BIOTROPICA 25(1): 15–27 1993

# Biomass and Nutrient Content of the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico, before and after Hurricane Hugo, 1989[1]

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## ABSTRACT

The biomass and nutrient content of two steepland watersheds were estimated using allometric equations and nutrient concentrations derived from a subsample of the vegetation. Prior to the passage of Hurricane Hugo in September 1989, the watersheds had a total vegetative biomass of 301 tons/ha, 75 percent of which was aboveground. The total nutrient content of this vegetation was 907, 49, 644, 653, and 192 kg/ha for N, P, K, Ca, and Mg, respectively and varied with topographic setting. Concentrations per unit dry weight of P (0.16), K (2.49), Ca (2.13), and Mg (0.62) in aboveground vegetation were similar to other steepland tropical forests, while the concentration of N (2.9) was greater. Following the passage of Hurricane Hugo, the standing aboveground biomass was reduced to 113 t/ha and the aboveground nutrient content of the forest was reduced 45 to 48 percent.

## RESUMEN

El contenido de biomasa y nutrientes de dos cuencas en zonas enpinadas, fueron estimadas usando ecuaciones allometricas y concentraciones de nutrientes de tejido vegetal. Con anteriodidad al Huracan Hugo en septiembre de 1989, las cuencas teían una biomasa vegetal de 301 tons/ha (75 por ciento aerea y 25 por ciento en raices). El contenido total de nutrientes de la vegetacion variaba de acuerdo a la posicion topografica y tuvo en promedio de 907, 49, 644, 653, y 192 kg/ha para N, P, K, Ca, y Mg, respectivamente. Concentraciones por unidad de peso seco de P (0.16), K (2.49), Ca (2.13), y Mg (0.62) en la vegetacion (excluyendo raices) fueron similares a otros bosques tropicales en zonas enpinadas, mientras que la concentracion de N (2.9) fue mayor. Despues del Huracan Hugo, la biomasa aerea se redujo a 113 t/ha y el contenido de nutrientes del bosque sobre el suelo se redujo en 45–48 por ciento.

*Key words:* *allometry; biomass; humid tropical steeplands; hurricanes; Luquillo Experimental Forest; nutrients.*

THIS PAPER DOCUMENTS THE BIOMASS AND NUTRIENT content of the tabonuco-type forest in the Bisley sector of the Luquillo Experimental Forest (LEF) immediately prior to and after the passing of Hurricane Hugo in September 1989. Allometric equations, above- and belowground biomass, and nutrient content are presented and compared. The objectives of this paper are to provide basic information needed for ecological studies at the site and to compare the site with similar tropical forests.

The Bisley watersheds 1 and 2 drain 13 ha of subtropical wet forest life zone (Ewel & Whitmore 1973) and receive 3000 to 4000 mm of precipitation each year (Scatena 1989). Elevations within the watersheds range between 260 to 400 m above sea level. The landscape is steep, highly dissected and covered with mature, secondary tabonuco-type

[1] Received 26 December 1991, revision accepted 23 June 1992.

forest. *Dacryodes excelsa* Vahl, commonly called tabonuco, *Sloanea berteriana* Choisy, and *Prestoea montana* (R. Graham) Nichols are the most important species at the site. Summaries of the ecology and history of the site and the surrounding forest are available elsewhere (Odum & Pigeon 1970, Brown *et al.* 1983, Scatena 1989).

## METHODS

Biomass subsampling.—During June 22–29, 1989, two 32 × 32 m plots were clearcut and subsampled for biomass. Before the harvest, all stems greater than 2.5 cm in diameter at 1.3 m (DBH) were identified, tagged, and mapped. A subset of 14 large trees was sampled for detailed allometry. These trees were selected to expand the existing set of allometric data from the tabonuco forest of the LEF (Ovington & Olson 1970) and obtain reliable biomass estimates for the two plots.

The allometry of the selected trees was determined by measuring stem diameter and bark thickness at 1 m intervals on the bole and the diameter of every major branch. For large trees with branches that could not be completely weighed, several branches were removed and separated into leaf and wood compartments. Regression equations using branch diameter and length were then developed and used to estimate the total leaf and branch biomass of the tree. Complete slices from each meter of bole and random subsamples of branches and leaves were kept for chemical analysis. All samples were weighed in the field and in the lab after they were oven dried at 60°C.

To determine the biomass and chemistry of herbaceous and woody vegetation with a DBH less than 2.5 cm, all vegetation was removed from 4 × 4 m subplots and sorted into sapling, herb, and fern compartments. The basal diameters of all "understory" palms, or mature palms without sufficient height to measure a DBH at 1.3 m, were measured in the plots and used to calculate the biomass of that compartment. The belowground biomass of fine roots (less than 5 mm diameter) was estimated from samples of roots sorted from 4.1 cm diameter, 35 cm deep root cores (Silver 1992). Coarse root biomass was estimated using the above- to belowground biomass ratios measured by Ovington and Olson (1970).

Allometric equations.—The allometry of the sampled Bisley vegetation was combined with existing data from the tabonuco forest of the LEF to develop general and species-specific biomass equations. When the 14 trees sampled in 1989 were combined with existing data (Ovington & Olson 1970), we had allometry for 101 stems from 37 species of the tabonuco forest (Fig. 1). Since a variety of stand-level data exists for these forests, biomass equations were developed for stems greater than 2.5 cm using combinations of DBH, height, and specific gravity as independent variables (Fig. 2, Appendix 1). Several linear and nonlinear models were tested; however, as other researchers have noted (Crow 1978, Brown *et al.* 1989), log-log models corrected for bias (Benjamin & Cornell 1970, Beauchamp & Olson 1973) were the most robust.

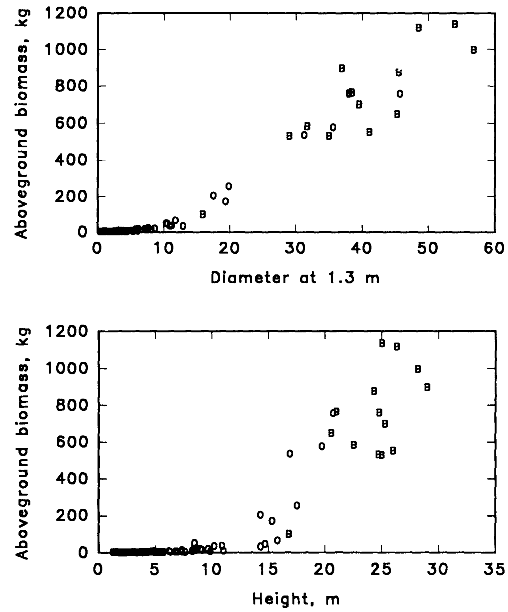


FIGURE 1. Total aboveground biomass (kg oven-dried weight) versus stem diameter (cm at 1.3 m), and tree height (m), for trees in the tabonuco forest of the Luquillo Experimental Forest, Puerto Rico.

Nutrient analysis.—Samples of bole wood with and without bark, branch wood with bark, leaves, and fruits of 18 species, plus composite samples of ferns, herbs, and seedlings, were analyzed for nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) (Fig. 3, Appendix 2). All samples were sorted, oven-dried, and ground in a wiley mill through a 0.85 mm (20-mesh) stainless steel sieve. Entire slices of tree trunks and leaves from several branches were ground to avoid bias due to variations in heartwood or leaf concentrations.

The ground samples were then digested with

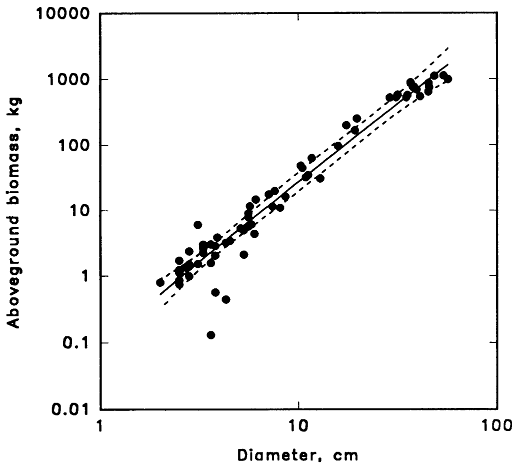


FIGURE 2. Total aboveground biomass (kg oven-dried weight) versus stem diameter (cm at 1.3 m) and total biomass equation [To = exp(2.475 ln(DBH) − 2.399)] and 99 percent confidence interval around equation.

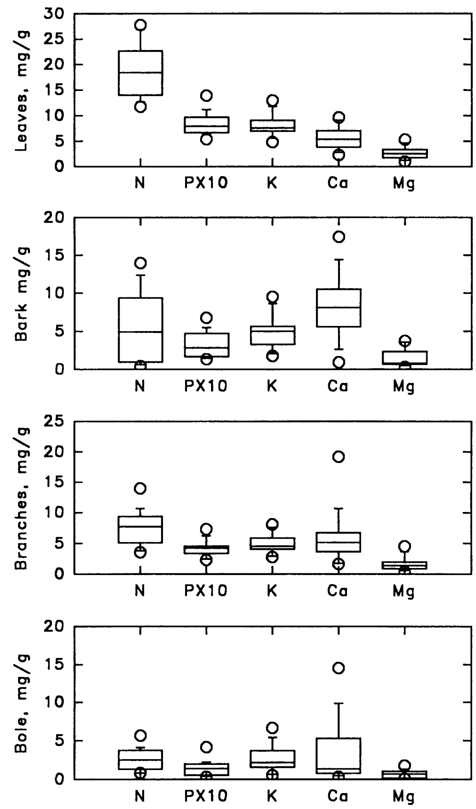


FIGURE 3. Box plots of average nutrient concentration by compartment for 19 selected species in the tabonuco forest of the Bisley watersheds, Puerto Rico. The box encompasses the 25th through 75th percentiles and has horizontal lines for the 10th, 50th, and 90th percentiles. Solid circles are data outside 10th and 90th percentiles. Phosphorous values are multiplied by 10.

$H_2O_2$ and concentrated $HNO_3$ (Luh Huang & Schulte 1985) and analyzed with a plasma emission spectrometer (Beckman Spectra Span V) at the Institute of Tropical Forestry (ITF). Nitrogen concentrations were determined using the semi-micro Kjeldahl method and $H_2SO_4$ digestion (Chapman & Pratt 1979). The nutrient concentrations of fine roots were determined at Yale University using a $H_2SO_3$ digest on roots less than 2 mm in diameter from 0 to 10 cm depth. In addition to running internal lab standards, samples of bole wood from 12 species were dried, ground, and analyzed at ITF, and digested and analyzed at Yale University for Ca, P and Mg using an ICP (Inductively Coupled Plasma spectrophotometer, Thermal-Jarrel Ash Atom Scan 25). No significant difference (0.01 level *t*-test) was found between the nutrient analysis performed on the same wood samples at the two laboratories.

WATERSHED-LEVEL BIOMASS AND NUTRIENT CALCULATIONS.—The biomass of the 13 ha area of Bisley watersheds 1 and 2 was estimated by applying the allometric equations and nutrient concentrations to stand data from 82 permanent plots within the watersheds (Table 1). These 10 m diameter permanent plots are located at the nodes of a 40 × 40 m grid that covers both watersheds and includes all stems equal to or greater than 2.5 cm DBH. Since the composition and structure of this forest is known to vary with topography, each plot was classified according to its topographic setting. Ridges were defined as local divides that receive no upland runoff, slopes as areas that receive and transmit upland runoff, and valleys as areas that concentrate runoff. Upland valleys include ephemeral channels, hollows, and chutes. Riparian valleys include valley areas within 20 m of perennial channels.

HURRICANE HUGO DAMAGE ASSESSMENT.—On September 17, 1989, 6 weeks after the biomass harvest, Hurricane Hugo passed over the site and caused extensive damage to the study area (Scatena & Larsen 1991). Estimates of posthurricane biomass were made by measuring the diameter and length of all downed wood greater than 2.5 cm in diameter in 59 transects (40 × 1 m) established between the permanent plots within the watersheds. The 2204 pieces of wood that occurred within the transects were classified into either branch or bole compart-

TABLE 1. *Biomass and nutrient content of vegetation in Bisley watersheds 1 and 2, Luquillo Experimental Forest, Puerto Rico in June 1989. The stand-level errors are the standard errors of the estimates of the 82 plots within the watersheds.*

| Vegetation unit | Biomass (t/ha) | Nutrients (kg/ha) | | | | |
|---|---|---|---|---|---|---|
| | | N | P | K | Ca | Mg |
| Stems (>2.5 cm DBH) | | | | | | |
| Leaves | 7.0 | 108.2 | 5.2 | 51.8 | 31.0 | 14.2 |
| Branches | 28.1 | 127.2 | 7.5 | 102.9 | 131.8 | 23.9 |
| Bole | 182.1 | 353.8 | 19.7 | 339.2 | 269.5 | 83.5 |
| Bark | 4.1 | 24.8 | 1.0 | 19.4 | 31.8 | 3.9 |
| Coarse root (>0.5 cm) | 72.4 | 202.7 | 10.9 | 79.6 | 155.7 | 50.7 |
| Fine root (<0.5 cm) | 2.2 | 34.6 | 1.2 | 2.4 | 17.0 | 2.2 |
| Understory palms | 3.6 | 44.6 | 2.7 | 40.8 | 11.3 | 11.2 |
| Saplings (<2.5 cm DBH) | 0.27 | 4.4 | 0.3 | 2.8 | 1.7 | 0.7 |
| Herbs | 0.31 | 4.6 | 0.3 | 3.9 | 2.4 | 1.2 |
| Ferns | 0.13 | 2.2 | 0.1 | 1.1 | 0.6 | 0.7 |
| Total | 300.9 | 907.0 | 48.9 | 643.9 | 652.8 | 192.2 |
| Stand-level standard error | 34.6 | 103.4 | 5.5 | 70.2 | 65.9 | 20.9 |

ments, and the total volume and mass of coarse woody debris per ha was calculated. The defoliation of leaves and fine wood biomass was determined from litter baskets within the Bisley forest (Lodge *et al.* 1991).

## RESULTS

ALLOMETRIC EQUATIONS.—Either the slope or the intercept of the biomass equation for the species reported in Appendix 1 was significantly different from the slope or intercept of the equations for other species (Fig. 4). The largest differences in slope and intercept occur for fast growing, low-wood-density species (*Cecropia peltata* L. and *Didymopanax morototoni* (Aubl.) Decne. & Planch.), shrubs (*Palicourea riparia* Benth.) and medium sized, high-wood-density trees (*Casearia arborea* (L. C. Rich.) Urban and *S. berteriana*).

The general biomass equation developed for the Bisley watershed (Fig. 5) is similar to a general equation developed for wet tropical forests (Brown *et al.* 1989) and an equation developed for the tabonuco forest of the LEF (Weaver & Gillespie 1992). All of these equations are similar for stems with diameters less than 60 cm and indicate that trees in wet forest life zones have less biomass than trees with identical girth in moist forest life zones.

PREHURRICANE BIOMASS AND NUTRIENT CONTENT.—Concentrations of nutrients generally decreased from leaves, to bark, to branch wood, to bole wood (Fig. 3). Nutrient concentrations in bark had the greatest between-species variations, while concentrations in bole wood had the least variation. The concentration of Ca had the greatest variation between compartments within the same species and between the same compartment of different species. The concentrations of both P and Mg were relatively constant between and within species.

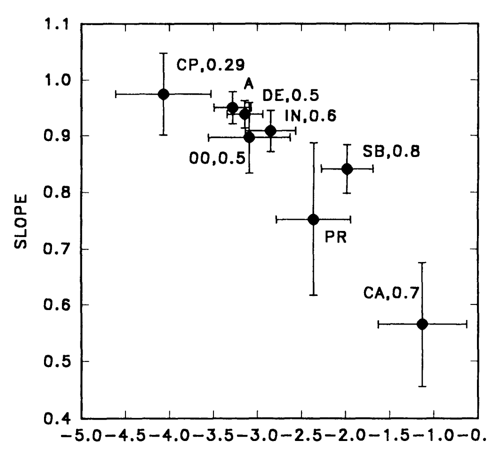


FIGURE 4. Slope (plus and minus 1 standard error) versus intercept (plus and minus 1 standard error) of total biomass equations for trees in the tabonuco forest of the Luquillo Experimental Forest, Puerto Rico. Letter and number adjacent to point indicates the species of the equation and its specific gravity where available: CP = *Cecropia peltata* and *Didymopanax morototoni*; A = all stems greater or equal to 2.5 cm; DE = *Dacryodes excelsa* and *Tetragastris balsamifera* (Sw.) Kuntze; IN = *Inga vera* and *I. laurina* (Sw.) Willd.; OO = *Ocotea* sp.; SB = *Sloanea berteriana*; PR = *Palicourea riparia*; CA = *Casearia* sp. All equations use $D^2H$ as an independent variable.

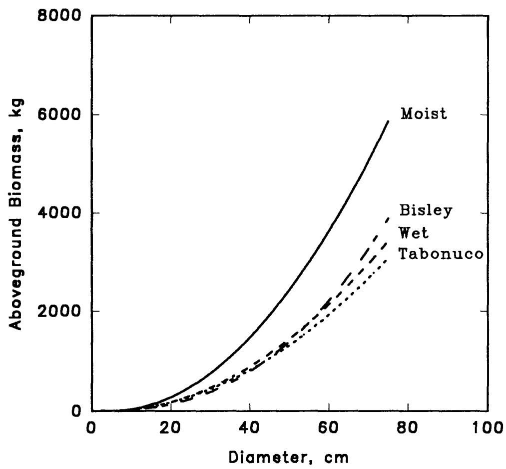


FIGURE 5. Estimated total aboveground biomass (kg oven-dried weight) of individual trees versus stem diameter at 1.3 m. Equations for moist and wet tropical forests are from Brown *et al.* 1989. Equation for tabonuco forest is from Weaver and Gillespie 1992. All equations use diameter as the only independent variable.

In the prehurricane Bisley watersheds, five species, *D. excelsa, Guarea guidonia* (L.) Sleumer, *S. berteriana, Buchenavia capitata* (Vahl) Eichl., and *P. montana,* accounted for 87 percent of the aboveground biomass and between 61 and 68 percent of the aboveground nutrient pool (Table 2). Tabonuco, the leading dominant in the forest, contained between 21 and 33 percent of the aboveground macronutrients. Understory vegetation comprised 1.4 percent of the biomass but between 2 and 8 percent of the total nutrients.

Aboveground biomass and nutrient content varied by topographic setting within the watersheds (Table 3). However, the aboveground nutrient content per unit weight of biomass for P, K, Ca and Mg in the prehurricane forest were not significantly different (0.01 level *t*-test) from the mean of the values reported from other moist steepland tropical forests (Table 4). Only the concentration of total N in the Bisley forest was significantly greater ($P < 0.01$ *t*-test) than the mean of the values reported for other forests. There were no significant differences between studies in the average nutrient concentrations of leaves from woody vegetation (Table 5).

Post-hurricane Hugo biomass and nutrient content.—Following Hurricane Hugo, the total standing aboveground biomass was reduced to 50 percent of the prehurricane value, while nutrient content decreased 45 to 48 percent (Table 6). The majority of the decrease in biomass was due to the snapping or uprooting of large trees. Branches accounted for 14 percent of the total woody biomass transferred by the hurricane. Woody debris with diameters greater than 24 cm accounted for 50 percent of the fallen biomass but only 6 percent of the fallen stems.

## DISCUSSION

Allometry and biomass.—The allometry of individual trees in the Bisley watersheds is similar for many canopy dominants and not significantly different from other wet tropical life zone forests. The similarity between general biomass equations developed for the LEF indicates that the general equations developed for tropical life zones (Brown *et al.* 1989) are applicable for most practical purposes.

TABLE 2. *Aboveground biomass and nutrient concentrations per unit dry weight of common species in Bisley watersheds 1 and 2 of the Luquillo Experimental Forest, Puerto Rico in June 1989.*

| Species | Biomass (t/ha) | Nutrients (mg/g) N | P | K | Ca | Mg |
|---|---|---|---|---|---|---|
| *Dacryodes excelsa* | 103.1 | 1.76 | 0.10 | 1.65 | 1.13 | 0.20 |
| *Sloanea berteriana* | 25.2 | 2.45 | 0.12 | 2.40 | 2.76 | 0.49 |
| *Guarea guidonia* | 24.0 | 2.93 | 0.23 | 1.99 | 1.88 | 0.88 |
| *Buchenavia capitata* | 10.4 | 3.13 | 0.14 | 2.44 | 2.63 | 0.60 |
| *Prestoea montana* | 6.8 | 6.78 | 0.37 | 5.68 | 3.37 | 1.50 |
| *Alchorneopsis portoricensis* | 6.2 | 3.53 | 0.18 | 2.48 | 1.19 | 1.05 |
| *Inga* spp. | 6.1 | 3.62 | 0.10 | 2.90 | 1.79 | 0.23 |
| *Didymopanax morototoni* | 3.9 | 1.05 | 0.05 | 0.85 | 1.54 | 0.82 |
| *Cecropia peltata* | 3.2 | 1.47 | 0.09 | 2.31 | 1.16 | 1.50 |
| Others and understory | 36.7 | 6.11 | 0.32 | 4.80 | 4.66 | 1.44 |
| Total aboveground | 225.6 | 2.97 | 0.16 | 2.49 | 2.13 | 0.62 |

TABLE 3. *Aboveground biomass, standard error (in parentheses), and nutrient content of stems equal to or greater than 2.5 cm diameter at 1.3 m, by topographic setting in the Bisley watersheds 1 and 2, Luquillo Experimental Forest, Puerto Rico.*

| Topographic setting | Drainage area (ha) | Stem density (stems/ha) | Basal area ($m^2$/ha) | Biomass (t/ha) | Nutrients (mg/g) | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | N | P | K | Ca | Mg |
| Total area | 13.0 | 1480 (78) | 36.7 (3.5) | 221 (26) | 2.77 | 0.15 | 2.32 | 2.10 | 0.57 |
| Ridges | 2.2 | 1772 (133) | 54.2 (7.9) | 312 (57) | 2.58 | 0.14 | 2.25 | 2.10 | 0.49 |
| Slopes | 8.5 | 1547 (155) | 33.4 (4.6) | 186 (31) | 2.82 | 0.15 | 2.40 | 2.14 | 0.54 |
| Upland valleys | 1.4 | 1157 (123) | 21.3 (4.0) | 121 (33) | 3.23 | 0.17 | 2.44 | 2.01 | 0.80 |
| Riparian valleys | 0.9 | 778 (177) | 20.9 (9.5) | 119 (63) | 3.11 | 0.19 | 2.20 | 2.07 | 0.79 |

If new equations are developed, they should concentrate on individuals with diameters greater than 60 cm. This size class is poorly represented in all biomass equations but typically accounts for the majority of aboveground biomass.

While the allometry of canopy dominants is similar within and between forests of the same life zone, differences do occur in the allometry of low density species, shrubs, and high density species. These differences are not easily related to the common architectural models assigned to the species (Hallé *et al.* 1978) but appear to be related to wood density and possibly canopy position (Fig. 4).

The estimated biomass of the Bisley forest is comparable to other estimates from the LEF. In 1964, the forest at El Verde, which is also in the LEF, had an estimated above- and belowground biomass of 265 tons/ha (Ovington & Olson 1970). An estimate of above- and belowground biomass made in 1959 for a well-stocked stand located 0.2 km due east of the Bisley watersheds was 358 t/ha (Odum *et al.* 1970). Given that the net woody biomass accumulation of this forest type is usually assumed to be 2.5 t/ha/yr (Weaver & Murphy 1990), in 1989 these stands would have had an expected total biomass of 327 and 433 t/ha, respectively. The mean of these estimates (380 t/ha) is within the range of the estimated total biomass of the entire Bisley watersheds (301 t/ha) and Bisley ridge sites (391 t/ha) in 1989. However, these previous estimates, like those for most other steepland forests (Tables 4 and 5) were based on well-stocked upland areas and do not consider variations in biomass across the landscape (Table 3). This variation can be considerable in these highly dissected terrains and should be considered in ecosystem-level estimates.

NUTRIENT CHEMISTRY.—While there is a general convergence in the allometry of dominants within the forest, there are considerable differences in the nutrient concentrations of tissue between species in

TABLE 4. *Aboveground biomass and average nutrient concentrations per unit dry weight in several tropical steepland forests.*

| Location | Reference | Biomass (t/ha) | Nutrients (mg/g) | | | | |
|---|---|---|---|---|---|---|---|
| | | | N | P | K | Ca | Mg |
| Bisley PR | This study | 226 | 2.9 | 0.16 | 2.49 | 2.13 | 0.62 |
| El Verde PR | Ovington and Olson 1970 | 365 | 2.22 | 0.12 | 1.42 | 2.45 | 0.93 |
| New Guinea | Grubb and Edwards 1982 | 310 | 2.20 | 0.12 | 2.14 | 4.13 | 0.60 |
| Venezuela | Grimm and Fassbender 1981 | 348 | 2.52 | 0.15 | 3.80 | 2.14 | 0.62 |
| Jamaica-Mul | Tanner 1985 | 337 | 2.5 | 0.12 | 2.5 | 2.8 | 0.57 |
| Jamaica-Mor | Tanner 1985 | 209 | 2.0 | 0.14 | 1.3 | 1.7 | 0.7 |
| Hawaii | Mueller-Dombois *et al.* 1984 | 176 | 2.09 | 0.16 | 2.16 | 4.30 | 0.41 |
| Average | | 282 | 2.35 | 0.14 | 2.26 | 2.81 | 0.64 |
| Coefficient of variation | | 27 | 13 | 13 | 37 | 36 | 25 |

TABLE 5. *Total leaf biomass and nutrient concentrations per unit dry weight of tree leaves in several tropical steepland forests.*

| Location | Reference | Biomass (t/ha) | Nutrients (mg/g) N | P | K | Ca | Mg |
|---|---|---|---|---|---|---|---|
| Bisley PR | This study | 7.0 | 15.5 | 0.74 | 7.4 | 4.43 | 2.03 |
| El Verde PR | Ovington and Olson 1970 | 10.2 | 11.6 | 0.69 | 6.1 | 5.49 | 1.96 |
| New Guinea | Grubb and Edwards 1982 | 7.2 | 12.0 | 0.77 | 6.0 | 11.01 | 2.42 |
| Venezuela | Grimm and Fassbender 1981 | 4.6 | 16.4 | 1.1 | 13.7 | 4.96 | 2.65 |
| Jamaica-Mul | Tanner 1985 | 6.4 | 14.5 | 0.65 | 9.3 | 9.1 | 3.7 |
| Jamaica-Mor | Tanner 1985 | 7.6 | 9.7 | 0.49 | 4.2 | 5.9 | 2.7 |
| Average | | 7.2 | 13.3 | 0.74 | 7.8 | 6.8 | 2.6 |
| Coefficient of variation | | 25 | 19 | 27 | 43 | 39 | 25 |

the Bisley forest (Fig. 3). Generally, understory vegetation had greater concentrations per unit dry weight than the dominant canopy species. However, the canopy trees account for a greater proportion of the total aboveground biomass and nutrient content of the forest. Some rapidly growing species, like *C. peltata* and *D. morototoni,* had relatively high concentrations of some nutrients in their leaves (Appendix 2), but high wood-biomass-to-leaf-biomass ratios, and therefore had low concentrations per tree (Table 2).

Except for the concentration of N in aboveground tissue, the nutrient content per unit dry weight in total biomass and leaves biomass of the Bisley forest was similar to other humid tropical steeplands (Tables 4 and 5). Differences in nutrient concentrations between the Bisley watersheds and the El Verde site, also within the LEF, are apparently due to both sampling methodology and plot location (Ovington & Olson 1970). The El Verde study did not include the biomass or nutrients of palms or any stems less than 1.3 m tall. In addition, the El Verde data were collected from a relatively small area, a 20 m diameter plot that contained one large emergent *Cyrilla racemiflora* L. that accounted for over 67 percent of the total biomass of the plot. The only reported nutrient analysis of *C. racemiflora* had relatively low concentrations of both N and P in both its bole and branch tissue (Ovington & Olson 1970). This species is the dominant of the colorado-type forest that occurs in the upper elevations of the LEF and does not occur in either of the Bisley watersheds.

The relatively high level of N in the aboveground biomass of the Bisley forest is apparently due to a combination of natural and anthropogenic factors. This highly dynamic steepland forest has an abundance of fast-growing species like *C. peltata, D. morototoni* and *Ormosia krugii* Urban. These species have high nitrogen contents in their tissue

TABLE 6. *Aboveground biomass, nutrient content and concentration per dry weight in Bisley watersheds 1 and 2, Luquillo Experimental Forest, Puerto Rico, after Hurricane Hugo, September 1989.*

| Vegetation unit | Biomass (t/ha) | Nutrients (kg/ha) N | P | K | Ca | Mg |
|---|---|---|---|---|---|---|
| Stems (>2.5 cm DBH) | | | | | | |
| Leaves | 0.6 | 9.2 | 0.5 | 4.4 | 2.6 | 1.2 |
| Branches | 12.9 | 58.4 | 3.4 | 47.4 | 60.2 | 10.9 |
| Bole | 94.7 | 184.0 | 10.2 | 176.4 | 140.2 | 43.4 |
| Bark | 2.1 | 12.7 | 0.5 | 9.8 | 16.2 | 2.0 |
| Understory palms | 2.5 | 31.2 | 1.9 | 28.6 | 7.9 | 7.8 |
| Saplings (<2.5 cm DBH) | 0.18 | 4.0 | 0.2 | 2.0 | 1.1 | 0.5 |
| Herbs | 0.21 | 2.3 | 0.1 | 1.9 | 1.2 | 1.0 |
| Ferns | 0.09 | 1.7 | 0.1 | 0.9 | 0.5 | 0.6 |
| Total | 113.3 | 303.5 | 16.9 | 271.4 | 229.9 | 67.4 |
| Concentration/dry weight (mg/g) | | 2.68 | 0.15 | 2.40 | 2.03 | 0.59 |
| Post-/prehurricane ratio | 0.50 | 0.45 | 0.46 | 0.48 | 0.48 | 0.48 |

and are known to be associated with ectotrophic mycorrhizae (Edmisten 1970). In addition, human activity associated with the establishment of coffee plantations at the end of the last century is known to have enriched forest slopes in *Inga vera* Willd. (García-Montiel 1991), a legume with a relatively high concentration of N in its branch wood and leaves. Although the coffee plantations have long been abandoned, regenerated *I. vera* is still abundant within the drainages.

While some of the differences in the concentrations per unit dry weight of various sites are due to differences in methodologies, two distinct groups of nutrients, low (N, P) and high (K, Ca) variation, can be defined (Tables 4 and 5). Nutrients with a low between-site variation are multivalent, usually derived from atmospheric sources (Likens *et al.* 1977) and are mobilized by living organisms. Since weathering of parent material is the principal source of nutrients in the high-variation group, differences in local bedrock and weathering processes may explain part of the wide range in their concentrations.

POST-HURRICANE HUGO BIOMASS AND NUTRIENT CONTENT.—The majority of the decrease in aboveground biomass caused by Hurricane Hugo was due to the snapping or uprooting of canopy trees. While differences in the extent of damage varied by forest compartments, the total percent transfer of the different nutrients from the forest was relatively constant (Table 6). This occurred because the greatest proportion of nutrients transferred from the standing aboveground pool came from bole wood, which has similar concentrations of most nutrients in all species (Fig. 3).

Following the hurricane, the remaining aboveground nutrient concentrations per unit dry weight in the Bisley forest (Table 6) were still greater than the lowest concentrations reported for other steepland tropical forests (Table 4). These relatively high concentrations attest to the nutrient-rich character of the biomass at this site.

## ACKNOWLEDGMENTS

This research was performed under grant BSR-8811902 from the National Science Foundation to the Institute of Tropical Forestry (U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station) and the Center for Energy and Environment Research (University of Puerto Rico) as part of the Long-Term Ecological Research Program in the Luquillo Experimental Forest, and a grant to A. H. Johnson from the A. W. Mellon Foundation of New York. Additional support was provided by the Forest Service and Yale University. J. Highland, S. Anderson, L. Migenis, and the timber crew of the Caribbean National Forest assisted in the 1989 field work.

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## Appendix 1

Allometric equations for the tabonuco forest of the Luquillo Experimental Forest, Puerto Rico. Weights are expressed in oven-dried kg, where Lf = leaves, Br = branches, Bo = Bole, To = total aboveground biomass, ln = natural log, D = Diameter in cm at 1.3 m, H = height in m, and S = specific gravity. Diameter range is the range of tree sizes that the equation was calculated with, in cm; RMES = root mean error squared; $N$ = sample size; $R^2$ = squared coefficient of correlation.

| Species and equation | Diameter range | RMES | $N$ | $R^2$ |
|---|---|---|---|---|
| All dicotyledonous trees | | | | |
| $To = \exp(0.994 \ln(D^2HS) - 3.098)$ | 2.5–57 | 0.502 | 47 | 0.964 |
| $To = \exp(0.950 \ln(D^2H) - 3.282)$ | 2.5–57 | 0.595 | 62 | 0.947 |
| $To = \exp(2.475 \ln(D) - 2.399)$ | 2.5–57 | 0.702 | 63 | 0.926 |
| $Lf = \exp(0.678 \ln(D^2HS) - 4.154)$ | 2.5–57 | 0.882 | 51 | 0.816 |
| $Lf = \exp(0.653 \ln(D^2H) - 4.307)$ | 2.5–57 | 0.816 | 51 | 0.882 |
| $Lf = \exp(1.792 \ln(D) - 3.758)$ | 2.5–57 | 1.019 | 63 | 0.741 |
| $Br = \exp(0.855 \ln(D^2HS) - 4.811)$ | 2.5–57 | 1.163 | 48 | 0.805 |
| $Br = \exp(0.758 \ln(D^2H) - 4.37)$ | 2.5–57 | 1.197 | 67 | 0.755 |
| $Br = \exp(1.982 \ln(D) - 3.69)$ | 2.5–57 | 1.242 | 68 | 0.736 |
| $Bo = \exp(1.021 \ln(D^2HS) - 3.482)$ | 2.5–57 | 0.520 | 47 | 0.964 |
| $Bo = \exp(0.983 \ln(D^2H) - 3.759)$ | 2.5–57 | 0.591 | 61 | 0.951 |
| $Bo = \exp(2.559 \ln(D) - 2.832)$ | 2.5–57 | 0.707 | 62 | 0.930 |

**Appendix 1.** *Continued.*

| Species and equation | Diameter range | RMES | *N* | $R^2$ |
|---|---|---|---|---|
| *Casearia* sp. | | | | |
| Lf = exp(0.543 ln($D^2H$) − 3.872) | 1.0–29 | 0.568 | 11 | 0.905 |
| Lf = exp(1.449 ln(D) − 3.370) | 1.0–29 | 0.548 | 11 | 0.912 |
| Br = exp(0.677 ln(D) − 4.149) | 1.0–29 | 0.988 | 11 | 0.831 |
| Br = exp(1.786 ln(D) − 3.504) | 1.0–29 | 1.023 | 11 | 0.819 |
| Bo = exp(0.563 ln($D^2H$) − 1.329) | 1.0–29 | 1.145 | 11 | 0.717 |
| Bo = exp(1.471 ln(D) − 0.779) | 1.0–29 | 1.194 | 11 | 0.692 |
| *Cecropia peltata* and *Didymopanax morototoni* | | | | |
| Lf = exp(1.449 ln(D) − 3.49) | 5.3–41 | 0.719 | 5 | 0.931 |
| Br = exp(2.062 ln(D) − 5.936) | 5.3–41 | 0.511 | 5 | 0.972 |
| Bo = exp(2.543 ln(D) = 3.139) | 5.3–41 | 0.416 | 5 | 0.973 |
| *Dacryodes excelsa* and *Tetragastris balsamifera* | | | | |
| Lf = exp(0.659 ln($D^2H$) − 3.553) | 2.8–46 | 0.536 | 8 | 0.936 |
| Lf = exp(1.701 ln(D) − 2.935) | 2.8–46 | 0.495 | 8 | 0.945 |
| Br = exp(1.703 ln($D^2H$) − 6.178) | 2.8–46 | 0.401 | 8 | 0.986 |
| Br = exp(2.760 ln(D) − 5.138) | 2.8–46 | 0.392 | 8 | 0.987 |
| Bo = exp(0.957 ln($D^2H$) − 3.594) | 2.8–46 | 0.208 | 8 | 0.995 |
| Bo = exp(2.454 ln(D) = 2.653) | 2.8–46 | 0.282 | 8 | 0.991 |
| *Inga vera* and *I. laurina* | | | | |
| Lf = exp(0.583 ln($D^2H$) − 3.627) | 2.0–45 | 0.579 | 6 | 0.925 |
| Lf = exp(1.523 ln(D) − 3.022) | 2.0–45 | 0.620 | 6 | 0.914 |
| Br = exp(0.602 ln($D^2H$) − 3.415) | 2.0–45 | 1.175 | 6 | 0.761 |
| Br = exp(1.572 ln(D) = 2.786) | 2.0–45 | 1.201 | 6 | 0.750 |
| Bo = exp(0.945 ln($D^2H$) − 2.355) | 2.0–45 | 0.167 | 6 | 0.998 |
| Bo = exp(2.479 ln(D) − 2.355) | 2.0–45 | 0.270 | 6 | 0.993 |
| *Ocotea leucoxylon* (Sw.) Mez, *O. spathulata* Mez, *O. portoricensis* Mez, *Ormosia krugii* | | | | |
| Lf = exp(0.603 ln($D^2H$) − 4.002) | 1.0–49 | 0.740 | 9 | 0.931 |
| Lf = exp(1.159 ln(D) − 3.593) | 1.0–49 | 0.909 | 9 | 0.896 |
| Br = exp(0.782 ln($D^2H$) − 5.182) | 1.0–49 | 1.315 | 9 | 0.878 |
| Br = exp(2.042 ln(D) − 4.609) | 1.0–49 | 1.569 | 9 | 0.827 |
| Bo = exp(0.944 ln(D) − 3.657) | 1.0–49 | 0.805 | 9 | 0.966 |
| Bo = exp(2.500 ln(D) − 3.031) | 1.0–49 | 1.108 | 9 | 0.935 |
| *Palicourea riparia* | | | | |
| To = exp(0.752 ln($D^2H$) − 2.362) | 0.8–3 | 0.299 | 7 | 0.861 |
| To = exp(1.924 ln(D) − 1.601) | 0.8–3 | 0.289 | 7 | 0.870 |
| *Prestoea montana,* where H = stem height (Frangi & Lugo 1985) | | | | |
| To = 7.7H + 6.8 | | | 25 | 0.90 |
| Lf = 1.7H + 6.1 | | | 25 | 0.50 |
| Bo = 5.9H − 1.6 | | | 25 | 0.85 |
| *Sloanea berteriana* | | | | |
| Lf = exp(0.676 ln($D^2H$) − 3.264) | 1.3–38 | 0.412 | 4 | 0.989 |
| Lf = exp(1.916 ln(D) − 3.165) | 1.3–38 | 0.296 | 4 | 0.994 |
| Br = exp(0.737 ln($D^2H$) − 3.750) | 1.3–38 | 0.943 | 4 | 0.953 |
| Br = exp(2.053 ln(D) − 3.568) | 1.3–38 | 1.205 | 4 | 0.924 |
| Bo = exp(0.881 ln($D^2H$) − 2.529) | 1.3–38 | 0.468 | 4 | 0.992 |
| Bo = exp(2.501 ln(D) − 2.403) | 1.3–38 | 0.187 | 4 | 0.999 |

## Appendix 2

Average nutrient concentrations (Avg.), sample size (N), and standard deviation (Std.) of selected species in the Bisley experimental watersheds of the Luquillo Experimental Forest, Puerto Rico.

| Species | | N (%) | Ca (mg/g) | P (mg/g) | Mg (mg/g) | K (mg/g) |
|---|---|---|---|---|---|---|
| *Alchornea latifolia* Sw. | | | | | | |
| Wood (*N* = 2) | Avg. = | 0.24 | 11.53 | 0.20 | 1.10 | 1.89 |
| | Std. = | 0.02 | 4.30 | 0.01 | 0.31 | 0.50 |
| Bark (*N* = 2) | Avg. = | 0.64 | 0.64 | 0.30 | 1.11 | 5.25 |
| | Std. = | 0.03 | 0.17 | 0.003 | 0.07 | 0.69 |
| *Alchorneopsis portoricensis* Urban | | | | | | |
| Wood | Avg. = | 0.30 | 0.58 | 0.15 | 1.01 | 2.25 |
| Bark | Avg. = | 0.64 | 12.88 | 0.23 | 0.86 | 3.96 |
| *Andira inermis* (W. Wright) HBK. | | | | | | |
| Leaves | | 2.66 | 2.70 | 1.13 | 2.58 | 8.34 |
| Branches | | 1.53 | 1.63 | 0.77 | 1.63 | 8.26 |
| Wood | | 0.41 | 0.78 | 0.22 | 0.39 | 3.54 |
| *Casearia arborea* | | | | | | |
| Fruits (*N* = 5) | Avg. = | 1.84 | 2.42 | 1.03 | 2.36 | 7.20 |
| | Std. = | 0.06 | 1.18 | 0.47 | 1.00 | 2.19 |
| Leaves (*N* = 7) | Avg. = | 2.12 | 4.04 | 0.71 | 2.91 | 6.01 |
| | Std. = | 0.19 | 1.18 | 0.09 | 0.42 | 2.33 |
| Branches (*N* = 7) | Avg. = | 0.73 | 2.55 | 0.34 | 1.76 | 4.59 |
| | Std. = | 0.31 | 0.93 | 0.11 | 0.24 | 1.45 |
| Wood (*N* = 9) | Avg. = | 0.40 | 1.99 | 0.21 | 0.99 | 4.24 |
| | Std. = | 0.40 | 2.43 | 0.20 | 0.69 | 1.98 |
| Bark (*N* = 6) | Avg. = | 1.04 | 7.38 | 0.48 | 3.49 | 9.67 |
| | Std. = | 0.06 | 1.03 | 0.03 | 0.24 | 0.47 |
| *Cecropia peltata* | | | | | | |
| Leaves (*N* = 2) | Avg. = | 1.82 | 9.57 | 1.05 | 5.57 | 8.82 |
| | Std. = | 0.23 | 0.82 | 0.26 | 0.04 | 0.86 |
| Branches (*N* = 2) | Avg. = | 0.42 | 3.45 | 0.35 | 3.72 | 7.43 |
| | Std. = | 0.02 | 0.003 | 0.01 | 0.02 | 0.04 |
| Wood (*N* = 8) | Avg. = | 0.11 | 0.89 | 0.07 | 1.42 | 2.12 |
| | Std. = | 0.02 | 0.14 | 0.01 | 0.18 | 0.73 |
| Bark (*N* = 8) | Avg. = | 0.74 | 7.82 | 0.28 | 3.75 | 8.14 |
| | Std. = | 0.05 | 0.97 | 0.02 | 0.36 | 0.59 |
| *Cordia borinquensis* Urban | | | | | | |
| Leaves | | 1.94 | 3.89 | 0.88 | 4.20 | 13.54 |
| Branches | | 0.89 | 4.43 | 0.46 | 1.55 | 7.66 |
| Wood | | 0.62 | 5.31 | 0.48 | 0.96 | 5.56 |
| *Dacryodes excelsa* | | | | | | |
| Leaves (*N* = 4) | Avg. = | 1.33 | 4.54 | 0.63 | 1.17 | 5.44 |
| | Std. = | 0.10 | 0.88 | 0.05 | 0.15 | 1.32 |
| Branches (*N* = 4) | Avg. = | 0.35 | 4.13 | 0.24 | 0.59 | 3.13 |
| | Std. = | 0.09 | 1.77 | 0.07 | 0.17 | 0.82 |
| Wood (*N* = 6) | Avg. = | 0.08 | 0.38 | 0.05 | 0.13 | 1.03 |
| | Std. = | 0.01 | 0.06 | 0.02 | 0.01 | 0.29 |
| Bark (*N* = 6) | Avg. = | 0.31 | 3.45 | 0.70 | 0.70 | 4.23 |
| | Std. = | 0.02 | 0.64 | 0.04 | 0.04 | 10.11 |
| *Didymopanax morototoni* | | | | | | |
| Fruits | Avg. = | 0.71 | 7.47 | 0.57 | 4.28 | 6.84 |
| Leaves (*N* = 5) | Avg. = | 1.56 | 6.49 | 0.94 | 3.12 | 7.50 |
| | Std. = | 0.08 | 0.97 | 0.16 | 0.49 | 1.56 |
| Branches (*N* = 5) | Avg = | 0.68 | 22.71 | 0.46 | 4.87 | 3.92 |
| | Std. = | 0.05 | 5.13 | 0.08 | 0.83 | 0.79 |

**Appendix 2.** *Continued.*

| Species | | N (%) | Ca (mg/g) | P (mg/g) | Mg (mg/g) | K (mg/g) |
|---|---|---|---|---|---|---|
| Wood ($N = 8$) | Avg. = | 0.08 | 1.10 | 0.04 | 0.76 | 0.72 |
| | Std. = | 0.004 | 0.12 | 0.01 | 0.07 | 0.14 |
| Bark ($N = 8$) | Avg. = | 0.35 | 9.13 | 0.15 | 1.74 | 2.24 |
| | Std. = | 0.04 | 0.91 | 0.02 | 0.08 | 0.47 |
| *Eugenia eggersii* Kiaersk. | | | | | | |
| Leaves | | 1.47 | 7.45 | 0.67 | 2.15 | 8.6 |
| Branches | | 0.54 | 4.97 | 0.32 | 0.77 | 4.21 |
| Wood | | 0.25 | 0.69 | 0.14 | 0.19 | 3.47 |
| *Guarea guidonia* | | | | | | |
| Fruits ($N = 12$) | Avg. = | 2.55 | 2.85 | 1.45 | 2.63 | 13.71 |
| | Std. = | 0.29 | 0.33 | 0.14 | 0.55 | 3.29 |
| Leaves ($N = 12$) | Avg. = | 2.69 | 5.17 | 1.53 | 3.90 | 11.84 |
| | Std. = | 0.22 | 0.85 | 0.11 | 0.69 | 1.01 |
| Branches ($N = 12$) | Avg. = | 0.90 | 6.31 | 0.45 | 2.18 | 5.84 |
| | Std. = | 0.24 | 1.98 | 0.12 | 0.22 | 1.24 |
| Wood ($N = 25$) | Avg. = | 0.20 | 1.24 | 0.19 | 0.71 | 1.54 |
| | Std. = | 0.04 | 0.43 | 0.08 | 0.11 | 0.82 |
| Bark ($N = 25$) | Avg. = | 1.10 | 17.92 | 0.48 | 2.88 | 5.74 |
| | Std. = | 0.11 | 2.72 | 0.08 | 0.81 | 1.88 |
| *Inga laurina* | | | | | | |
| Fruits ($N = 2$) | Avg. = | 2.15 | 3.36 | 1.36 | 1.28 | 10.10 |
| | Std. = | 0.13 | 0.4 | 0.07 | 0.03 | 0.56 |
| Leaves ($N = 8$) | Avg. = | 2.82 | 5.40 | 1.06 | 1.51 | 7.40 |
| | Std. = | 0.10 | 1.18 | 0.09 | 0.15 | 0.81 |
| Branches ($N = 8$) | Avg. = | 0.94 | 7.49 | 0.36 | 0.97 | 4.43 |
| | Std. = | 0.21 | 1.43 | 0.06 | 0.34 | 0.65 |
| Wood ($N = 16$) | Avg. = | 0.25 | 1.35 | 0.06 | 0.18 | 2.72 |
| | Std. = | 0.02 | 0.24 | 0.02 | 0.04 | 0.58 |
| Bark ($N = 16$) | Avg. = | 1.46 | 8.37 | 0.28 | 0.63 | 5.83 |
| | Std. = | 0.14 | 1.11 | 0.03 | 0.07 | 0.52 |
| *Khaya nyasica* Stapf. ex Baker | | | | | | |
| Leaves ($N = 8$) | Avg. = | 1.84 | 5.63 | 0.90 | 2.26 | 8.95 |
| | Std. = | 0.31 | 1.33 | 0.23 | 0.40 | 1.03 |
| Branches ($N = 8$) | Avg. = | 0.69 | 5.39 | 0.43 | 1.12 | 5.90 |
| | Std. = | 0.11 | 1.03 | 0.14 | 0.18 | 1.44 |
| Wood ($N = 13$) | Avg. = | 0.09 | 1.37 | 0.04 | 0.13 | 0.62 |
| | Std. = | 0.03 | 0.25 | 0.02 | 0.06 | 0.48 |
| Bark ($N = 13$) | Avg. = | 0.32 | 7.49 | 0.13 | 0.72 | 2.52 |
| | Std. = | 0.05 | 0.98 | 0.02 | 0.18 | 1.23 |
| *Myrcia deflexa* (Poir.) DC. | | | | | | |
| Fruits | Avg. = | 1.10 | 4.56 | 1.24 | 1.32 | 19.15 |
| Leaves ($N = 2$) | Avg. = | 1.13 | 7.14 | 0.49 | 2.55 | 6.76 |
| | Std. = | 0.08 | 0.85 | 0.03 | 0.20 | 0.44 |
| Branches ($N = 2$) | Avg. = | 0.38 | 3.93 | 0.23 | 0.58 | 2.94 |
| | Std. = | 0.10 | 1.11 | 0.07 | 0.22 | 0.96 |
| Wood ($N = 2$) | Avg. = | 0.40 | 5.75 | 0.17 | 0.67 | 3.68 |
| | Std. = | 0.24 | 4.40 | 0.09 | 0.35 | 2.58 |
| *Ocotea leucoxylon* | | | | | | |
| Fruits ($N = 3$) | Avg. = | 3.51 | 4.26 | 2.71 | 2.35 | 13.17 |
| | Std. = | 0.02 | 0.96 | 0.35 | 0.20 | 0.87 |
| Leaves ($N = 4$) | Avg. = | 2.13 | 6.97 | 0.84 | 1.75 | 7.61 |
| | Std. = | 0.08 | 2.29 | 0.19 | 0.27 | 1.34 |
| Branches ($N = 4$) | Avg. = | 1.07 | 6.09 | 0.42 | 1.22 | 5.15 |
| | Std. = | 0.36 | 1.23 | 0.17 | 0.31 | 1.15 |

**Appendix 2.** *Continued.*

| Species | | Nutrients | | | | |
|---|---|---|---|---|---|---|
| | | N (%) | Ca (mg/g) | P (mg/g) | Mg (mg/g) | K (mg/g) |
| Wood ($N = 8$) | Avg. = | 0.25 | 1.38 | 0.08 | 0.15 | 1.94 |
| | Std. = | 0.03 | 0.38 | 0.01 | 0.03 | 0.22 |
| Bark ($N = 8$) | Avg. = | 1.27 | 10.57 | 0.46 | 0.60 | 4.76 |
| | Std. = | 0.06 | 1.22 | 0.06 | 0.12 | 0.56 |
| *Ormosia krugii* | | | | | | |
| Fruits ($N = 3$) | Avg. = | 1.27 | 1.75 | 0.41 | 0.77 | 3.69 |
| | Std. = | 0.08 | 0.42 | 0.14 | 0.07 | 0.79 |
| Leaves ($N = 8$) | Avg. = | 2.13 | 2.12 | 0.76 | 0.91 | 4.48 |
| | Std. = | 0.09 | 0.47 | 0.06 | 0.10 | 0.57 |
| Branches ($N = 8$) | Avg. = | 0.93 | 1.71 | 0.43 | 0.41 | 2.73 |
| | Std. = | 0.22 | 0.45 | 0.25 | 0.17 | 1.37 |
| Wood $N = 11$) | Avg. = | 0.21 | 0.29 | 0.03 | 0.06 | 0.43 |
| | Std. = | 0.02 | 0.12 | 0.01 | 0.03 | 0.17 |
| Bark ($N = 11$) | Avg. = | 0.90 | 3.83 | 0.17 | 0.27 | 1.67 |
| | Std. = | 0.05 | 3.83 | 0.02 | 0.09 | 0.47 |
| *Palicourea riparia* | | | | | | |
| Fruits | | 2.92 | 6.60 | 1.73 | 3.86 | 13.48 |
| Leaves | | 2.68 | 9.65 | 0.79 | 4.75 | 9.51 |
| Branches | | 1.02 | 11.02 | 0.44 | 3.53 | 4.32 |
| Wood | | 1.68 | 16.53 | 0.54 | 1.98 | 7 38 |
| *Prestoea montana* | | | | | | |
| Leaves | | 1.25 | 3.05 | 0.75 | 3.17 | 11.47 |
| Bole | | 1.10 | 4.12 | 0.57 | 2.48 | 9.74 |
| *Sloanea berteriana* | | | | | | |
| Fruits | Avg. = | 0.55 | 0.70 | 0.73 | 0.47 | 10.87 |
| Leaves ($N = 5$) | Avg. = | 1.40 | 3.76 | 0.64 | 1.89 | 7.02 |
| | Std. = | 0.09 | 0.63 | 0.07 | 0.33 | 0.64 |
| Branches ($N = 5$) | Avg. = | 0.81 | 7.20 | 0.64 | 1.78 | 5.58 |
| | Std. = | 0.14 | 2.97 | 0.15 | 0.55 | 0.51 |
| Wood ($N = 7$) | Avg. = | 0.12 | 2.23 | 0.05 | 0.30 | 1.80 |
| | Std. = | 0.02 | 0.62 | 0.01 | 0.02 | 0.32 |
| Bark ($N = 7$) | Avg. = | 0.49 | 10.44 | 0.16 | 0.67 | 5.35 |
| | Std. = | 0.06 | 1.17 | 0.02 | 0.06 | 0.37 |
| *Tetragastris balsamifera* | | | | | | |
| Leaves ($N = 3$) | Avg. = | 1.40 | 5.67 | 0.67 | 1.66 | 7.20 |
| | Std. = | 0.03 | 1.19 | 0.002 | 0.11 | 0.41 |
| Branches ($N = 3$) | Avg. = | 0.48 | 5.54 | 0.33 | 1.01 | 4.53 |
| | Std. = | 0.09 | 2.39 | 0.09 | 0.18 | 1.03 |
| Wood ($N = 3$) | Avg. = | 0.50 | 5.94 | 0.34 | 1.10 | 5.07 |
| | Std. = | 0.09 | 2.22 | 0.07 | 0.14 | 0.61 |
| Understory vegetation | | | | | | |
| Ferns ($N = 6$) | Avg. = | 1.74 | 4.48 | 0.77 | 5.03 | 8.59 |
| | Std. = | 0.34 | 1.21 | 0.18 | 0.96 | 1.58 |
| Herbs ($N = 6$) | Avg. = | 1.48 | 7.50 | 0.94 | 3.99 | 12.47 |
| | Std. = | 0.45 | 2.31 | 0.29 | 1.92 | 2.11 |
| Saplings ($N = 6$) | Avg. = | 1.89 | 5.49 | 0.92 | 2.85 | 9.44 |
| | Std. = | 0.33 | 1.39 | 0.14 | 0.67 | 0.86 |