

An international network to monitor the structure, composition and dynamics of Amazonian forests (RAINFOR)

Malhi, Y.^{1*}; Phillips, O.L.²; Lloyd, J.⁸; Baker, T.²; Wright, J.¹; Almeida, S.³; Arroyo, L.²⁰; Frederiksen, T.⁴; Grace, J.¹; Higuchi, N.⁵; Killeen, T.⁶; Laurance, W.F.⁷; Leão, C.⁴; Lewis, S.²; Meir, P.¹; Monteagudo, A.⁹; Neill, D.¹⁰; Núñez Vargas, P.⁹; Panfil, S.N.¹¹; Patiño, S.^{8,21}; Pitman, N.¹²; Quesada, C.A.¹⁶; Rudas-Ll., A.¹³; Salomão, R.³; Saleska, S.¹⁴; Silva, N.¹⁵; Silveira, M.^{16,22}; Sombroek, W.G.¹⁷; Valencia, R.¹⁸; Vásquez Martínez, R.¹⁹; Vieira, I.C.G.³ & Vinceti, B.¹

¹Institute of Ecology and Resource Management, University of Edinburgh, Darwin Building, Mayfield Road, Edinburgh EH9 3JU UK; ²Centre for Biodiversity and Conservation, School of Geography, University of Leeds, UK.; ³Museu Paraense Emilio Goeldi, Belém, Pará, Brazil; ⁴Proyecto BOLFOR, Santa Cruz, Bolivia; ⁵Departamento de Silvicultura Tropical, Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, Brazil; ⁶Center for Applied Biodiversity Science, Conservation International, Washington DC, USA; ⁷Smithsonian Tropical Research Institute, Balboa, Republic of Panama, and Biological Dynamics of Forest Fragments Project, National Institute for Amazonian Research (INPA), Manaus, AM, Brazil; ⁸Max-Planck-Institut für Biogeochemie, Postfach 100164, D-07701 Jena, Germany; ⁹Herbario Vargas, Universidad Nacional San Antonio Abad del Cusco, Cusco, Peru; ¹⁰Fundacion Jatun Sacha, Quito, Ecuador, and Missouri Botanical Garden, St. Louis, MO, USA; ¹¹Department of Botany, University of Georgia, Athens, GA, USA; ¹²Center for Tropical Conservation, Duke University, Durham, NC, USA.; ¹³Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia; ¹⁴Harvard University, Cambridge, MA, USA; ¹⁵CIFOR, Tapajos, Pará, Brazil, and EMBRAPA Amazonia Oriental, Belem, Pará, Brazil; ¹⁶Depto de Ecologia, Universidade de Brasilia, Brasilia DF, Brazil; ¹⁷ISRIC, Wageningen, The Netherlands; ¹⁸Departamento de Ciencias Biológicas, Herbario QCA, Pontificia Universidad Catolica del Ecuador, Quito, Ecuador; ¹⁹Proyecto Flora del Perú, Jardín Botánico de Missouri, Jaen, Cajamarca, Peru; ²⁰Museo Noel Kempff Mercado, Santa Cruz, Bolivia; ²¹Alexander von Humboldt Institute, Bogotá DC, Colombia; ²²Depto de Ciencias da Natureza/Parque Zoobotanico, Universidade Federal do Acre, AC, Brazil; *Corresponding author; Fax +441316620478; E-mail ymalhi@ed.ac.uk

Abstract. The Amazon basin is likely to be increasingly affected by environmental changes: higher temperatures, changes in precipitation, CO₂ fertilization and habitat fragmentation. To examine the important ecological and biogeochemical consequences of these changes, we are developing an international network, RAINFOR, which aims to monitor forest biomass and dynamics across Amazonia in a co-ordinated fashion in order to understand their relationship to soil and climate. The network will focus on sample plots established by independent researchers, some providing data extending back several decades. We will also conduct rapid transect studies of poorly monitored regions. Field expeditions analysed local soil and plant properties in the first phase (2001-2002). Initial results suggest that the network has the potential to reveal much information on the continental-scale relations between forest and environment. The network will also serve as a forum for discussion between researchers, with the aim of standardising sampling techniques and methodologies that will enable Amazonian forests to be monitored in a coherent manner in the coming decades.

Keywords: Amazon; Basal area; Carbon; Climate; Long-term monitoring; Permanent plot; Soil; Tropical forest.

Abbreviation: PSP = Permanent sample plot.

Introduction

The tropical forests of Amazonia constitute one of the most important ecosystems of the Earth. They account for 45% of the world's tropical forest, storing ca. 20% of the carbon residing in terrestrial vegetation and annually processing about 3 × as much carbon through photosynthesis and respiration as humans release to the atmosphere through fossil fuel combustion (Malhi et al. 1999; Malhi & Grace 2000). Amazonia also accounts for a large portion of land surface evapotranspiration, and a significant part of the world's known species. Small changes in the structure and/or function of these forests could therefore have global consequences for biodiversity, the carbon cycle and climate.

Recent research has suggested that apparently undisturbed tropical forests, remote from areas of deforestation or other significant human influences, are undergoing unexpected changes. Long-term monitoring of tropical forest plots indicates that tree populations experienced increased rates of mortality and recruitment ('turnover') in the latter part of the last century (Phillips & Gentry 1994; Phillips 1997). These plots also showed

that the basal area and biomass of mature forests increased over the same period (Phillips et al. 1998, 2002), pointing to a sink for atmospheric CO₂ in South American forests of 0.5 - 1 Pg C.yr⁻¹ (1 Pg = 10¹⁵ g), equivalent to the fossil fuel emissions of the entire European Union. Meanwhile, researchers using micrometeorological techniques and inverse modelling of atmospheric CO₂ concentrations found that tropical ecosystems globally probably contribute a gross C sink of 0-3 Pg C.yr⁻¹ (Bousquet et al. 2000; Malhi & Grace 2000), while modelling and laboratory studies imply changes in the physiology and productivity of forests in response to global atmospheric change (e.g. Lloyd 1999; Norby et al. 1999).

Several mechanisms have been suggested to account for the changes in tropical forest dynamics, including increases in atmospheric CO₂ and climate change. However, there has been, to our knowledge, no attempt to systematically collate these hypotheses and investigate whether they account for recent changes in tropical forest dynamics. Moreover, changes may be transient and of an uncertain long-term direction: for example, a recent vegetation-atmosphere simulation, using the UK Hadley Centre GCM, predicted that the Amazon forest increases in biomass, but would suffer large-scale dieback later this century as drought-temperature effects become important, leading to a rapid acceleration of global warming (Cox et al. 2000; White et al. 2000). Monitoring and understanding what is happening *on the ground* in Amazonian forests today is crucial, both for the future of these forests and possibly for the global climate.

The paper describes a new attempt to obtain and collate such 'ground-truth' data by utilizing long-term permanent sample plots (PSPs) to monitor forest biomass and dynamics, and relate these to soil and climate. Many of these plots were established in the past to investigate specific local ecological or forest management questions. However, by compiling and comparing these studies on a *regional* scale a new level of information becomes available: information that may provide insights into the mechanisms underlying the current responses of Amazonian ecosystems to climate trends and the possible future of Amazonia under global change scenarios.

The study is called the Amazonian Forest Inventory Network (RAINFOR; Spanish 'Red Amazónica de Inventarios Forestales', Portuguese 'Rede Amazônica de Inventarios Florestais'). It is associated with the international Large-Scale Biosphere Atmosphere Study in Amazonia (LBA). For details of the RAINFOR project see <http://www.geog.leeds.ac.uk/projects/rainfor/>.

Field expeditions associated with RAINFOR commenced in 2001. Although new results are already being found, the main purpose of this paper is to outline the methodological issues raised in attempting to set up an international forest plot network.

More specifically, this paper: (1) introduces the aims of the RAINFOR network; (2) describes the environment of Amazonia; (3) discusses issues related with protecting the rights of field data collectors; (4) outlines the RAINFOR field sampling protocols; (5) discusses potential methodological problems in field site selection and field data sampling, and how these can be tested for in field data; (6) examines approaches to quantifying the spatial and environmental coverage of the field sites, and (7) presents some preliminary field data.

Background: The environment of Amazonia

Climate

Amazonia is composed of a vast lowland continental basin, slowly rising in altitude to 300 m a.s.l. at its western fringe, surrounded to the north and south by the crystalline shields of Guyana and Brazil, and to the west by the Andes mountains. The region shows little variation in surface temperature, which rises above a daily maximum of ca. 32 °C only in regions and at times where water supply is limited. Total annual rainfall is typically 2000 mm, but ranges between 4000 mm in the northwest and less than 1200 mm at the savanna fringes. The spatial variation in total annual rainfall is shown in Fig. 1a. The data are derived from the University of East Anglia observed climatology for the period 1960-1998 (New et al. 1999), and are available from the IPCC Data Distribution Centre (http://ipcc-ddc.cru.uea.ac.uk/cru_data/datadownload/download_index.html). The data are superimposed on a map of forest cover derived from the FAO world forest map (Anon. 2000a). The FAO definition of forest is crown cover >10% and potential tree height >5 m.

Rainfall patterns are seasonal in the south and east parts of the region, and here there are several months of the year where rainfall rates drop below 100 mm / month. Observational studies show that a wet tropical forest transpires ca. 100 mm.mo⁻¹ (e.g. Hodnett et al. 1996; Malhi et al. 2002), and hence can be expected to experience water limitation effects when precipitation drops below this threshold, which therefore can be defined as an indicator of dry season conditions. The mean length of the dry season is shown in Fig. 1b.

This description is derived from a limited precipitation data set (1960-1998), and it is likely that forests endure occasional much more severe droughts, perhaps once a century (there is documentary evidence for such an intense El Niño in 1925/1926). Forest structure may reflect adaptation and response to these severe droughts.

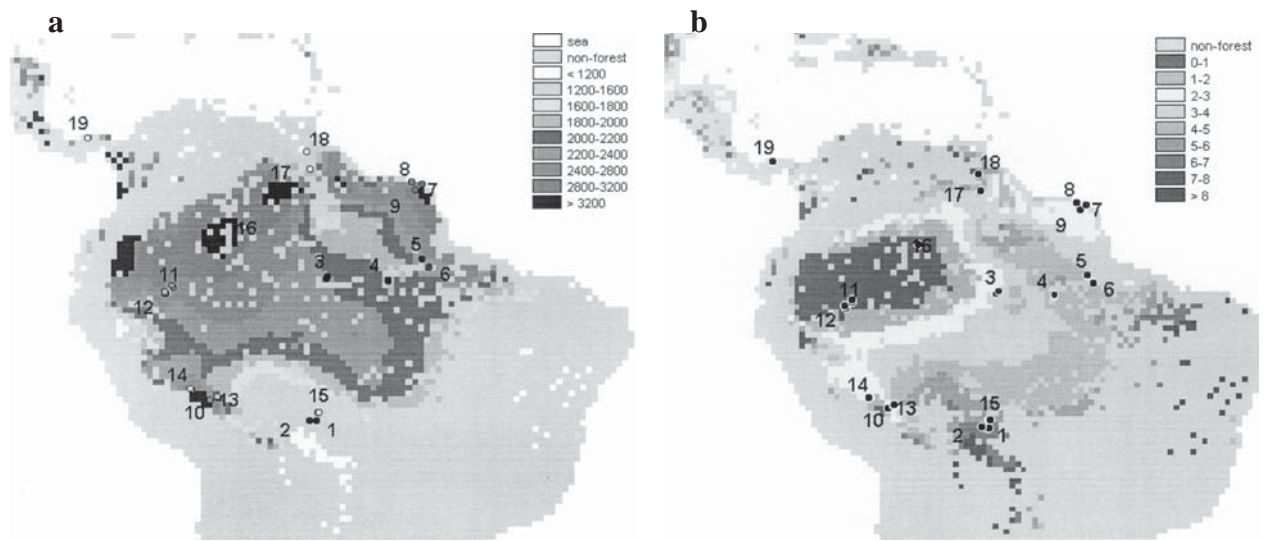


Fig. 1. a. Mean annual rainfall (mm) in Amazonia, 1960-1998 (data from the University of East Anglia). Only forested regions are shown, with the map of forest cover derived from Anon. (2001). **b.** Mean length of dry season, 1960-1998, indicated by the number of consecutive months with less than 100 mm rainfall. Data derived from same source. The numbered points correspond to forest plot locations (plots shown do not exactly match all those in Table 4): 1 = Los Fierros (Bo); 2 = Cerro Pelao (Bo); 3 = BDFFP/Bionte (Br); 4 = Tapajos (Br); 5 = Jari (Br); 6 = Caxiuana (Br); 7 = Paracou (FG); 8 = St Elie (FG); 9 = Nouragues (FG); 10 = Tambopata (Pe); 11 = Yanamono/Sucusari (Pe); 12 = Allpahuayo/Mishana (Pe); 13 = Cuzco Amazonica (Pe); 14 = Manu (Pe); 15 = Huanchaca (Bo); 16 = San Carlos (Ve); 17 = El Dorado (Ve); 18 = Rio Grande (Ve); 19 = BCI (Pa). Country codes: Bo = Bolivia, Br = Brazil, FG = French Guyana, Pe = Peru, Ve = Venezuela, Pa = Panama.

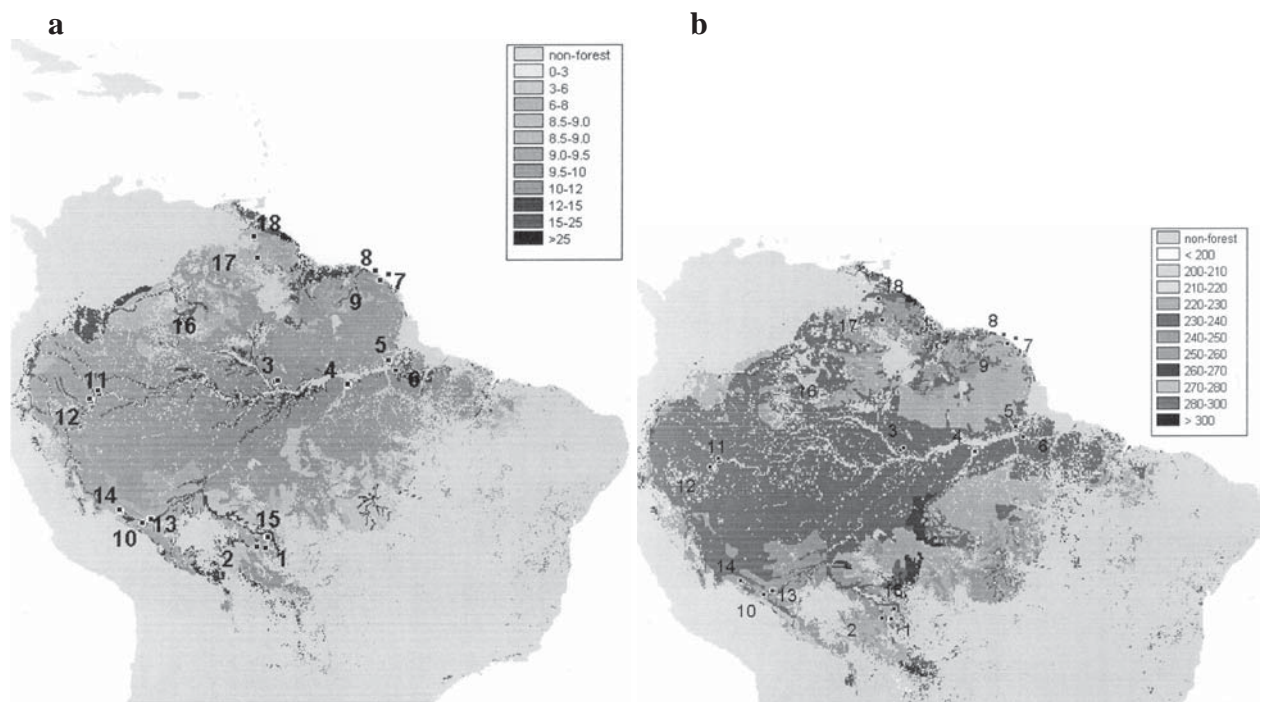


Fig. 2. Variation of soil properties across Amazonia. Data derived from the IGBP Global Soil Data Task (2000). **a.** Total carbon content (kg.m^{-2}) in the top 1 m. $1 \text{ kg.m}^{-2} = 10 \text{ t.ha}^{-1}$. **b.** Total available water capacity in the top 1 m (mm). In many Amazonia regions soils data are very sparse and these maps are only approximate. Plot numbers as in Fig. 1.

Soils

An example of the cover in terms of soil environmental space is shown in Fig. 2. The data are derived from the IGBP Global Soils Data Task (Anon. 2000b). The two variables selected are soil carbon content (which is strongly correlated with soil nutrient variables such as nitrogen content), and plant available water capacity, an indicator of the hydraulic properties of the soil (both in the top 1 m of the soil). The carbon content is typically 10 kg C.m⁻² in most of the Amazonian lowlands, with values slightly higher in the western Amazonian lowlands and the highest values (> 20 kg C.m⁻²) in the Amazon floodplain. Values are lower on the crystalline uplands and lowest (< 3 kg C.m⁻²) in mountain regions. In terms of hydraulic properties, wet lowland soils can typically hold about 230 mm.m⁻¹ of plant available water, whereas high values tend to be found in mountain regions.

Variation in soil parent material causes important differences in soil fertility. Within the Guyana and Brazilian shields, active weathering of the crystalline basement rocks results in areas with relatively high nutrient concentrations, whereas the sedimentary lowland areas that border the crystalline shield are derived from weathered shield material, and are comparatively infertile (Sombroek 2000). By contrast, the soils of western Amazonia derive from the Andean Cordillera and have higher fertility and higher ion exchange capacities. In addition to these broad regional scale patterns, large differences also occur within these land forms. For example, in the Iquitos area of the Peruvian Amazon the small hills characteristically have white, sandy soils, whereas clay rich soils with higher nutrient concentrations are found in the lowest sites (Vormisto et al. 2000). Variations in soil type at this 10-100 km scale are very common. The most limiting macro-nutrient in many Amazonian soils is thought to be phosphorus rather than nitrogen, and hence the tightness of the phosphorus cycling between vegetation and soil may be very important (Vitousek 1984; Lloyd et al. 2000). Micronutrients such as calcium are also likely to play an important role.

A principal aim of RAINFOR is to understand how the productivity and dynamics of Amazonian forests are constrained by environmental factors, by utilizing the spatial variability of these factors. The major factors are likely to be: (1) water – in months where precipitation drops below ca. 100 mm, the forest has the potential to become water-limited; (2) light – tree growth may be limited by light availability when total insolation drops below ca. 12 MJ.day⁻¹; (3) soil fertility – higher fertility soils might be expected to support higher forest productivity (in the absence of other climatic constraints), although this is not yet clear from field studies.

Field strategy to date

In the first phase (2001-2002), clusters of plots have been selected to span the full Amazon climate gradient. Within each cluster we have prioritized old-growth plot recensuses and attempted to sample the full edaphic range, establishing new plots if existing plots have not achieved this. The field expeditions to date have been:

1. Iquitos region, Peru (NW Amazonia); Jan-Apr 2001, 10 plots;
2. Noel Kempff National Park, – soil sampling at La Chonta – Bolivia (SW); May-Jul 2001, 9 plots;
3. Jatun Sacha and Yasuni, Ecuador (NW); Jan-Feb 2002, 5 plots each;
4. Madre de Dios, Peru (SW);
5. Rondonia, Mato Grosso, Brazil (S).

Many of these sites may become long-term ecosystem monitoring sites.

Issues raised in the establishment of the RAINFOR Network

In attempting to construct this forest plot network, we have confronted a number of methodological issues. The major issues are outlined below. Some of these issues are discussed in greater detail in Phillips et al. (2002), and the field protocols are outlined in documents available at the RAINFOR web site (<http://www.geog.leeds.ac.uk/projects/rainfor/>). In this paper we will pay particular attention to the issue of spatial and environmental coverage of Amazonia.

Issue 1: Protection of rights of data collectors

An important component of RAINFOR is the encouragement of discussion and data exchange between researchers in different Amazonian countries. However, whilst maximal exchange of data will be encouraged, the rights of data ownership of the local field researchers will be conscientiously protected at all times. We have established an explicit participation agreement, which is available at the RAINFOR website.

Issue 2: Common protocols for data collection

One of the primary difficulties in comparing forest plot data from different sources is the different forest sampling methodologies used. We sample biomass non-destructively using measurements of tree-diameter and height, and rely to some extent on allometric relationships in the literature determined from destructive harvests. In our field studies we have not attempted to post-correct previous data sets, but have tried to develop a consistent forest plot sampling protocol. The protocol describes the issues of plot shape, size, orientation, topog-

raphy, seasonal timing of re-measurements, procedures for tagging trees etc. A summary of all variables measured is given in Table 1.

A protocol was also established for soil and foliar sampling. Soils are sampled from five cores within each 1 ha plot, at eight depths up to 2 m depth. Furthermore, a soil description to 2 m depth is carried out using a soil pit, which is then cored up to 4 m depth. Leaves and branches are sampled from the upper crown of 20 trees in each plot, and at three different heights within the canopy for a subset of trees.

Both the forest biomass and the soil and foliar sampling protocols are available from the RAINFOR website.

Issue 3: Biases in site selection

One potential criticism of the use of forest sample plots is that there may be a bias in site selection. For example, foresters may favour particularly mature, gap-free forest stands in which to locate their plots (the 'majestic forest bias'), may favour accessible sites that are vulnerable to fragmentation and edge-effects, or, conversely, may favour immature forests recovering from disturbance. The first two biases would be expected to lead to decreases in stand biomass over time, the last to an increase in biomass. We test for these biases by looking for auxiliary signatures that such biases would cause. These tests are outlined in Table 2.

Descriptions of the results of these tests on forest plot data are given in companion papers (Phillips et al. 2002; Lewis et al in prep.). The tests indicated that the majority of forest plot sites did not appear to be recovering from a natural disturbance (for example, both turnover and basal area were increasing). There may, however, be a slight bias towards majestic forest stands that would result in a negative bias on basal area growth estimates.

Issue 4: Methodological errors in measurements

In addition to the potential problems caused by site selection bias, there are a number of ways that the field measurements and post-measurement data-checking may

Table 1. Variables to be determined at each site.

Forest structure parameters	
Tree basal area, basal area growth and mortality, stem density, growth, mortality and recruitment (≥ 10 cm diameter)	
Liana basal area, basal area growth and mortality, stem density, growth, mortality and recruitment (≥ 10 cm diameter)	
Tree height (to derive plot level diameter/height relationships for accurate modelling of tree-by-tree volumes and growth for each plot, and test whether tree shape differs between stands in different environmental conditions)	
Species names where known unambiguously; in all cases of doubt voucher collections are made	
Leaf area index, from hemispherical photographs	
Soil fertility parameters	
pH; calcium, potassium, magnesium, sodium, cation exchange capacity	
Nitrogen, as extractable ammonium and nitrate	
Phosphorus (organic labile, organic non-labile, inorganic labile, inorganic non-labile, microbial, available (Bray method), total)	
Soil organic carbon (Loss on ignition at 420 °C)	
Total C, and carbon isotopic signature (Mass spectrometer)	
Soil physical properties	
Moisture loss at 70 °C	
Bulk density	
Particle size fractions	
Porosity	
Soil profile description	
Leaf properties	
Specific leaf area	
Concentrations of carbon, nitrogen, phosphorus, calcium, and magnesium, in leaves and wood, at various canopy heights	
Wood density for a subset of trees from selected species	
Other measurements	
Topographic survey of plots	
Installation of automatic weather stations where possible	

bias the plot measurements. These biases may not normally be important in classical forestry studies of tree growth and death, or of the recovery of forest stands from disturbance, but in our search for shifts in the structure and composition of old-growth forests it is important to address this issue. In Tables 3 and 4 we have listed a number of possible biases caused by field methodologies. Each of these errors would leave a signature in the data, and in the final column we list tests that can be performed to check for the presence of these errors. The tests and their results are discussed in greater detail in Phillips et al. (2002).

Table 2. Possible biases in site selection and additional signatures that should be visible in the data.

Issue	Description	Additional signatures
'Majestic forest bias'	Biased selection of mature phase, gap-free sites in the landscape (negative effect on basal area change)	Decline in number of big trees with increasing time. Mortality and recruitment increase with increasing time. Basal area correlates negatively with plot size
'Progressive fragmentation and edge effects'	Biased selection of accessible sites vulnerable to fragmentation and edge effects (negative effect on basal area change)	Mortality correlates with increasing time. Mortality and negative changes in basal area correlate with fragment size and/or distance to edge
'Immature forest bias'	Biased selection of successional forest; positive effect on basal area change	Stem density declines as basal area increases ('self-thinning')

Table 3. Methodological biases that may cause apparent decreases in total plot basal area.

Issue	Description	Additional signatures
The effect of the research on the sample plot: degradation of the forest plot	E.g. researchers compacting soil, tagging trees, climbing and collecting trees, drawing attention of others to plot, etc.	Growth negatively correlated with time Mortality positively correlated with time Climbed or collected trees have depressed growth and elevated mortality Infection rates of climbed/collected trees positively correlate with time
Incomplete recensusing	New recruits may be missed, and some surviving trees may be missed and assumed dead ('ghost mortality')	Apparent sudden 'recruitment' of large trees
Post-measurement data checking: reducing extreme increments	Exceptional increments eliminated <i>a priori</i> or reduced in case measurement is in error	Effect only on the latest census interval (since most trees discovered to have been rounded-down incorrectly previously will be corrected)

Issue 5: Spatial and environmental coverage of the study region

An idealized network and a practical strategy

As a guide to identifying the most important gaps in our study, we first consider an ideal forest sampling network. An idealized network would span the environmental space (i.e. cover the range of climate regimes and soil types), in a stratified random fashion, whilst having sufficient spatial sampling density to cover sites with similar environments in different geographical areas. These would tease out spatial effects, such as historically determined phytogeographical patterns.

If there are F determining (independent) environmental factors, each of which can be approximated into S states; the minimum number of sites required to span environmental space is S^F . For example, if there are five environmental factors to be investigated (for example, rainfall seasonality, interannual rainfall variability, soil

phosphorus, soil nitrogen, soil texture), each of which can be composed of three states (for example, low, medium, high), we would require $243 (= 3^5)$ sites to evenly span the environmental space. In reality, correlation between different environmental factors (for example, rainfall and soil fertility) reduces the number of sites required, but also reduces the power to discriminate between factors.

In designing a real trans-Amazonian network, there are a number of practical constraints on this idealized distribution that need to be considered: (1) there is incomplete *a priori* knowledge of the values of environmental variables and prior human disturbance at the study sites, and incomplete knowledge of their variation across Amazonia; (2) existing plot locations are not randomly located within each major environmental strata across Amazonia; (3) much of the region is remote, and there are logistical constraints on setting up and revisiting remote sites; (4) there are differences in methodologies

Table 4. Methodological biases that may cause apparent increases in total plot basal area.

Issue	Description	Additional signatures
The effect of the research on the sample plot: nail swelling	Increasing swelling around nail used to place tag on tree	Effect increases with time No evidence of increase in recruitment No evidence of researchers moving point of measurement
Field measurement errors: 'Buttress creep'	Bole irregularities move up with time, becoming more likely to affect point of measurement with increasing time	Effect increases with time Effect especially marked in trees with large diameter No evidence of increase in recruitment No evidence of researchers moving point of measurement
Field measurement errors: 'Basal area inflation'	Disproportionately rapid radial increment of buttresses; bole irregularities will compound the over-estimation of [stand] biomass increase (Clark 2001, but see Phillips et al. 2002)	Effect especially marked in trees with large diameter Effect increases with increasing time Some trees with implausibly large diameters
Field measurement errors: 'Rounding-up negative increments'	In evaluating changes in diameter, 'false negatives' are rounded up to 0, but 'false positives' kept because they can not be distinguished from trees that have genuine increases in diameter	Effect size small and diminishes with increasing length of interval. No negative changes in researchers' tree-by-tree data sets

(to assess biomass, to sample soils and plants, and to identify species), and difficulties in scientific communications between research groups in different countries.

Whilst trying to approximate the idealized network design, we focused initially on sites where existing research groups have already collected data. These sites have historical data (enabling analysis of change through time), complementary scientific data (e.g. local rainfall records, soil analysis, root biomass), enhanced prospects of future security and local researchers interested in maintaining studies. Where possible, the network will help secure long-term support for these key monitoring sites. We have then identified major gaps in environmental space and geographical space that are not covered by PSPs (see below), and now aim to fill these gaps with ‘snapshot’ transects, and the establishment of new PSP sites in critical gaps.

Existing forest plot sites and their coverage of environmental space

Table 5 describes a selection of the existing long-term sites that are currently planned to be included in the network. The list is not comprehensive and is still growing. Sites currently within RAINFOR are plotted in Fig. 1.

The importance of logistical constraints is evident: most sites cluster close to cities hosting research institutions. The major plot clusters are:

(1) an Eastern Amazonian constellation close to the Amazon river cities of Belém, Santarem and Manaus. This relatively well-studied region is also a major research focus of the wider LBA project. However, many of the research sites are relatively similar, hosting tall forests on old, nutrient-poor, well-drained soils in a moderately seasonal climate occasionally subject to drought.

(2) a NW Amazonian constellation focused around N Peru (Iquitos) and Ecuador, with some sites in Colombia and Venezuela, covering a region with high rainfall and little or no dry season.

(3) a SW Amazonian constellation around S Peru, SW Brazil (Acre) and NE Bolivia, often sitting on richer soil near the base of the Andes and on the Brazilian crystalline shield and subject to a more seasonal rainfall regime.

Fig. 3 shows how the sites span climatic space. Two axes of environmental variability have been selected: the mean length of the dry season (number of months with < 100 mm of rain), and the interannual variability (represented by the standard deviation of the length of the dry season).

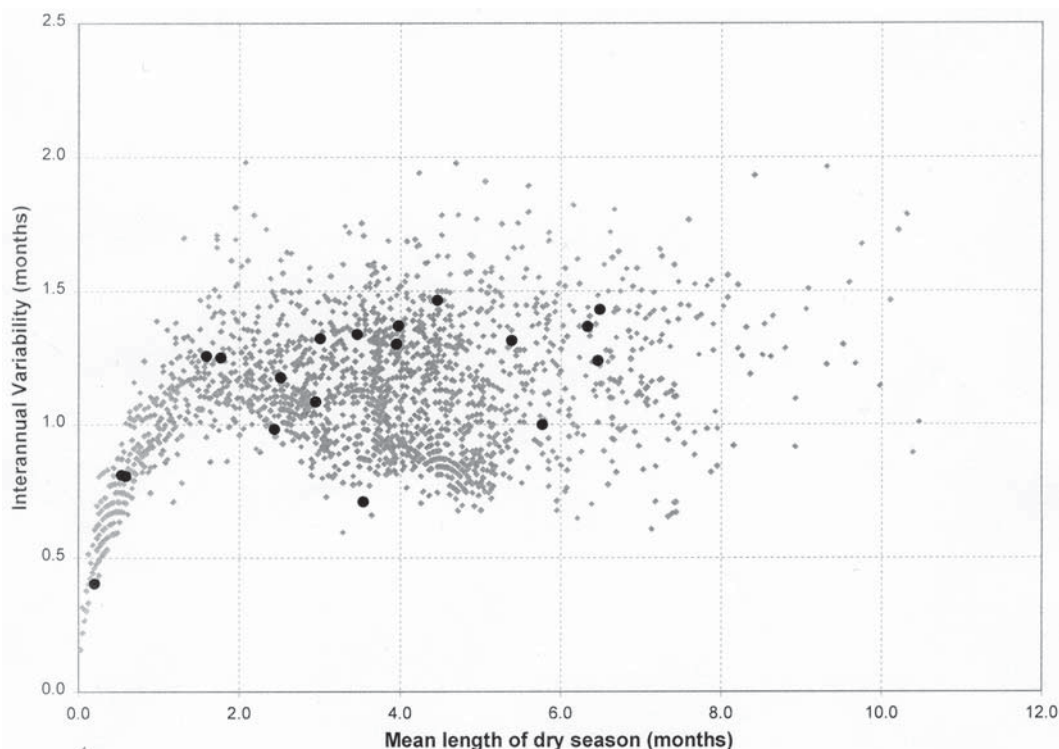


Fig. 3. How the forest plot network spans climatic space. A scatter plot of mean length of the dry season in months and annual variation (standard deviation) in the length of the dry season. Each light grey point represents a 0.5° area of neotropical forest. Solid black circles indicate the location of RAINFOR forest plot sites.

Table 5. The RAINFOR network. ^aCountry; Bo, Bolivia; Br, Brazil; C, Colombia; E, Ecuador; P, Peru; V, Venezuela. ^bNumber of edaphically or geographically distinct sites within any one cluster of plots. ^cMean annual rainfall calculated from UEA observed climatology, apart from those marked * derived from local data or estimated from Sombroek (2001). ^dDry season defined as months < 100 mm rainfall. ^eSoil fertility and drainage estimated from Sombroek (2000), or local information. Fertility: H, high; M, medium; L, low. Drainage: G, good; A, average; P, poor. ^fStem number and basal area calculated for stems ≥ 10 cm DBH, per ha, as mean of values at start and end of measurement period.

Name	City ^a	State	Site ^b		Location (degs, mins)		Rainfall ^c mm	Dry season ^d		Dry season ^e SD	Soil ^f		Area Ha.	Year		# censuses	Stems ^g No.	BA ^h m ²	Mn tree BA	Principal investigators	Institution
			No.	S	W	Months		Fert	Drain		Start	End		No.	cm ²						
Bosque Chimanes	Bo	Beni	3	15.04	66.33	2110	4.00	1.29	L	G	26	1995	1997	2	513	25.25	492	Leano, Panfil	BOLFOP		
Phlón Lajas	Bo	Beni	2	c.15.00	c.67.00	2559*	5.84	1.73	M	G	2	1990	1999	1	618	28.50	461	Killeen	MBG		
BOLFOP	Bo	Santa Cruz	2	c.15.00	c.62.00	1580/1870	5.68/4.79	1.73	L	G	35.2	1995	1999	5/2	397	20.55	518	Leano, Fredericksen	BOLFOP		
BDFPP	Br	Amazonas	5	c.2.30	ca 60	2398	2.27	1.52	L	G	27	1981	1999	3-5	607	28.20	465	Laurance	BDFDDP, INPA		
BIONTE	Br	Amazonas	1	2.38	60.10	2376	2.37	1.42	L	G	3	1980	1999	14	626	29.73	475	Higuchi	INPA		
Jacaranda	Br	Amazonas	2	2.38	60.10	2376	2.37	1.42	L	G	10	1996	2000	2	583	27.98	480	Higuchi	INPA		
Fazenda Nova	Br	Acre	1	10.07	69.13	1800*	4.32*	0.82*	M	G	1	1995	1995	1	632	34.16	541	Silveira	UB		
Ollinda	Br	Acre	5	c.8.00	c.73.00	2225/2326*	2.16/1.68*	1.21/1.29*	L/M	G	5	1996	1999	1-2	498	22.18	445	Silveira	UB		
PARNA	Br	Acre	6	c.10.00	c.70.00	1879-1988*	4.37-3.42*	0.76-0.84*	L/M	G	6	1991	2000	1-2	488	21.38	438	Silveira	UB		
RESEX	Br	Acre	1	10.04	67.37	1900*	4.32*	0.82*	M	G	1	1999	1999	1	484	21.59	446	Selhorst	FUA		
Rio Branco	Br	Para	1	c.6.00	c.51.00	1924	4.37	1.17	H	G	1	1986	1993	4	484	21.59	446	Salamao	Museu Goeldi		
Carajás	Br	Para	3	5.21	49.04	2059	4.89	1.10	H	G	6	1988	1995	4	525	27.83	530	Salamao	Museu Goeldi		
Marabá	Br	Para	1	c.1.27	c.48.27	2863	3.26	1.05	L	G	2	1956	1999	10	418	28.35	678	Salamao	Museu Goeldi		
Mocambo	Br	Para	1	c.1.00	c.47.30	2893	3.32	0.96	L	G	3	1991	1999	4	439	23.30	531	Salamao	Museu Goeldi		
Peixe-Boi	Br	Para	1	2.45	55.00	2067	4.68	1.80	L	G	3	1983	1995	4	460	27.25	583	Silva	CIFOR		
Tapajós 1	Br	Para	1	2.51	54.57	2067	4.68	1.80	L	G	4	1999	1999	1	460	27.25	583	Saleska, Hammond-Pyle, Hutyra, Wofsy, de Camargo, Vieira	HU/USP		
Tapajós 2	Br	Para	1	2.51	54.57	2067	4.68	1.80	L	G	4	1999	1999	1	460	27.25	583	Saleska, Hammond-Pyle, Hutyra, Wofsy, de Camargo, Vieira	HU/USP		
Trombetas	Br	Para	2	c.1.30	c.56.30	2039	4.05	1.58	L	G	2	1997	1999	2	491	26.30	536	Salamao	Museu Goeldi		
Caxiuaña 1	Br	Para	2	1.42	51.32	2508	2.84	1.30	L	G	2	1995	1999	2	525	33.73	642	Almeida	Museu Goeldi		
Caxiuaña 2	Br	Para	2	1.42	51.32	2508	2.84	1.30	L	G	2	2000	2000	1	516	31.59	612	Almeida	Museu Goeldi		
S. F. do Para	Br	Para	1	1.04	47.47	2600*	3.42*	0.96*	L	G	1	1997	2000	2	499	26.26	526	Vieira	Museu Goeldi		
Vizeu	Br	Para	1	1.53	46.45	2400*	3.42*	0.96*	L	G	2	1998	1998	1	505	30.37	601	Vieira	Museu Goeldi		
Amacayacu	C	Amazonas	2	c.3.21	c.70.09	3216*	0.89	1.03	H	G	3	1989	1998	1	610	33.29	546	Rudas	UNC		
Jatun Sueba	E	Napo	2	1.04	77.36	2800*	1.21	1.03	H	G	3	1989	1998	3	634	31.59	498	Neill	MBG		
Yasuni 1	E	Napo	1	0.41	76.24	3080*	0.37	1.21	M/H	P-G	50	1995	1995	1	664	26.7	402	Valencia	PUCE		
Yasuni 2	E	Napo	3	c.0.30	c.76.00	2563	0.37	1.21	M/H	P-G	15	1997	1997	1	664	26.7	402	Valencia	PUCE		
Allpahuayo	P	Loreto	2	3.57	73.25	2845	0.84	0.83	L/M	A/G	1.8	1990	1996	2	588	26.54	451	Phillips, Vasquez	UL/PPP/IIAP		
Mishana	P	Loreto	1	3.47	73.30	2899	0.95	0.97	L	A	1	1983	1990	2	823	29.05	353	Phillips, Vasquez	UL/PPP		
Sucusari	P	Loreto	2	3.14	72.54	2836	0.58	0.84	M	A	2	1992	1996	2	609	28.92	475	Phillips, Vasquez	UL/PPP		
Yanamono	P	Loreto	1	3.26	72.51	2844	0.68	0.89	H	A	1	1983	1996	5	573	31.42	548	Phillips, Vasquez	UL/PPP		
Cuzco	P	Madre de Dios	4	12.34	69.08	2451*	3.50*	1.20*	H	P/A	4	1989	1998	3	525	26.40	503	Phillips, Vasquez, Nunez	UL/PPP/UNSAAC		
Amazonico	P	Madre de Dios	6	12.49	69.43	2248*	4.08*	1.44*	L-H	P-G	5.4	1979	1998	4-7	590	28.44	482	Phillips, Vasquez	UL/PPP		
Tambopata	P	Madre de Dios	3	-1.45	67.00	3174	0.16	0.37	L	A/G	3.25	1975	1986	2	874	29.59	359	Herrera	IVIC, Caracas		
San Carlos de Rio Negro	V	Amazonas	3	-1.45	67.00	3174	0.16	0.37	L	A/G	3.25	1975	1986	2	874	29.59	359	Herrera	IVIC, Caracas		

This climatic information can be used to calculate which regions are poorly covered by the PSPs for particular environmental variables. Using the example of these length and variability of the dry season, the approach we have used is as follows:

1. Normalize each of the axes in Fig. 3 by subtracting the mean value for all the tropical forest pixels, and dividing by the standard deviation.
2. For each pixel, calculate the 'standardized environmental distance', D_i , from each of the forest plots on each environmental axis i .
3. Use these values to locate the 'closest' forest plot (in that environmental variable) to that plot.
4. For each pixel, plot the environmental distance of the plot from the 'nearest' plot. Examples for the two dry season variables are shown in Fig. 4a, b. For the mean length of the dry season, the coverage of the plot

network is good for much of Amazonia, except at the fringes, and to a lesser extent in an arc in central-west Amazonia. In terms of interannual variability, the coverage of the plot network is poorer, particularly in the northwest Amazon, and in south-central Amazonia.

5. The two maps can be combined by repeating the calculation of minimum environmental distance in two dimensional space (using Pythagoras' rule). The result is shown in Fig 4c. In this combined variable space, the poorest coverage is clearly in northwestern Amazonia, and at the extreme dry fringes of Amazonia.

This approach can be used to prioritize new field-work sites, and can be extended to include other environmental factors such as soil properties.

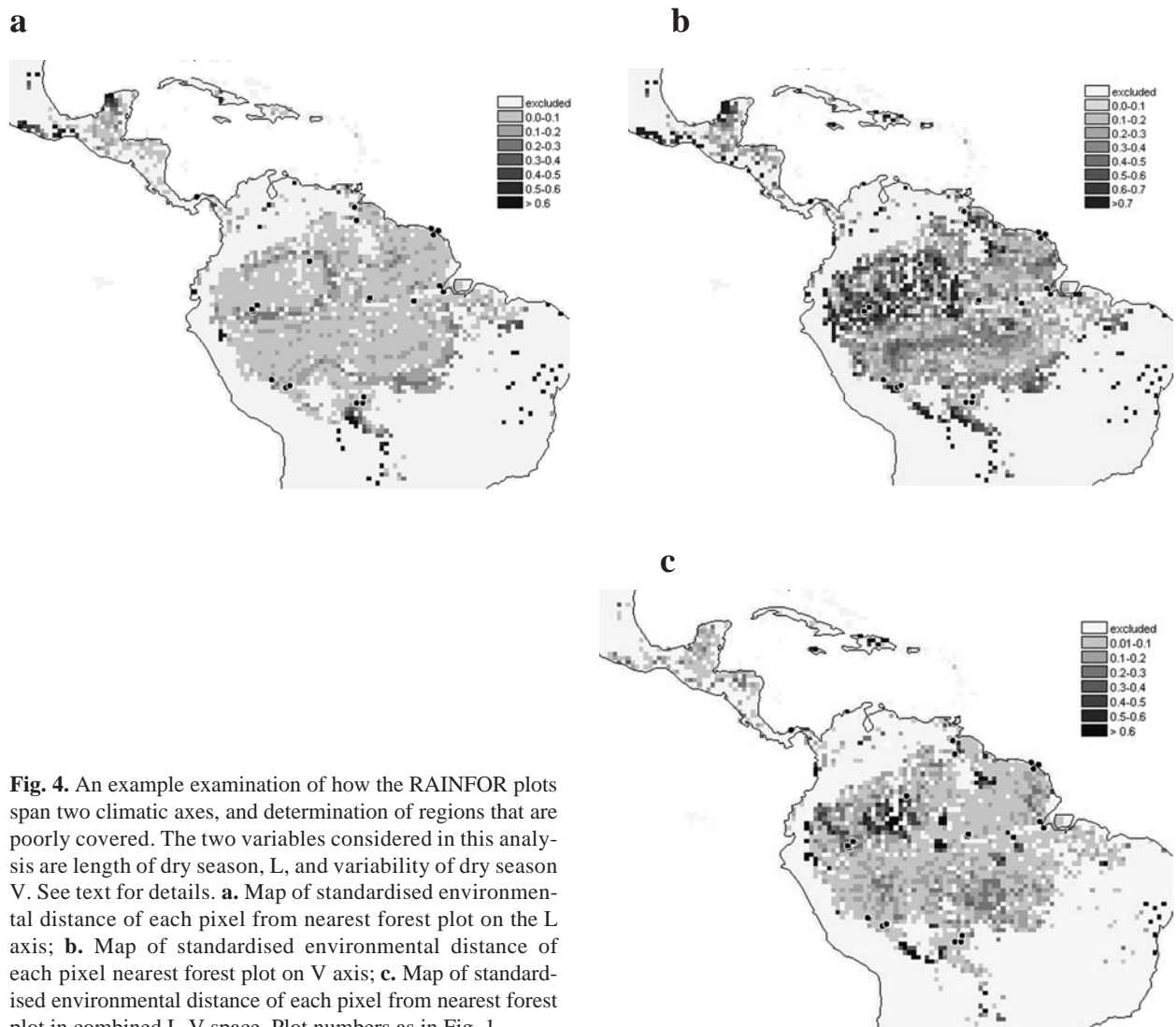


Fig. 4. An example examination of how the RAINFOR plots span two climatic axes, and determination of regions that are poorly covered. The two variables considered in this analysis are length of dry season, L , and variability of dry season V . See text for details. **a.** Map of standardised environmental distance of each pixel from nearest forest plot on the L axis; **b.** Map of standardised environmental distance of each pixel nearest forest plot on V axis; **c.** Map of standardised environmental distance of each pixel from nearest forest plot in combined L - V space. Plot numbers as in Fig. 1.

Some early results

Fig. 5a-c shows some early results from the data so far assembled. Results are still being collected and analysed, and these graphs should therefore only be taken as an indication of the type of trans-Amazonian analyses that will be possible when the data sets are fully checked and compiled, when precipitation data are assembled, and when soil samples have been analysed. Here we concentrate on simple stand characteristics (basal area and tree stem density per ha). Future analyses will concentrate on the more complex questions of forest dynamics (forest growth and mortality rates, total above-ground productivity), and more rigorous multifactorial analytical techniques will be applied when the data set has achieved the desired degree of quality assurance.

Fig. 5a plots the stem density (no. of trees with DBH ≥ 10 cm.ha⁻¹) against the mean length of dry season. Each site is also labelled according to estimated soil fertility (high, medium, low). There is a clear trend for low fertility sites with the more aseasonal conditions (dry season < 2 mo) to show higher stem densities. For more seasonal sites stem density stays relatively fixed between 400 and 700 stems per ha, though perhaps begins to reduce again for the most seasonal sites. The correlations of stem density with total rainfall or interannual variability are weaker; mean dry season length seems to be the best precipitation-based predictor. It is unclear to what extent the trends are caused directly by climatic factors, or by covarying soil fertility. Analysis of soil samples collected in 2001 and 2002 should help to refine and explain these patterns.

Fig. 5c plots basal area (cross-sectional area at 1.3 m height of all stems ≥ 10 cm DBH) against mean length of dry season. The basal area at most sites ranges between 25 and 35 m².ha⁻¹; this lower limit begins to break down for some sites with dry seasons > 3 mo long. There is little evidence of higher basal area at low seasonality sites: although there are more trees per ha at these sites, they are also smaller on average (Fig. 5b), and so total basal area per ha therefore appears to be fairly conservative across Amazon precipitation regimes.

Conclusions and future directions

This paper has provided an overview of the trans-Amazonian forest network, and some indications of the type of results to be expected over the coming years. This will be the first attempt to study tropical forest dynamics at a continental scale. In addition to being a compilation of field results, the network also hopes to become a forum for discussion of a number of methodological issues related to the correct use and inter-

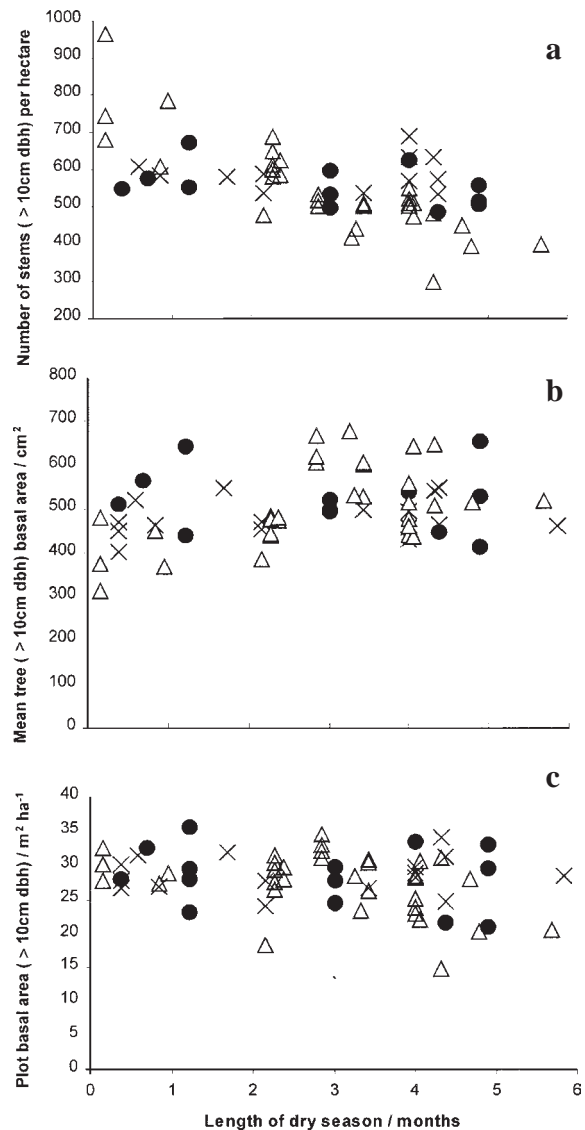


Fig. 5. The relationship between the mean length of the dry season in months and (a) the number of stems, ≥ 10 cm dbh, per ha, (b) mean stem size, ≥ 10 cm dbh, (c) total basal area, ≥ 10 cm dbh, per ha. Mean dry season length and the standard deviation of dry season length are calculated from the interpolated precipitation data analysed by the University of California at Santa Barbara. Site classifications of soil fertility are tentatively drawn from Sombroek (2000). Δ = low fertility sites, \times = medium fertility sites, \bullet = high fertility sites.

pretation of PSPs. Issues that will need to be tackled include:

1. Is there a bias (at local scale) in the sites which researchers select for PSPs? This can be examined by employing the tests described in Table 1.
2. How vulnerable are forest dynamics to nearby deforestation? A number of the plots in eastern Amazonia

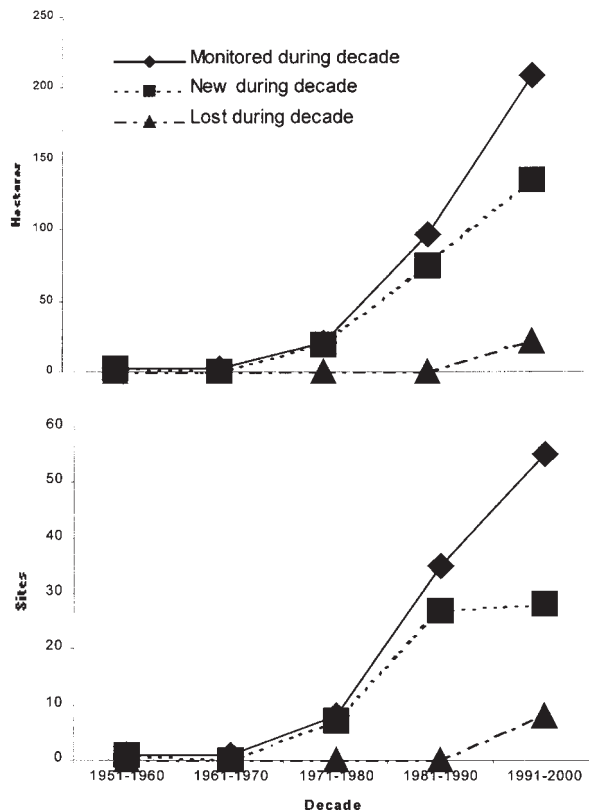


Fig. 6. The number of (a) ha, and (b) sites, monitored, 1951-2000, for sites within RAINFOR.

are situated in large forest fragments, and others are within landscapes that are becoming progressively disturbed by, for example, selective logging.

3. What is the relationship between basal area and above-ground and below-ground biomass? Can empirical relations determined at one site be applied to other sites?

4. What is the relationship between basal area growth, total net primary production (NPP) and total photosynthesis? This can be investigated at the intensive sites in eastern Amazonia, where many complementary eco-physiological measurements are being conducted as part of LBA.

Once fully functioning, RAINFOR has the potential to yield a vast amount of information and new understanding of the ecology, dynamics and biomass of the world's largest area of rain forest. However, its potential lies not only in the science that can be done now, but also in the long-term collaborations, connections and standardized protocols that will be discussed and developed between researchers in all Amazonian countries. If successful, these may allow the forests of Amazonia to be monitored in a systematic and spatially coherent way for decades to come. Fig. 6 shows how the number of forest census sites has increased since 1950. Although some

sites have been lost to deforestation and degradation, there are currently more than 40 sites being monitored covering more than 100 ha in total. In addition, these sites are only those currently known to the authors – there are likely to be more that we hope to include in the future, and within RAINFOR new plots may also be set up in undersampled regions. Many of the existing PSPs were initially censused in the 1980s and 1990s, and although they are already yielding valuable scientific information, their full potential will be realised if they can be monitored for several more decades. Then they will provide unique valuable information on the effects of global change that are likely to sweep Amazonia over the coming century (whether in the form of climate change, biodiversity loss, fragmentation or CO₂ fertilization), and also on the feedback between Amazonia and the global climate through its influence on the carbon cycle. This is information that will be crucial to the understanding and protection of this immense and important ecosystem.

Acknowledgements. Cross-Amazonian work within RAINFOR is funded by the EU Fifth Framework Programme (CARBON-SINK-LBA), by the U.K. Natural Environment Research Council (grants GR9/04635 and NER/A/S/2000/01002), and by the Max Planck Institute for Biogeochemistry, Jena, Germany. YM is funded by a Royal Society University Research Fellowship. We gratefully acknowledge the support of the numerous funding agencies and organizations who have contributed to research at individual sites: in Bolivia (TK), U.S. National Science Foundation (DEB 92011026), the Nature Conservancy/Mellon Foundation (Ecosystem Function Program); in Brazil (SA): Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Museu Goeldi, Estação Científica Ferreira Penna; in Brazil (WL): NASA-LBA, Andrew W. Mellon Foundation, U.S. Agency for International Development, Smithsonian Institution; in Brazil (RS): CNPq, Fundo Nacional do Meio Ambiente, Companhia Vale do Rio Doce, Mineração Rio do Norte, EMPBRAPA-CPATU, and the Woods Hole Research Center; in Brazil (IV): CNPq/MCT; in Colombia (AR): Missouri Botanical Garden and the McArthur Foundation; in Ecuador (RV): Center for Tropical Forest Science; in Peru (OP, TB, AM, PN, RV, BV): Natural Environment Research Council (Postdoctoral Fellowship to OP, Research Assistantship to BV, SL), U.S. National Geographic Society (5472-95) (6837-00), National Science Foundation (BSR-9001051), WWF-U.S./Garden Club of America, Conservation International, MacArthur Foundation, Andrew W. Mellon Foundation, ACEER, Albergue Cuzco Amazonico, Explorama Tours S.A., Explorers Inn, IIAP, INRENA, UNAP, and UNSAAC.

References

- Anon. (FAO) 2000. *Global forest resources assessment 2000*, FAO Forestry Paper 140, data available online at <http://www.fao.org/forestry/fo/fra/index.jsp>.
- Anon. (Global Soil Data Task) 2000. *Global gridded surfaces of selected soil characteristics (IGBP-DIS)*. International Geosphere-Biosphere Programme - Data and Information Services. Available on-line [<http://www.daac.ornl.gov/>] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, TN.
- Bousquet, P., Peylin, P., Ciais, P., Le Quere, C., Friedlingstein, P. & Tans, P.P. 2000. Regional changes in carbon dioxide fluxes of land and oceans since 1980. *Science* 290: 1342-1346.
- Clark, D. 2002. Are tropical forests an important carbon sink? Reanalysis of the long-term plot data. *Ecol. Appl.* 12: 3-7.
- Cox P.M., Betts, R.A., Jones, C.D., Spall, S.A. & Totterdell, I.J. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* 408: 184-187.
- Grace, J. et al. 1995. Carbon dioxide uptake by an undisturbed tropical rain-forest in Southwest Amazonia, 1992 to 1993. *Science* 270: 778-780.
- Hodnett, M.G., Oyama, M.D., Tomasella, J. & de O. Marques Filho, A. 1996. Comparisons of long-term soil water storage behaviour under pasture and forest in three regions of Amazonia. In: Gash, J.H.C., Nobre, C.A., Roberts, J.M. & Victoria, R.L. (eds.) *Amazonian deforestation and climate*, pp. 57-77. Wiley, New York, NY.
- Lloyd J. 1990. The CO₂ dependence of photosynthesis, plant growth responses to elevated CO₂ concentrations and their interaction with soil nutrient status, II. Temperate and boreal forest productivity and the combined effects of increasing CO₂ concentrations and increased nitrogen deposition at a global scale. *Funct. Ecol.* 13: 439-459
- Lloyd, J. & Farquhar, G.D. 2000. Do slow-growing species and nutrient-stressed plants consistently respond less to elevated CO₂? A clarification of some issues raised by Poorter (1998). *Global Change Biol.* 6: 871-876
- Malhi, Y., Nobre, A.D., Grace, J., Kruijt, B., Pereira, M.G.P., Culf, A. & Scott, S. 1998. Carbon dioxide transfer over a Central Amazonian rain forest. *J. Geophys. Res.* D24: 31593-31612.
- Malhi, Y., Baldocchi, D.D. & Jarvis, P.G. 1999. The carbon balance of tropical, temperate and boreal forests. *Plant Cell Environ.* 22: 715-740.
- Malhi, Y. & Grace, J. 2000. Tropical forests and atmospheric carbon dioxide. *Trends Ecol. Evol.* 15: 332-337.
- Malhi, Y., Pegoraro, E., Nobre, A.D., Pereira, M.G.P., Grace, J., Culf, A.D. & Clement, R. In press. The water and energy dynamics of a central Amazonian rain forest. *J. Geophys. Res. Atmosph.*
- Norby, R.J., Wullschlegel, S.D., Gunderson, C.A., Johnson, D.W. & Ceulemans, R. 1999. Tree responses to rising CO₂ in field experiments: implications for the future forest. *Plant Cell Environ.* 22: 683-714.
- Phillips, O.L. 1997. Long-term environmental change in tropical forests: increasing tree turnover. *Environ. Conserv.* 23: 235-248.
- Phillips, O.L. & Gentry, A.H. 1994. Increasing turnover through time in tropical forests. *Science* 263: 954-958.
- Phillips, O.L. et al. 1998. Changes in the carbon balance of tropical forest: evidence from long-term plots. *Science* 282: 439-442.
- Phillips, O.L. et al. 2002. Changes in the biomass of tropical forests: evaluating potential biases. *Ecol. Appl.* 12: 576-587.
- Rudas-Ll., A. & Prieto-C., A. 1998. Análisis florístico del Parque Natural Amacayacu e Isla Mocagua, Amazonas (Colombia). *Caldasia* 20: 142-172.
- Shuttleworth, W.J. 1988. Evaporation from Amazonian rain-forest. *Proc. R. Soc. Lond. Ser. B* 233: 321-346.
- Sombroek, W.G. 2000. Amazon land forms and soils in relation to biological diversity. *Acta Amazon.* 30: 81-100.
- Sombroek, W.G. In press. Annual rainfall and dry season strength in the Amazon region and their environmental consequences. *Ambio*.
- Vitousek, P.M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65: 285-298.
- Vormisto J., Phillips O.L., Ruokolainen, K., Tuomisto, H. & Vásquez, R. 2000. A comparison of fine-scale distribution patterns of four plant groups in an Amazonian rainforest. *Ecography* 23: 349-359.
- White, A., Cannell, M.G.R. & Friend, A.D. 2000. CO₂ stabilization, climate change and the terrestrial carbon sink. *Global Change Biol.* 6: 817-833.
- Williams, M., Malhi, Y., Nobre, A.D., Rastetter, E.B., Grace, J. & Pereira, M.G.P. Seasonal variation in net carbon exchange and evapotranspiration in a Brazilian rain forest: a modelling analysis. *Plant Cell Environ.* 21: 953-968.

Received 11 December 2000;

Revision received 1 March 2002;

Accepted 8 April 2002.

Coordinating Editors: J. Canadell & P.S. White.