Journal of Tropical Ecology (2009) **25**:473–482. Copyright © 2009 Cambridge University Press
doi:10.1017/S0266467409990095 Printed in the United Kingdom

Dissecting biomass dynamics in a large Amazonian forest plot

Renato Valencia*,[1], Richard Condit†, Helene C. Muller-Landau‡, Consuelo Hernandez*
and Hugo Navarrete*

* Laboratorio de Ecología de Plantas y Herbario QCA, Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Apartado 17-01-2184, Quito, Ecuador
† Global Forest Observatory Network, Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Balboa, Ancón, Panamá, República de Panamá
‡ Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Balboa, Ancon, Panamá, República de Panamá

(*Accepted 30 May 2009*)

Abstract: Above-ground biomass (AGB) is increasing in most of the Amazon forests. One hypothesis is that forests are responding to widespread and intense human intervention prior to the European conquest ($>$500 y ago). In this study we confront this hypothesis with changes in AGB over 6.3 y in a large western Amazonian forest plot ($>$150 000 shrubs and trees and 1100 species with dbh $\geq$ 10 mm in 25 ha). We examined AGB flux in different habitats and across diameter classes. The forest lost small stems (4.6%), gained large trees (2.6%), and gained biomass (0.7%). The change in AGB stock was due entirely to this upward shift in size leading to more canopy trees and fewer saplings after just 6 y. Across habitats, the biggest increment in biomass was in the secondary-forest patch (3.4% y^{-1}) which we know was cleared about 27 y ago, whereas mature forest on ridges and valleys had small increases (0.10% and 0.09% y^{-1}, respectively). In both censuses, AGB stocks were $>$50% higher on the ridge than in the valley while relative growth and mortality were higher in the valley. Mean wood specific gravity (WSG) decreased with increasing diameter class; WSG did not change much between censuses in mature forests and did not contribute to the change in AGB stocks. Our forest increased its standing biomass, but far less than the average reported for other Amazonian forests (i.e. 0.30 vs. 0.98 Mg ha^{-1} y^{-1}). We find no evidence to support the notion that this forest is recovering from long-past human intervention. Instead of a long-term recovery, we believe the forest changed in response to natural fluctuations of the environment (e.g. changes in precipitation, higher CO_2), windstorms or other more recent events. The significant differences in AGB stocks between valley and ridge suggest that the terra firme forests are a mosaic of natural habitats, and that this mosaic is in part responsible for the variation in biomass stocks detected in Amazonian terra firme forests.

Resumen: La biomasa aérea de la mayoría de los bosques amazónicos está incrementando. Una hipótesis es que los bosques están respondiendo a un disturbio humano intenso y ampliamente distribuido, anterior a la llegada de los conquistadores europeos ($>$500 años atrás). En este estudio se confronta esta hipótesis con los cambios en biomasa encontrados en 6.3 años en una parcela de gran escala de la Amazonia occidental ($>$150.000 arbustos y árboles con diámetro a la altura del pecho $\geq$10 mm y 1100 especies en 25 ha). Los resultados se examinan por categorías de diámetro y hábitat. En este período el bosque perdió tallos pequeños (4.6%), ganó árboles grandes (2.6%) y ganó biomasa (0.7%). La ganancia en biomasa fue debida enteramente al incremento de árboles de gran tamaño que significó más árboles de dosel y menos juveniles en apenas 6 años. Entre los hábitats, el mayor incremento en biomasa se encontró en un parche de bosque secundario de colina (3.4%/año), cuya edad es de 27 años, mientras el bosque maduro de las colinas y los valles incrementó escasamente (0.10% y 0.09%/año, respectivamente). Tanto al inicio como al final del estudio, el stock de biomasa fue $>$50% más grande en la colina que en el valle mientras que el crecimiento y la mortalidad relativa fueron mayores en el valle. La media de la gravedad específica de la madera (GEM) fue menor a mayor clase diamétrica; en el bosque maduro, el cambio en la GEM fue insignificante y no contribuyó al aumento en stocks de biomasa. El bosque incrementó la biomasa aérea pero mucho menos que el promedio reportado para otros bosques amazónicos (i.e. 0.30 vs. 0.98 Mg ha^{-1}/año). No se encontró evidencia que apoye la noción de que el bosque se está recuperando de un disturbio de gran escala ocurrido en el pasado. En su lugar, se cree que el bosque cambió en respuesta a fluctuaciones naturales del ambiente (e.g. cambios en precipitación, mayor concentración de CO_2), vendavales u otro tipo de eventos más recientes. La diferencia significativa en los stocks de biomasa encontrada entre el valle y la colina sugiere que la tierra firme es un mosaico de hábitats naturales y que este mosaico podría explicar en parte la variación encontrada en los stocks de biomasa de bosques amazónicos de tierra firme.

Key Words: Amazonia, biomass dynamics, climate change, Ecuador, growth, tropical trees, Yasuni National Park

---

[1] Email: lrvalencia@puce.edu.ec

INTRODUCTION

Evidence from both tree plots and eddy flux measurements suggests Amazonian forests are carbon sinks (Baker *et al.* 2004, Grace *et al.* 1995, Phillips *et al.* 1998). Tree biomass, recruitment and death all appear to be increasing through time. One hypothesis for the biomass increase is CO_2 fertilization, or more broadly, any climatic fluctuation favouring higher growth. Alternatively, changes might be due to long-term succession after a major disturbance, perhaps a climatic event (Chave *et al.* 2008) or widespread anthropogenic disturbances that ended about 500 y ago, when human populations decreased due to diseases brought by European conquerors (Heckenberger *et al.* 2007, Roosevelt *et al.* 1991, Wright 2005).

Nearly all inferences about forest and carbon dynamics of Amazonia, the largest tropical rain-forest formation of the world ($\sim$6 million km^2) are based on measurements on relatively large trees (diameter $\geq$10 cm), measured in small forest plots (1 ha), loosely scattered in this area. We propose here a different approach based on data from a 25-ha forest plot in which all stems $\geq$1 cm dbh were measured, tagged and identified to species or morphospecies. The plot dataset consists of >150 000 shrubs and trees with dbh $\geq$10 mm, in 1100 species (Valencia *et al.* 2004). Our approach is to dissect the details of forest change by intensive inventory at a single site. We have already shown overall biomass increase in our plot (Chave *et al.* 2008). Here, we examine diameter distributions and change through time, and differences across local habitats, in order to shed light on the possible causes. We also predict that if the forest is recovering from past disturbance, then the wood specific gravity should increase through time, as is expected to occur in successional forests (Brown & Lugo 1990). Finally, we examined differences between major topographic habitats (ridge and valley) as well as the changes in a secondary forest patch.

MATERIALS AND METHODS

Study site

Yasuni National Park is the largest protected forest in continental Ecuador, covering 980 000 ha, and adjacent to an additional 600 000 ha of forest in the Huaorani Indian territory. The terrain is undulating, dissected throughout by streams of many sizes, varying in elevation generally by <100 m. Soils are acidic (pH inside the plot averages 4.63), dominated by silt and clay and moderately low in nutrients (Tuomisto *et al.* 2003); details about nutrient concentration inside the plot are published elsewhere (John *et al.* 2007).

Upland forest dominates most of the landscape, dotted by inundated forests on floodplains and small swampy depressions. It is visually homogeneous, tall, evergreen forest, lacking large disturbances, and highly diverse. The canopy is 10–25 m tall punctuated with emergents to 50 m and small gaps created by fallen trees. Pottery remains indicate Native Americans occupied the site (Netherly 1997), but presently the human population density is very low. Areas near roads and rivers, including our study site, are hunted. More information about the study site is published elsewhere (Valencia *et al.* 2004).

Climate

Rainfall and temperature are largely aseasonal, and every month averages >100 mm precipitation. During the past 7 years of records at the research station, the longest rainless period was 3 weeks and the least rainy month was August (Valencia *et al.* 2004).

The forest census

A 50-ha plot of forest at 0°41′S, 76°24′W, just south of the Tiputini River, was demarcated in 1995 (Figures 1 and 2 in Valencia *et al.* 2004 show plot location). We report here on the western 25 ha, where we have completed two censuses (March 1995–June 1999 and October 2002–November 2003) of stems dbh $\geq$ 1 cm. This section ranges from 216 to 248 m asl, and includes two ridges and an intervening valley, plus a small section of another valley on the north boundary. The valley occasionally floods but only for brief periods.

Habitat categories

We considered three major habitat divisions based on topography and history: ridge, valley and secondary forest (Valencia *et al.* 2004). These three habitats were defined after evaluating finer divisions by elevation, slope and convexity, and finding that the bulk of the variation in tree species composition in the plot is associated with these three units. The valley was defined as all 20 × 20-m subquadrats with mean slope <12.8° and mean elevation <227.2 m. The remaining quadrats were defined as the ridge, which also included a 0.48-ha patch of secondary forest. This patch was a heliport during oil exploration, abandoned around 1982 and inadvertently included into the plot. Valencia *et al.* (2004) provide more details, along with a map of the habitat units and species distribution maps.

Enumeration and censuses

Tree enumeration followed the standardized methods used in a worldwide network of large forest plots (Condit 1998). Stems were tagged, mapped and identified to morphospecies in 1995–1999, then recensused in 2002–2003. Diameter measurements were taken at 1.3 m above the ground. In stems with swellings at this height, diameters were taken above or below, and the position always paint-marked and recorded (as height above the ground). Diameters were taken well above large buttresses (Condit 1998), and in rare cases, this meant 5–7 m up the stem. In individuals with more than one stem, the largest was always painted so it could be re-identified in subsequent censuses. We always abbreviate diameter as dbh, for 'breast-height', even when the height varied somewhat.

Most dead trees were identified as such because they were completely missing, fallen, or standing but obviously decayed (Condit 1998, Condit *et al.* 1995). Equivocal cases arose, though, where leafless trunks showed little sign of decay. In these cases, death was recorded when the entire stem circumference had soft, decaying wood at the surface. We know from other long-term censuses that a proportion of these trees will reappear alive in the future, but in Panama, the number is so small that it is barely detectable in estimated mortality rates (Condit *et al.* 2004).

Trees that lost a principal stem but resprouted were considered alive. They were excluded from estimates of diameter growth, but not excluded in tallying biomass change. If the sprout was < 10 mm dbh, its diameter was not recorded, and it counts as zero in biomass estimates.

Diversity and taxonomy

In the first census, 1104 morphospecies were recorded, including 151 230 individual trees; 116 151 were identified to species, 27 798 only to genus, 1724 to family alone, and 5557 were not identified at all (Romoleroux *et al.* 1997, Valencia *et al.* 2004). In the second census, there were 1112 morphospecies (it included 32 new and excluded 24 lost) and 145 751 individuals, 115 094 identified to species, 27 644 to genus alone, 1542 to family alone, and 1471 could not be assigned to any taxonomic entity. Among the species, we also recognize 32 subspecies. Although future work will collapse some of the species or subspecies, it will also uncover further species, and we suspect the total richness will remain about what it is now.

Biomass

Above-ground biomass was estimated as

$$AGB = \rho \times \exp(-a + b\ln(dbh) + c(\ln(D))^2 - d(\ln(D))^3)), \qquad (1)$$

where $a = 1.500$, $b = 2.148$, $c = 0.207$, $d = 0.0281$, and ρ is wood specific gravity; AGB is in Mg and dbh is in cm (Chave *et al.* 2005). Wood specific gravity was taken from the literature for 246 species, and for 93 other species we obtained direct measurements in the surroundings of the plot or areas of Yasuni National Park (including 51 species having the highest basal area in the plot). Wood specific gravity at species level was assigned to 75 354 individuals. For 658 species (78 436 individuals) we used the mean published value for congeneric species and for 127 species (11 932 individuals) the mean value of the species in their families. For all remaining species (12 and 7584 individuals), ρ was set to 0.582, the mean density for the known species. Throughout this article, we use biomass to refer to above-ground biomass; nowhere do we mention or consider below-ground stocks.

Confidence limits on biomass and wood specific gravity change were estimated by bootstrapping across 20 × 20-m subquadrats. That is, a random draw of all quadrats was made, with replacement, 1000 times, and each time the total biomass was summed across individuals. The central 95% of the 1000 bootstrap estimates were taken as the 95% confidence range. Relative rates (% y^{-1}) of above-ground biomass (AGB) were calculated as follows:

Relative growth rate = 100 × (log((AGB2–R)/(AGB1–D–L))/ time); where AGB1 and AGB2 corresponds to the AGB in census 1 and 2, respectively, R = AGB of new recruits, D = AGB of dead trees, and L = AGB of stems alive but broken below 1.3 m by the second census (lost stems). Relative mortality rate was estimated as 100 × (log(AGB1/(AGB1–D))/time) and relative net change as 100 × (log(AGB2/AGB1))/time.

Measurement errors

We discarded extreme growth rates in calculations of diameter and biomass change. Trees which increased by more than 40 mm y^{-1} were considered erroneous outliers, as were any which decreased by more than $4s$, where $s = 0.0062$ dbh ± 0.904; s is the estimated SD due to measurement error for the census methods used (Condit 1998). We thus discarded any tree where diameter shrunk by more than 4 SD of error, presuming that such extremes are not simple mis-measurement, but are rather misplaced numbers or decimal places (i.e., recording a 120-mm tree as 12 mm). A total of 180 individuals were excluded by these criteria (~0.1% of all individuals).

For biomass change, these trees could not simply be excluded, since we are interested in total biomass turnover, not the mean per tree. Instead, each of the 180 outliers was assigned the mean growth rate of all other

Table 1. Overall changes in stem size, number of individuals and above-ground biomass (AGB) stocks of trees ≥10 mm dbh in a 25-ha forest plot and its three different major habitats. Ridge (16.64 ha^{-1}) and valley (7.88 ha^{-1}) are topographic habitats, whereas secondary is a young successional forest patch on a ridge (0.48 ha^{-1}). 95% confidence intervals shown in parentheses. Wood specific gravity (WSG) was calculated using all levels of identification and then weighted by volume. Recruitment rate is the entry of stems newly above 10 mm dbh, while loss rate is the loss of stems broken below 10 mm dbh.

	Forest-wide	Ridge	Valley	Secondary
Individuals in census 1 (ha^{-1})	6049 (5947–6143)	6405 (6294–6513)	5123 (4996–5243)	8927 (8165–9550)
Individuals in census 2 (ha^{-1})	5830 (5735–5917)	6132 (6029–6238)	5057 (4939–5180)	8060 (7385–8667)
Change in stem density (ha^{-1})	219 (−165 to 267)	−273 (−331 to −209)	−66 (−140 to 10)	−867 (−1134 to −609)
AGB census 1 (Mg ha^{-1})	272 (261–283)	309 (296–324)	200 (188–213)	152 (139–167)
AGB census 2 (Mg ha^{-1})	274 (262–286)	310 (297–326)	201 (189– 214)	185 (163–205)
AGB change (Mg ha^{-1})	1.9 (−3.3 to 6.5)	1.5 (−5.1 to 7.7)	0.8 (−7.8 to 7.0)	33.0 (22.4–44.1)
WSG 1 (g cm^{-3})	0.530 (0.524–0.537)	0.537 (0.530–0.545)	0.519 (0.505–0.532)	0.371 (0.343–0.408)
WSG 2 (g cm^{-3})	0.527 (0.520–0.534)	0.535 (0.527–0.544)	0.515 (0.500–0.528)	0.366 (0.347–0.393)
Growth rate (Mg ha^{-1} y^{-1})	6.4 (6.1–6.7)	6.8 (6.5–7.2)	5.3 (4.9–5.6)	9.7 (8.0–11.1)
Mortality rate (Mg ha^{-1} y^{-1})	6.1 (5.5–6.9)	6.6 (5.7–7.6)	5.2 (4.3–6.4)	4.5 (3.6–5.4)
Recruitment rate (Mg ha^{-1} y^{-1})	0.162 (0.135–0.190)	0.151 (0.119–0.188)	0.184 (0.138–0.239)	0.242 (0.099–0.489)
Loss rate (Mg ha^{-1} y^{-1})	0.099 (0.081–0.120)	0.096 (0.078–0.118)	0.101 (0.063–0.154)	0.202 (0.097–0.323)
Net AGB change (Mg ha^{-1} y^{-1})	0.30 (−0.53 to 1.05)	0.24 (−0.82 to 1.25)	0.13 (−1.18 to 1.19)	5.24 (3.67–6.76)
Relative AGB mortality rate (%y^{-1})	2.42 (2.17–2.73)	2.30 (1.97–2.65)	2.83 (2.28–3.41)	3.23 (2.45–4.15)
Relative AGB growth (% y^{-1})	2.52 (2.42–2.62)	2.36 (2.25–2.48)	2.86 (2.67–3.07)	6.38 (5.48–7.25)
Relative net change (% y^{-1})	0.11 (−0.19 to 0.38)	0.08 (−0.25 to 0.41)	0.07 (−0.59 to 0.59)	3.44 (2.43–4.35)

trees in the plot in its dbh class in the first census, with dbh classes (10–20), (20–30), (30–40), (40–50), (50–100), (100–200), (200–300), (300–500), (500–1000) and (≥ 1000) mm.

In calculating rates of change, we used the mean time interval for the relevant trees. For example, to calculate the net change in above-ground biomass per year in the valley, we calculated the total net change in above-ground biomass per area in the valley, and then divided by the mean intercensus interval for trees in the valley.

RESULTS

Overall forest change

In 6.3 y, stem density decreased by 3.6%, while the above-ground biomass (AGB) increased 0.7% (Table 1). Confidence intervals on the change in stems did not include zero, while those on biomass change did, meaning spatial variation was sufficient that 25 ha of randomly chosen 20 × 20-m subplots would sometimes (> 2.5% of the time) show biomass decrease. Because our census includes saplings down to 1 cm in stem diameter, the impact of recruitment on biomass was negligible: nearly all the change was due to growth and death (6.4 Mg ha^{-1} y^{-1} growth vs. 6.1 Mg ha^{-1} y^{-1} death).

Overall changes by habitat

All habitats lost stems. The valley lost the fewest, while the secondary forest patch lost 9.7% and the ridge 4.3% (Table 1). At the same time, all habitats showed a trend towards increasing biomass. The patch of secondary forest gained 3.4% y^{-1}, whereas the mature forest gained just 0.08% y^{-1} and 0.07% y^{-1}, in ridge and valley, respectively. Only the change in secondary-forest biomass was significantly greater than zero. Growth was highest in the secondary forest, which grew significantly more than either of the mature forest habitats, gaining 9.7 Mg ha^{-1} y^{-1}, nearly twice as much than in the valley (5.3 Mg ha^{-1} y^{-1}), while the ridge grew an intermediate amount ~30% more than the valley (6.8 Mg ha^{-1} y^{-1}). Absolute mortality rate was highest in ridge and lowest in the secondary forest (Table 1).

Forest changes by diameter categories

The decrease in the number of trees was due almost entirely to a reduction in the number of stems less than 100 mm as a result of mortality, growth out of the size class, and breakage below 10 mm dbh. The number of large trees, greater than 300 mm dbh, actually increased (Table 2). Likewise, biomass declined in the smaller size classes, and the increase in forest biomass was due to an increase in the number of large trees, dbh >300 mm (Table 2, Figure 1). In the forest as a whole, the average dbh increased 0.9 mm between censuses as a result of the shift toward larger trees. The mean biomass per stem decreased in the smallest and largest size classes, but increased in intermediate size classes.

Habitat differences by diameter category

Ridge and valley had parallel changes in stem number and mean diameter, though slightly different in detail

Table 2. Forest-wide above-ground biomass (AGB) in a 25-ha forest plot and stem counts and sizes in two censuses (C1 and C2) separated by an average time interval of 6.3 y.

	Mean dbh (mm)		Stem density (ha^{-1})		AGB per stem (Mg)		AGB (Mg ha^{-1})		
dbh class (mm)	C 1	C 2	C 1	C 2	C 1	C 2	C 1	C 2	C2-C1
10–50	22.8	22.7	4439	4235	0.0014	0.0013	6.1	5.7	−0.38
50–100	68.6	68.3	908	897	0.0166	0.0166	15.1	14.9	−0.22
100–200	140	140	483	477	0.0972	0.0974	46.9	46.5	−0.41
200–300	236	236	138	137	0.358	0.359	49.3	49.2	−0.15
≥300	431	431	82	84	1.89	1.88	154	157	3.07
Total	49.4	50.2	6049	5830	0.045	0.047	272	274	1.90

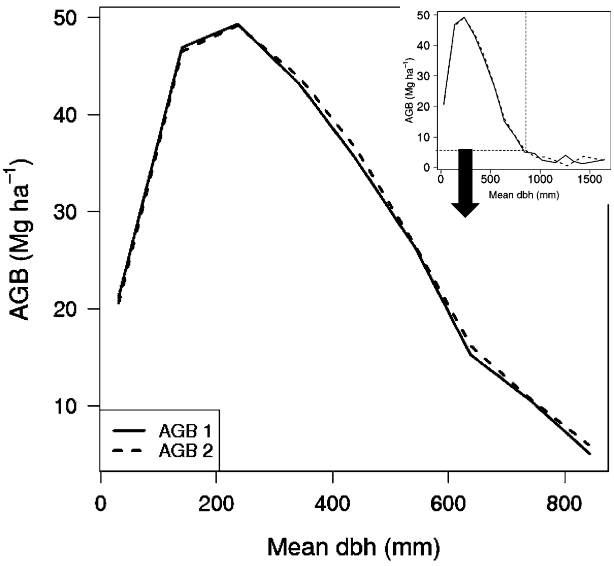

Figure 1. Forest-wide distribution of above-ground biomass (AGB) among 100-mm dbh classes in the two censuses (AGB 1 and AGB 2, respectively) of a 25-ha plot, located at Yasuni National Park. Censuses were done with a time interval of 6.3 y. The difference between lines shows the tiny losses and gains. Inset is the figure for the entire forest.

(Table 3). The secondary forest also had parallel changes, but showed a much larger increase in the number of large trees (Table 3).

Biomass stocks were significantly different between habitats in nearly all 50-mm diameter categories, with ridge > valley (Figure 2). Secondary forest had most biomass concentrated in a narrow dbh range, about 200–500 mm (Figure 2).

Relative to the difference between ridge and valley, the 6-y change in AGB stock was almost trivial (Figure 2). The one exception was the increase in large trees in the secondary forest. Growth was generally higher than death in each diameter class, and the whole distribution of AGB shifted upward in dbh (Figure 3, Table 4).

Mean wood specific gravity

In both censuses, forest-wide mean wood specific gravity (WSG) tended to decrease from smaller to larger individuals (Table 5).

In both censuses and in all diameter categories, wood was consistently heavier on the ridge (~2–7%) than in the valley by an average of ~3.5%. The difference was slightly greater in the second census (Table 6). Between censuses, there were only marginal (<1%) changes in WSG in any given size class on either ridge or valley but major increases (~5–10%) in secondary forest in stems with dbh <200 mm. Secondary forest had the lowest WSG of the plot, particularly among the largest trees and in the second census (Table 6). Overall, changes in WSG between censuses were small relative to changes in AGB, contributing little relative to the increased density of large trees.

Table 3. Changes in stem density and diameter size in different habitats of the 25-ha plot. The values correspond to two censuses (C1 and C2) conducted in a time interval of 6.3 y. N1 = individuals in census 1, N2 = individuals in census 2.

	Ridge				Valley				Secondary			
	Mean dbh (mm)		Stem density (ha^{-1})		Mean dbh (mm)		Stem density (ha^{-1})		Mean dbh (mm)		Stem density (ha^{-1})	
dbh class (mm)	C1	C2	C1	C2	C1	C2	C1	C2	C1	C2	N1	N2
10–50	22.6	22.5	4764	4509	23.5	23.2	3622	3555	22.5	22.8	6590	5919
50–100	68.4	68.1	916	905	69.0	68.6	863	859	68.5	69.5	1375	1263
100–200	140	141	492	486	140	139	451	456	145	141	679	531
200–300	237	237	140	139	235	235	125	124	237	244	260	258
≥300	439	440	92.8	93.1	407	410	61.4	63.5	361	353	22.9	89.6
Total	48.9	49.8	6405	6132	51.1	51.4	5123	5057	46.1	48.7	8927	8060

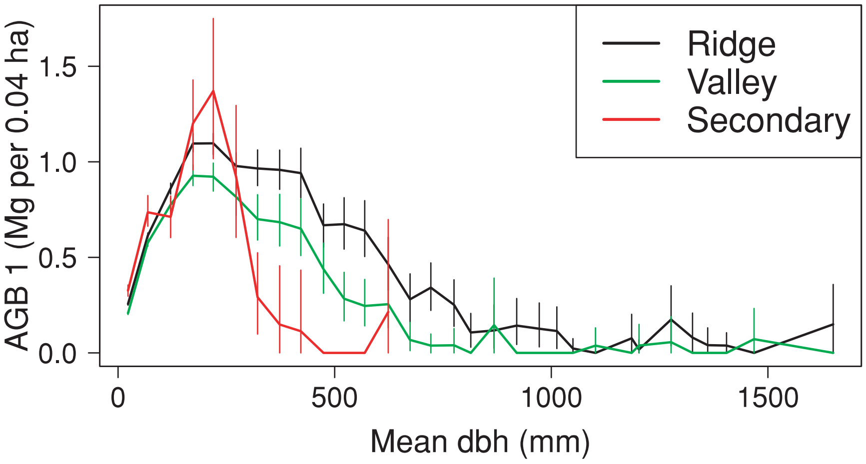

Figure 2. Between-habitat differences in above-ground biomass in census 1 (AGB 1) stocks plotted by 50-mm diameter classes and 95% confidence intervals (vertical lines). Continuous lines unite points of the 50% percentile of each diameter class. Habitats of the Yasuni 25-ha plot were divided in subplots of 20 × 20 m: ridge (416 subplots) valley (197) and secondary (12). Confidence intervals were minuscule in stems < 100 mm but average values were different in mature habitats. A similar pattern (not illustrated) was also found when AGB of census 2 was used.

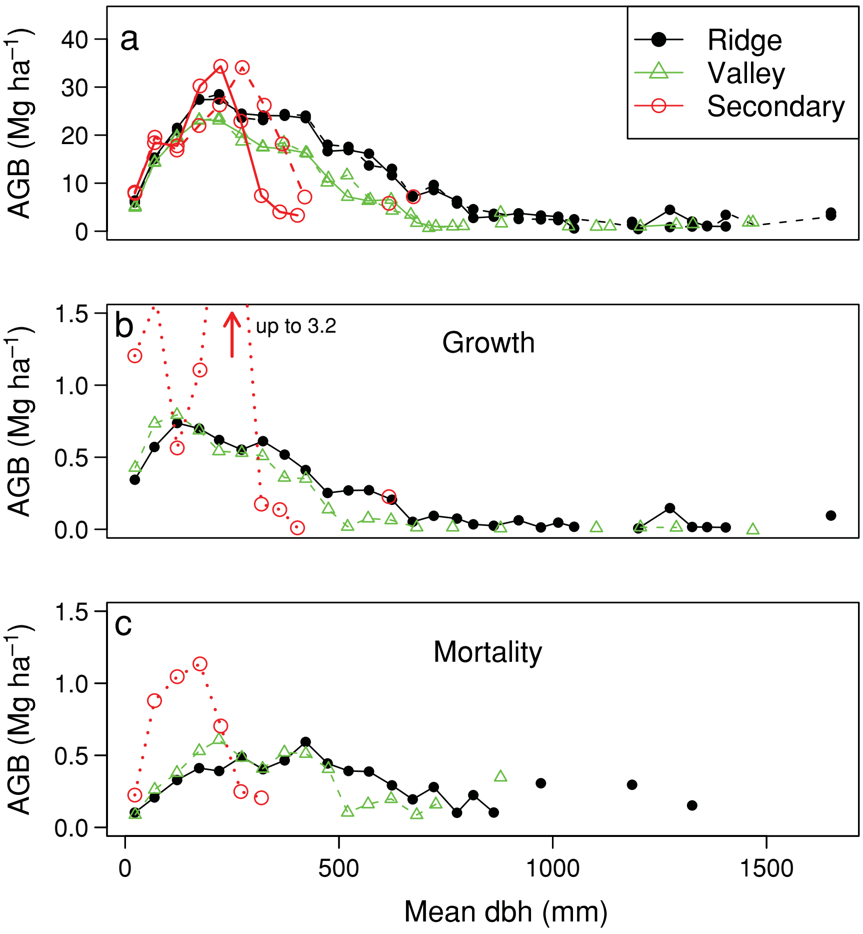

Figure 3. Above-ground biomass (AGB) changes by habitat in 6.3 y as a function of 50-mm diameter class: AGB in census 1 (solid line) and AGB in census 2 (dashed line) (a), growth in AGB (b) and mortality in AGB (c). Growth and mortality (averaged by year) refer to the original diameter class regardless of any shift to a larger dbh category during the 6.3 y.

Table 4. Above-ground biomass (AGB) by habitat of the 25-ha plot. The values correspond to two censuses conducted in a time interval of 6.3 y. C = census.

	Ridge				Valley				Secondary			
	AGB per stem (Mg)		AGB (Mg ha^{-1})		AGB per stem (Mg)		AGB (Mg ha^{-1})		AGB per stem (Mg)		AGB (Mg ha^{-1})	
dbh class (mm)	C 1	C 2	C 1	C 2	C 1	C 2	C 1	C 2	C 1	C 2	C 1	C 2
10–50	0.00134	0.00132	6.4	6.0	0.00143	0.00138	5.2	4.9	0.00124	0.00133	8.1	7.9
50–100	0.0167	0.0166	15.3	15.1	0.0167	0.0166	14.4	14.2	0.0134	0.0155	18.4	19.6
100–200	0.0994	0.0998	48.9	48.5	0.0945	0.0938	42.6	42.8	0.0707	0.0732	48.0	38.9
200–300	0.371	0.374	51.9	52.1	0.346	0.340	43.4	42.2	0.220	0.234	57.3	60.4
≥300	2.01	2.03	186	189	1.54	1.53	94.8	97.0	0.896	0.655	20.5	58.7
Total	0.048	0.051	309	310	0.0391	0.0398	200.4	201.2	0.0171	0.0230	152	185

Table 5. Forest-wide mean wood specific gravity (WSG, g cm^{-3}) changes in two censuses (WSG 1 for census 1 and WSG 2 for census 2) carried out in an average time interval of 6.3 years. Reported values correspond to all levels of identification (i.e. 339 species, 658 congeneric, 127 confamilial, and 12 set to mean density of known species). To calculate the mean WSG, each individual tree was assigned to a dbh class in each census. Values in parentheses represent 95% confidence intervals.

dbh class (mm)	WSG 1	WSG 2	Change
10–50	0.597	0.601	0.0033
50–100	0.604	0.610	0.0057
100–200	0.538	0.540	0.0026
200–300	0.539	0.537	−0.0014
≥300	0.518	0.512	−0.0058
≥10	0.531 (0.524–0.531)	0.527 (0.520–0.534)	−0.0033 (−0.0037 to 0.0012)

DISCUSSION

Mature forest biomass increased by 0.13 and 0.24 Mg ha^{-1} y^{-1}, in valley and ridge, respectively. This was due entirely to an increase in the number of large trees. Small diameter categories (dbh < 10 cm) lost 0.1 Mg ha^{-1} y^{-1} of biomass. Because of the decrease among small trees, had we considered only trees ≥ 10 cm dbh, we would have overestimated AGB increase by 62% and 46%, at 0.19 and 0.35 Mg ha^{-1} y^{-1}, in valley and ridge, respectively. Our spatial bootstrapping procedure showed that overall, the increase we observed was not statistically significant.

Changes in biomass and carbon flux in tropical forests have created controversy among ecologists for the past 15 y or so. There is wide belief that both growth rates and standing stocks are increasing through time, though reasonable scepticism still seems warranted. Our forest also increased its standing biomass, although far less than the Amazonian forest average (i.e. 0.30 overall or 0.13–0.24 in mature forest vs. 0.98 Mg ha^{-1} y^{-1} reported by Baker *et al.* 2004). Why Amazonian forests are increasing in biomass stocks by such large amounts remains controversial.

One hypothesis for Amazonian forest is that they are still recovering from long-past human intervention. That populations of native Americans were higher before the Columbian interchange than they were 200 y later seems certain, and it is plausible that large areas of agricultural land in 1500 have reforested since. Ceramic fragments of pre-Hispanic human occupation were found under a terra firme forest near our plot (Netherly 1997), but unfortunately no age has been reported to date (in 1994, during the archaeological fieldwork, a rough preliminary estimate was ~500 y; P. Netherly pers. comm.). However, ethnohistoric evidence as well as pollen of cultivated plants or charcoal do not support dense settlements at Yasuni: pollen and charcoal in three study lakes at Yasuni National Park suggest localized human activity near one swamp but not in two nearby study lakes, which is interpreted as a sign that human settlements in the area were few (Bush & Silman 2007). Altogether, available evidence suggests that our study area had low population densities before the Spanish conquest (~0.3 persons km^{-2}, Newson 1996).

The results we present from a large plot in Yasuni seem hard to reconcile with the long-past human intervention hypothesis. In a period of 6 y, the number of small stems in the mature forest section of the plot fell ~4%, while the number of large stems increased more than 2.5%. The overall increase in biomass of the mature forest can be attributed entirely to this increase in the number of large trees and thus a shift in mean diameter. Wood specific gravity barely changed in the mature forest. The decline in small-stem population size would be expected if canopy trees became more abundant and light less available in the understorey. It is therefore reasonable to believe that the increasing numbers of large trees is a leading factor in explaining the observed changes in our forest dynamics.

These are the patterns to be expected during succession, but they are happening too rapidly to fit long-term succession from a disturbance more than 200 y ago. Obviously, the population size of small stems cannot change at a rate of ~4% every 6 y for long. Likewise, it seems difficult

Table 6. Mean wood specific gravity (WSG, g cm^{-3}) in different habitats over a period of 6.3 y. Values correspond to all levels of identification (i.e. 339 species, 658 congeneric, 127 confamilial, and 12 set to mean density of known species). To calculate the mean WSG, each individual tree was assigned to a habitat and a dbh class in each census (1 and 2). Values in parentheses represent 95% confidence intervals.

	Ridge			Valley			Secondary		
dbh class (mm)	WSG 1	WSG 2	Change in WSG	WSG 1	WSG 2	Change in WSG	WSG 1	WSG 2	Change in WSG
10–50	0.604	0.608	0.0042	0.583	0.582	−0.0009	0.564	0.593	0.0290
50–100	0.613	0.618	0.0055	0.598	0.599	0.0010	0.477	0.532	0.0551
100–200	0.549	0.551	0.0017	0.530	0.528	−0.0024	0.360	0.399	0.0386
200–300	0.557	0.558	0.0010	0.521	0.516	−0.0050	0.328	0.323	−0.0055
>300	0.522	0.518	−0.0038	0.501	0.495	−0.0057	0.416	0.340	−0.0757
Total	0.537 (0.499–0.545)	0.535 (0.528–0.543)	−0.0020 (−0.0032 to 0.0026)	0.519 (0.506–0.532)	0.515 (0.501–0.529)	−0.0048 (−0.0082 to −0.0004)	0.371 (0.343–0.404)	0.365 (0.348–0.390)	−0.0060 (−0.0177 to 0.0058)

to sustain the notion that the canopy of the forest is still gaining 0.1% y^{-1} 200 y or more after recovery.

The recovering helicopter pad does not lend support to the notion of long-term recovery either. This patch was largely cleared only 15 y before our first census, yet its biomass is nearly 60% of that of the neighbouring mature ridge-top forest, and it gained ∼22% of its biomass in 6 y. At the current rate of increase, the secondary forest patch would attain biomass similar to the surrounding mature forest in ∼20–60 y. This is consistent with published accounts of secondary forest recovery (Alves *et al.* 1997, Brown & Lugo 1990, Scatena *et al.* 1996, Steininger 2000). At one site in Mexico, total AGB of secondary forests attained values equivalent to primary forests in 73 y (Hughes *et al.* 1999).

The ridge and valley of the Yasuni forest are remarkably different in biomass, with the ridge having more than 35% higher standing stock. The difference is due almost entirely to a higher number of very large trees on the ridge, and to a lesser extent from higher density wood on the ridge. In our plot, the bottomland valley was more dynamic than the surrounding ridges, having higher relative (not absolute) growth and mortality rates. The higher dynamism and the relatively low stocks of biomass seem to be caused by natural environmental conditions. Valley soils are more humid than ridges since superficial water drains downwards and some proportion of absorbed water in the ridge runs horizontally under the ground and eventually reaches parts of the bottomland. We also found that biomass in the valley is persistently lower in each diameter size category. Nevertheless, both ridge and valley changed in parallel, losing saplings while gaining large trees, and neither showed a systematic change in wood specific gravity. The significant differences between valley and ridge suggest that terra firme forests are a mosaic of natural habitat types, and that this habitat variation is responsible in part for the observed variation in biomass stocks of Amazonian forests.

Overall, we believe the change in diameter distribution and biomass of the Yasuni forest is most likely due to some recent event, not long-term succession. This is consistent with ideas relating to climatic or atmospheric changes (Lewis *et al.* 2004): higher CO_2 or shifts in precipitation or rainfall that change the equilibrium in tree size favouring increase in density of larger trees. Alternatively, it also fits with recovery from a relatively recent disturbance, such as a large storm or drought that removed big trees in the canopy. Although we do not have systematic records, there are moderate windstorms every decade or so, and one occurred in 2002 and removed several big trees in our plot. It seems very likely to us that over scales of decades, forest structure is seldom stable, even in the absence of human intervention. Discrete climatic events or oscillations in precipitation cause forest structure to fluctuate (Condit *et al.* 2004). We believe that when we have 150 y of censuses in the Yasuni plot, we will observe periods of biomass increase and periods of biomass decrease, with different species coming and going in different ways. Certainly, wherever there are long-term tree ring records of forests, continuous fluctuations are observed (Fichtler *et al.* 2003).

But a single forest lacks much weight in arguments about large-scale and concerted change. Just because many Amazonian forests show steady biomass increase, and Yasuni does too, does not mean that the causes of the increase at Yasuni will be the same as elsewhere. More large-scale and intensive plot inventories are needed to elucidate the detailed fingerprint of forest change. In addition, studies of the response of individual species may provide clues about drivers of forest change, and large plots offer details on demography of many species.

ACKNOWLEDGEMENTS

The Yasuni Forest Dynamics Plot (YFDP) was established with contributions from many professional workers, students, field assistants and volunteers; some of them have worked with us for over a decade. We wish to thank Robin Foster, Álvaro Pérez, Gorky Villa, Margot Bass, Pablo Alvia and Katya Romoleroux for the taxonomic identifications; Anelio Loor, Jairo Zambrano, Milton Zambrano, Gabriel Grefa, Jugalio Suárez, Wilson Loor and Milton Pabón carefully mapped and measured trees. Carolina Altamirano provided unpublished data on wood specific gravity. Funding for the study plot was provided by the government of Ecuador (Donaciones deI impuesto a la Renta 2004–2006), the National Science Foundation (grants DEB-0090311 and DEB-9806828); the Mellon Foundation, the Tupper Family Foundation, and the Smithsonian Tropical Research Institute (STRI). Pontificia Universidad Católica del Ecuador (PUCE) and, in particular, Dr Manuel Corrales Pascual and Dr Laura Arcos, enthusiastically supported the project. We gratefully acknowledge the support of a STRI Latin American Senior Scholar Award (August 2008–February 2009) to RV, which allowed him to focus on the present publication, and HSBC Climate Partnership funding to HM. RV thanks Catalina, Julián, Martín and Sebastián for their support while he was abroad. The Ecuadorian Ministerio del Ambiente granted permission for our work in Yasuni National Park.

LITERATURE CITED

ALVES, D. S., SOARES, J. V., AMARAL, S., MELLO, E. M. K., ALMEIDA, S. A. S., FERNANDES, DA, SILVA, O. & SILVEIRA, A. 1997. Biomass of primary and secondary vegetation in Rondônia, Western Brazilian Amazon. *Global Change Biology* 3:451–461.

BAKER, T. R., PHILLIPS, O. L., MALHI, Y., ALMEIDA, S., ARROYO, L., DI FIORE, A., ERWIN, T., HIGUCHI, N., KILLEEN, T. J., LAURENCE, S. G., LAURENCE, W. F., LEWIS, S., MONTEAGUDO, A., NEILL, D. A., NÚÑEZ, P., PITMAN, N. C. A., SILVA, J. N. M. & VÁSQUEZ, R. 2004. Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society B* 359:353–365.

BROWN, S. & LUGO, A. 1990. Tropical secondary forests. *Journal of Tropical Ecology* 6:1–32.

BUSH, M. & SILMAN, M. 2007. Amazonian exploitation revisited: ecological asymmetry and the policy pendulum. *Frontiers in Ecology and Environment* 5:457–465.

CHAVE, J., ANDALO, C., BROWN, S., CAIRNS, M. A., CHAMBERS, J. Q., EAMUS, D., FÖLSTER, H., FROMARD, F., HIGUCHI, N., KIRA, T., LESCURE, J.-P., NELSON, W., OGAWA, H., PUIG, H., RIÉRA, B. & YAMAKURA, T. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145:87–99.

CHAVE, J., CONDIT, R., MÜLLER-LANDAU, H. C., THOMAS, S. C., ASHTON, P. S., BUNYAVEJCHEWIN, S., CO, L. L., DATTARAJA, H. S., DAVIES, S. J., ESUFALI, S., EWANGO, C. E. N., FEELEY, K. J., FOSTER, R. B., GUNATILLEKE, N., GUNATILLEKE, S., HALL, P., HART, T. B., HERNÁNDEZ, C., HUBBELL, S. P., ITOH, A., KIRATIPRAYOON, S., LAFRANKIE, J. V., LOO, DE, LAO, S., MAKANA, J.-R., NOOR, M. N. S., RAHMAN KASSIM, A., SAMPER, C., SUKUMAR, R., SURESH, H. S., TAN, S., THOMPSON, J., TONGCO, M. D. C., VALENCIA, R., VALLEJO, M., VILLA, G., YAMAKURA, T., ZIMMERMAN, J. K. & LOSOS, E. C. 2008. Assessing evidence for a pervasive alteration in tropical tree communities. *PLOS Biology* 6:455–462.

CONDIT, R. 1998. *Tropical forest census plots*. Springer-Verlag, Berlin. 211 pp.

CONDIT, R., HUBBELL, S. P. & FOSTER, R. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* 65:419–439.

CONDIT, R., SALOMON, A., HERNÁNDEZ, A., PÉREZ, R., LAO, S., ANGEHR, G., HUBBELL, S. P. & FOSTER, R. B. 2004. Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *Journal of Tropical Ecology* 20:51–72.

FICHTLER, E., CLARK, D. A. & WORBES, M. 2003. Age and long-term growth of trees in an old-growth tropical rain forest based on analyses of tree rings and ^{14}C. *Biotropica* 35:306–317.

GRACE, J., LLOYD, J., McINTYRE, J., MIRANDA, A. C., MEIR, P., MIRANDA, H. S., NOBRE, C., MONCRIEFF, J., MASSHEDER, J., MALHI, Y., WRIGHT, I. & GASH, J. 1995. Carbon dioxide uptake by an undisturbed tropical rain forest in southwest Amazonia 1992 to 1993s. *Science* 270:778–780.

HECKENBERGER, M. J., CHRISTIAN RUSSELL, J., TONEY, J. R. & SCHMIDT, M. J. 2007. The legacy of cultural landscapes in the Brazilian Amazon: implications for biodiversity. *Philosophical Transactions of the Royal Society B* 362:197–208.

HUGHES, R. F., KAUFFMAN, J. & JARAMILLO, V. J. 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology* 80:1892–1907.

JOHN, R., DALLING, J. W., HARMS, K. E., YAVITT, J. B., STALLARD, R. F., MIRABELLO, M., HUBBELL, S. P., VALENCIA, R., NAVARRETE, H., VALLEJO, M. & FOSTER, R. B. 2007. Soil nutrients influence spatial distributions of tropical species. *Proceedings of the National Academy of Sciences* 104:864–869.

LEWIS, S. L., MALHI, Y. R. & PHILLIPS, O. L. 2004. Fingerprinting the impacts of global change on tropical forests. *Philosophical Transactions of the Royal Society B* 359:437–462.

NETHERLY, P. 1997. Loma y ribera: patrones de asentamiento prehistórico en la Amazonía ecuatoriana. *Fronteras de la Ciencia* 1:3–54.

NEWSON, L. 1996. The population of the Amazon basin in 1492: a view from the Ecuadorian headwaters. *Transactions of the Institute of British Geographers, New Series* 21:5–26.

PHILLIPS, O. L., MALHI, Y., HIGUCHI, N., LAURENCE, W. F., NUÑEZ, P. V., VASQUEZ, R. M., LAURENCE, S. G., FERREIRA, L. V., STERN, M., BROWN, S. & GRACE, J. 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* 282:439–442.

ROMOLEROUX, K., FOSTER, R., VALENCIA, R., CONDIT, R., BALSLEV, H. & LOSOS, E. 1997. Especies leñosas (dap $\geq$1 cm) encontradas en dos hectáreas de un bosque de la Amazonía ecuatoriana. Pp. 189–215 in Valencia, R. & Balslev, H. (eds.). *Estudios Sobre Diversidad y Ecología de Plantas*. Pontificia Universidad Católica del Ecuador, Quito.

ROOSEVELT, A. C., HOUSLEY, R. A., IMAZIO, DA, SILVEIRA, M., MARANCA, S. & JONHNSON, R. 1991. Eight millennium pottery from prehistoric shell midden in the Brazilian Amazon. *Science* 254:1621–1624.

SCATENA, F. N., MOYA, S., ESTRADA, C. & CHINEA, J. D. 1996. The first five years in the reorganization of aboveground biomass and nutrient use following hurricane Hugo in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico. *Biotropica* 28:424–440.

STEININGER, M. 2000. Secondary forest structure and biomass following short and extended land-use in central and southern Amazonia. *Journal of Tropical Ecology* 16:689–708.

TUOMISTO, H., POULSEN, A. D., RUOKOLAINEN, K., MORAN, R. C., QUINTANA, C., CELI, J. & CAÑAS, G. 2003. Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. *Ecological Applications* 13:352–371.

VALENCIA, R., FOSTER, R., VILLA, G., CONDIT, R., SVENNING, C. J., HERNÁNDEZ, C., ROMOLEROUX, K., LOSOS, E., MAGAARD, E. & BALSLEV, H. 2004. Tree species distributions and local habitat variation in the Amazon: a large forest plot in eastern Ecuador. *Journal of Ecology* 92:214–229.

WRIGHT, S. J. 2005. Tropical forests in a changing environment. *Trends in Ecology and Evolution* 20:553–560.