United States Department of Agriculture
Forest Service

Forest Products Laboratory

Research Paper FPL–RP–677

Wood Specific Gravity Variation with Height and Its Implications for Biomass Estimation

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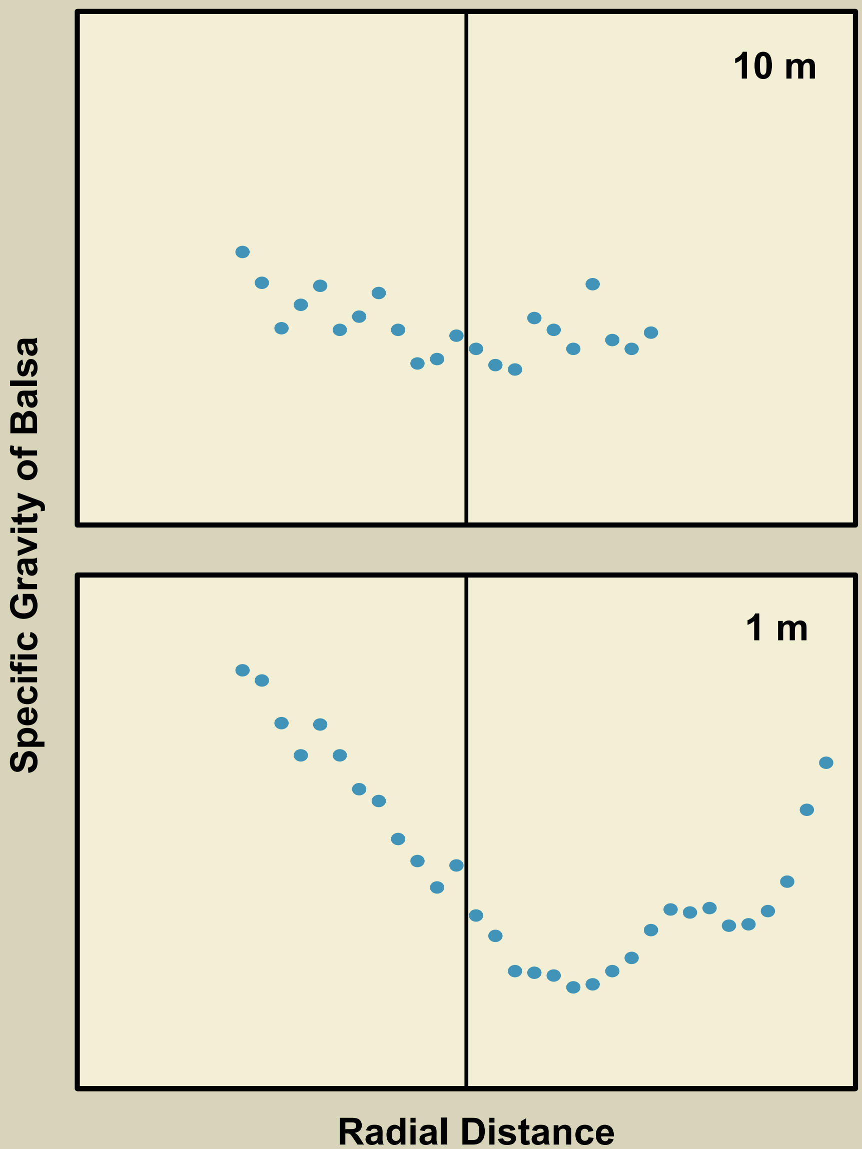

Abstract

Wood specific gravity (SG) is widely employed by ecologists as a key variable in estimates of biomass. When it is important to have nondestructive methods for sampling wood for SG measurements, cores are extracted with an increment borer. While boring is a relatively difficult task even at breast height sampling, it is impossible at ground level and arduous at heights above a couple of meters. Therefore, if a nondestructive estimate of the biomass of a whole stem is required, the variation of SG with height must be known. Here we look at the SG variation with height of five tropical trees, four of which belong to species that have been shown to have extreme variation in pith to bark SG. The results suggest that patterns of variation in SG with height are different among species, and there is no generalized pattern across species.

Keywords: biomass, increment borers, tree cores, height, wood specific gravity

This research was supported by a grant from the Michaux Fund of the American Philosophical Society. Sayra Navas, Sonia Vargas, and Ana Gómez helped with the collecting. Scott Kosiba, Scott Bowe, and Samuel Glass gave critical reviews that improved the manuscript. We gratefully acknowledge the cooperation of the Organization for Tropical Studies. GBW was supported by a grant from the US NSF (DEB 1147434).

January 2014

Wiemann, Michael C.; Williamson, G. Bruce. 2014. Wood specific gravity variation with height and its implications for biomass estimation. Research Paper FPL-RP-677. Madison, WI: U.S. Department of Agriculture, Forest Service, Forest Products Laboratory. 9 p.

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Introduction

Woody biomass of trees can be determined by weighing whole stems or by measuring stem volume and applying estimates of wood specific gravity. Weighing whole stems requires that trees be felled, weighed, and a correction applied to account for moisture content. Nondestructive measurement requires that tree volume be measured and then multiplied by an estimate of wood specific gravity. Basic specific gravity (SG) is used because it directly gives the dry weight contained by a green (undried) volume of wood. SG is defined as the oven-dry weight of wood in a sample divided by the volume of the sample in the green condition, divided by the density of water (= 1 g/cm^3) (Williamson and Wiemann 2010). Green volume of wood from a living tree is easily determined by water displacement. Oven-dry weight is relatively easy to determine by drying a sample in an oven at 101–105 °C, then weighing it quickly before it adsorbs atmospheric moisture (ASTM 2012).

Nondestructive determination of tree volume and biomass requires that diameters and heights be measured, with adjustments made to include branches and below-ground components, if these are desired. Diameters below a height of 2 m can be measured easily using a diameter tape or tree calipers. To make height and diameter measurements higher on the stem without the difficult task of climbing a tree requires more specialized equipment, such as altimeters, hypsometers, clinometers, or relascopes. Because these instruments are expensive and difficult to use in dense forests, an alternative is to use the diameter at breast height (DBH) (1.4 m) and apply factors to estimate other diameters, height, volume, and/or biomass. For example, Molto et al. (2013) compare models used to predict tree height from DBH. Gray (1956) gives a comprehensive analysis of tree form, and its relation to underbark and overbark tree volume, with equations for volume computation. Hahn (1984) and Zianis et al. (2005) give volume equations based on diameter and height for North American and European trees, respectively. For trees from tropical forests, Chave et al. (2005) present equations for calculating biomass from combinations of diameter, height, adjustment for taper, and SG, and Brown et al. (1989) examine regression models for the calculation of biomass using DBH, height, and SG. Some of the models presented by Brown et al. (1989), Chave et al. (2005), and Jenkins et al. (2003, 2004) estimate volume or biomass based on diameter alone.

If a green volume of wood is multiplied by its SG and then by the density of water, the result is the oven-dry weight of the volume of wood. Although this process seems straightforward, a problem arises because SG is not necessarily uniform within a stem. It varies with tree age, across diameters, and with height. This variation has been well documented for some commercial species, but not for the majority of noncommercial, tropical species. One source of SG values is the database described by Chave et al. (2009) and maintained by Zanne et al. (2009), available at the Dryad website (http://datadryad.org/handle/10255/dryad.234). The data come from a wide variety of sources, and although very useful, they are biased toward temperate species and small trees. As such, they are not necessarily representative of mean values for the species included.

For some species, SG is constant from bark to pith. Examples include the temperate angiosperm *Magnolia grandiflora* L. (Fig. 1a) and the tropical angiosperm *Simarouba glauca* DC. (Fig. 1b). Other radial trends have been recorded: a steady increase from pith to bark, linear in *Heliocarpus appendiculatus* Turcz. (Fig. 1c); curvilinear in *Schizolobium parahyba* (Vell.) S.F. Blake (Fig. 1d); a steady decrease from pith to bark in *Quercus copeyensis* C.H. Mull. (Fig. 1e); a decrease outward from pith, then an increase to bark in *Apeiba aspera* Aubl. (Fig. 1f); an increase outward from pith, then a decrease to bark in *Astronium graveolens* Jacq. (Fig. 1g); and finally, erratic variation in *Brunellia costaricensis* Standl. (Fig. 1h) and *Cochlospermum vitifolium* (Willd.) Willd. ex Spreng. (Fig. 1i). The data for Figure 1 were collected by the authors, and the trends are summarized in Wiemann and Williamson (2013).

If SG estimates are required at heights that cannot be sampled easily using an increment borer (such as near ground level or high in the stem), knowledge of the SG variation with height is required. Zobel and van Buijtenen (1989) assert that whole-tree SG can be reliably estimated from breast height SG for both gymnosperms and angiosperms, but their list of species is heavily biased toward temperate trees.

In temperate gymnosperms, SG typically decreases from tree base to top, with many exceptions (Panshin and

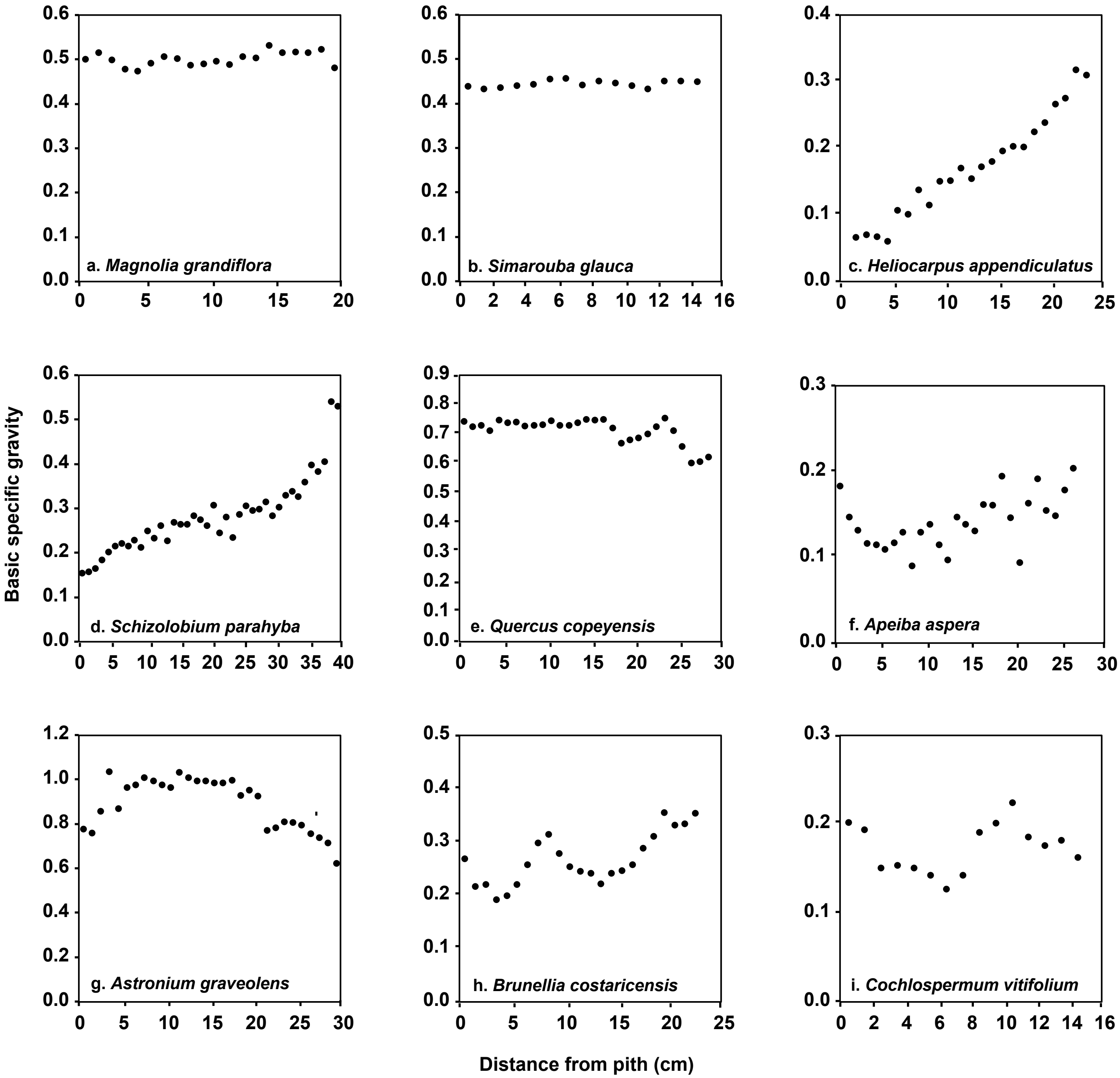

Figure 1. Specific gravity (SG) versus distance from pith (cm) for representative species.

de Zeeuw 1980). Wahlgren and Fassnacht (1959) compared SG measured from a single increment core taken at breast height to SG measured from disks taken along the entire bole of southern pine (*Pinus* spp.); they found SG decreased curvilinearly with height and that core-based SG at breast height was higher than whole-tree SG. Okkonen et al. (1972) presented plots of SG as a function of height in the stem for 27 gymnosperm species of the United States and they reported three trends: an overall decrease in SG with height for species having high percentages of latewood, an overall increase in SG with height for species with low percentages of latewood, and a decrease followed by an increase in SG with height for other species. Pong et al. (1986) developed algorithms to be used to calculate green and oven-dry densities at any height in *Pseudotsuga menziesii* (Mirb.) Franco and *Tsuga heterophylla* (Raf.) Sarg.

In angiosperms, studies on individual species may be necessary to make whole bole estimates of SG, because there are no consistent patterns across species. In *Carya ovata* (Mill.) K. Koch, *Liquidambar styraciflua* L., *Quercus stellata* Wangenh., *Liriodendron tulipifera* L., *Quercus falcata* Michx., *Quercus nigra* L., and *Carya tomentosa* Nutt., Taylor (1979) reported SG increases of 1%–13% with height from 1.5–15 m, but in *Nyssa sylvatica* Marsh. he found a 6% decrease. From breast height to about 20 m, SG increased by 1%–8% in *Platanus occidentalis* L. (Taylor 1969a), *Quercus phellos* L. (Wooten 1968), *Salix nigra* Marsh. (Wooten and Taylor 1968), *Carya illinoensis* (Wangenh.) K. Koch (Taylor 1969b) and *Celtis laevigata* Willd. (Taylor 1971). In contrast, SG decreased by 3% over this height in *Liriodendron tulipifera* L. (Taylor 1968).

The above trends characterize temperate species. For subtropical and tropical species, data on SG with height are very limited. In plantation-grown *Eucalyptus grandis* Hill ex Maiden, Taylor (1973) reported an average increase of 12% in SG from 1.5-m to 26-m height. Whitmore (1973) found a SG decrease of 28% between 0.6-m and 3-m height in Costa Rican *Ochroma pyramidale* (Cav. ex Lam.) Urban. Also in Costa Rican *Ochroma pyramidale*, Rueda and Williamson (1992) found SG increasing with height for wood adjacent to the pith, but remaining relatively constant with height for wood adjacent to the bark. Omolodun et al. (1991) found that, for *Hildegardia barteri* (Mast.) Kossern, SG of wood adjacent to the pith increased with height, whereas it varied erratically with height for wood midway between pith and bark, and wood adjacent to the bark.

In tropical pioneer species, low wood SG early in life has been associated with rapid height growth. This is followed by increasing SG (and therefore increasing wood strength) with distance from pith as a tree attains stature (Wiemann and Williamson 1988, 1989a,b). This offers a selective advantage to increasing SG across a tree radius. To apply the same logic to SG variation with height requires a rationale for how radial variation should vary with height. To maximize growth in stature, SG above the base should reflect the inner portion of the stem base, therein maximizing the volume of wood produced. In contrast, to insure no loss of mechanical strength up the bole, SG above the base should reflect the outer portion of the stem base. These alternative strategies require different mechanisms to control the SG of wood produced along the bole. In the first alternative, all wood produced at the same time (i.e., the outer wood) would exhibit decreasing SG from bottom to top along the bole. In the second alternative, all wood produced at the same time would have the same SG from bottom to top along the bole. Differences among species may reflect selection for different growth strategies. In this report we present and compare data on wood SG with height up the stem for five trees from tropical forests in Costa Rica, documenting how radial variation changes with height.

Materials and Methods

One tree each of *Rollinia microsepala* Standl., *Trema micrantha* (L.) Blume, *Cecropia obtusifolia* Bertolini, and *Ochroma pyramidale* (Cav. ex Lam.) Urban were felled in the canton of Sarapiquí in the province of Heredia (10°20′N, 83°50′W, 100-m elevation). The site is classified as Tropical Wet Forest in Holdridge's Life Zone Classification (Hartshorn 1983). One tree of *Cecropia peltata* L. was felled near Palo Verde (10°20′N, 85°20′W, 100-m elevation), which is classified as Tropical Dry Forest by Holdridge (Hartshorn 1983). *R. microsepala* is slow-growing (Finegan et al. 1999); the other species are fast-growing (Davis 1970; Greenhouse 1935; Silvera et al. 2003).

Tree diameter was measured at breast height, except in the *Cecropia* species, which had stilt roots. In *C. obtusifolia*, tree diameter was measured at 2 m, and in *C. peltata* it was measured at 1.5 m.

The trees were felled near ground level and disks were cut along the boles at regular intervals that depended upon individual tree characteristics. On each disk, a strip approximately 1–2 cm wide was marked across a diameter. The length of each strip was measured, corresponding to the diameter outside the bark (DOB) of the disk. The strips were then cut from the disks, labeled, and wrapped in cellophane to maintain their green condition. Subsequently, the strips were cut into 1-cm segments, each labeled with its distance from the pith (or central hole in the case of *Cecropia*). The number of 1-cm segments from the pith to the bark of each half of the disk is the distance from pith to bark for that half at that height. The total number of 1-cm segments from bark to bark for each disk is the diameter inside the bark (DIB) for that disk at that height.

The green volume of each segment was measured by water displacement (i.e., the weight of water displaced by the green sample). The segments were then placed in a drying oven set at a temperature of 103 °C until dry (24–48 h), after which the dry segments were quickly weighed to 0.001 g. Basic SG was calculated as oven-dry weight/green volume/density of water for each segment.

Each disk was analyzed as two separate halves, referenced arbitrarily as disk side 1 and disk side 2, separated by the pith (or the central holes). The average SG based on each side was computed as a weighted mean (SG_W) of all segments taken from a disk side, calculated as ($SG_W = SG_1 + 3SG_2 + 5SG_3 + \ldots + (2n-1)SG_n)/n^2$. SG_W weights each segment by its relative contribution to the overall cross-sectional area, assuming a circular cross-sectional area. For each half-disk, the SG of the inner wood (SG_I) was calculated as the arithmetic mean of the innermost three segments, and the SG of the outer wood (SG_O) was calculated as the arithmetic mean of the outermost three segments (Wiemann and Williamson 2012). Whole-disk SG values were calculated as the means of the two half-disk values at each height; these means are referred to as Disk SG_I, Disk SG_O, and Disk SG_W.

We compared the changes in SG across each radius using SG_O/SG_I and by plotting segment SG as a function of distance from the pith or central hole. SG values with height were compared for each of the trees.

Results

Tree species, diameters at indicated heights, and total tree heights are given in the first column of Table 1. Then Table 1 gives the height above ground and DOB of each sample disk, the distance from pith to bark, specific gravities (SG_W, SG_I, SG_O), and the ratio of SG_O to SG_I, for each half-disk (disk side 1 and disk side 2), and the DIB, specific gravities, and ratio of SG_O to SG_I for the whole disks.

SG_O was greater than SG_I in every radius from the pioneer species, with SG_O/SG_I ratios of 1.12 to 2.66. The SG_O/SG_I ratio was generally, but not always, greater than 1.0 for the late-successional *Rollinia*, whose ratios were 0.87 to 1.60 (Table 1). Bark to bark SG trends for each tree at each sampled height are presented in Figure 2. Large pith to bark SG increases were evident on the lower boles of the pioneers (*Cecropia, Ochroma, Trema*) but not the *Rollinia*. In the *Cecropia* species, the slopes varied little with height, although SG_I increased with height. In contrast, for *Ochroma*, SG_I was relatively constant with height but pith to bark SG slopes decreased with height. In *Ochroma*, to a height of 8 m, the lowest SG segments were on the wider side of disks with eccentrically located pith, so that the lowest SG wood was in the center of the stem rather than closest to the pith; further up the bole the pith was centered in the disk. SG of *Trema* SG was similar to that of *Cecropia* as far as maintaining steep pith to bark increases up the bole, but similar to *Ochroma* in that SG_I remained constant with height.

In the slow-growing *Rollinia*, SG varied erratically across the radii at different heights, sometimes showing increases, occasionally a decrease, and sometimes random ups and downs. There were marked inconsistences between side 1 and side 2 disks at the same height (Fig. 2).

The changes in SG_I, SG_O, and SG_W with height for the whole disks (Disk SG_I, Disk SG_O, Disk SG_W, respectively), given in Table 1, can be seen graphically in Figure 3. SG_I showed a dramatic increase (127%) with height in *C. obtusifolia*, much more than in any of the other species. *C. peltata* showed a modest increase in SG_I with height, but the values were more erratic and the trend less obvious. *Trema* showed a slight decrease in SG_I, *Ochroma* was constant, and *Rollinia* was erratic. SG_O decreased (by about 35%) with height in *Ochroma* but was relatively constant in the other species (Table 1, Fig. 3). In *Ochroma*, the highest Disk SG_W was at the lowest height; it decreased with height to 4 m, then remained relatively constant. A similar trend was found in *Trema*, although the magnitude of the change was much lower.

In *C. obtusifolia*, SG_W was low at the bottom of the stem and gradually increased with height. The changes were more erratic in the other two species, *Rollinia* and *C. peltata*.

Figure 4 compares the patterns of Disk SG_W with height for the five species. The dashed line on Figure 4 indicates breast height (1.4 m), illustrating the sampling bias that can result by assuming that a breast height increment core represents the whole stem.

Discussion

There is no consistent SG pattern across the five species. At all heights, the four fast-growing pioneer species (*C. obtusifolia*, *C. peltata*, *O. pyramidale*, *T. micrantha*) showed the shift from lower SG wood near the pith to higher SG wood adjacent to the bark that characterize these species, although the magnitude of the shift varied with height. Three factors account for radial variation with height: an increase in SG_I with height (*Cecropia* species) resulting in lower SG_O/SG_I ratios, a decrease in SG_O with height (*O. pyramidale*) also resulting in lower SG_O/SG_I ratios, or relatively constant SG_O and SG_I with height (*T. micrantha*), resulting in stable SG_O/SG_I ratios. SG_O/SG_I ratios varied from 1.12 to 2.66 in these pioneer species (Table 1).

The trends in *R. microsepala* were erratic and hard to characterize. At 1 m, the pith was centered, and SG seemed to increase, then decrease, increase again, and finally decrease adjacent to the bark. At 2 m and 4 m, SG with distance from pith seemed random across the diameter, with a slight tendency to increase near the bark at both sides of the stem at 2 m and one side at 4 m. At 6 m, the trend of increasing SG was not centered on either the pith or the middle of the tree, and at 8 m and 10 m, there were trends of increasing SG with distance from pith on one side of the stem but not the other (Fig. 2).

The decrease in mean SG with height that we found in *Ochroma* (Fig. 4), was also reported by Whitmore (1973). SG_I was relatively constant with height in *Ochroma* in this study (Fig. 3), but Rueda and Williamson (1992) showed an increase in inner wood SG with height in *Ochroma*. All three studies, Whitmore (1973), Rueda and Williamson (1992), and this one found that outer wood SG decreased with height (Table 1, Fig. 3).

Conclusions

This initial study gives an idea of the magnitude of the errors that would occur if breast height SG were assumed to represent whole stem SG. Like change in SG with distance from the pith, change in SG with height seems to characterize the fast-growing tropical pioneer species sampled here.

Although we found differences among species, with only one tree per species we cannot distinguish variation among species from variation within them. Noteworthy in this regard are the two studies on many individuals of *Ochroma*

Table 1. Tree species, diameter (at breast height or above stilt roots at indicated height), and tree height of each disk. Maximum values are in bold, minimum values are in italics for SG columns for each species.

Tree species, diameter, and height	Disk measurements		Disk side 1					Disk side 2					Whole disk DIB, SG averages, and outer/inner ratios				
	Ht, (m)[a]	DOB, (cm)[b]	Pith to bark, (cm)	SG_W[c]	SG_I[d]	SG_O[e]	SG_O/SG_I	Pith to bark, (cm)	SG_W	SG_I	SG_O	SG_O/SG_I	DIB[f] (cm)	SG_W	SG_I	SG_O	SG_O/SG_I
Cecropia	2	46	22	*0.31*	*0.14*	0.38	**2.66**	13	*0.33*	*0.16*	0.42	**2.59**	35	*0.32*	*0.15*	0.40	**2.62**
obtusifolia,	4	37	15	0.31	0.20	*0.35*	1.73	12	0.34	0.23	**0.43**	1.88	27	0.33	0.22	*0.39*	1.81
47 cm at 2 m,	6	31	14	0.35	0.24	0.38	1.57	10	0.38	0.25	0.42	1.67	24	0.36	0.25	0.40	1.62
27 m	8	33	11	0.36	0.28	0.40	1.44	12	0.36	0.26	*0.39*	1.48	23	0.36	0.27	0.40	1.46
	10	30	13	0.35	0.28	0.38	1.36	11	0.38	0.27	0.42	1.57	24	0.37	0.27	0.40	1.47
	12	28	12	0.35	0.30	0.39	1.30	8	0.39	0.33	0.42	1.29	20	0.37	0.31	0.40	1.29
	14	22	8	**0.39**	0.33	**0.42**	1.28	8	**0.40**	0.34	0.42	1.25	16	**0.40**	0.33	**0.42**	1.26
	16	20	8	0.38	**0.33**	0.39	*1.18*	7	0.38	**0.34**	0.40	*1.17*	15	0.38	**0.34**	0.39	*1.17*
Cecropia peltata,	1.5	29	19	0.30	*0.20*	*0.30*	1.48	8	0.34	0.24	0.36	1.51	27	0.32	0.22	0.33	1.49
29 cm at 1.5 m,	2	26	16	*0.28*	0.21	0.31	**1.53**	7	*0.31*	*0.22*	0.34	**1.56**	23	*0.29*	*0.21*	0.33	**1.55**
14 m	4	23	12	0.29	0.22	0.30	1.40	7	0.32	0.27	*0.33*	1.20	19	0.31	0.25	*0.32*	1.29
	6	21	7	0.32	**0.28**	**0.35**	1.23	9	**0.42**	**0.39**	**0.44**	*1.13*	16	**0.37**	**0.34**	**0.39**	*1.17*
	8	18	7	**0.32**	0.28	0.34	*1.22*	7	0.34	0.27	0.37	1.38	14	0.33	0.27	0.35	1.30
Ochroma	1	36	19	0.13	0.10	**0.18**	1.82	12	**0.24**	0.15	**0.27**	**1.83**	31	**0.18**	0.12	**0.23**	**1.83**
pyramidale,	2	34	18	0.11	0.09	0.16	1.75	11	0.20	**0.15**	0.21	1.42	29	0.15	0.12	0.19	1.54
36 cm (DBH),	4	34	16	*0.11*	0.08	0.15	1.78	11	0.15	0.14	0.17	1.18	27	*0.13*	0.11	0.16	1.40
20 m	6	31	14	0.12	*0.07*	0.16	**2.21**	11	0.15	0.15	0.17	*1.12*	25	0.14	0.11	0.16	1.47
	8	29	12	0.13	0.07	0.16	2.16	12	*0.15*	0.14	*0.16*	1.13	24	0.14	*0.11*	0.16	1.49
	10	27	10	**0.13**	**0.11**	*0.13*	*1.13*	12	0.15	*0.12*	0.16	1.38	22	0.14	0.11	*0.14*	1.26
	12	24	8	0.13	0.11	0.13	1.21	12	0.16	0.15	0.18	1.21	20	0.14	**0.13**	0.16	*1.21*
Rollinia	1	32	16	0.30	0.24	0.30	1.25	15	0.29	0.26	0.35	**1.32**	31	0.29	0.25	0.32	**1.29**
microsepala,	2	29	15	0.26	0.22	0.29	1.34	11	0.27	*0.26*	0.31	1.19	26	0.26	*0.24*	0.30	1.26
32 cm (DBH),	4	25	13	*0.24*	*0.21*	*0.25*	1.22	10	0.28	0.28	0.31	1.10	23	*0.26*	0.24	*0.28*	1.15
18 m	6	25	15	0.25	0.29	0.26	*0.87*	8	**0.41**	**0.39**	**0.42**	1.09	23	0.33	0.34	0.34	*1.00*
	8	20	8	0.32	0.22	0.36	**1.60**	10	*0.25*	0.28	*0.26*	0.92	18	0.28	0.25	0.31	1.22
	10	18	6	**0.38**	**0.33**	**0.39**	1.17	10	0.31	0.35	0.32	*0.92*	16	**0.35**	**0.34**	**0.36**	1.04
Trema micrantha,	1	22	9	**0.31**	**0.20**	0.34	*1.67*	11	**0.32**	0.20	**0.36**	1.80	20	**0.32**	**0.20**	**0.35**	*1.73*
22 cm (DBH),	2	20	9	0.31	*0.17*	0.33	**1.98**	9	0.30	*0.17*	0.32	1.91	18	0.30	*0.17*	0.33	**1.94**
16 m	4	18	9	0.31	0.17	**0.34**	1.97	8	0.30	**0.18**	*0.32*	*1.71*	17	0.30	0.18	0.33	1.83
	6	17	6	*0.28*	0.17	*0.30*	1.74	8	*0.28*	0.17	0.33	**1.93**	14	*0.28*	0.17	*0.32*	1.83

[a] Height above ground of the disk.
[b] Diameter outside of the bark.
[c] Weighted mean specific gravity.
[d] Inner specific gravity.
[e] Outer specific gravity.
[f] Diameter inside of the bark.

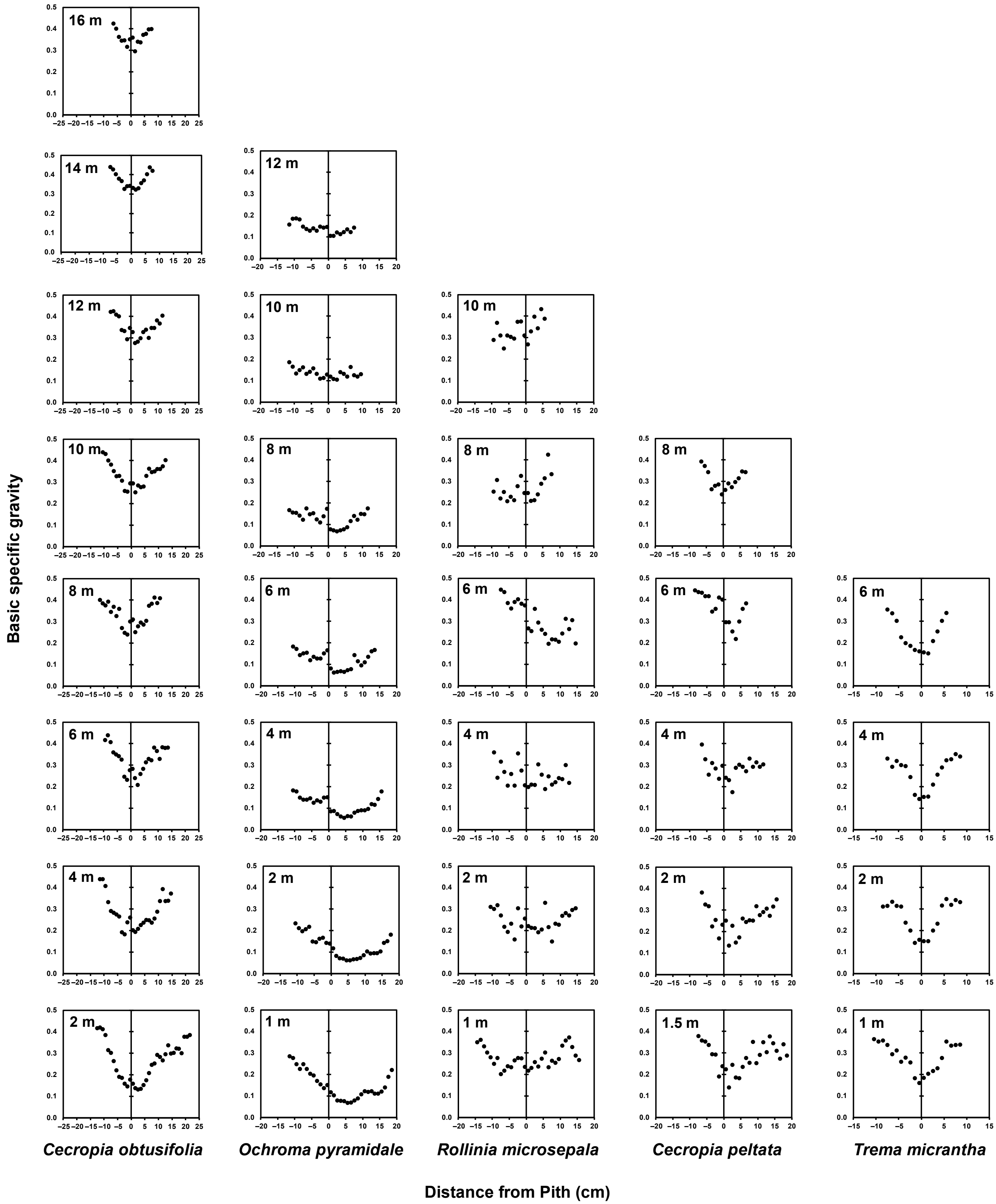

Figure 2. Specific gravity (SG) versus distance from pith (cm) for each species at each height.

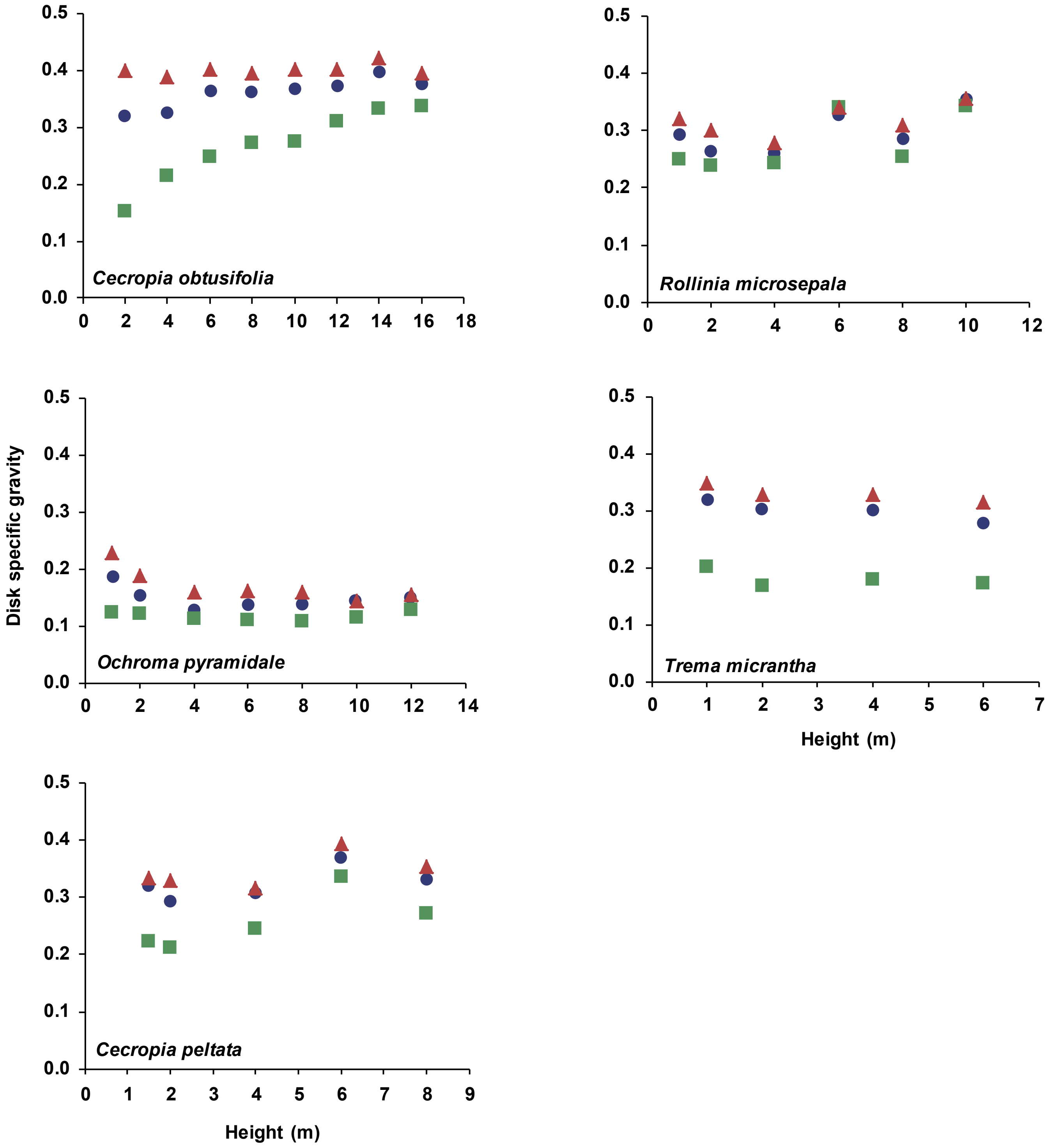

Figure 3. Disk SG_I (squares), Disk SG_O (triangles), and Disk SG_W (circles) as a function of height for the five species.

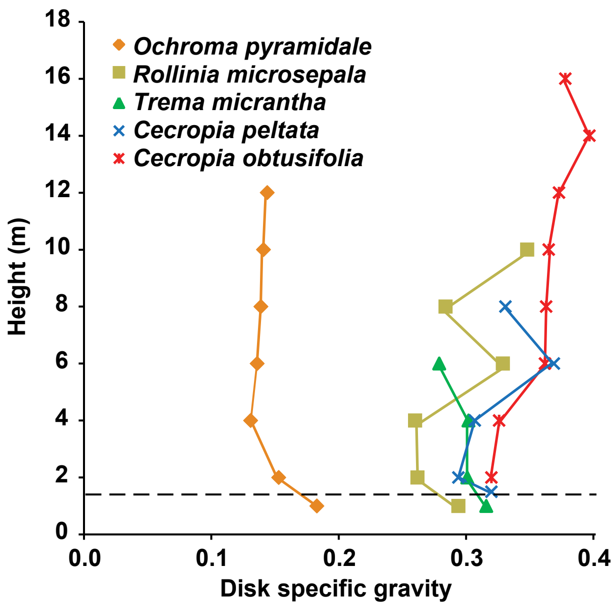

Figure 4. Disk SG_W as a function of height in tree for the five species. Dashed line shows breast height, 1.4 m.

pyramidale in Costa Rica that showed increases with height at one site (Rueda and Williamson 1992) and decreases at the other (Whitmore 1973). Despite the absence of general trends, the presence of variation in SG with height illustrates the importance of understanding how SG varies with height if biomass is to be estimated from wood samples taken only at breast height.

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