

Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography

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Abstract

We used forest inventories, conducted in seventy-two 1-ha permanent plots to assess the variation in tree and palm aboveground live biomass (AGLB), and its relation with soil gradients (texture and nutrients) and topography (altitude and slope). Our plots, located at Reserva Florestal Adolpho Ducke, a 10,000 ha reserve in central Amazonia, near the city of Manaus, were systematically spread over 64 km². The plots were long (250 m) and narrow (up to 40 m), following elevational contours. Chemical and physical soil analyses were undertaken using topsoil samples, collected in each plot. The plots covered a soil textural gradient ranging from 8% to 98% percent of sand, slopes varying from 0.5° to 27°, and the maximum difference of altitude among plots was 70 m, ranging from 39 to 109 m a.s.l. The mean total AGLB (palm + trees) for stems over 1 cm diameter breast height (dbh = 1.3 m), was 327.8 Mg/ha (ranging from 210.9 to 426.3) and was similar to other studies in the region. We found a two-fold variation in total AGLB estimates among plots, with soil or topography explaining around 20% of this variation. **AGLB was positively related to either a soil textural gradient (represented by the percentage of clay) or altitude, but was insensitive to slope.** Although slope had no detectable effect on the mean variation of AGLB per plot, it explained 14% of the AGLB in understory and emergent trees. On slopes, AGLB is concentrated mostly in tree classes of small size ($1 \leq \text{dbh} < 10$ cm), whereas in flat areas, most of the biomass is concentrated in a few big trees. When considering palms and trees separately, we found that tree biomass tended to increase in clay-rich soils (mostly located in high areas), whereas palm biomass was higher in sandy soils (low slopes and bottomlands). This study shows that forests in central Amazonia grow in a heterogeneous environment in relation to soil and topography, and this heterogeneity seems to be in part responsible for differences in structure and AGLB accumulation. In the forest around Manaus, topography can be used to predict aboveground live biomass as an alternative to soil variables, with similar predictive power. Topographic variables can be easily assessed using satellite imagery and could improve current estimates of carbon stocks over large areas in the Amazon.

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1. Introduction

Tropical forest biomass estimates are a useful way to assess the forest carbon stocks and emissions to the atmosphere during deforestation and changes in land cover (Fearnside, 1996; Malhi and Grace, 2000). Carbon content in plant tissue is approximately, half of the dry weight of aboveground live biomass (Higuchi et al., 1998; Malhi and Grace, 2000), which is strongly correlated with trunk diameter; therefore it is possible

to use regressions models to convert trunk diameter data into an estimate of biomass (Brown, 1997).

Knowing the spatial variation of forest biomass is important because the emissions of carbon from deforestation are determined by the biomass of the forest actually deforested, not necessarily by the average biomass for a region (Houghton, 2005). Therefore, it is essential to describe the variation of biomass at multiple scales. Biomass varies across broad environmental gradients of moisture and temperature, and it varies at fine scales as a result of natural disturbances (Houghton, 2005). Tropical forests exhibit large spatial variability in tree biomass (e.g. Laurance et al., 1999; Chave et al., 2001, 2003) but this variation is poorly documented (Houghton, 2005). For example, most studies recognize

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differences in the aboveground biomass among different forest types in the Amazon (e.g. Houghton et al., 2001), but there is little information to evaluate the variation in carbon stocks within a single forest type (for an exception, see Laurance et al., 1999). Most available data were obtained either from small plots (≤ 1 ha, see examples in Brown and Lugo, 1992), which are not representative, or very large plots (e.g. 50 ha in Chave et al., 2003), which generally lack replicates and are rarely randomly located in the landscape (Brown and Lugo, 1992; Clark and Clark, 2000; Keller et al., 2001; Clark, 2002; Chave et al., 2004). Furthermore, there is a tendency for researchers to select 'attractive' forests (Sheil, 1995) or to avoid naturally disturbed ones (Körner, 2003). Consequently, these plots may not be useful to assess all the conditions that affect forest biomass. One approach is to replicate the measurements in many plots of the same forest, to encompass the environmental variability across the landscape (Clark and Clark, 2000; Chave et al., 2004).

The first landscape-scale study addressing AGLB distribution in central Amazonia found a two-fold variation in biomass estimates across 1000 km² of terra-firme forest (Laurance et al., 1999). Around 30% of the AGLB variation was explained by soil factors, supporting the idea that biomass accumulation in tropical forest is related to soil quality. However, the plots used by Laurance et al. (1999) were square in shape and, although they covered a wide range of edaphic conditions, were not completely representative of the area. The location of some of these plots were biased because, in smaller reserves (1 and 10 ha), the plots were placed to avoid streams (Fearnside, pers. comm.). Additionally, square 1-ha plots may include a wide variation in topographic and edaphic variables, where part of the plot may be on sandy soil and another on heavy clay.

Magnusson et al. (2005) developed a method to evaluate floristic variation in long, thin plots that follow topographic contour lines. This method was designed to minimize altitudinal variation within plots, increasing the precision of estimates of predictor variables. Long, thin plots, however, have a high perimeter–area ratio, which could lead to errors in the inclusion of individual trees, and reduce the precision of biomass estimates. Therefore, it is important to determine whether the new methodology, which permits the cost-efficient inclusion of trees of all size classes, produces biomass estimates similar to those from conventional square 1-ha plots.

In central Amazonia, soil characteristics are often related to local altitude, i.e. to the position along a soil catena (Chauvel et al., 1987). Soil maps of central Amazonia are very imprecise, but altitude can be determined from topographic maps, or using digital elevation models (DEM) derived from SRTM radar (shuttle radio topographic mission), with a high degree of confidence. Therefore, we tested whether altitude can be used as a surrogate for soil characteristics to predict AGLB.

In this paper, we describe the variation in AGLB in 72 1-ha plots spanning 64 km² of old growth *terra-firme* forest in Reserva Florestal Adolpho Ducke. The permanent plots installed at Reserva Ducke (Magnusson et al., 2005) offer a unique opportunity to evaluate the distribution of AGLB in relation to topographic and edaphic variables over a meso-scale landscape.

The sampling method was designed to replicate the AGLB measurements in plots of the same forest. The main concern was to delineate sample units that maintain similar terrain features by keeping elevation and soil characteristics relatively constant within each plot. The plots were distributed systematically, and represent the topographic and edaphic variation typical of the geological formation *Alter do Chão* underlying about 25% of central Amazonia (Sombroek, 2000). Detailed data on soil chemistry and texture offer a unique opportunity to assess fine-scale variability in central Amazonian soils and to investigate the potential significance of this variability to natural vegetation, influencing the amount of AGLB in each plot. Specifically, we addressed the following questions:

- (1) Do soil and topography explain the variation in tree and/or palm AGLB estimates at Reserva Ducke?
- (2) Based on the strong correlation between soil texture and altitude, can we use only topographic variables to predict AGLB spatial variation in central Amazonia?
- (3) Do soil and topography affect different forest components, such as tree and palm AGLB in the same way?
- (4) Do all tree size classes respond in the same way to topography or are the effects related to size class?

2. Materials and methods

2.1. Study site

This research was conducted at Reserva Florestal Adolpho Ducke, Manaus, Amazonas, Brazil (02°55'S, 59°59'W) between December 2000 and February 2003. The reserve covers 10,000-ha (10 km × 10 km) of old-growth forest located 26 km north-east of Manaus. The vegetation is classified as *terra-firme* forest with a closed canopy, and an understory covered with abundant acaulescent palms (Ribeiro et al., 1999). Canopy height of trees is generally 30–37 m with individuals that reach 40–45 m (Ribeiro et al., 1999). Average annual rainfall at this site is about 2300 mm, with a distinct dry season during July–September with usually less than 100 mm of rain per month during 3 months (Marques-Filho et al., 1981). Mean monthly temperature is stable throughout the year, at around 26 °C (Marques-Filho et al., 1981).

The reserve lies within the geological formation *Alter do Chão*. The soils are derived from Tertiary fluvio-lacustrine deposits, which are sediments derived from the deeply weathered Precambrian Guianan and Brazilian Shields (Chauvel et al., 1987; Sombroek, 2000). The reserve is covered mostly by Oxisols (allic yellow latosols in the Brazilian system) on the plateaus, Ultisols (podzol in the Brazilian system) on slopes, and Spodosols associated with small streams in small valley bottoms (Chauvel et al., 1987; Bravard and Righi, 1989). These soils are typically acidic and very low in nutrients, such as phosphorus, calcium, and potassium (Chauvel et al., 1987). Intensive studies at Reserva Ducke have shown that the clay content of the top 5 cm of soil is highly correlated with altitude (Pearson correlation = 0.94; R. Luizão, unpublished data). When moving from a plateau to a

valley, clay content decreases strongly and sand content increases (Chauvel et al., 1987).

The topography of the reserve is undulating with a dense drainage network forming a pattern of plateaus and valleys with a maximum altitudinal difference of about 100 m (from 40 to 140 m a.s.l.) (Ribeiro et al., 1999). A ridge that runs from north to south through the middle of the reserve separates two major watersheds. Streams to the east flow to tributaries of the Amazon River, and those to the west flow to the Negro River.

2.2. Sampling design

A grid of 18 8 km trails covers an area of 64 km² within Reserva Ducke. We used this grid to systematically distribute permanent plots in the reserve. We established eight plots on each of the nine east-west trails, (72 plots total). All plots were at least 1 km from the edge of the reserve and from one another.

Each permanent plot was 250 m long and was established following the topographic contour. The advantage of this design is that narrow plots following contour lines tend to keep soil conditions homogeneous, given that soil types vary with altitude (Chauvel et al., 1987). By orienting the plots to follow the altitudinal contours, we were able to use long thin plots to capture within-habitat variation in vegetation, while minimizing within-plot variation in topographic variables (Magnusson et al., 2005).

Within plots, trees were mapped, and their diameters at breast height (dbh) were measured (see biomass estimates for details). We established a hierarchical design to sample trees and palms. Trees with dbh ≥ 30 cm were sampled in 1-ha (40 m \times 250 m). Sub-samples of 0.5 ha (20 m \times 250 m) and 0.1 ha (4 m \times 250 m) were used to sample trees with 10 cm \leq dbh < 30 cm and 1 cm \leq dbh < 10 cm, respectively. To map trees and define the area of the plot we used the horizontal area. Although most researchers define plot area using a slope correction, we used horizontal area to provide the same available area for tree crowns, independent of the topography. Plots that have 1-ha of ground area, in steep areas, will have less than 1-ha available for tree crowns (horizontal area). Another advantage of using a horizontal area is that it facilitates transfer of the limits of the plot to maps or satellite imagery.

2.3. Topography

The topographic variables used in this study were altitude and slope. A professional surveyor determined the altitude with the use of a theodolite. The slope across the plot was measured perpendicular to the elevational contour with a clinometer every 50 m along each plot, totaling five measurements per plot. We used the mean of the five measurements to represent the slope of the plot.

2.4. Soil data

A total of 23 soil attributes were recorded from soil-surface samples (0–5 cm) collected within each plot. The field and

laboratory methods used for soil analyses are presented in detail in Mertens (2004), and are briefly summarized here. Soil textural analyses were conducted at INPA (National Institute for Research in the Amazon) and nutrients analyses were conducted at EMBRAPA (Brazilian Agricultural Research Corporation) soil laboratories.

To assess soil properties, a composite sample was made from six topsoil (0–5 cm) cores taken every 50 m along the centerline of the plot. Composite samples for each plot were oven-dried, cleaned by removing stones and fine roots, and passed through a 2 mm sieve. The hydrometer method was used to estimate percent of clay, silt, and sand (<0.002 , 0.002–0.05, and 0.05–2 mm, respectively) (Mathieu and Pielain, 1998). Soil acidity in distilled H₂O was measured with a pH meter. Total N was determined by wet oxidation (Kjeldahl method) converting organic N to ammonium (NH₄⁺) for measurement. Total organic C was determined by wet oxidation in an acid dichromate solution followed by titration with 0.5N FeSO₄ and *o*-phenalpthroline as indicator. The determination of available phosphorus was done by the ammonium molybdate–ascorbic acid method (Murphy and Riley, 1962). The blue color complex formed was read photometrically at 712 nm. K⁺, Na⁺, Cu, Fe, Mn²⁺, Zn⁺ were extracted by the Mehlich 1 method (Nelson et al., 1953) and measured by atomic absorption. Ca²⁺ and Mg²⁺ were also measured by atomic absorption spectrophotometry after extraction with a concentrated 1N KCl solution. The concentrations of Al³⁺ and H⁺ in the soil were determined by titration with 0.025N NaOH solution containing 1% of phenolphthalein as indicator. Cation measures included cation exchange capacity (CEC), which is the sum of K⁺, Ca²⁺, Mg²⁺, Na⁺, Al³⁺ + H⁺; and total exchangeable bases (TEB), which is the sum of K⁺, Ca²⁺, Mg²⁺ + Na⁺. Cations were extracted in a 1 M KCl solution at unbuffered pH of the soil (EMBRAPA, 1997).

2.5. Biomass estimates

We estimated the aboveground dry biomass (AGLB) of live trees and palms for each of the 72 plots. AGLB was estimated by carefully measuring (to the nearest 1 mm) the diameters of trees ≥ 1 cm at breast height (dbh = 1.3 m above the ground). Protocols for diameter measurements depended on tree size. For individuals < 6 cm in diameter, maximum stem diameter was measured with calipers. Boles > 6 cm in diameter were measured with a fabric diameter tape (Forestry Suppliers, model 283D). When the point of measurement (1.3 m above the ground) was affected by buttresses or major stem deformities, measurements were taken 50 cm above any deformity. Measurements of dbh were converted to biomass estimates with a combination of allometric models developed for local forests, depending on the life form and diameter class (Table 1).

The allometric equation used to estimate biomass of arborescent palms is based on dbh and height, but we did not directly measure height. Palm dbh was measured only for individuals with exposed stems, after removal of any old petiole bases. For palm height, we defined a species-specific value based on species descriptions in the “Palm Florula of Reserva

Table 1
Allometric equations used to estimate tree and palm aboveground dry biomass (AGLB, kg ha⁻¹)

Life form	Allometric equations
Trees	
dbh ≥ 1 cm and dbh < 5 cm ^a	AGLB = exp(−1.7689 + 2.3770 × ln(dbh))
dbh ≥ 5 cm and dbh < 20 cm ^b	AGLB = exp(−1.754 + 2.665 × ln(dbh)) × 0.6 ^c
dbh ≥ 20 cm ^b	AGLB = exp(−0.151 + 2.170 × ln(dbh)) × 0.6 ^c
Palms	
dbh ≥ 1 cm ^d	AGLB = exp(−6.3789 − 0.877 × ln(1/dbh ²) + 2.151 × ln(H))

The equations were based on diameter at breast height (dbh, cm) and/or height (H, m).

^a Nascimento and Laurance (2002).

^b Higuchi et al. (1998).

^c The Higuchi et al. (1998) equations, in contrast to the others used in this study, provide wet weight biomass estimates. To correct for that, we assumed that dry weight is 60% of wet weight and we multiply the values obtained by 0.6 to provide dry biomass estimates (Higuchi et al., 1998).

^d Saldarriaga et al. (1988).

Ducke” (Henderson and Scariot, 1993). First, we calculated the median dbh of each species measured in the field and compared this with literature data. If the median dbh of our sample for the target species was coincident with the minimum dbh registered in the Florula, we used the minimum height registered for this species as the value of height for all individuals of this species.

When the median dbh of our species sample was the maximum dbh recorded in the Florula, we use the maximum height for biomass estimates.

2.6. Data analysis

We used Principal Components Analysis (PCA) as the ordination method to describe major gradients in the soil, using a subset of 14 variables (see Table 2 for a list of the soil variables recorded in each plot). We initially conducted all analyses including and excluding carbon and nitrogen, because these are mainly derived from vegetation, and including them in analyses to predict vegetation characteristics would be circular reasoning. Nutrient cations in the topsoil are also derived from vegetation as the soil at greater depth in the Manaus area contains almost no nutrient cations. However, available carbon and nitrogen are cycled directly from atmosphere to soil, mainly thorough plants and are not derived from mineral soil at any depth. The addition of these elements had little effect on the PCA axes. Therefore, we only present the results excluding carbon and nitrogen.

To test the effects of soil gradients and topography on biomass estimates, we used several multiple regression analyses. Pearson correlations were used to test for collinearity between soil gradients (PCA axis) and topography. As altitude was highly correlated with the first PCA axis, we excluded it from analyses involving soils. We ran separate regressions for palms and other trees in order to assess the individual effects of the soil and topography on each of these forest components. We also ran multiple regressions using only the topographic variables slope and altitude to test whether they could predict variation in tree and/or palm biomass estimates. We used the SYSTAT 8.0 package for all analyses (Wilkinson, 1990).

3. Results

3.1. Topography and soil gradients

Soil and topographical variables varied widely among plots (Table 2). The clay content of superficial soil varied

Table 2
Summary statistics of soil and topographic variables measured in 72 permanent plots at Reserva Ducke

Variables	Min	Max	Mean	S.D.
Topography				
Slope (°)	0.50	27.00	9.99	7.48
Altitude (a.s.l.)	39.00	109.00	75.61	20.08
Soil texture				
Clay (%)	1.62	87.74	47.44	33.32
Silt (%)	0.29	14.15	3.37	1.99
Sand (%)	8.00	98.09	49.15	33.84
Acidity				
pH in water	3.45	4.87	4.04	0.27
Carbon				
Organic C (g/kg)	7.31	73.03	28.21	12.27
Primary nutrients				
N (g/kg)	0.52	3.16	1.79	0.71
P (mg/dm ³)	1.00	12.00	3.21	2.28
K (mg/dm ³)	12.00	52.00	24.64	7.89
Secondary nutrients				
Ca ²⁺ (c.mol/dm ³)	0.01	0.25	0.05	0.04
Mg ²⁺ (c.mol/dm ³)	0.01	0.12	0.05	0.03
Na ²⁺ (mg/dm ³)	5.00	24.00	11.96	3.85
Micronutrients				
Cu ⁺ (mg/dm ³)	0.00	0.40	0.15	0.12
Fe ²⁺ (mg/dm ³)	6.00	449.00	164.07	104.45
Mn ²⁺ (mg/dm ³)	0.10	1.90	0.76	0.44
Zn ²⁺ (mg/dm ³)	0.23	2.94	0.52	0.34
Other ions				
Al ³⁺ (c.mol/dm ³)	0.56	2.88	1.68	0.52
Al ³⁺ + H ⁺ (c.mol/dm ³)	5.06	15.11	9.42	2.37
Cations				
Total exchangeable bases (TEB)	25.23	111.26	52.87	18.22
Cation exchange capacity (CEC)	90.09	338.95	204.22	55.65

Table 3

Correlations of 14 topsoil variables (0–5 cm) and three ordination axes produced by Principal Components Analysis

Variables	Axis 1	Axis 2	Axis 3	Altitude	Slope
Clay	0.83	−0.32	0.09	0.94	−0.27
Silt	0.29	−0.12	−0.78	0.25	0.07
pH _(H₂O)	−0.54	0.59	0.07	−0.37	−0.01
P	−0.27	0.56	−0.52	−0.45	−0.08
K ⁺	0.66	0.65	−0.10	0.38	−0.40
Ca ²⁺	0.28	0.70	−0.12	0.05	−0.25
Mg ²⁺	0.44	0.76	0.15	0.18	−0.32
Na ⁺	0.80	0.07	−0.11	0.60	−0.22
Cu ⁺	0.38	−0.14	0.09	0.12	0.06
Fe ²⁺	0.55	−0.56	−0.08	0.48	0.34
Mn ²⁺	0.42	0.57	0.32	0.14	−0.29
Zn ²⁺	0.01	0.48	0.04	−0.12	−0.17
Al ³⁺	0.91	−0.25	0.01	0.74	−0.27
Al ³⁺ + H ⁺	0.92	0.11	0.04	0.63	−0.37
Altitude ^a	0.76	−0.23	0.06	–	–
Slope ^a	−0.28	−0.33	−0.11	–	–
Variation explained (%)	34.12	22.97	7.67	–	–

^a Altitude and slope were not included in soil ordinations but we tested the correlation between these variables and each soil variable alone and PCA axes.

from 1.6% to 87.7%. Clay soils were more frequent in the eastern watershed of the reserve, whereas soils in 60% of plots in the western watershed contained 50% or more sand. Altitude varied from 39 to 109 m a.s.l., and slope within plots ranged from 0.5° to 27°.

The ordination analysis revealed three main soil gradients in the study area (Table 3). Axis 1, which captured 34% of the total variation in the dataset, described a gradient between plots with high clay content (and higher K⁺, Mg²⁺, Na⁺, Al³⁺ and Al³⁺ + H⁺), and those with high sand content. Axis 2, which explained 23% of the variation, mainly described a continuum in soil pH, with more acidic sites having higher Fe²⁺ and Al³⁺, and less P, K⁺, Ca²⁺, Mg²⁺, Mn²⁺, and Zn²⁺. Axis 3 explained 8% of the variation and described a gradient in silt and P.

Soil gradients and topography were related. Axis 1 was correlated to altitude ($r^2 = 0.76$; $P < 0.001$), but was not correlated to slope ($r^2 = -0.28$; $P = 0.18$). The soil variables associated with this axis were also correlated with altitude (data not shown). Axis 2 reflects mainly the soil fertility and was not correlated with altitude ($r^2 = -0.23$; $P = 0.57$), but was moderately correlated with slope ($r^2 = -0.33$; $P = 0.04$). None of the variables associated with the axis 2 were individually correlated with slope (data not shown).

3.2. Variation in tree and palm density and AGLB

In the 72 plots, total AGLB (tree + palm) of stems over 1 cm dbh had a two-fold variation, ranging from 210.9 to 426.3 Mg/ha (Fig. 1), with a mean of 327.8 ± 41.9 Mg/ha (\pm S.D.). The mean tree biomass per plot (palms excluded) was 325.6 Mg/ha (S.D. = 43.2), ranging from 189.8 to 422.8 Mg/ha (Appendix A). The class containing trees with

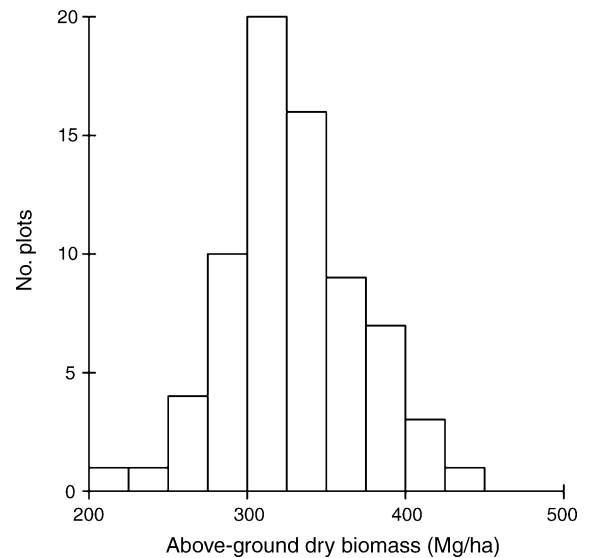


Fig. 1. Frequency distribution of aboveground dry biomass of live trees in seventy-two 1-ha plots in central Amazonia.

dbh < 10 cm held the majority of the individuals, but represented only 6% of the total tree biomass. Around 38% of AGLB estimates per plot were due to trees with dbh between 20 and 40 cm (Table 4). Emergent trees (dbh \geq 70 cm, *sensu* Clark and Clark, 1996) occurred in low densities (\sim 4 individuals/ha) but represented, on average, 12% of total tree biomass per plot. Giant trees (dbh \geq 150 cm, *sensu* Laurance, 2001) were found only in six plots, always in very low density (\sim 1 individual/ha). An individual of this size could contain around 10% of the entire plot biomass (40 Mg/ha; S.D. = 10.7 Mg/ha, $n = 7$).

The number of individuals and the biomass of palms varied greatly among plots (Appendix A). Around 3.4% of the individuals of each plot were palms (range: 0–18.7%). Most palms had dbh < 20 cm, but some species, such as *Mauritia flexuosa*, attained dbh greater than 50 cm. The mean palm biomass per plot was 2.1 Mg/ha, ranging from 0.0 to 21.2 Mg/ha. Most plots (76%) had palm biomass estimates lower than 2 Mg/ha. Palm biomass represented less than 1% of the total biomass in all plots combined, but palm biomass attained 10% of the total biomass in one plot.

Table 4

Mean AGLB of trees and number of individuals of different diameter size classes in seventy-two 1-ha plots at Reserva Ducke, Manaus, Brazil

Classes of dbh (cm)	AGLB (Mg/ha)	No. of individuals (ha ⁻¹)	% AGLB (Mg/ha)
≥ 1 , <10	19.4 (4.5)	4307.5 (1085.2)	6.1 (1.8)
≥ 10 , <20	45.8 (7.7)	363.1 (63.0)	14.3 (3.0)
≥ 20 , <30	63.5 (13.0)	59.8 (11.9)	19.7 (4.1)
≥ 30 , <40	58.0 (10.3)	51.4 (9.0)	17.9 (2.8)
≥ 40 , <50	45.9 (11.1)	23.7 (5.8)	14.1 (2.8)
≥ 50 , <60	32.4 (12.1)	10.8 (3.9)	9.8 (3.2)
≥ 60 , <70	20.7 (10.2)	4.8 (2.4)	6.0 (3.1)
≥ 70	41.3 (27.3)	4.5 (2.8)	12.2 (7.1)

Values are mean \pm standard deviation (in parentheses).

Table 5
Results of multiple regressions relating aboveground dry biomass of live trees and/or palms to soil (PCA axes 1, 2 and 3) and topography (slope and altitude)

Biomass components	$b_{\text{soil gradients}}$			$b_{\text{topography}}$		R^2	P
	PCA1	PCA2	PCA3	Slope	Altitude		
Tree + palm	–	–	–	–0.206	0.347*	0.21	<0.000
	0.353*	–0.017	0.021	–0.231	–	0.22	0.002
Palm	–	–	–	–0.310*	–0.429*	0.18	0.001
	–0.247*	0.694*	–0.070	–0.006	–	0.55	<0.001
Tree	0.364*	–0.074	0.026	–0.224	–	0.22	0.002
	–	–	–	–0.174	0.372*	0.21	<0.001

The values represent the standard coefficient (b) associated with each predictor variable. This coefficient indicates the magnitude of the effect of the independent variable on AGLB estimate. * $P \leq 0.005$.

3.3. Effects of soil gradients and topography on AGLB estimates

Around 20% of the spatial variation in AGLB estimates could be predicted from soil characteristics and slope (Table 5). AGLB was positively related to mineral soil PCA axis 1 ($t = 3.13$; $P = 0.003$) indicating higher biomass on more clay-rich substrates (Fig. 2). In all analyses, the plot with smallest AGLB estimates was a statistical outlier. This plot was located near a second order stream, characterized by poorly drained soil with predominance of large arborescent palms, such as *M. flexuosa* and *Oenocarpus bataua*. Excluding this outlier increased the predictive power of the regression: slope and soil gradients explained 29% of the AGLB variation ($F_{4,66} = 6.66$, $P < 0.001$). PCA axis 1 was positively related to AGLB estimates ($t = 3.23$, $P = 0.002$).

The model using only topographic variables explained 21% of the variation in AGLB estimates (Table 5). The total biomass increased with altitude ($t = 3.05$; $P < 0.001$) but was not affected by slope. The model excluding the outlier explained 24% of the AGLB variation ($F_{2,68} = 10.74$, $P < 0.001$), with a positive effect of altitude ($t = 2.76$, $P = 0.007$) and a negative effect of the slope ($t = -2.47$, $P = 0.016$).

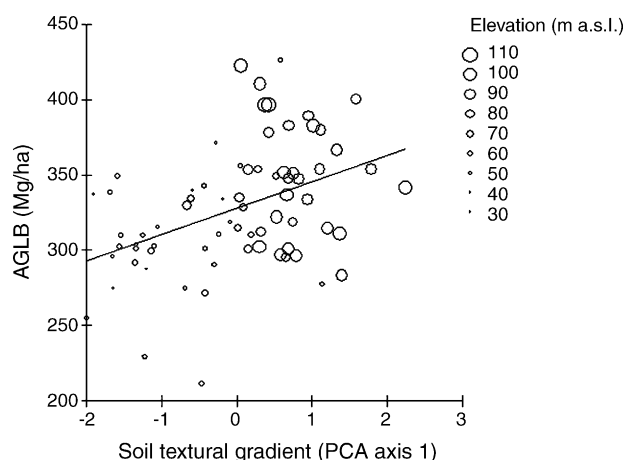


Fig. 2. Relationship between PCA axis 1 and aboveground biomass of live trees in seventy-two 1-ha plots located at Reserva Florestal Adolpho Ducke. Positive values in the soil textural gradient represent plots with high clay soil. The size of the dots indicates the elevation of each plot. Higher AGLB estimates were found in plots with clay soils and these are generally located at higher elevation.

The trends observed for tree AGLB estimates excluding palms were very similar to the total AGLB estimates (Table 5). However, variation in palm AGLB did not follow the same pattern. Palm biomass was highly affected by soil and topography. The multiple regressions of PCA axes and slope explained 55% of the variation in palm AGLB. The slope of the terrain and the PCA axis 3 did not contribute significantly to the model, but the two soil variables (PCA axes 1 and 2) did (Table 5). The relation between PCA axis 1 and palm AGLB was negative, indicating that higher palm biomass was found in soils with more sand. However, the relationship between PCA axis 2 and palm AGLB was positive, indicating a strong positive effect of soil pH, P and or base availability on palm AGLB. The model using only topographic variables explained 18% of the variation in palm AGLB (Table 5). Palm biomass was negatively related to altitude ($t = -3.71$, $P < 0.001$) and slope ($t = -2.68$, $P = 0.009$).

3.4. Effects of topography on AGLB by tree size class

The effects of topography on AGLB estimates depended on tree size class. Slope affected mainly the AGLB of small ($1 \text{ cm} \leq \text{dbh} < 10 \text{ cm}$) and big trees ($\text{dbh} \geq 70 \text{ cm}$). The AGLB of small trees increased with slope, but the opposite trend occurred for emergent trees (Table 6). Slope alone explained 14% of the AGLB variation in trees $1 \text{ cm} \leq \text{dbh} < 10 \text{ cm}$ ($F_{1,70} = 11.19$; $P = 0.001$) or $\text{dbh} \geq 70 \text{ cm}$ ($F_{1,70} = 11.18$; $P = 0.001$).

Table 6
Results of multiple regressions relating AGLB estimates of different tree size class to topography (slope and altitude)

Size class	Slope	Altitude	F	P	R^2
$\geq 1, < 10$	(0.41)**	NS	5.99	0.004	0.15
$\geq 10, < 20$	(0.31)*	(0.31)*	5.01	0.009	0.13
$\geq 20, < 30$	(0.29)*	NS	2.76	0.070	0.07
$\geq 30, < 40$	NS	NS	1.86	0.163	0.05
$\geq 40, < 50$	NS	(0.42)**	11.04	<0.000	0.24
$\geq 50, < 60$	NS	(0.26)*	2.97	0.057	0.08
$\geq 60, < 70$	NS	NS	3.21	0.047	0.09
≥ 70	(–0.35)**	NS	5.62	0.005	0.14

The values in parentheses represent the standard coefficient (b) of variables that contributed significantly to the model. This coefficient indicates the magnitude of the effect of the independent variable on AGLB estimate. NS = $P > 0.05$; * $P < 0.05$; ** $P < 0.005$.

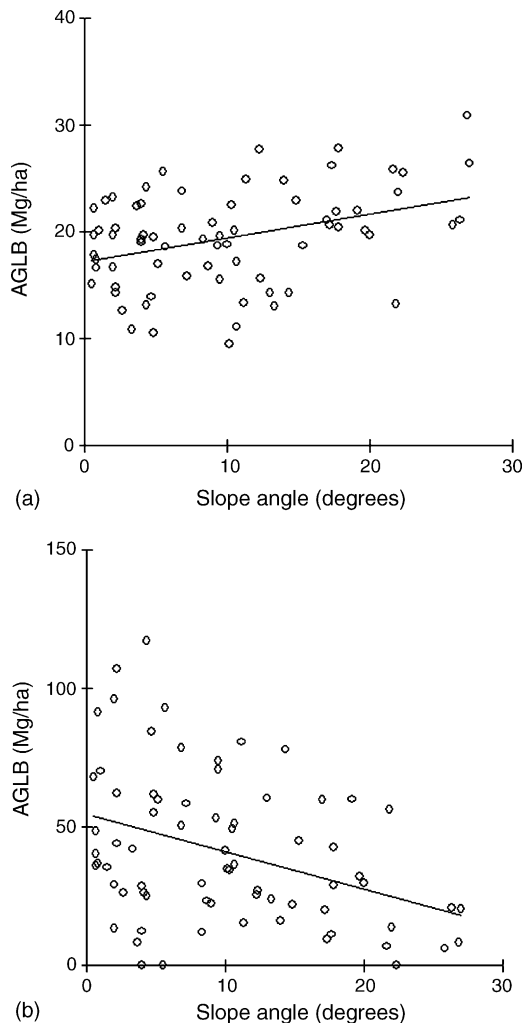


Fig. 3. Effects of slope (°) on aboveground live biomass (AGLB, Mg/ha) of (a) understory and sub-canopy trees (1 cm ≤ dbh < 10 cm) and (b) emergent trees (dbh ≥ 70 cm). The lines on parts a and b represent linear regressions ($AGLB = 17.1 + 0.23 \text{ slope}$, $r^2 = 0.14$, $F_{1,70} = 11.19$, $P = 0.001$ and $AGLB = 54.5 - 1.348 \text{ slope}$, $r^2 = 0.14$, $F_{1,70} = 11.18$, $P = 0.001$, respectively).

(Fig. 3). AGLB estimates of trees with 30 cm ≤ dbh < 40 cm were not affected by topography. Slope did not explain the spatial variation in AGLB of canopy trees (40 cm ≤ dbh < 60 cm), but altitude positively affected their biomass. The size class (40 cm ≤ dbh < 50 cm) with small canopy trees was the most affected by topography ($F_{2,69} = 11.04$, $P < 0.001$). Altitude ($t = 3.75$, $P < 0.001$) and slope ($t = -1.36$, $P = 0.18$) explained 24% of the AGLB variation in this tree size class, but altitude alone explained 22% (Fig. 4).

4. Discussion

4.1. Effects of soil and topography on aboveground tree live biomass

Soil and topography explained almost one third of the variation of the aboveground tree live biomass in our study site. Although a large proportion of the variation remains unexplained, we have evidence that small differences in soil texture and

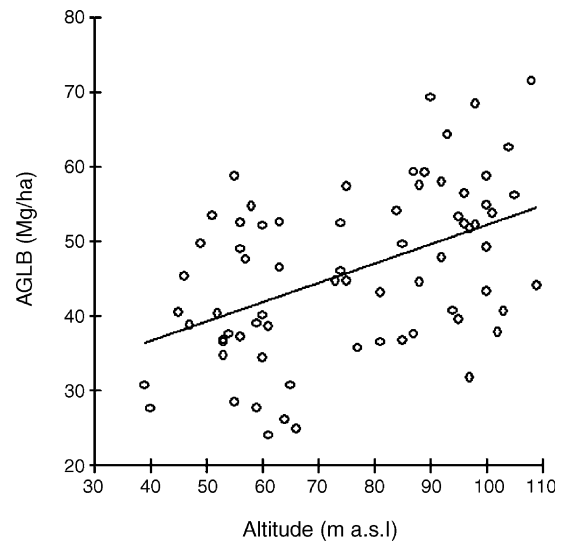


Fig. 4. Effects of altitude on canopy-tree (40 cm ≤ dbh < 50 cm) aboveground live biomass (AGLB, Mg/ha). The line represents a linear regression ($AGLB = 36.4 + 0.85 \text{ altitude}$, $r^2 = 0.22$, $F_{1,70} = 19.99$, $P < 0.001$).

fertility could affect biomass accumulation. The soil textural gradient (PCA axis 1) was the main variable associated with AGLB variation in this study. Texture is one of the most important characteristics of the soil, influencing directly and indirectly a cascade of relations between organic matter, ions, and soil drainage (Fearnside and Leal Filho, 2001; Silver et al., 2000). Zarin et al. (2001) considered soil texture as a constraint on aboveground biomass accumulation in an Amazonian second-growth forest, because sandier soils are characterized by lower productivity. The influence of soil texture on productivity may be related to moisture, nutrient availability, and nutrient cycling. Soil nutrients (PCA axis 2) were not strongly associated with the variation in AGLB. The limited variation in soil fertility in the tropics and the seasonal variation in key indicators of soil fertility, such as cations, phosphorus, and pH, could explain the lack of a relationship between nutrients and biomass (Sollins, 1998).

Laurance et al. (1999) attributed the great spatial variation on AGLB estimates to nitrogen availability. However, we excluded this element from our analyses and obtained similar results suggesting that tree live biomass might not be limited by nitrogen. Tropical plants play a vital role in controlling nutrient losses. Plants act as source of nutrients (deposition of litter) and sink of nutrients by increasing nutrient sequestration when they are more available. Higher tree biomass could provide more litter, resulting in a positive relationship between biomass and nutrients; higher biomass could also be the result of more nutrient availability. Plants have the potential to affect nutrient levels, to which they respond. Luizão et al. (2004) found a significant difference between soil total nitrogen and nitrogen leaf concentration and topographic positions in central Amazonia. Plateau and slope areas had more nitrogen in the topsoil and leaves than *baixio* areas, emphasizing the close relationship between the amount of nitrogen in the soil and in living tissues. This also could indicate that the rates of decomposition and mineralization are perhaps slower on sandy soils.

Soil and topography could also indirectly affect AGLB variation through changes in species composition, forest dynamics, and physiological constraints driven by soil and topography. Several studies have described the effects of soil and topography on the distribution of trees (Lescure and Boulet, 1985; Sabatier et al., 1997; Clark et al., 1999; Tuomisto et al., 2003) and understory plants (Kinupp and Magnusson, 2005; Costa et al., 2005). If species characterized by large individuals were associated with a particular soil type, this pattern will be related to forest biomass (Fearnside and Leal Filho, 2001). Any effect of soil on the occurrence of emergent species could have a large effect on plot AGLB estimates, because few large individuals can account for a large portion of the plot's AGLB (Brown and Lugo, 1992; Clark and Clark, 1996). This seems to be the case at Ducke, where bigger trees were more frequent in high and flat areas dominated by clay soils.

Differences in forest biomass can also be imposed by physiological constraints of soil and topography. In general, higher forest biomass is expected on more fertile soils, independent of species composition, simply because there are more resources available for plant growth. However, Silva et al. (2002) studied the growth rates of trees along a topographic gradient in central Amazonia and did not detect a topographic influence on growth rate.

It is difficult to establish causal relationships between topography and biomass because topography is a composite variable that covaries with other variables such as soil type (Chauvel et al., 1987), canopy openness (Robert, 2003) and soil water potential (Becker et al., 1988; Daws et al., 2002). Topography also affects forest dynamics (Gale and Barfod, 1999; Bellingham and Tanner, 2000) and nutrient cycling (Luizão et al., 2004). There is some evidence that topography affects the frequency of gaps (Bellingham and Tanner, 2000) and the way trees die (Gale and Barfod, 1999). Therefore, the AGLB variation could represent variation in the natural disturbance regime of the forest. The topographic effects on tree biomass accumulation described here are certainly not due to the topography *per se*, but to environmental conditions defined by the topography.

In contrast to our results, AGLB estimates from other tropical forests were insensitive to soil type and/or topography (Clark and Clark, 2000; Chave et al., 2001, 2003). However, most studies were not specifically designed to address soil or topographic effects on AGLB estimates. Results from Panama (Chave et al., 2003) and French Guiana (Chave et al., 2001) were from large and continuous plots (50 and 20 ha, respectively) that could be biased by site selection and too large to detect gradients along the catena.

4.2. The contribution of palms to aboveground live biomass estimates

Although palms are conspicuous components of tropical forests, they are frequently excluded from AGLB assessments or are treated as trees (e.g. Laurance et al., 1999), mostly because general palm allometric equations are scarce (e.g. Saldarriaga et al., 1988; Cummings et al., 2002) or species-

specific (e.g. Frangi and Lugo, 1985; Hughes et al., 1999). In contrast to trees, most palms change little in diameter while growing in height. The use of tree equations probably overestimates palm biomass, but this should have a modest effect on total estimates (Clark and Clark, 2000), since palms are a relatively minor component of AGLB. In our study, palms represented less than 1% of AGLB estimates per plot. However, palm biomass was highly variable between plots and, in some plots, the biomass of palms represented 10% of the total biomass. Palm biomass also varies between forest types (Cummings et al., 2002) and sites (Clark and Clark, 2000; DeWalt and Chave, 2004). Fearnside (1994) suggested that palms generally contribute about 3.5% of the aboveground biomass in the Brazilian Amazon. At large spatial scales, forests dominated by large palms covered about 20% of the original forest area in the Brazilian Amazon (IBGE, 1997). This means that, at least in some areas, arborescent palms are especially abundant, and make up large proportions of the aboveground live biomass.

Considering palms separately from other life forms should be useful to better understand the structural differences between tropical forests and the role of non-tree components in models of carbon balance in changing landscapes (Brown and Lugo, 1992). It is possible that the high palm biomass in certain areas will affect nutrient cycling processes, such as decomposition rates. Palm leaves on the ground decompose slowly, while palm trunks decompose faster than tree boles (Frangi and Lugo, 1985) and this could potentially affect the carbon cycle.

In this study, we only sampled stemmed palms. Stemless palms are very common in understory of forest around Manaus and, on average, represent 0.4% of AGLB (Nascimento and Laurance, 2002).

4.3. Comparing results with other studies

The shape of the plot apparently had little influence on our estimate of the aboveground live biomass in terra-firme forests around Manaus. In this region, both studies (Laurance et al., 1999, this study) dealing with large-scale variation in aboveground live biomass produced similar results, despite using different methodologies. Laurance et al. (1999) used 65 1-ha square plots, obtaining an AGLB mean value of 356 ± 47 Mg/ha, while in this study we used 72 1-ha thin plots that followed topographic contours and obtained an AGLB mean value of 328 ± 41.9 Mg/ha. A study comparing the effect of different methodologies (circular plots vs. square plots) found a 10–16% difference in basal area and aboveground live biomass estimates between the methods, but the authors considered that those differences were likely to be due to measurement protocols rather than the form of the plot (Clark and Clark, 2000). The results of our study and those of Laurance et al. (1999) indicate that different plot shapes can produce similar estimates when tree-measurement protocols and allometric regressions are similar. Although the allometric regressions (Santos, 1996) used by Laurance et al. (1999) make higher biomass estimates for trees over 90 cm dbh, those equations probably make lower biomass estimates for medium size trees,

and some sort of compensation may have acted to level off the overall estimates (B. Nelson, pers. comm.).

In this study, we investigated a more complete soil textural gradient than Laurance et al. (1999). However, after excluding one outlier, we found similar results to those of Laurance et al. (1999). The outlying plot presented the lowest biomass of our sample and one of the extremes of the soil gradient investigated. It had much sandier soil than any plot studied by Laurance et al. (1999), but also may have had a much higher water table. This result indicates a greater variation in AGLB biomass than that due simply to soil texture, and future studies should investigate other variables, such as soil drainage, that may inhibit AGLB accumulation.

4.4. Implications for regional biomass estimates

The relationships between soil, topography and AGLB estimates could improve our predictions of the responses of the forest to natural or anthropogenic perturbations. This could generate differences in carbon fluxes between patches of soil types, even when carbon stocks are similar between areas (Clark and Clark, 2000). Therefore, long-term biomass dynamics could depend on soil and topographic variation, at least in central Amazonia.

At present, it is not easy to use the relationship between biomass and soils to predict AGLB in other areas. The spatial variability of soil properties in the Amazon region, although recognized, has not been well documented or mapped at high resolution (Richter and Babbar, 1991). This creates problems for extrapolating results from plot-level studies to estimate effects over large areas (Holmes et al., 2004). However, this study

showed that topography could be used as a proxy for soil texture in central Amazonia, where the effects of soil and AGLB spatial variation are well documented (Laurance et al., 1999; this study). Topographic variables (altitude and slope) can be obtained from maps, or using digital elevation models (DEM) derived from SRTM radar. As an alternative to soil variables, topography could be used to predict aboveground live biomass over large areas in central Amazonia with almost the same predictive power.

The Amazon forest has an important role in the global carbon budget (Fearnside, 2003), but we still have little data to make reliable predictions. The methodology used at Reserva Ducke is efficient and feasible for long term studies of tree biomass. We believe that similar ongoing studies in other areas (see <http://www.ppbio.inpa.gov.br>) are an efficient way to improve our knowledge on AGLB spatial variation over the entire Brazilian Amazon.

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Appendix A

Total AGLB (tree + palm) estimates and topographic features of each one of the 72 permanent plots installed at Reserva Ducke, Manaus, Brazil. The estimates were based on plots with 1-ha of planar area. Soil data are available in <http://ppbio.inpa.gov.br/Port/inventarios/ducke/>.

Plot code	Total AGLB (Mg/ha)	Tree AGLB (Mg/ha)	Palm AGLB (Mg/ha)	Slope angle (°)	Altitude (m a.s.l.)	Ground area (ha)
LO2T0	211.0	189.8	21.2	2.0	61	1.00
LO9T500	229.0	226.0	3.1	17.0	60	1.05
LO4T1500	254.7	245.0	9.7	10.7	55	1.02
LO2T4500	271.1	269.8	1.3	25.8	65	1.11
LO8T6500	274.4	273.1	1.3	12.3	47	1.02
LO1T7500	274.5	274.3	0.2	15.3	54	1.04
LO6T7500	277.2	276.2	1.0	22.0	60	1.08
LO9T6500	282.8	280.4	2.4	4.0	96	1.00
LO5T7500	287.2	284.0	3.2	17.3	39	1.05
LO5T5500	290.1	289.3	0.8	5.5	60	1.00
LO6T500	291.5	291.4	0.2	26.3	64	1.12
LO9T4500	295.1	294.4	0.6	17.8	85	1.05
LO3T7500	295.7	295.0	0.7	4.0	51	1.00
LO7T2500	296.0	295.1	1.0	13.0	101	1.03
LO8T7500	296.7	295.1	1.6	4.3	95	1.00
LO4T6500	299.0	298.2	0.8	11.3	66	1.02
LO6T5500	300.7	300.4	0.3	26.8	77	1.12
LO8T5500	300.7	299.1	1.6	0.7	97	1.00
LO2T6500	300.8	300.7	0.1	10.7	59	1.02
LO6T2500	300.9	291.5	9.3	2.7	60	1.00
LO7T4500	302.0	301.7	0.3	2.0	100	1.00
LO3T1500	302.3	302.1	0.2	8.3	61	1.01

Appendix A (Continued)

Plot code	Total AGLB (Mg/ha)	Tree AGLB (Mg/ha)	Palm AGLB (Mg/ha)	Slope angle (°)	Altitude (m a.s.l.)	Ground area (ha)
LO6T1500	302.5	297.5	4.9	21.8	53	1.08
LO8T500	303.4	294.8	8.6	4.8	52	1.00
LO9T5500	309.6	307.9	1.7	14.8	57	1.03
LO7T500	309.8	309.1	0.7	13.3	58	1.03
LO7T7500	310.1	309.8	0.3	27.0	63	1.12
LO3T3500	310.1	295.0	15.2	10.2	55	1.02
LO4T3500	310.5	309.7	0.8	4.0	105	1.00
LO7T1500	312.0	309.0	3.0	17.7	84	1.05
LO9T7500	314.1	312.7	1.4	4.2	97	1.00
LO2T2000	314.5	314.2	0.3	17.8	75	1.05
LO6T6500	315.1	314.6	0.6	17.2	53	1.05
LO3T2500	318.6	317.7	0.9	10.3	53	1.02
LO3T500	318.6	316.8	1.8	12.3	81	1.02
LO7T5500	321.8	321.7	0.0	0.8	100	1.00
LO1T5500	328.2	328.2	0.0	20.0	74	1.06
LO2T3000	329.8	329.1	0.7	19.7	81	1.06
LO5T1500	333.5	330.6	2.9	10.5	93	1.02
LO3T6500	333.9	327.3	6.6	9.3	40	1.01
LO6T4500	334.2	333.7	0.5	14.0	75	1.03
LO1T0	334.6	334.1	0.6	22.3	85	1.08
LO4T2500	336.3	334.6	1.7	6.8	100	1.01
LO4T500	337.0	337.0	0.1	2.2	46	1.00
LO8T3500	338.4	333.9	4.5	5.2	56	1.00
LO2T7500	339.9	339.5	0.4	6.8	45	1.01
LO5T3500	341.4	340.7	0.7	0.7	103	1.00
LO1T6500	342.7	341.8	0.8	19.2	59	1.06
LO7T6500	347.1	346.6	0.6	8.7	95	1.01
LO4T7500	347.6	347.5	0.2	1.0	88	1.00
LO8T2500	349.0	347.1	1.9	10.0	63	1.02
LO3T5500	349.2	348.8	0.4	21.7	74	1.08
LO4T4500	351.0	350.8	0.2	1.5	98	1.00
LO6T3500	351.4	349.7	1.7	8.3	100	1.01
LO4T5500	353.4	352.9	0.5	0.7	92	1.00
LO9T2500	353.6	353.4	0.1	9.0	87	1.01
LO5T2500	353.8	353.3	0.4	9.5	73	1.01
LO5T4500	353.9	353.8	0.1	3.7	94	1.00
LO5T500	356.1	345.9	10.2	3.3	56	1.00
LO2T5500	366.3	365.8	0.5	0.5	96	1.00
LO8T1500	371.3	368.8	2.5	5.7	49	1.00
LO9T1500	378.0	376.7	1.3	11.2	87	1.02
LO5T6500	379.6	379.2	0.3	2.2	90	1.00
LO8T4500	382.1	379.6	2.4	2.0	102	1.00
LO7T3500	382.6	382.1	0.5	4.8	92	1.00
LO1T4000	389.2	389.2	0.0	7.2	89	1.01
LO1T2000	396.3	395.4	0.9	2.2	109	1.00
LO1T1000	396.5	395.3	1.2	0.8	108	1.00
LO3T4500	400.0	399.4	0.6	9.5	88	1.01
LO2T1000	410.3	409.3	1.1	14.3	98	1.03
LO1T3000	422.3	419.6	2.7	4.7	104	1.00
LO9T3500	426.3	422.8	3.5	4.3	56	1.00

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