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Biomass and production of southern Appalachian cove forests reexamined

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Aboveground biomass and aboveground net primary production (ANPP) were determined for leaf, branch, and bole compartments of cove forests in the Great Smoky Mountains, Tennessee. The sample plots included young stands (42-63 years following agricultural abandonment) and old stands with no history of logging or catastrophic fire. Tree species, diameter at breast height (DBH), and 10-year radial growth increment data were collected on plots of 0.4–1.0 ha. Biomass was estimated with species-specific allometric equations for the Great Smoky Mountains and eastern Tennessee. ANPP was estimated using diameter growth measurements to determine biomass accumulation over the preceding 10-year interval. Biomass estimates for the predominantly deciduous old-growth stands ranged from 326 to 394 $Mg \cdot ha^{-1}$ on plots ≥0.4 ha. These were consistently greater than the corresponding estimates of 216–277 $Mg \cdot ha^{-1}$ for young stands. The old *Tsuga*-dominated stands had the highest biomass estimates of 415–471 $Mg \cdot ha^{-1}$ for 1.0-ha plots. Annual ANPP estimates were high (11.7–13.1 $Mg \cdot ha^{-1}$) among the young stands. These stands had particularly high bolewood production. ANPP of the old-growth plots ≥0.4 ha ranged from 6.3 to 8.6 $Mg \cdot ha^{-1} \cdot year^{-1}$ for the deciduous stands and 8.0–10.1 $Mg \cdot ha^{-1} \cdot year^{-1}$ for the coniferous–deciduous stands. Previous biomass estimates for primeval cove forests were well above temperate forest means of 300–350 $Mg \cdot ha^{-1}$. Our estimates based on larger plots were lower than previous estimates of 500–610 $Mg \cdot ha^{-1}$, but they still exceeded temperate forest means. Our deciduous values were 26–94 $Mg \cdot ha^{-1}$ above the temperate deciduous forest mean of 300 $Mg \cdot ha^{-1}$, and our *Tsuga*–deciduous values were 65–121 $Mg \cdot ha^{-1}$ above the temperate coniferous forest mean of 350 $Mg \cdot ha^{-1}$.

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La biomasse aérienne et la production primaire nette ont été mesurées pour les feuilles, les branches et la tige dans les forêts des vallons encaissés dans les montagnes Great Smoky du Tennessee, aux États-Unis. Les parcelles-échantillons incluaient de jeunes peuplements de 42 à 63 ans sur des terres agricoles abandonnées et de vieux peuplements jamais exploités ni perturbés de façon importante par le feu. Des données sur l'espèce, le diamètre à hauteur de poitrine (dhp) et l'accroissement radial sur 10 ans furent collectées dans des parcelles de 0,4 à 1,0 ha. La biomasse a été estimée à partir d'équations allométriques spécifiques à chaque espèce des montagnes Great Smoky et de la partie est du Tennessee. La production primaire nette a été estimée à l'aide des mesures de croissance en diamètre pour déterminer l'accumulation de biomasse au cours de l'intervalle des 10 années précédentes. Les estimations de biomasse pour les vieux peuplements, pour la plupart à dominance feuillue, allaient de 326 à 394 $Mg \cdot ha^{-1}$ pour des parcelles de ≥0,4 ha. Ces estimations étaient toujours plus élevées que celles de 216 à 277 $Mg \cdot ha^{-1}$ pour les jeunes peuplements correspondants. Les vieux peuplements dominés par le *Tsuga* avaient les estimations de biomasse les plus élevées, soit 415 à 471 $Mg \cdot ha^{-1}$ pour des parcelles de 1,0 ha. Les estimations de production primaire nette annuelle étaient élevées (11,7–13,1 $Mg \cdot ha^{-1}$) chez les jeunes peuplements. Ces peuplements avaient une production particulièrement forte de bois dans la tige. La production primaire nette dans les parcelles ≥0,4 ha des vieilles forêts allait de 6,3 à 8,6 $Mg \cdot ha^{-1} \cdot an^{-1}$ pour les peuplements feuillus et de 8,0 à 10,1 $Mg \cdot ha^{-1} \cdot an^{-1}$ pour les peuplements mélangés. Les estimations antérieures de biomasse pour les forêts vierges dans les vallons encaissés se situaient bien au-dessus des moyennes de 300 à 50 $Mg \cdot ha^{-1}$ pour la forêt tempérée. Nos estimations basées sur des parcelles-échantillons plus grandes sont plus faibles que les estimations précédentes de 500 à 610 $Mg \cdot ha^{-1}$ mais excèdent quand même les moyennes de la forêt tempérée. Nos valeurs pour la forêt décidue sont de 26 à 94 $Mg \cdot ha^{-1}$ plus élevées que la moyenne de 300 $Mg \cdot ha^{-1}$ pour la forêt tempérée décidue et nos valeurs pour la forêt décidue avec *Tsuga* sont de 65 à 121 $Mg \cdot ha^{-1}$ plus élevées que la moyenne de 350 $Mg \cdot ha^{-1}$ pour la forêt tempérée résineuse.

[Traduit par la rédaction]

Introduction

Estimates of primeval cove forest biomass are among the highest for deciduous forests of the temperate zone (ca. 500 $Mg \cdot ha^{-1}$ above ground), and aboveground net primary production (ANPP) estimates for these forests range from 10 to 12 $Mg \cdot ha^{-1} \cdot year^{-1}$ (Whittaker 1966). Young cove forests generally have lower total aboveground biomass, but ANPP may exceed 20 $Mg \cdot ha^{-1} \cdot year^{-1}$ (Whittaker 1966). On poor sites ANPP may fall below 10 $Mg \cdot ha^{-1} \cdot year^{-1}$, even for young stands (Day and Monk 1977; Monk and Day 1988). ANPP, nutrient accumulation rates, and nitrogen fixation rates (by symbionts of *Robinia pseudoacacia*, a colonizing tree species) are high following clear-cutting (Boring *et al.* 1981, 1988; Boring and Swank 1984*a*, 1984*b*). Thus, cove forests exhibit a potential for rapid ecosystem recovery following major disturbance.

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Previous aboveground biomass estimates for old cove forests of the Great Smoky Mountains, based on 0.1-ha plots (Whittaker 1966), are well above temperate forest means of 300–350 $Mg \cdot ha^{-1}$ (Whittaker and Likens 1975; DeAngelis *et al.* 1981; Cannell 1982; Greller 1988). Estimates range from 500 to 610 $Mg \cdot ha^{-1}$ for old-growth plots in cove forests of the Great Smoky Mountains. These high values could be the result of sampling design elements such as plot size and site selection. For example, small plots in areas with high biomass such as stands of large trees, lacking disturbance patches, may produce high estimates. Sampling scale is a critical consideration in the measurement of forest attributes, including biomass (Busing and White 1993). Recently, the mosaic nature of the forested landscape and the role of patch dynamics in community structure have been emphasized (Whittaker and Levin 1977; Bormann and Likens 1979*a*, 1979*b*; Pickett and White 1985). Spatial heterogeneity of this nature must be accounted for in ecosystem-level studies for the findings to be representative of the forest as a whole. In cove forests of the southern Appalachians, small gaps created by individual-tree mortality are important determinants of spatial heterogeneity (Runkle 1982, 1985). Gap size typically ranges from 0.02 to 0.1 ha in temperate deciduous forests (Lorimer 1989). For these reasons, a biomass estimate from one 0.1-ha plot on a nonrandomly selected site cannot be expected to accurately represent stand-wide (1–10 ha) values.

In a previous paper we presented the results of a long-term study on cove forest succession following agricultural abandonment (Clebsch and Busing 1989). Species composition, community structure, and gap processes of adjacent young and old stands were compared in that study. Here we examine ecosystem properties at the same site and at several other cove forest sites in the Great Smoky Mountains. Aboveground biomass and ANPP are determined for leaf, branch, and bole compartments of young stands (42–63 years) and old stands (>400 years). Reasons for the discrepancies between our estimates and those of Whittaker (1966) are examined. We focus on the effects of site selection, sampling scale, and biomass equations on estimated biomass values. We examine (*i*) whether Whittaker's 0.1-ha plots were placed in areas with biomass levels that reflect stand-wide biomass levels at scales approaching 1 ha and (*ii*) whether Whittaker's allometric equations give similar biomass estimates to our more recent equations based on data from the southern Appalachians. In this way the reliability and applicability of Whittaker's initial cove forest biomass estimates can be determined.

Study sites

The primary study site was located in Long Branch cove (83°25′W, 35°41′N), Great Smoky Mountains National Park, Tennessee. Forest plots at the site included young stands following agricultural abandonment circa 1920 and old stands in a "topographic climax" state (Whittaker 1956). All stands at this site were predominantly deciduous. See Clebsch and Busing (1989) for detailed site and community descriptions.

The Long Branch data were supplemented with information from five additional old-growth sites in the park (Table 1). These included two deciduous stands: (*i*) the Indian Camp Creek stand, which contained several large trees (>120 cm DBH), and (*ii*) the Porters Creek stand sampled by Whittaker (1966) and Becking and Olson (1978). Whittaker chose the Porters Creek stand for his "deciduous cove forest" estimates (Whittaker sample 18). We resampled the Porters Creek stand with a much larger plot (0.6 ha) in 1989. The remaining old-growth stands were located in a *Tsuga canadensis* – deciduous forest of the Roaring Fork watershed near Roaring Fork or Surrey Fork (Table 1). All three of the Roaring Fork stands were sampled with 1.0-ha plots in 1990. The Surrey Fork stand was sampled by Whittaker in 1960 for his "hemlock – mixed forest" estimates (Whittaker sample 24).

Methods

Aboveground biomass and production were estimated using species-specific DBH to mass equations for the Great Smoky Mountains and eastern Tennessee (Shanks and Clebsch 1962; Clebsch 1971). These equations were based on logarithmically transformed linear regressions for a variety of tree species over a wide size range of trees (Table 2). Predicted dry weights were adjusted for transformation bias with a correction factor calculated from the standard error of the estimate (Sprugel 1983). Equations for congeneric species were used if regressions were lacking for a species. An equation for a red oak species group was based on data from *Quercus rubra*, *Quercus velutina*, *Quercus coccinea*, and *Quercus falcata* trees. An equation for miscellaneous deciduous species was based on data from *Halesia carolina*, *Sassafras albidum*, *Fraxinus americana*, *Prunus pensylvanica*, *Amelanchier arborea*, *Acer saccharum*, *Betula lenta*, and *Tilia heterophylla* trees. Stand summaries included all live trees >2 cm DBH.

Production in stands YNG1, YNG2, and YNG3 was estimated using average radial growth rates for (*i*) understory and (*ii*) overstory trees. In old-growth stands OLD1 and OLD2, individual growth rates were used for all trees >10 cm and average rates for each species were used for smaller individuals. Species-specific growth rate averages for each dominance class (dominant, codominant, subdominant, or suppressed) were used for the remaining old-growth stands.

Tree species and DBH data were collected in 0.4-ha young-growth plots in 1962, 1968, and 1983. The young forest was initiated circa 1920 following agricultural abandonment, and we estimated the stands to be 42, 48, and 63 years old (Table 1). Ten-year radial growth increments were taken from a sample of understory and overstory trees at breast height. In stands OLD1 and OLD2, 10-year radial growth increments were taken from all trees >10 cm DBH. Tree growth increments were taken from a sample of trees in the remaining old-growth stands, except OLD3; growth data were not collected from this stand.

Net branch and bole production were calculated as the difference in stand mass values obtained from DBH, and DBH minus the 10-year diameter increment. Production was not corrected for ingrowth or for biomass losses from mortality and litter fall over the 10-year period. Leaf production was estimated as the standing leaf mass for deciduous species and as a fraction of standing leaf mass for evergreen species. Based on a maximum leaf retention time of approximately 7 years for the evergreen species, we estimated mean leaf retention time to be 3.5 years, half the maximum. The amount of leaf mass contributing to ANPP was calculated as 3.5^{-1} of the standing evergreen leaf mass.

Results

Total aboveground biomass estimates were consistently greater in the old deciduous stands than in the young deciduous stands (Table 3). Old stands at the Long Branch study site (OLD1 and OLD2) had biomass levels in the 329–394 $Mg \cdot ha^{-1}$ range; the young stands had lower levels, <280 $Mg \cdot ha^{-1}$. There was a trend of increasing biomass up to the 63rd year of stand development. Bole mass increased during this period, but leaf and branch biomass did not.

Aboveground biomass estimates for the old deciduous stands ranged from 326 to 521 $Mg \cdot ha^{-1}$ (Table 3). Estimates for the deciduous stands at Indian Camp Creek (OLD3) and lower Long Branch (OLD1) approached 400 $Mg \cdot ha^{-1}$. The 0.1-ha plot data of Whittaker (OLD4) and Becking (OLD5)

TABLE 1. Study plot descriptions

Code	Stand age (years)	Plot size[a] (ha)	Location	Elev. (m)	Slope (deg.)	Aspect	Basal area ($m^2 \cdot ha^{-1}$)	Dominants	Data collection: Collector	Data collection: Year
Young deciduous stands										
YNG1	42	0.4	Long Branch	945	10	N	41	*Liriodendron*	R.E. Shanks and E.E.C. Clebsch	1962
YNG2	48	0.4	Long Branch	910	10	N	45	*Liriodendron*	E.E.C. Clebsch	1968
YNG3	63	0.4	Long Branch	910	10	N	49	*Liriodendron*	E.E.C. Clebsch	1983
Old deciduous stands										
OLD1	>400	0.6	Long Branch	920	11	N	45	*Acer–Tsuga–Halesia*	R.T. Busing	1987
OLD2	>400	0.6	Long Branch	950	16	N	39	*Halesia–Acer–Tsuga–Aesculus*	R.T. Busing	1988
OLD3	>400	0.4	Indian Camp Creek	975	15	N	47	*Halesia–Acer–Tsuga*	E.E.C. Clebsch	1962
OLD4	>400	0.1	Porters Creek	720	17	N	53	*Acer–Aesculus–Magnolia*	R.H. Whittaker	1959
OLD5	>400	0.1	Porters Creek	720	17	N	56	*Aesculus–Halesia–Magnolia*	R.W. Becking	1977
OLD6	>400	0.6	Porters Creek	720	18	N	40	*Halesia–Aesculus–Acer*	R.T. Busing	1989
Old coniferous–deciduous stands										
OLD7	>400	1.0	Roaring Fork	995	10	N	48	*Tsuga–Halesia–Fagus–Acer*	R.T. Busing	1990
OLD8	>400	1.0	Roaring Fork	960	10	N	55	*Tsuga–Halesia–Acer–Fagus*	R.T. Busing	1990
OLD9	>400	1.0	Roaring Fork	1140	20	N	40	*Tsuga–Halesia–Aesculus*	R.T. Busing	1990
OLD10	>400	0.1	Surrey Fork	870	7	N	66	*Tsuga–Acer–Fagus–Aesculus*	R.H. Whittaker	1960

[a] Dimensions are 20 × 50 m for the 0.1-ha plots, 40 × 100 m for the 0.4-ha plots, 50 × 120 m for the 0.6-ha plots, and 100 × 100 m for the 1.0-ha plots.

gave substantially higher biomass values of 478 and 521 $Mg \cdot ha^{-1}$, respectively, than the 0.6-ha plot (OLD6) estimate of 326 $Mg \cdot ha^{-1}$ from the same site at Porters Creek. Whittaker (1966) obtained an estimate of 500 $Mg \cdot ha^{-1}$ from the OLD4 data. Using the same DBH data, but with bias-corrected species-specific equations, we obtained a comparable estimate of 478 $Mg \cdot ha^{-1}$. At a scale of 0.1 ha it did appear that deciduous stand biomass could reach levels near 500 $Mg \cdot ha^{-1}$ (e.g., plots OLD4 and OLD5). This was not typical of larger land areas, however. The large plot (0.6 ha) estimate at this site (OLD6) more closely resembled the large plot (0.6 ha) estimates of the deciduous stands at the Long Branch site (OLD1 and OLD2). None of the 0.6-ha plot estimates exceeded 400 $Mg \cdot ha^{-1}$.

The *Tsuga*-dominated stands had the highest biomass levels, ranging from 415 to 621 $Mg \cdot ha^{-1}$ (Table 3). As above, the 0.1-ha plot (OLD10) estimate of 621 $Mg \cdot ha^{-1}$ is considerably higher than all the estimates from larger plots (415–471 $Mg \cdot ha^{-1}$). Whittaker (1966) obtained a similar estimate of 610 $Mg \cdot ha^{-1}$ from the data of this 0.1-ha plot.

Annual ANPP exceeded 11 $Mg \cdot ha^{-1}$ in all but the old-growth stands with large sample plots (≥0.4 ha, Table 4). The three young stands, dominated by *Liriodendron tulipifera*, had ANPP in the 11–14 $Mg \cdot ha^{-1} \cdot year^{-1}$ range. There was a weak trend of increasing ANPP during the 42–63 year period of stand development. Annual bolewood production was consistently higher in the young stands (6.5–7.7 $Mg \cdot ha^{-1}$ for young; vs. 2.5–4.7 $Mg \cdot ha^{-1}$ for old), whereas annual leaf production and bole production estimates were approximately equal among stands, regardless of age. The leaf ANPP estimate for the 0.1-ha plot at Porters Creek (OLD4) was considerably higher than all other estimates, however.

The 0.6-ha plots in deciduous stands OLD1, OLD2, and OLD6 gave total ANPP estimates ranging from 6.3 to 8.6 $Mg \cdot ha^{-1} \cdot year^{-1}$, whereas the 0.1-ha plot (OLD4) gave a high estimate, 11.8 $Mg \cdot ha^{-1} \cdot year^{-1}$. Our OLD4 estimate closely resembled Whittaker's (1966) estimate of 11.5 $Mg \cdot ha^{-1} \cdot year^{-1}$ from the same 0.1-ha plot data. The effect of sampling scale on ANPP estimation was clearly demonstrated by the discrepancy between our 0.1-ha plot estimate (OLD4) and our 0.6-ha plot estimate (OLD6) at Porters Creek. The large-plot value was 27% lower. It should be noted that our 1989 (OLD6) growth increment measurements compared favorably with those from 1959 (OLD4).

The old coniferous–deciduous ANPP estimates were similar among stands, regardless of sampling scale. Total ANPP ranged from 8.0 to 10.1 $Mg \cdot ha^{-1}$. These values were lower than Whittaker's (1966) estimate of 11.5 $Mg \cdot ha^{-1}$ for the 0.1-ha plot at Surrey Fork.

Discussion

Whittaker's (1966) biomass estimates for deciduous and *Tsuga*–deciduous stands from individual 0.1-ha plots are considerably higher than our estimates from larger plots,

TABLE 2. Linear regressions of log(dry weight (g)) versus log(DBH (cm))

Species and compartment	Sample size	Diameter range (cm DBH)	m	b	SEE[a]	R^2
Acer rubrum						
Branch	7	3.6–45.5	1.727	4.956	0.632	0.900**
Bole	7	3.6–45.5	2.347	4.707	0.238	0.992**
Acer saccharum						
Leaf	9	7.4–60.7	1.383	4.081	0.286	0.931**
Branch	9	7.4–60.7	2.216	4.048	0.346	0.959**
Bole	9	7.4–60.7	2.240	5.440	0.111	0.996**
Aesculus octandra						
Leaf	5	7.9–48.0	3.338	−3.259	0.225	0.994**
Branch	20	2.8–55.9	2.025	4.267	0.750	0.897**
Bole	20	2.8–55.9	2.475	3.997	0.189	0.995**
Amelanchier arborea						
Bole	4	8.9–25.4	1.514	7.217	0.147	0.976*
Betula lenta						
Leaf	5	6.1–25.9	2.391	1.659	0.129	0.994**
Branch	5	6.1–25.9	3.463	1.230	0.303	0.984**
Bole	5	6.1–25.9	2.452	4.697	0.131	0.994**
Fagus grandifolia						
Leaf	8	7.6–51.6	1.252	3.929	0.171	0.958**
Branch	8	7.6–51.6	2.376	3.414	0.191	0.985**
Bole	8	7.6–51.6	2.405	4.431	0.162	0.989**
Liriodendron tulipifera						
Leaf	16	2.5–54.0	1.415	3.947	0.369	0.897**
Branch	16	2.5–54.0	1.794	4.537	0.453	0.902**
Bole	16	2.5–54.0	2.395	4.478	0.133	0.995**
Prunus pensylvanica						
Leaf	6	6.3–41.9	1.913	2.359	0.011	0.946**
Branch	6	6.3–41.9	2.517	2.537	0.528	0.925**
Bole	6	6.3–41.9	2.289	4.739	0.090	0.997**
Quercus (red oak group)						
Leaf	11	2.3–72.9	1.735	3.358	0.788	0.867**
Branch	14	11.4–72.9	2.934	1.683	0.431	0.949**
Bole	14	11.4–72.9	2.024	6.009	0.147	0.987**
Sassafras albidum						
Bole	5	6.1–15.2	2.651	3.807	0.231	0.961**
Tilia heterophylla						
Leaf	6	8.1–32.8	2.868	−1.559	0.365	0.958**
Branch	6	8.1–32.8	2.939	0.945	0.376	0.957**
Bole	6	8.1–32.8	2.415	4.222	0.239	0.974**
Tsuga canadensis						
Leaf	10	5.8–85.1	1.294	5.154	0.150	0.990**
Branch	10	6.1–85.1	2.504	2.973	0.354	0.980**
Bole	10	6.1–85.1	2.624	3.486	0.131	0.996**
Deciduous species group						
Leaf	41	4.8–60.7	1.808	2.473	0.674	0.787**
Branch	41	4.8–60.7	2.564	2.638	0.728	0.864**
Bole	41	4.8–60.7	2.385	4.672	0.316	0.967**

NOTE: Form of the regression equation is $\ln(\text{mass}) = m[\ln(\text{DBH})] + b$. *, $p \le 0.05$; **, $p \le 0.01$.

[a] Standard error of the estimate; a correction factor (CF) multiplied by values predicted by regression equations can be obtained as follows: $\text{CF} = \exp(\text{SEE}^2/2)$.

0.4–1.0 ha. He obtained an estimate of 500 $\text{Mg}\cdot\text{ha}^{-1}$ for a deciduous stand and an even greater estimate of 610 $\text{Mg}\cdot\text{ha}^{-1}$ for a *Tsuga*–deciduous stand. After examining his raw data, we conclude that these were probably not randomly chosen plot sites. The deciduous stand plot (0.1 ha) at Porters Creek contained three trees greater than 100 cm DBH. Although our plot was six times larger, only one additional tree >100 cm DBH was encountered. Apparently, the 0.1-ha plot was placed in an area of the stand with higher than average biomass. Similarly, Whittaker's 0.1-ha *Tsuga*–deciduous plot contained more large trees than would be expected to occur in a randomly placed plot. Three individuals of *Tsuga* exceeded 100 cm DBH in the plot. Yet, the average density of *Tsuga* >100 cm DBH was <5 $\cdot\text{ha}^{-1}$ in our 3-ha sample of *Tsuga*–deciduous forest. All the *Tsuga*–deciduous samples, including the 0.1-ha plot, were from the same watershed. Again, the 0.1-ha *Tsuga*–deciduous plot was apparently placed in an area of higher than average biomass for the stand. It is not surprising that Whittaker's cove forest biomass estimates are well above average temperate forest values of 300–350 $\text{Mg}\cdot\text{ha}^{-1}$

TABLE 3. Aboveground biomass of tree leaves, branches, and boles in young and old cove forest stands

Plot	Biomass ($Mg \cdot ha^{-1}$) Leaf	Branch	Bole	Total
Young deciduous stands				
YNG1	4	32	180	216
YNG2	4	36	214	254
YNG3	4	35	238	277
Old deciduous stands				
OLD1	4	89	301	394
OLD2	4	69	255	329
OLD3	5	92	295	392
OLD4	7	85	386	478
OLD5	9	93	420	521
OLD6	4	64	257	326
Old coniferous–deciduous stands				
OLD7	5	97	313	415
OLD8	7	108	326	441
OLD9	6	107	358	471
OLD10	7	152	463	621

TABLE 4. Aboveground net primary production (ANPP) of tree leaves, branches, and boles in young and old cove forest stands

Plot	ANPP ($Mg \cdot ha^{-1} \cdot year^{-1}$) Leaf	Branch	Bole	Total
Young deciduous stands				
YNG1	4.0	1.2	6.5	11.7
YNG2	4.3	1.1	6.4	11.8
YNG3	4.3	1.1	7.7	13.1
Old deciduous stands				
OLD1	3.1	0.8	2.7	6.6
OLD2	3.1	0.7	2.5	6.3
OLD4	7.3	0.8	3.7	11.8
OLD6	4.0	1.0	3.6	8.6
Old coniferous–deciduous stands				
OLD7	3.3	1.1	3.6	8.0
OLD8	3.7	1.5	3.8	9.0
OLD9	4.0	1.4	4.7	10.1
OLD10	3.0	1.2	3.9	8.1

(Whittaker and Likens 1975), as they were based on small plots with large trees.

Another potential source of discrepancy between our estimates and those of Whittaker (1966) is our use of species-specific allometric equations based on data from the Great Smoky Mountains. Whittaker used allometric equations published by other researchers in his estimates, and he states that "mean values for broadleaf deciduous trees were applied to the mixed cove forests." Thus, his deciduous tree equations were not species specific. Applying our equations to the raw data of his 0.1-ha plots at Porters Creek and Surrey Fork, we obtain comparable biomass estimates in both cases. So the major source of discrepancy between our estimates and those of Whittaker is related to sampling scale rather than the equations employed. Our use of plots 4–10 times larger than Whittaker's allowed us to capture more spatial heterogeneity, including small-scale disturbance patches.

In conclusion, while all of Whittaker's (1966) old-growth cove forest biomass estimates were well above temperate forest means, our estimates were less extreme. Our deciduous stand estimates were 26–94 $Mg \cdot ha^{-1}$ greater than the deciduous forest mean (300 $Mg \cdot ha^{-1}$), and our *Tsuga*–deciduous values were 65–121 $Mg \cdot ha^{-1}$ greater than the coniferous forest mean (350 $Mg \cdot ha^{-1}$). Thus, Tsuga–deciduous cove forests do have higher than average stand biomass for coniferous forests of the temperate zone. Earlier estimates from 0.1-ha plots placed in areas with large trees cannot be taken as estimates of average stand biomass. They are best interpreted as maximum cove forest biomass estimates at the scale of 0.1 ha.

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