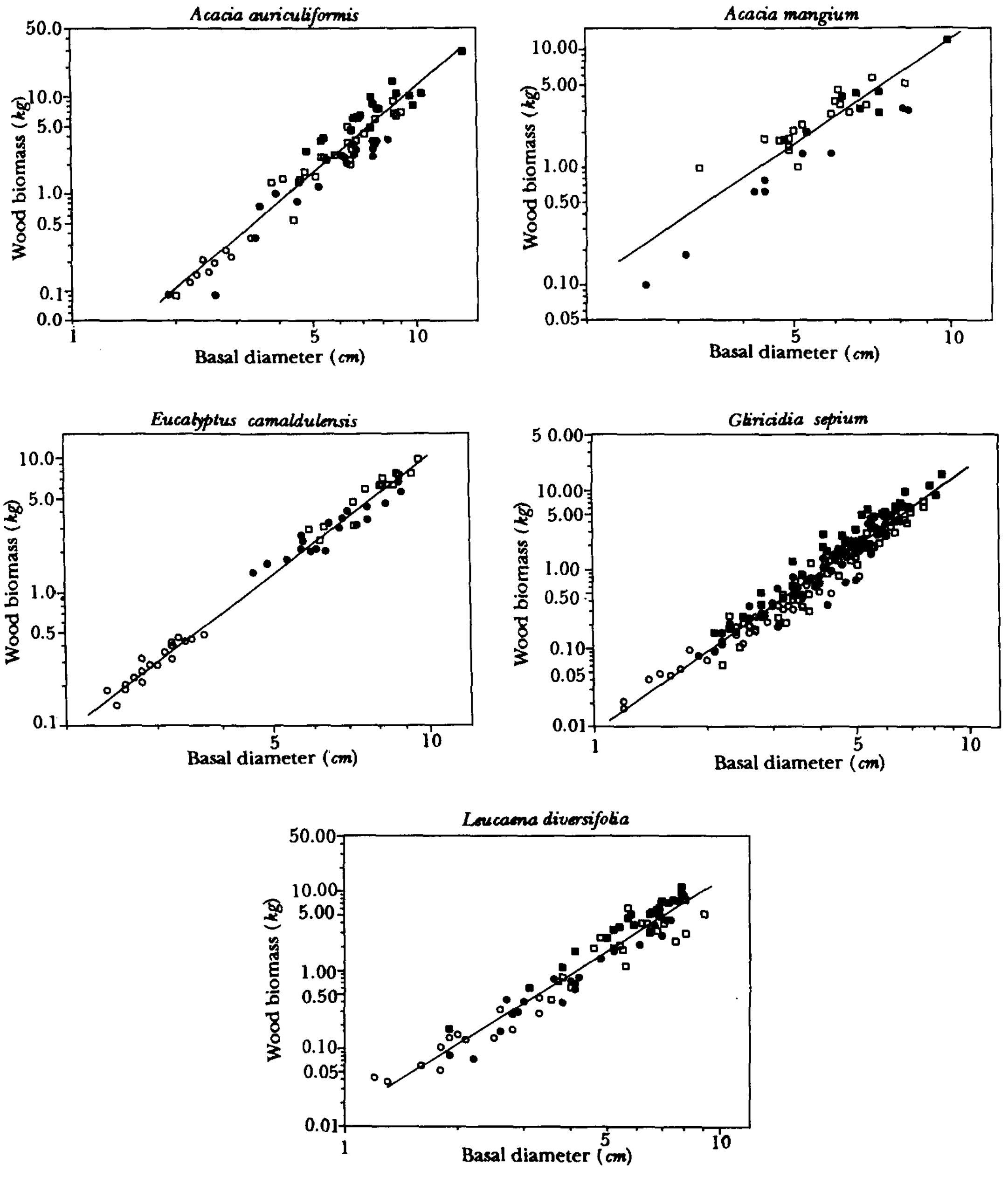

Figure 1. Relationship between tree woody biomass (WB, *kg*) and basal diameter (D, *cm*) for *Acacia auriculiformis, Acacia mangium, Eucalyptus camaldunlensis, Gliricidia sepium* and *Leucaena diversiolia* at 6 (○), 12 (●), 18 (☐) and 24 (■) months (solid lines are the allometric relationships WB = a D^b for each species based on all ages combined; coefficients and statistics are given in Table 3)

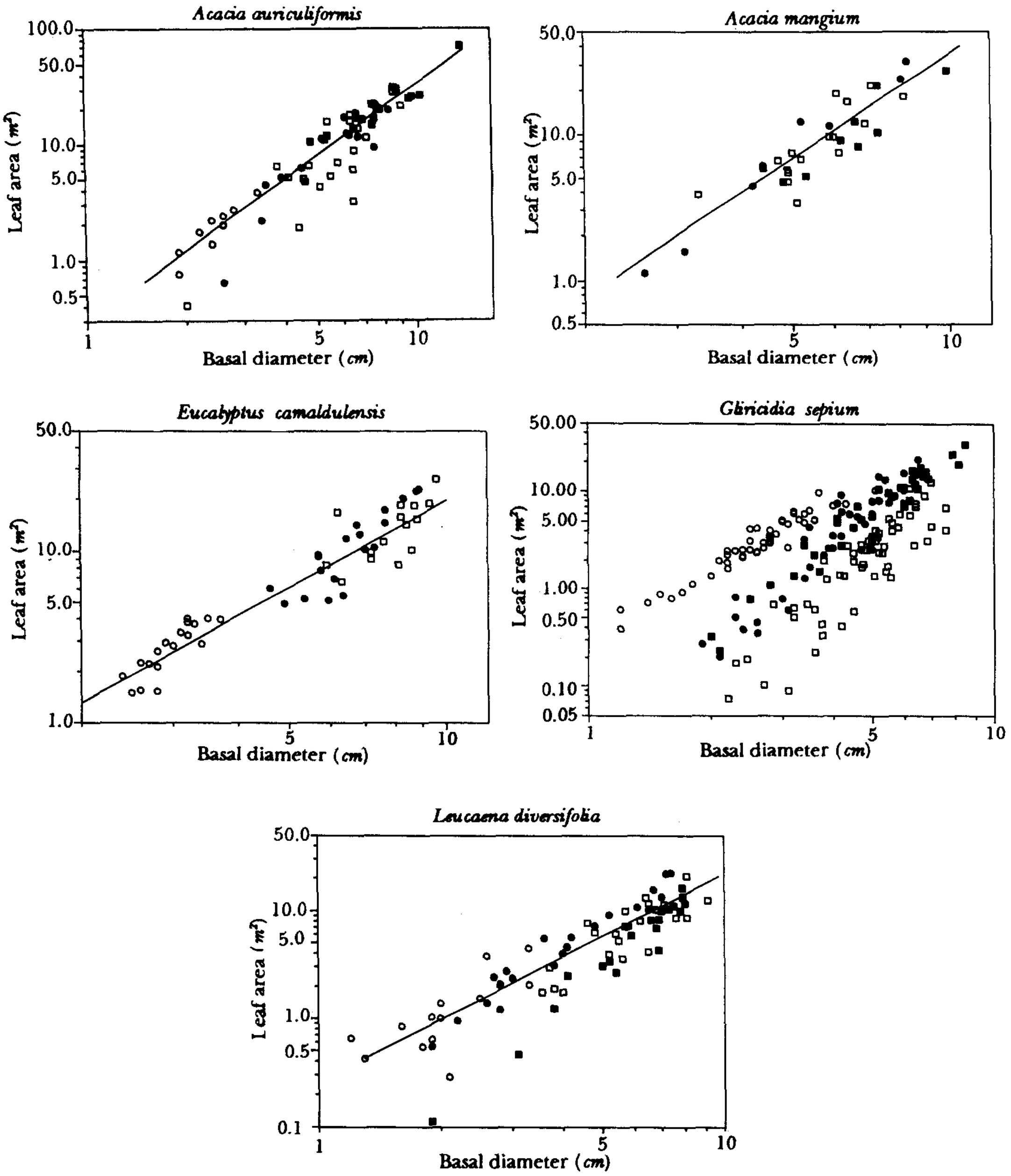

Figure 2. Relationship between tree leaf area (LA, m^2) and basal diameter (D, *cm*) for *Acacia auriculiformis*, *Acacia mangium*, *Eucalyptus camaldulensis*, *Gliricidia sepium* and *Leucaena diversifolia* at 6 (○), 12 (●), 18 (☐) and 24 (■) months (solid lines are the allometric relationships LA = a D^b for each species based on all ages combined; Coefficients and statistics are given in Table 3)

Allometry of woody biomass did not differ among different spacings harvested at 24 months for *A. auriculiformis* or *L. diversifolia* ($P > 0.05$, Figure 3). Allometry of leaf area did not differ among spacings for either species ($P > 0.05$, Figure 4).

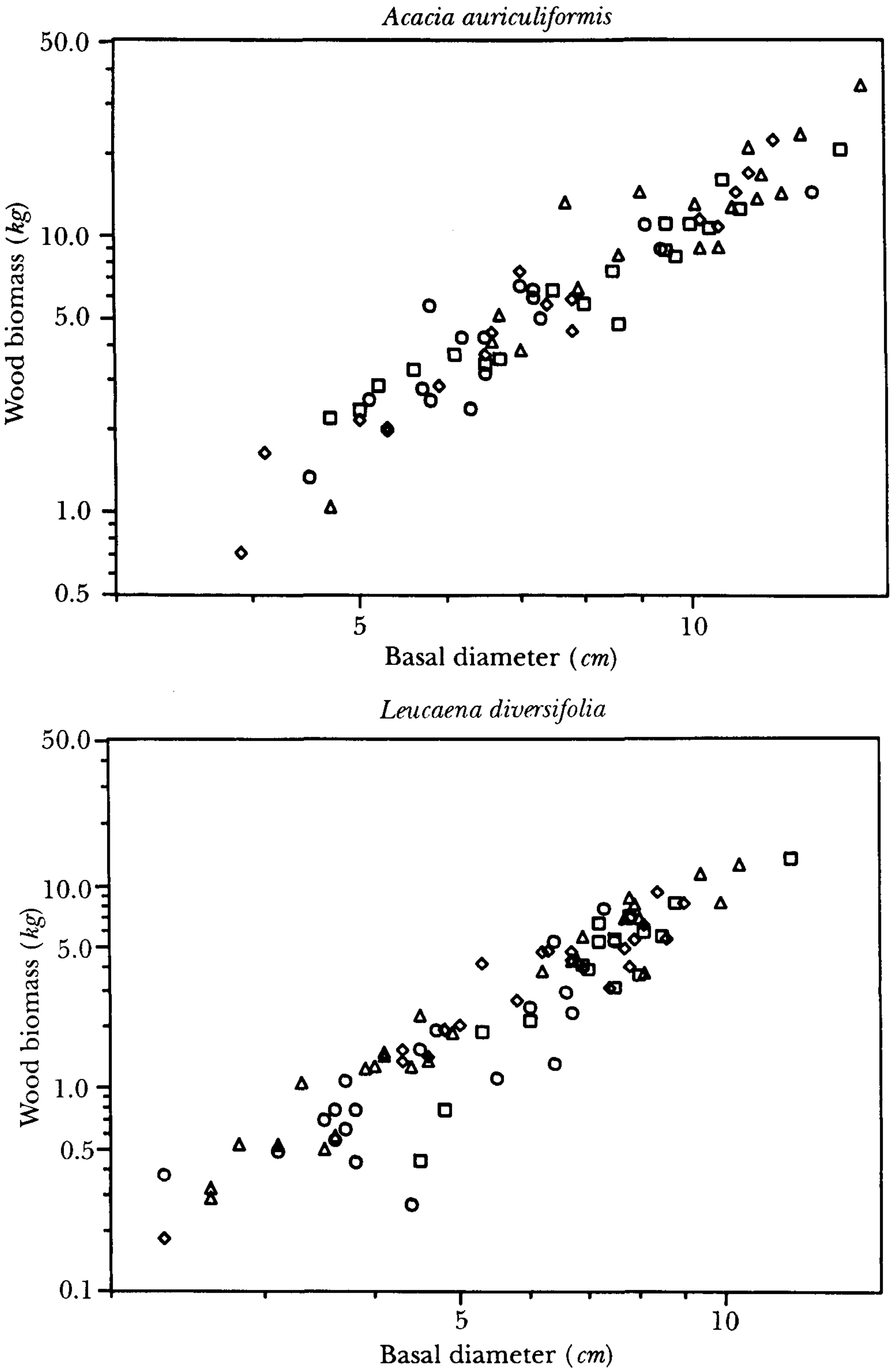

Figure 3. Relationship between tree woody biomass (WB, *kg*) and basal diameter (D, *cm*) for *Acacia auriculiformis* and *Leucaena diversifolia* at 1 × 1 (○), 2 × 1 (□), 2 × 2 (Δ) and 4 × 0.5 *m* (◇) spacings

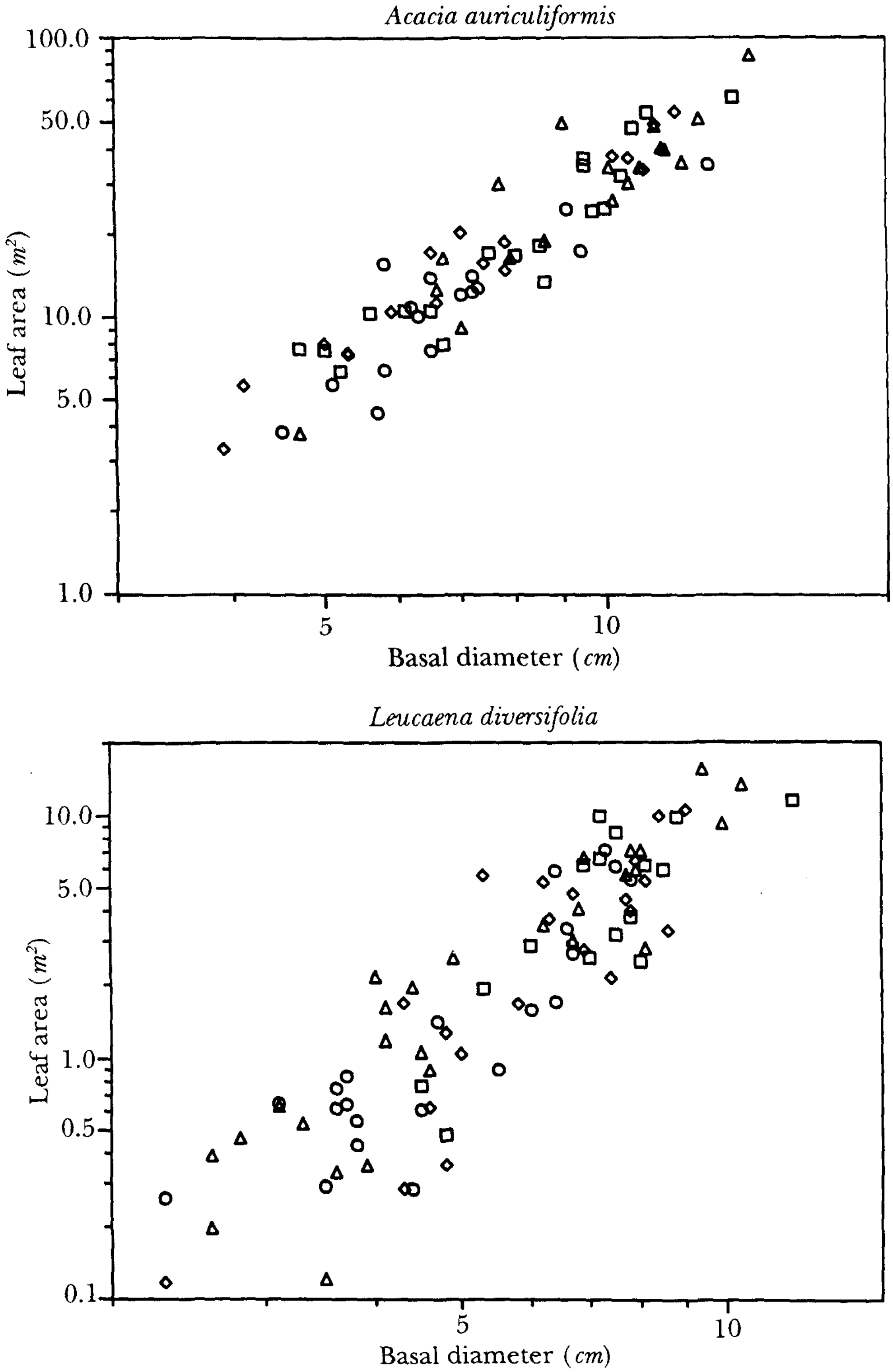

Figure 4. Relationship between tree leaf area (LA, m^2) and basal diameter (D, *cm*) for *Acacia auriculiformis* and *Leucaena diversifolia* at 1 x 1 (○), 2 x 1 (□), 2 x 2 (Δ) and 4 x 0.5 *m* (◇) spacings

Summary equations were generated from all harvests of the first experiment based on diameter alone (Table 2) and based on diameter and height where height contributed significantly to the regression (Table 3). The exponent of the leaf area-diameter equations was not significantly different from 2.0 in four of the five species, the exception being *E. camaldulensis*, thus supporting the pipe model theory for these young trees. Variation in leaf biomass was similar to variation in leaf area: approximate conversions may be done with the average specific leaf mass of 0.099 $kg\,m^{-2}$ for *A. auriculiformis*, 0.106 for *A. mangium*, 0.118 for *E. camaldulensis*, 0.054 for *G. sepium* and 0.066 for *L. diversifolia*. The exponents of the woody biomass-diameter equations were all significantly different from 2.0 and were close to 3.0 (Table 2). The woody biomass equations using height tended to have exponents of D close to 2 and exponents of H close to 1, suggesting a similarity to the frequently used transformation D^2H. The improvement in prediction from the inclusion of height can be judged by the increase in r^2 in the second model. In general, the improvements were only a few percent, ranging from less than 1% for *E. camaldulensis* woody biomass to 13% for *A. mangium* woody biomass.

Table 2. Summary of regression coefficients and statistics for allometric models of leaf area (m^2) and woody biomass (*kg*) versus basal diameter (D, *cm*) (n = number of trees, a' = intercept of log-log regression, b = slope, $S_{y.x}$ = standard error of estimate, r^2 = coefficient of determination, a = corrected coefficient of allometric equation $Y = a\,D^b$)

Component and species	n	Min D	Max D	a'	b	$S_{y.x}$	r^2	a
Leaf area								
Acacia auriculiformis	82	1.9	13.7	-1.324	2.064	0.371	0.895	0.285
Acacia mangium	34	2.6	9.9	-1.971	2.384	0.314	0.831	0.146
Eucalyptus camaldulensis	51	2.4	9.6	-0.911	1.688*	0.298	0.869	0.421
Gliricidia sepium	209	1.2	8.5	-1.739	2.044	0.934	0.435	0.272
Leucaeana diversifolia	87	1.2	9.1	-1.487	1.934	0.487	0.830	0.255
Woody biomass								
Acacia auriculiformis	82	1.9	13.7	-4.362	2.972*	0.362	0.949	0.0136
Acacia mangium	34	2.6	9.9	-4.397	2.953*	0.419	0.809	0.0136
Eucalyptus camaldulensis	51	2.4	9.6	-4.358	2.900*	0.163	0.985	0.0130
Gliricidia sepium	209	1.2	8.5	-4.740	3.347*	0.354	0.935	0.0093
Leucaena diversifolia	87	1.2	9.1	-4.260	2.989*	0.392	0.947	0.0152

* Exponent of equations differed significantly from 2.0 ($P < 0.001$ in all cases)

Table 3. Summary of regression coefficients and statistics for allometric equations where height was significant (Footnote shows significance of height term; c = slope of height term; a = corrected coefficient of allometric equation $Y = a D^b H^c$; all other symbols as in Table 2)

Species	a'	b	c	$S_{y.x}$	r^2	a
Leaf area						
Eucalyptus camaldulensis	- 1.100	2.388	-0.659*	0.287	0.881	0.347
Gliricidia sepium	- 1.813	3.754	-1.742***	0.850	0.534	0.234
Leucaena diversifolia	- 1.488	2.503	-0.599**	0.468	0.845	0.252
Woody biomass						
Acacia auriculiformis	- 4.259	2.152	0.991***	0.256	0.975	0.0146
Acacia mangium	- 4.606	2.138	1.089***	0.242	0.938	0.0103
Eucalyptus camaldulensis	- 4.100	1.949	0.896***	0.110	0.993	0.0167
Gliricidia sepium	- 4.706	2.563	0.798***	0.306	0.952	0.00948
Leucaena diversifolia	- 4.259	1.979	1.063***	0.298	0.970	0.0148

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Discussion

Allometry of woody biomass was independent of age, season, or spacing, suggesting that these equations may be applied to trees grown under other treatments or conditions. However, these equations should be applied cautiously to trees larger than those sampled here, because extrapolation of curves beyond the region of fit is subject to error. The allometry of leaf area was not affected by age in three of the five species, or by the different spacings for the two species tested, *A. auriculiformis* and *L. diversifolia.* Our findings agree with the results of Hungerford (1987) and Thompson (1989) who found that for stand densities greater than 3000 trees per hectare, leaf area: sapwood area ratio was not affected by plant density. However, our results contrast with those of others who found differing leaf biomass allometry among sites (Adams & Lockaby 1988, Canadell *et al.* 1988) or nutrient regimes (Cromer & Williams 1982, Snowdon 1985). Our unpublished results from another experiment also suggest leaf area allometry could be strongly affected by fertilization. Taken together, these findings suggest the hypothesis that trees vary leaf area allometry in response to differences in nutrient status but not to differences in spacing or light environment.

For those species which did differ in leaf area allometry over time, *L. diversifolia* and *G. sepium,* the situation is more complex. Although *L. diversifolia* differed significantly, the summary equation could probably be applied with error falling within the scatter of the data from the other harvests. It is not known whether the attacks by the psyllid affect growth primarily by reduction in leaf area or whether there are additional effects (*e.g.* loss of carbon and nutrients, or killing of apical meristems). For *G. sepium,* the reduction in leaf area at 18 months was quite marked and the summary leaf area equations should be used with extreme caution.

The actual cause of the defoliation is not known, but could be associated with lower winter temperatures and light (Whiteman *et al.* 1986) or the cumulative effective of the preceding dry summer. The fact that older (18 month) trees were more severely affected than younger trees (6 month) also agrees with our observations elsewhere, and suggests that defoliation may be triggered by the onset of flowering in mature trees.

The fact that the exponents of the woody biomass-diameter equations were significantly different from 2 and closer to 3 has important ramifications for measuring tree growth. Average diameter of a stand of trees is not a good estimate of average tree biomass, and average diameter cannot be inserted into allometric equations to estimate stand biomass. For multiple-stemmed trees, calculation of a single diameter as the square root of the sum of the squared individual stem diameters (*e.g.* MacDicken & Brewbaker 1988, Stewart 1989, Briscoe 1990) would lead to errors in biomass estimates. For example, two stems of *L. diversifolia*, each with a diameter of 5 *cm*, would have the same basal area as a single stem of $\sqrt{50}$ = 7.07 *cm.* Together they would weigh 3.73, *versus* 5.26 *kg* calculated from 7.07 *cm* diameter, a 41% overestimate. This finding also suggests that in sampling trees to create biomass equations, one should not pool multi-stem diameters based on basal area.

The finding that the exponents of the leaf area-diameter equations were all near 2 may be due to the relation between leaf area and cross-sectional area of sapwood as suggested by the pipe model theory (Shinozaki *et al.* 1964). It is not known why the exponent of *E. camaldulensis* was significantly lower than 2, but it may have reflected early heartwood formation.

The improvements to the regressions from including height in addition to diameter were relatively modest, although height may be more important where the H *versus* D relationship (growth form) differs among sites (Whitesell *et al.* 1988). Although tree height may be of interest itself (*e.g.* in assessing competition for light), its use solely to improve biomass predictions should be questioned on practical grounds.

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