GEOGRAPHIC VARIATION IN WOOD SPECIFIC GRAVITY: EFFECTS OF LATITUDE, TEMPERATURE, AND PRECIPITATION

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ABSTRACT

Wood basic specific gravity (SG) was compared at sites located along a gradient from 52°N latitude to the equator. Mean SG increased by 0.0049 per °C mean annual temperature (MAT), and decreased by 0.00017 per cm of mean annual precipitation (MAP). Considered alone, MAT was a better predictor of mean SG across the temperate zone (3–22°C MAT, latitude north of 29°N; $r^2 = 0.80$) than it was across the entire MAT range ($r^2 = 0.62$) or across warm tropical sites alone (MAT $> 23°C$; $r^2 = 0.33$, $p = 0.67$). In contrast, MAP considered alone was a better predictor of mean SG in the warm tropical sites ($r^2 = 0.62$) than across all sites ($r^2 = 0.04$, $p = 0.39$).

Variability in SG among the sites was compared using two measures of dispersion: range and standard deviation. As MAT increased across the temperate zone, maximum SG increased and minimum SG remained constant, resulting in an increase in SG range; SG standard deviation, however, remained constant. Both SG range and SG standard deviation increased dramatically in the warm tropical zone relative to the temperate zone, demonstrating that variability in SG in the warm tropics is much greater than would be predicted from greater species richness alone.

Keywords: Specific gravity, climate, temperate woods, tropical woods, temperature, precipitation, biomass.

INTRODUCTION

Angiosperm wood anatomical characters have been shown to vary with latitude, exhibiting particularly sharp contrasts between temperate and tropical woods (Wiemann et al. 2001). Such changes in physiognomy of woods are likely to be reflected in their physical properties as well. The single best indicator of wood physical and mechanical behavior is specific gravity, measured either green, air-dry, or oven-dry (Panshin and de Zeeuw 1980). One of the most commonly used wood specific gravity measures is basic specific gravity, which is defined as the ratio of oven-dry weight to the weight of water displaced by the green (undried) volume (Panshin and de Zeeuw 1980). Basic specific gravity (SG) can be converted to the ecologist's measure of

stem allocation, defined as weight of dry bio-mass per volume of living wood tissue (Harper 1977).

The mean and variation in SG among tree species in a forest has important implications for forest management, community ecology, and regional carbon cycles (Fearnside 1997). In closed canopy forests, species with low specific gravity wood are generally colonizers or pioneers, species with intermediate SG values are usually mature forest species or emergents, and those with exceptionally high SG values are often slow-growing species confined to the sub-canopy (Wiemann and Williamson 1988, 1989a). In the absence of growth rate data, SG may be used as a correlate of species growth rates, having important consequences for forest management, nutrient cycling, and carbon sequestration; estimates of above-ground biomass generally are based on one or a few tree measurements, combined with an average SG, where the average may have been derived from one species or a mean of published values for a geographic region (Adams and Owens 2001; Brown et al. 1989; Fearnside 1996). Rarely, species-specific biomass equations are derived from species SG values and growth equations (Nelson et al. 1999). Thus, the mean and variation in SG among species in a forest can provide insightful information; however, most SG data are tabulated by species in technical publications and are not available by forest stand (Fearnside 1997).

Where comparisons of SG among forest stands have been made, notable differences have been recorded. For example, Williamson (1984), compared means and standard deviations of SG in wet forests from Indiana, Trinidad, and Costa Rica, and found that mean SG was similar in the three geographic areas but that variability in SG was significantly greater in the tropical stands. Chudnoff (1976) found that, in tropical America, moist forests had higher proportions of dense (SG > 0.69) species than either wetter or drier forests.

Here, we analyze the SG of woody angiosperms growing across an extensive latitudinal range (0–52°N). We also look for associations between SG and climatic variables—namely, mean annual temperature (MAT), cold month mean temperature (CMMT), and mean annual precipitation (MAP). The forests sampled extend from northern Minnesota and central England to equatorial Africa. They span an MAT range of 3–27°C, and an MAP range of 58–396 cm.

MATERIALS AND METHODS

Lists of angiosperm tree species at 19 sites in the United States, Mexico, Guatemala, Costa Rica, Panama, England, Gabon, and Nigeria were obtained from forest inventories. Data on the location, climate, and sampling of these sites are given in Table 1, and the sources of information about the sites and the species growing on them are given in Appendix 1. Mid-site latitude and longitude, site elevation and area, as well as climatic data (MAT, CMMT, and MAP) were obtained from previously published records (Wernstedt 1972; NOAA 1985; Sanford et al. 1994).

For each species a SG value, considered representative of the species regardless of provenance and sample location within a tree, was obtained from the literature (Llach-Cordero, no date; Markwardt and Wilson 1935; Dickinson et al. 1949; Hess et al. 1950; Wangaard and Muschler 1952; Wangaard et al. 1954, 1955; Longwood 1962; Kukachka et al. 1968; van der Slooten 1968; Kukachka 1970; Chudnoff 1973, 1984; Bendtsen and Ethington 1975; Panshin and de Zeeuw 1980; Lavers 1983; USDA Forest Service 1999; Toennisson 1992; Rijsdijk and Laming 1994; Alden 1995). Obviously, one limitation of this methodology was its inability to track geographic variation in SG within a species, as was done by Howe (1974), Whitmore (1973), and Wiemann and Williamson (1989b).

With the exceptions of Avery County, NC (elevation 800–1,600 m) and the central Adirondack Preserve (elevation 300–1,200 m), the sites represented elevations of less than 600 m. We were unable to find sufficient published SG data on tropical montane species to

TABLE 1. *Location and weather data for sites.*

Site	Location				Climate			Number of angiosperm tree species		Percentage of species with SG data
	Latitude	Longitude	Elevation (m)	Area (km²)	MAT (°C)	CMMT (°C)	MAP (cm)	At site	With SG data	
Warwickshire, UK	52.3°N	2°W	20–260	2,500	9.5	3.1	72	50	18	36
Beltrami County, MN	48.0°N	95°W	360–460	6,500	3.2	−17.0	58	30	19	63
Adirondack upland, NY	44.4°N	74°W	300–1,200	7,000	5.4	−9.1	100	40	24	60
Kalamazoo County, MI	42.2°N	86°W	230–320	1,500	9.8	−4.6	88	80	50	62
King George County, VA	38.3°N	77°W	0–50	450	13.4	1.5	104	70	51	73
Hill Demonstration Forest, NC	36.2°N	79°W	100–220	10	15.1	4.3	116	70	48	69
Avery County, NC	36.1°N	82°W	800–1,600	650	9.6	−0.3	128	50	35	70
Haywood County, TN	35.6°N	89°W	70–130	1,400	16.0	3.7	130	70	51	73
Caddo Parish, LA	32.6°N	94°W	40–110	2,300	17.9	7.1	118	100	56	56
Ichauway, GA	31.2°N	84°W	30–100	100	19.6	10.6	131	90	43	48
Marion County, FL	29.2°N	82°W	10–50	4,200	21.7	14.6	137	90	32	36
Collier County, FL	26.2°N	81°W	0–10	5,000	23.8	19.0	140	70	18	26
Los Tuxtlas Biological Station, Mexico	18.6°N	95°W	150–530	10	24.4	20.5	211	150	23	15
Central Peten, Guatemala	16.8°N	90°W	150–250	1,500	25.4	22.4	201	150	25	17
Santa Rosa National Park, Costa Rica	10.9°N	86°W	0–320	100	24.0	22.8	191	150	40	27
La Selva Biological Station, Costa Rica	10.4°N	84°W	30–140	15	25.8	24.7	396	350	43	12
Costa Rican montane forest	9.6°N	84°W	2,200–3,000	150	7.3	6.0	280	30	19	63
Barro Colorado Island, Panama	9.2°N	80°W	20–160	15	26.7	26.1	272	350	60	17
Okomu Forest Reserve, Nigeria	6.3°N	5°W	10–80	1,500	26.2	24.3	201	150	43	29
Lope Reserve, Gabon	0.2°S	12°W	100–600	50	25.2	23.3	169	300	57	19

match previously published forest species lists. Therefore, we sampled woods in one montane forest region of Costa Rica located within 10 km of the Carretera Interamericana between Km 50 and Km 82. Sampling included San Gerardo de Dota (elevation 2,500 m, 9.6°N, 85.8°W; two species), Finca Madre Selva de La Trinidad de Dota (elevation 2,400 m, 9.7°N, 83.9°W; 11 species), and six species taken within a few hundred meters of the Carretera Interamericana from El Empalme (Km 50, elevation 2,200 m, 9.7°N, 83.9°W) to Ojo de Agua (Km 82, elevation 3,000 m, 9.6°N, 83.8°W). A pith-to-bark sample was taken from each tree, usually with a 12-mm-diameter increment borer but in some instances from disks cut from felled trees. A 4-cm-long segment located midway between pith and bark was used to determine SG of each tree. We consider these samples to be representative of the overall tree SG because they avoid the effects of juvenile wood found adjacent to the pith and the sometimes lower SG characteristic of the outer sapwood of some species. The segments were stored in sealed tubes or plastic bags until further processing to prevent moisture loss. Each segment was cut into four 1-cm-long pieces, and the volume of each piece was determined by water displacement. This was done by suspending each piece at the end of a teasing needle, submerging each one in a small beaker of water on a tared balance, and recording the weight displaced by the submerged piece. The pieces were then dried at 103°C until they achieved constant weight. The measurements on the 1-cm pieces were summed to give values for whole segments, and segment SG was calculated as oven-dry weight divided by the weight of water displaced. The combined species list and SG values became the Costa Rican montane forest site (Table 1).

For each of the 20 sites, we calculated mean SG and three measures of dispersion, the range, variance, and standard deviation of the SG values. Range is intuitively interpretable, but it usually increases as the number of species included increases, and it is affected strongly by extreme values. Variance is unbiased by sample size, but its units, being squares, are not as useful as those of the standard deviation. Standard deviation is biased by sample size, but the bias is small for large samples. Gurland and Tripathi (1971) derived a correction for the bias; the correction is only 1.5% for a sample size of 18 (our smallest sample), and less than 0.5% for a sample size of 60 (our largest sample). The SG variables— mean, range, and standard deviation—subsequently were treated as dependent variables of latitude, MAT, CMMT, and MAP, and were examined using regression and correlation analysis.

RESULTS

The percentage of species in each stand for which SG data could be found varied greatly (12–73%), with temperate sites being more comprehensively represented than tropical sites (Table 1). The percentage ranged from only 12% in the extremely diverse tropical forest of La Selva, Costa Rica, to more than 50% in eight of the eleven sites located in the United States. The actual number of species with SG data was less variable than the percentage, ranging from 18 species in Warwickshire, UK, and Collier County, Florida, to 60 species at Barro Colorado Island, Panama (Table 1). The montane forest of Costa Rica had a high percentage of woods with SG values because we directly sampled as many species as possible. The SG values based on tabulated data may have a bias toward mature forest and canopy emergent species, since these comprise the majority of commercial woods. Nonetheless, data were available for many understory and small-diameter species.

Mean SG per site varied from 0.445 in Beltrami Co., Minnesota, to 0.608 in Collier County, Florida (Table 2). In linear regressions with a single independent variable, the mean SG was strongly dependent (Fig. 1A–D) on latitude ($r^2 = 0.33$, $p = 0.008$), MAT ($r^2 = 0.62$, $p < 0.0001$), and CMMT ($r^2 = 0.54$, $p = 0.0002$), but not on MAP ($r^2 = 0.04$, $p =$

TABLE 2. *MAT, mean SG, minimum SG, maximum SG, SG range and SG standard deviation for the sites, arranged by ascending MAT.*

Site	MAT (°C)	Mean SG	Minimum SG	Maximum SG	SG Range	SG standard deviation
Beltrami Co., MN	3.2	0.445	0.31	0.58	0.27	0.082
Adirondack upland, NY	5.4	0.475	0.31	0.66	0.35	0.098
Costa Rican montane forest	7.3	0.488	0.30	0.75	0.45	0.113
Warwickshire, UK	9.5	0.486	0.34	0.70	0.36	0.095
Avery Co., NC	9.6	0.517	0.32	0.66	0.34	0.099
Kalamazoo Co., MI	9.8	0.511	0.32	0.66	0.34	0.098
King George Co., VA	13.4	0.518	0.32	0.66	0.34	0.089
Hill Demonstration Forest, NC	15.1	0.529	0.32	0.66	0.34	0.087
Haywood Co., TN	16.0	0.539	0.36	0.66	0.30	0.082
Caddo Parish, LA	17.9	0.542	0.32	0.80	0.48	0.092
Ichauway, GA	19.6	0.533	0.36	0.80	0.44	0.093
Marion Co., FL	21.7	0.534	0.37	0.80	0.43	0.093
Collier Co., FL	23.8	0.608	0.32	0.89	0.57	0.178
Santa Rosa National Park, Costa Rica	24.0	0.565	0.14	0.96	0.82	0.218
Los Tuxtlas Biological Station, Mexico	24.4	0.547	0.16	0.94	0.78	0.207
Lope Reserve, Gabon	25.2	0.588	0.20	0.94	0.74	0.155
Central Peten, Guatemala	25.4	0.548	0.24	0.87	0.63	0.180
La Selva Biological Station, Costa Rica	25.8	0.523	0.16	0.96	0.80	0.194
Okomu Forest Reserve, Nigeria	26.2	0.581	0.20	0.94	0.74	0.172
Barro Colorado Island, Panama	26.7	0.511	0.12	0.94	0.82	0.195

0.39). However, in a stepwise multiple regression, MAP was the second variable included after MAT, and it significantly explained an additional 9% of the variance in SG, increasing the R^2 from 0.62 to 0.71. With MAT and MAP included in the model, neither latitude nor CMMT explained additional variance in SG. In the final regression, mean SG increased by 0.0049 per 1°C of MAT and decreased by 0.00017 per cm of MAP. All dependent and independent variables were significantly correlated with one another except for mean SG with MAP and minimum SG (Table 3).

Elevation exhibited no observable effect on mean SG although there were only three high-elevation sites. The Costa Rican montane site (latitude = 9.6°N, MAT = 7.3°C), the Avery Co. site (latitude = 36.1°N, MAT = 9.6°C), and the Adirondack upland site (latitude = 44.4°N, MAT = 5.4°C) fell along the regression line of mean SG on MAT (Fig. 1B), even though the three diverged widely in latitude.

SG minimum was relatively constant across the sites whose MAT was less than 24°C; it then decreased abruptly at the tropical sites

(Fig. 2A). In contrast, SG maximum increased gradually with MAT, although there appeared to be a step increase above 17°C and another step above 23°C (Fig. 2A). The high SG maximum (0.75) for the montane forest of Costa Rica (Fig. 2A, open circle) was a consequence of the dominant species, *Quercus copeyensis* C.H. Muller. *Q. copeyensis* is more similar in anatomy and in SG to the diffuse-porous live oak of the southern United States (*Quercus virginiana* Mill., SG = 0.80) than it is to the ring-porous oaks that are widely distributed throughout the eastern United States (SG = 0.52–0.64) (USDA Forest Service 1999).

The occurrence of both denser and less dense woods at warmer sites resulted in an increase in SG range with MAT (Fig. 2B). With the exception of the unusually high value for the montane forest of Costa Rica, the SG range increased gradually with MAT, showing the step increase at about 17°C, and then increasing dramatically in the tropics where SG maxima increase and SG minima decrease (Fig. 2A, B).

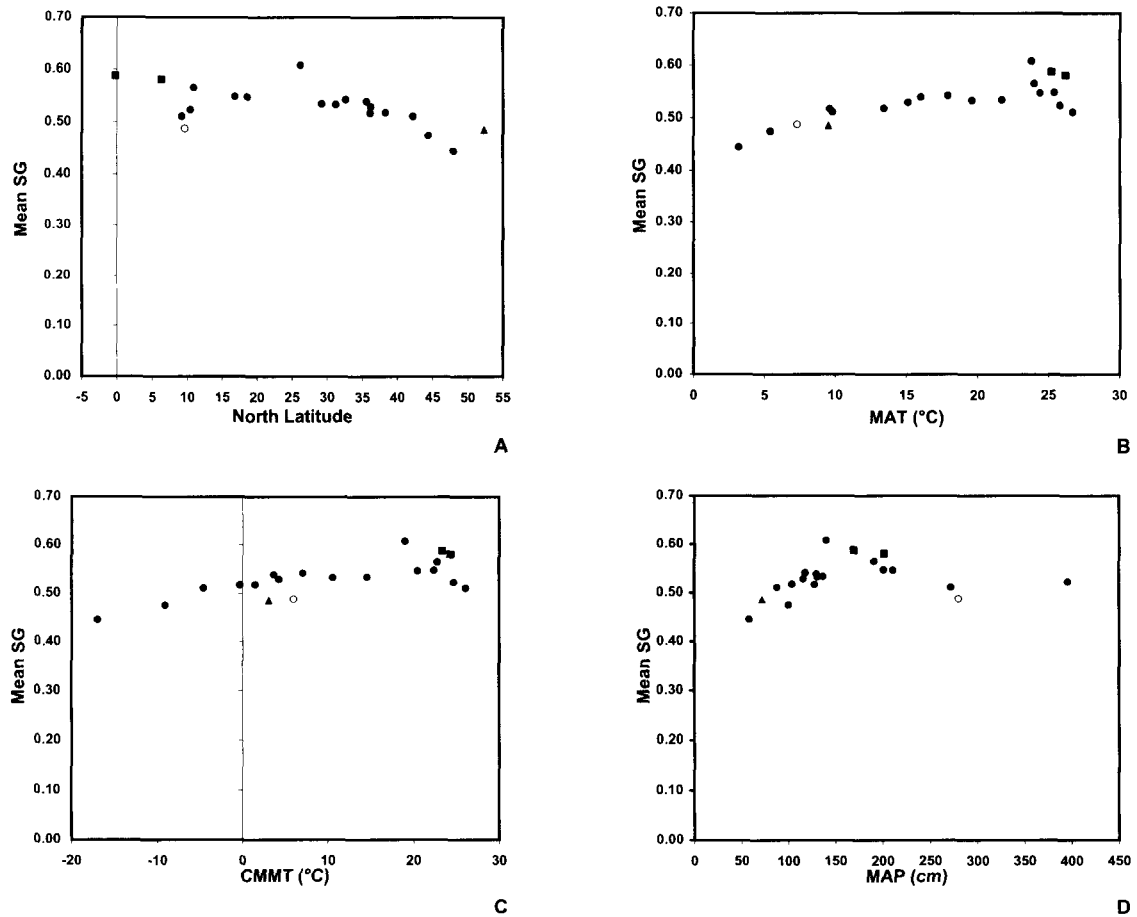The standard deviation in SG was relatively

FIG. 1.   Mean basic specific gravity (SG) as a function of latitude, MAT, CMMT, and MAP. Closed symbols: data from literature; open symbols: data measured from wood samples. Circles: American sites; squares: African sites; triangles: Warwickshire, UK.

TABLE 3.   *Correlation coefficients among the independent and dependent variables. Correlations significant at the 0.05 level unless marked (ns).*

|	Latitude	MAT	CMMT	MAP	Mean SG	Min. SG	Max. SG	SG range	SG St. Dev.
Latitude	1.00	−0.75	−0.85	−0.79	−0.58	0.75	−0.86	−0.86	−0.76
MAT	−0.75	1.00	0.95	0.56	0.79	−0.62	0.91	0.84	0.76
CMMT	−0.85	0.95	1.00	0.69	0.74	−0.69	0.95	0.90	0.83
MAP	−0.79	0.56	0.69	1.00	0.20 (ns)	−0.70	0.70	0.74	0.68
Mean SG	−0.58	0.79	0.74	0.20 (ns)	1.00	−0.28 (ns)	0.68	0.56	0.53
Min. SG	0.75	−0.62	−0.69	−0.70	−0.28 (ns)	1.00	−0.78	−0.91	−0.89
Max. SG	−0.86	0.91	0.95	0.70	0.68	−0.78	1.00	−0.97	0.89
SG Range	−0.86	0.84	0.90	0.74	0.56	−0.91	0.97	1.00	0.94
SG St. Dev.	−0.76	0.76	0.83	0.68	0.53	−0.89	0.89	0.94	1.00
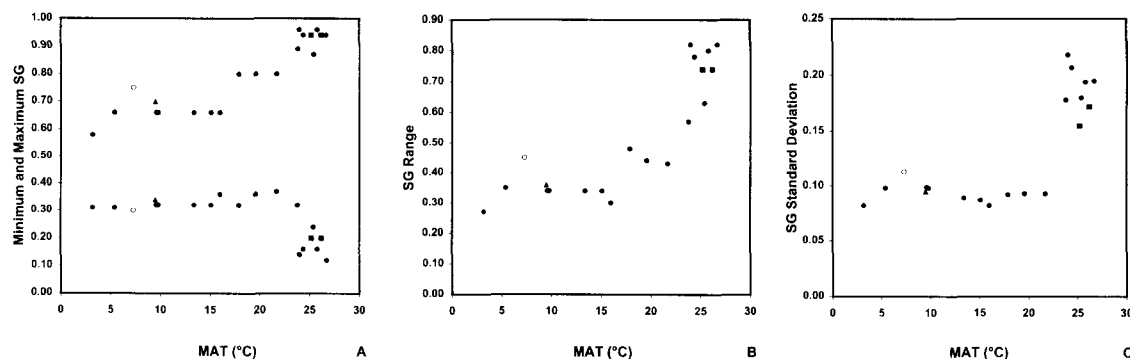
FIG. 2. Maximum and minimum basic specific gravity (SG), SG range, and SG standard deviation as a function of MAT. Closed symbols: data from literature; open symbols: data measured from wood samples. Circles: American sites; squares: African sites; triangles: Warwickshire, UK.

constant (0.082–0.099) for MAT of 3–22°C. Above a MAT of 23°C SG standard deviation jumped to 0.155–0.218 (Fig. 2C). The SG standard deviation of 0.113 for the montane forest of Costa Rica was intermediate between those for the lowland temperate and tropical forests.

DISCUSSION

In a comparison of temperate and tropical woods, Williamson (1984) found no difference in mean SG between woods in Indiana and those in Costa Rica and Trinidad. Here, with a more extensive dataset, we found that mean SG responds to a fundamental change in the environment—namely, temperature. The regression of mean SG on MAT for all 20 sites gave a coefficient of determination of 0.62, as mean SG increased by 0.0049 per °C. Furthermore, variation in mean SG was better explained by temperature than by latitude. Obviously, latitude and temperature are correlated, but not perfectly, for example $r^2 = 0.56$ in our dataset. Therefore, it is important to distinguish which factor is a better predictor of variation in mean SG.

Changes in mean SG with MAT can best be understood by dissecting the changes in the underlying SG distributions. Williamson (1984) noted the lack of extremely low SG woods (<0.30) and extremely high SG woods (>0.80) in forests in Indiana, and he suggested

that a two-step loss of the extremes occurred in Florida, where low SG disappeared prior to the loss of high SG woods. Our dataset confirms that the temperate forests are deficient in both low and high SG woods, but the pattern of disappearance of these woods appears more complicated than previously supposed. Wood SG minimum does make a one-step shift from the tropical to the temperate sites, as all sites with an MAT <24°C had an SG minimum >0.30. Every site with an MAT ≥24°C had at least one tree species with SG in the range 0.12–0.24. Only a few extremely low SG woods, such as balsa (*Ochroma pyramidale* (Cav.) Urban) and ceiba (*Ceiba pentandra* (L.) Gaertn.), have commercial value. Therefore low SG woods are probably under-represented in the literature, and tropical forests may actually exhibit a lower and more uniform SG minimum than we have documented here. Wood SG maximum increased with MAT along the entire temperature range. The increase appeared to involve at least two steps, one at an MAT of about 17°C, and another at an MAT of about 24°C (Fig. 2A). Clearly more sites are needed to confirm this pattern.

Changes in the range and standard deviation in SG mirrored the aforementioned changes in SG minimum and SG maximum. The step increases in the SG maximum (Fig. 2A) were reflected in apparent step increases in the SG range as MAT increased (Fig. 2B). In contrast,

the SG standard deviation, which measures overall dispersion, not just the extremes, was nearly constant over MAT of 3–22°C, and then increased dramatically for the warmer sites (MAT 23–27°C) (Fig. 2C).

The increases in the SG minimum, maximum, and range were potentially attributable to sample size, since larger sample sizes can increase the likelihood of including extreme values. Although there were significantly more tree species in the warmer sites, there were not necessarily more trees with SG data (Table 1). In fact, the sample size of available SG values explained little of the variation in the SG minimum ($r^2 = 0.04$, $p = 0.39$), the SG maximum ($r^2 = 0.02$, $p = 0.52$), and the SG range ($r^2 = 0.03$, $p = 0.44$). Evidence that the variation in SG increased with MAT was provided by the SG standard deviations. Here the higher variability in SG in the tropics was clearly due to intrinsic variability in tropical woods (Table 2; Fig. 2C).

What causes the loss of extreme SG woods in the temperate zone is still unknown. However, Wiemann et al. (2001) found that wood anatomical characters change from a temperate physiognomy to a tropical physiognomy when frosts become rare, in Florida somewhere between 25° and 29°N latitude. This latitudinal range includes our Florida sites in Marion County (latitude 29.2°N, MAT = 21.7°C, SG maximum = 0.80) and Collier County (latitude 26.2°N, MAT = 23.8°C, SG maximum = 0.89) and includes one of the step changes in the SG maximum. Earlier, Williamson (1984) suggested that the changes in SG occurring in Florida were probably related to solar radiation or cold temperatures, but the change in the SG minimum appeared at a lower latitude than the change in the SG maximum. The data here suggest that the changes in both the maximum and the minimum occur at about the same latitude, but the change in the minimum is much more abrupt (Fig. 2A).

Williamson (1984) showed that elevational changes in SG minimum and SG maximum in Costa Rica were similar to changes across latitudes. As our sample here included only three

sites with elevations above 600 m, and as they occurred at different latitudes and exhibited different MAT values, no conclusions are forthcoming. The two temperate sites, Avery County in North Carolina and the Adirondack upland in New York, showed SG distributions similar to lowland sites with comparable MAT values. However, the Costa Rican montane site was different in that it maintained a higher SG maximum, and concomitantly a greater SG range and standard deviation, than lowland sites of similar MAT. This is perhaps not surprising since tropical montane sites exhibit less extreme cold temperatures than temperate sites with the same MAT and have potentially different precipitation patterns. For example, the Costa Rican montane site had an MAT in the range of north temperate sites (3–10°C), but exhibited a CMMT comparable to the south temperate site at Caddo Parish, LA, and an MAP comparable to the tropical sites (Table 1). Therefore, future comparisons of SG changes across tropical elevations with those across lowland latitudes may be especially fruitful in separating effects of mean temperatures from effects of minimum temperatures and precipitation.

Over our 20 sites, mean annual precipitation explained only 9% of the variance in mean SG, after controlling for MAT (Fig. 1D). This result was somewhat contrary to the finding of Barajas-Morales (1987) that mean oven-dry specific gravity was 34% higher in Mexican dry forest (MAP = 61 cm, MAT = 24.5°C) than in Mexican wet forest of comparable latitude and nearly identical MAT (MAP = 400 cm, MAT = 23.4°C). Comparison of our two lowland sites in Costa Rica showed a mean SG only 9% higher at the dry site (Santa Rosa; MAT = 24.0°C, MAP = 191 cm) than at the wet site (La Selva; MAT = 25.8°C, MAP = 396 cm), but the Mexican dry forest was considerably drier than the Costa Rica dry forest, and this may account for its much larger mean specific gravity. It is also probable that the inclusion of latitudinal variation in our dataset masked the effects of precipitation, since the temperate sites were generally drier, as well as

colder, than the tropical sites, and because MAP showed only modest variation among the temperate sites (Table 1). For the eight sites with an MAT of at least 23°C, corresponding to the high SG standard deviation subgroup (Fig. 2C, Table 2), MAP explained 62% of the variance in mean SG (p = 0.02), but none of the variance in SG minimum (r^2 = 0.29, p = 0.17), maximum (r^2 = 0.22, p = 0.24), range (r^2 = 0.30, p = 0.16), or standard deviation (r^2 = 0.09, p = 0.48). Mean SG decreased 0.00033 per cm of MAP at these sites, and MAT alone explained none of the variance in any SG measure (r^2 = 0.03–0.33, p = 0.13–0.67) among the sites. Therefore, within the tropics MAP may be an important determinant of mean SG, a conclusion certainly supported by Chudnoff (1976), who found that, in low elevation tropical forests, a high proportion of heavy timbers are produced where MAP is 200–400 cm, but regions with lower (100–200 cm) or higher (400–800 cm) rainfalls produce a preponderance of medium SG woods. MAP may be important in the temperate zone as well, but for our 11 temperate sites (MAT < 22°C, latitude north of 29°N) MAP was highly correlated with MAT (r^2 = 0.63), and MAT was a better predictor of mean SG (r^2 = 0.80) than was MAP (r^2 = 0.74) for these sites.

There were several important limitations to our dataset. First, the sites are mostly New World from the Northern Hemisphere. Second, geographically proximal sites are not strictly independent, as they share some species. This is always a difficulty in field-based studies although here it is perhaps more obvious because we employed a single published SG value for species found at more than one site. Third, the number of species with SG data per site was a function of the total number of species growing on a site, the comprehensiveness of wood testing programs (which tend to focus on commercial species), and the availability of test results. No doubt there is much information on tropical species that was not readily available to us. In some instances, extensive specific gravity measurements have been made, but only on an air-dry or an oven-dry

volume basis. For example, Barajas-Morales (1987) compared wet and dry Mexican forests using wood specific gravities determined from oven-dry volumes. It is possible to apply corrections for volumetric shrinkage in order to convert oven-dry SG values to basic SG, but such corrections sometimes have a tropical-temperate bias (Williamson 1984), so we chose to use only data determined and reported as basic SG. Even given the limitations of the dataset, the results that SG mean varies with MAT and MAP are important conclusions for forest management and for estimation of global carbon stocks. Especially where species SG values are not yet determined, as is the case in many tropical forests, local climatic data could provide a proxy for SG mean in biomass estimates. For example, in the Amazon Basin, local MAT isotherms and MAP isohyets could provide more refined SG estimators for mixed species biomass determinations than those based solely on a single SG mean for the entire region (Brown et al. 1989; Fearnside 1996).

CONCLUSIONS

Angiosperm mean wood SG increases gradually with decrease in latitude. However, mean annual temperature is a much stronger correlate of mean SG than is latitude. In addition, mean wood SG decreases with increasing mean annual precipitation, especially among tropical sites. Variability in SG among species at a site increases much more dramatically with mean annual temperature than does the mean SG. Both SG range and standard deviation show steep increases from temperate to subtropical/tropical habitats. Although the much larger number of tree species growing at subtropical/tropical sites could account for the larger ranges in SG, the larger standard deviations can only be attributed to greater overall diversity in woods.

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REFERENCES

ADAMS, M. B., AND D. R. OWENS. 2001. Specific gravity of coarse woody debris for some central Appalachian hardwood forest species. Res. Paper NE-716. USDA Forest Service, Northeastern Research Station. 4 pp.

ALDEN, H. A. 1995. Hardwoods of North America. Gen. Tech. Rep. FPL-GTR-83. USDA Forest Serv., Forest Products Lab. 136 pp.

BARAJAS-MORALES, J. 1987. Wood specific gravity in species from two tropical forests in Mexico. IAWA Bulletin n.s. 8:143–148.

BENDTSEN, B. A., AND R. L. ETHINGTON. 1975. Mechanical properties of 23 species of eastern hardwoods. Res. Note FPL-0230. USDA Forest Serv., Forest Products Lab. 12 pp.

BRAHAM, R. R. 1992. Woody plants of Hill Forest. College of Forest Resources Tech. Rep. #68, Raleigh, NC. 75 pp.

BROWN, S., A. J. R. GILLESPIE, AND A. E. LUGO. 1989. Biomass estimation methods for tropical forests with applications to forestry inventory data. Forest Science 35:881–902.

CADBURY, D. A., J. G. HAWKES, AND R. C. READETT. 1971. A computer-mapped flora: A study of the county of Warwickshire. Academic Press, London, UK. 768 pp.

CHUDNOFF, M. 1973. Physical, mechanical, and other properties of selected secondary species in Surinam, Peru, Colombia, Nigeria, Gabon, Philippines, and Malaysia. FPL-AID-PASA TA(AJ):2–73.

———. 1976. Density of tropical timbers as influenced by climatic life zones. Commonw. Forestry Rev. 55: 203–217.

———. 1984. Tropical timbers of the world. Agric. Handbook No. 607. USDA Forest Serv., Forest Products Lab. 464 pp.

CROAT, T. B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, CA. 943 pp.

DICKINSON, F. E., R. W. HESS, AND F. F. WANGAARD. 1949. Properties and uses of tropical woods, I. Tropical Woods 95:1–145.

DREW, M. B., L. K. KIRKMAN, AND A. K. GHOLSON. 1998. The vascular flora of Ichauway, Baker County, Georgia:

A remnant longleaf pine/wiregrass ecosystem. Castanea 63:1–24.

FEARNSIDE, P. M. 1996. Amazonian deforestation and global warming: Carbon stocks in vegetation replacing Brazil's Amazon forest. Forest Ecol. Mgmt. 80:21–34.

———. 1997. Wood density for estimating forest biomass in Brazilian Amazonia. Forest Ecol. Mgmt. 90:59–87.

GURLAND, J., AND R. C. TRIPATHI. 1971. A simple approximation for unbiased estimation of the standard deviation. American Statistician 25:30–32.

HANES, C. R., AND F. N. HANES. 1947. Flora of Kalamazoo County, Michigan. Schoolcraft. 295 pp.

HARPER, J. L. 1977. Population biology of plants. Academic Press, London UK. 892 pp.

HARTSHORN, G. S., AND L. J. POVEDA. 1983. Checklist of trees. Pages 158–183 *in* D. H. Janzen, ed. Costa Rican natural history. University of Chicago Press, Chicago, IL.

HESS, R. W., F. F. WANGAARD, AND F. E. DICKINSON. 1950. Properties and uses of tropical woods, II. Tropical Woods 97:1–132.

HOWE, J. P. 1974. Relationship of climate to the specific gravity of four Costa Rican hardwoods. Wood Fiber 5: 347–352.

IBARRA MANRÍQUEZ, G., AND S. SINACA COLÍN. 1987. Listados florísticos de México VII, Estación Tropical Los Tuxtlas, Veracruz. Universidad Nacional Autónoma de México, México, Distrito Federal. 51 pp.

JONES, E. W. 1956. Ecological studies on the rain forest of southern Nigeria, IV, The plateau forest of the Okomu Forest Reserve. J. Ecology 44:83–117.

KUDISH, M. 1992. Adirondack upland flora: an ecological perspective. Chauncy Press, Saranac, NY. 320 pp.

KUKACHKA, B. F. 1970. Properties of imported tropical woods. Research Paper FPL 125. USDA Forest Serv., Forest Products Lab. 67 pp.

———, T. A. McCLAY, and E. BELTRANENA-M. 1968. Selected properties of 52 timber species from the department of El Petén, Guatemala. 54 pp.

LAKELA, O., AND F. C. CRAIGHEAD. 1965. Annotated checklist of the vascular plants of Collier, Dade, and Monroe Counties, Florida. University of Miami Press, Coral Gables. 95 pp.

LAVERS, G. M. 1983. The strength properties of timbers (3rd ed.). Forest Products Research Laboratory, London, UK. 60 pp.

LEWIS, P. O., AND E. T. BROWNE. 1991. The vascular flora of Haywood County, Tennessee. J. Tenn. Acad. Science 66:37–44.

LLACH-CORDERO, L. no date. Physical and mechanical properties of 113 species. Report on a wood testing programme carried out for UNDP/SF Project 234, Inventory and Forest Demonstrations Panama. 288 pp.

LONGWOOD, F. R. 1962. Present and potential commercial timbers of the Caribbean. Agric. Handbook No. 207. USDA Forest Serv. 167 pp.

LUNDELL, C. L. 1937. The vegetation of Petén. Carnegie Institution of Washington, Washington, DC. 244 pp.

MACROBERTS, D. T. 1979. Checklist of the plants of Caddo Parish, Louisiana. Bull. Museum of Life Sciences 1:1–54.

MARKWARDT, L. J., AND T. R. C. WILSON. 1935. Strength and related properties of woods grown in the United States. Tech. Bull. No. 479. USDA Forest Serv., Forest Products Lab. 99 pp.

NELSON, B. W., R. MESQUITA, J. L. G. PEREIRA, S. GARCIA AQUINO DE SOUZA, G. TEIXEIRA BATISTA, AND L. BOVINO COUTO. 1999. Allometric regressions for improved estimate of secondary forest biomass in the central Amazon. Forest Ecol. Mgmt. 117:149–167.

NOAA. 1985. Climates of the states, 3rd ed. Gale Research Co., Detroit, MI. 1572 pp.

OWNBEY, G. B., AND T. MORLEY. 1991. Vascular plants of Minnesota. University of Minnesota Press, Minneapolis, MN. 307 pp.

PANSHIN, A. J., AND C. DE ZEEUW. 1980. Textbook of wood technology, 4th ed. McGraw-Hill Book Co., New York, NY. 722 pp.

RADFORD, A. E., H. E. AHLES, AND C. R. BELL. 1968. Manual of the vascular flora of the Carolinas. University of North Carolina Press, Chapel Hill, NC. 1183 pp.

RIJSDIJK, J. F., AND P. B. LAMING. 1994. Physical and related properties of 145 timbers. Kluwer Academic Publishers, Dordrecht, Netherlands. 380 pp.

SANFORD, R. L., P. PAABY, J. C. LUVALL, AND E. PHILLIPS. 1994. Climate, geomorphology, and aquatic systems. Pages 19–33 in L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, eds. La Selva: Ecology and natural history of a neotropical rain forest. University of Chicago Press, Chicago, IL.

SIMMONS, M. P., D. M. E. WARE, AND W. J. HAYDEN. 1995. The vascular flora of the Potomac River watershed of King George County, Virginia. Castanea 60:179–209.

TOENNISSON, R. L. 1992. A collection of wood properties. Forest Resources Development Program. Tennessee Valley Authority. 21 pp.

TUTIN, C., L. J. T. WHITE, E. A. WILLIAMSON, M. FERNANDEZ, AND G. McPHERSON. 1994. List of plant species identified in the northern part of the Lope Reserve, Gabon. Tropics 3:249–276.

USDA FOREST SERVICE, FOREST PRODUCTS LABORATORY.

1999. Wood handbook. General Technical Report FPL-GTR-113.

VAN DER SLOOTEN, H. J. 1968. Report on a wood testing program carried out for UNDP Project 192, survey and development of selected forest areas, Costa Rica. 133 pp.

WANGAARD, F. F., AND A. F. MUSCHLER. 1952. Properties and uses of tropical woods, III. Tropical Woods 98:1–190.

———, A. KOEHLER, AND A. F. MUSCHLER. 1954. Properties and uses of tropical woods, IV. Tropical Woods 99:1–187.

———, W. L. STERN, AND S. L. GOODRICH. 1955. Properties and uses of tropical woods, V. Tropical Woods 103:1–139.

WERNSTEDT, F. L. 1972. World climatic data. Climatic Data Press, Lemont. 523 pp.

WHITMORE, J. L. 1973. Wood density variation in Costa Rican balsa. Wood Science 5:223–229.

WIEMANN, M. C., AND G. B. WILLIAMSON. 1988. Extreme radial changes in wood specific gravity in some tropical pioneers. Wood Fiber Sci. 20:344–349.

———, AND ———. 1989a. Radial gradients in the specific gravity of wood in some tropical and temperate trees. Forest Science 35:197–210.

———, AND ———. 1989b. Wood specific gravity gradients in tropical dry and montane rain forest trees. American J. Botany 76:924–928.

———, D. L. DILCHER, AND S. R. MANCHESTER. 2001. Estimation of mean annual temperature from leaf and wood physiognomy. Forest Science 47: 141–149.

WILBUR, R. L. 1994. Vascular plants: An interim checklist. Pages 350–378 in L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, eds. La Selva: Ecology and natural history of a neotropical rain forest. University of Chicago Press, Chicago, IL.

WILLIAMSON, G. B. 1984. Gradients in wood specific gravity of trees. Bulletin of the Torrey Botanical Club 111: 51–55.

WOFFORD, B. E. 1989. Guide to the vascular plants of the Blue Ridge. University of Georgia Press, Athens, GA. 384 pp.

WUNDERLIN, R. P. 1982. Guide to the vascular plants of central Florida. University Presses of Florida, Tampa, FL. 472 pp.

APPENDIX TABLE 1. *References for species lists and climate data.*

Site	Species list	Weather Station and Reference
Adirondack upland, NY	Kudish 1992	Tupper Lake; NOAA 1985
		Chasm Falls; Wernstedt 1972
Avery Co., NC	Wofford 1989; Radford et al. 1968	Banner Elk; NOAA 1985
Barro Colorado Island	Croat 1978	Barro Colorado; Wernstedt 1972
		Gatún; Wernstedt 1972
		Madden Dam; Wernstedt 1972
Beltrami Co., MN	Ownbey and Morley 1991	Bemidji; NOAA 1985
		Baudette; NOAA 1985
Caddo Parish, LA	MacRoberts 1979	Plain Dealing; NOAA 1985
		Shreveport; NOAA 1985
Central Petén, Guatemala	Lundell 1937	Flores; Wernstedt 1972
Costa Rica montane forest	—	Villa Mills; Wernstedt 1972
Collier Co., FL	Lakela and Craighead 1965	Naples; NOAA 1985
		Everglades; Wernstedt 1972
		Tamiani Trail; Wernstedt 1972
Haywood Co., TN	Lewis and Browne 1991	Brownsville; NOAA 1985
Hill Demonstration Forest, NC	Braham 1992	Durham; NOAA 1985
		Oxford; NOAA 1985
Ichauway, GA	Drew, Kirkman, and Gholson 1998	Camilla; NOAA 1985
Kalamazoo Co., MI	Hanes and Hanes 1947	Kalamazoo; NOAA 1985
King George Co., VA	Simmons, Ware, and Hayden 1995	Fredericksburg; NOAA 1985
La Selva Biological Station, Costa Rica	Hartshorn and Poveda 1983; Wilbur 1994	La Selva bridge; Sanford et al. 1994
		Rafael's Point; Sanford et al. 1994
Lope Reserve	Tutin et al. 1994	Booue; Wernstedt 1972
		Lambarene; Wernstedt 1972
		Lastourville; Wernstedt 1972
Los Tuxtlas Biological Station, Mexico	Ibarra and Sinaca 1987	San Andres Tuxtla; Wernstedt 1972
Marion Co., FL	Wunderlin 1982	Ocala; NOAA 1985
Okomu Forest Reserve	Jones 1956	Benin City; Wernstedt 1972
Santa Rosa National Park, Costa Rica	Hartshorn and Poveda 1983	Quebrada Grande; Wernstedt 1972
Warwickshire, UK	Cadbury, Hawkes, and Readett 1971	Birmingham; Wernstedt 1972
		Coventry; Wernstedt 1972
		Shipston; Wernstedt 1972