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Ecophysiology of Forest and Savanna Vegetation

J. Lloyd,¹ M. L. Goulden,² J. P. Ometto,³ S. Patiño,⁴ N. M. Fyllas,¹ and C. A. Quesada⁵

Ecophysiological characteristics of forest and savanna vegetation are compared in an attempt to understand how physiological differences within and between these vegetation types relate to their geographical distributions. A simple ordination first shows that although precipitation exerts a key effect on Amazonian vegetation distributions, soil characteristics are also important. In particular, it is found that under similar precipitation regimes, deciduous forests tend to occur on more fertile soils than do cerrado vegetation types. A high subsoil clay content is also important in allowing the existence of semievergreen forests at only moderate rainfall. Such observations are consistent with biome specific physiological characteristics. For example, deciduous trees have higher nutrient requirements than do evergreen ones which also tend to have characteristics associated with severe water deficits such as a low specific leaf area. Nutrient contents and photosynthetic rates are lower than for savanna than for forest species with several ecosystem characteristics suggesting a primary limitation of nitrogen on savanna productivity. By contrast, phosphorus seems to constrain the productivity of most Amazonian forest types. Differentiation is made between the fast-growing, high-nutrient-requiring forest types of western Amazonia and their counterparts in eastern Amazonia, which tend to occupy infertile but deeper soils of high water-holding ability. On the basis of observed physiological characteristics of the various vegetation forms, it is argued that, should Amazonian precipitation decline sharply in the future, the slower growing forests of eastern Amazonia will transform directly into an evergreen cerrado type vegetation but with the more fertile western Amazonian forests being replaced by some form of drought-deciduous vegetation.

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1. INTRODUCTION

In this chapter, we first consider the various vegetation types of Amazonia and the underlying factors influencing their distribution. We then look at their contrasting physiological characteristics in some detail, first at the leaf and plant and then at the whole stand level. Finally, in the spirit of *Schimper* [1903], we speculate on the extent to which observed differences between the various vegetation types studied as part of Large-Scale Biosphere-Atmosphere Experiment in Amazonia (LBA) reflect adaptations to the different soil and climatic environments in which they occur.

2. CONTRAST OF AMAZONIAN VEGETATION TYPES

Although dominated by tropical evergreen and semievergreen forest, here we adopt the terminology of *Eyre* [1963] to delineate the various tropical forest types; see also section 2.3. Amazonia also contains significant amounts of other vegetation types of a contrasting physiology, especially toward its southern and eastern margins. These include large areas of both well-drained savanna, often referred to as cerrado, along with seasonally flooded savannas such as those that occur in the Pantanal (Brazil) and the “Llanos de Moxos” (Bolivia and Colombia). Also, along the southern fringe, especially in northern Bolivia, large areas of (semi) deciduous seasonal forest occur (Chiquitano). Savannas are also scattered along the northern borders of the basin, for example, in Roraima State in Brazil and in the La Sabana region of Venezuela. An overview of the lowland tropical vegetation types of South America, including Amazonia, is given by *Daly and Mitchell* [2000]. In this review, we focus on terre firme forest and cerrado only.

2.1. Primary Determinants of the Different Vegetation Types

It has long been apparent that the main factor delimiting tropical forest and savanna is rainfall and its seasonality. *Schimper* [1903] and *Nix* [1983] developed seven criteria to predict the occurrence of tropical savannas throughout the world, four of which involved precipitation, two of which involved temperature, and one of which involved incoming radiation. Recently, *Huytra et al.* [2005] extended the water availability notion, arguing that frequency of drought is also an excellent predictor of the forest savanna boundary, overall supporting the notion of *Oyama and Nobre* [2003] that seasonality of soil moisture is a critical factor in determining forest-savanna boundaries. *Schimper* [1903] expressed this point himself, saying that savannas generally are found where there are clearly defined wet and dry seasons, the latter being characterized by very dry soil and a very dry atmosphere, with wet seasons occurring every year and rarely broken by significant dry periods. *Malhi et al.* [2009] also developed a simple model of Amazonian vegetation distribution based on rainfall and its seasonality: their savanna zone being defined as where the mean annual precipitation was less than 1500 mm a⁻¹ and with a mean cumulative water deficit (MCWD) as defined by *Malhi et al.* [2009] as the maximum climatological water deficit (CWD) attained over a year with CWD calculated using a “bucket model” and with no feedback effect of CWD on evaporation, greater than 300 mm. *Malhi et al.* [2009] also differentiated between “rain

forest” and “seasonal forest,” the latter apparently being most prevalent where rainfall is reasonably high (between 1300 and 2000 mm) but with moderate MCWD (350–450 mm) also occurring.

Although precipitation and its seasonality are no doubt important factors controlling the relative distributions of forest and savanna across Amazonia, it is also clear that additional factors must be involved. This is because within the Amazon forest domain itself, there are many occurrences of savanna vegetation despite high rainfall (>2000 mm) with unusually adverse physical and/or chemical conditions for tree growth apparently responsible [*Beard*, 1953; *Anderson*, 1981; *Brown*, 1987]. Examples of this include the savannas of the relict sandstone cover that once made up much of the land portion of the Guyanas [*van Donselaar*, 1969]; these include the savannas of Roraima (Brazil) as well as the Rupunini savannas of Guyana [*Myers*, 1936] and the Sipalwini savanna of southern Suriname [*van Donselaar*, 1968], the Grand Sabana area of Venezuela [*Dezseo et al.*, 2004] as well as scattered “islands” across the northeast of Brazilian Amazonia [*Andrae Lima*, 1959; *Egler*, 1960; *Ratter et al.*, 2003]. Although in some cases the presence of such “Amazonian savannas” can clearly be attributed to water-logging [e.g., *Huber*, 2006], in other cases, the generally poor nutrient status of the sandy soils seems to be the primary cause [*Beard*, 1953; *Anderson*, 1981; *Brown*, 1987]. The possibility of poor water-holding capacity of the sandy soils associated with many of the “dry” savannas giving rise to unusually severe water deficits in the dry season preventing the establishment of forest does not seem to have been investigated. In areas usually associated with (semi)evergreen forest, savannas may also occur on unusually shallow and/or rocky soils [*Reatto et al.*, 1998].

2.2. Variation in Savanna Structure

Within the savanna biome itself, considerable variation exists and explanations for the various physiognomic forms, especially the degree of woodiness, have concentrated on the degree to which variations in the density of woody plants is a function of degradation due to fire and human activity [*Rizzini*, 1963; *Coutinho*, 1990; *Bond et al.*, 2005] as opposed to variations in soils such as effective rooting depth, waterlogging, and fertility [*Eiten*, 1993]. Nevertheless, on balance, there seems little to suggest that burning and other human activities account for large-scale variations in savanna form, although this is no doubt the case under certain circumstances in Brazil as elsewhere [*Eiten*, 1983; *Sarmiento*, 1983; *Cavelier et al.*, 1998; *Dezseo et al.*, 2004]. That factors other than fire are important in determining woodiness of cerrado vegetation is also suggested by

plant ordination studies [Ribeiro and Tabarelli, 2002; Miranda et al., 2003] and points to soil fertility being a major determinant of woodiness in Brazilian savanna at the landscape scale [Lopes and Cox, 1977a, 1977b]. For example, it is well established that some woodland types, *cerradão*, tend to occur only on unusually fertile soils [Furley et al., 1988; Morriera, 2000; Chapuis-Lardy et al., 2001], and on the basis of soil pH and exchangeable cation measurements, a distinction is sometimes made between “mesotrophic facies *cerradão*” and “dystrophic facies *cerradão*,” which are characterized by different species compositions. Nevertheless, despite these differences, both vegetation forms seem to be characterized by relatively high soil-soluble phosphorus concentrations [Furley and Ratter, 1988]. Whether the grassland *cerrado* forms such as *campo sujo* occur because of soils with an exceptionally low nutrient status is less clear [Alvim and Araújo, 1952; Askew et al., 1970; Goodland and Pollard, 1973; Lopes and Cox, 1977a, 1977b; Furley and Ratter, 1988; Furley, 1992; Ruggiero et al., 2002]. Fire frequencies must also be important. What is clear in any case is that the Brazilian *cerrado* occupies an area much of which on the basis of climate alone would be expected to be occupied by forests [Bond et al., 2005], and one significant factor accounting for the actual vegetation is the relatively infertile soil there [Montgomery and Askew, 1983]. It is also interesting to note that the seasonally dry tropical forest, which occurs on the southern edges of Amazonia, is considered to exist because of the more fertile soils occurring there, with areas of *cerrado* vegetation in the same regions occurring where soils are of the more infertile type typically associated with Amazonia [Prado and Gibbs, 1993; Prado, 2000; Oliveira-Filho and Ratter, 2002].

2.3. A Basin-Wide Ordination of Forest and Savanna Vegetation Types

In an effort to formalize the above vegetation/climate/soil relationships, we have undertaken a constrained ordination of Amazonian vegetation types from the spatially explicit database of Cochrane et al. [1985], which also includes both soil chemical and physical characteristics, also investigating effects of temperature and precipitation, these coming from New et al. [2000]. Results from this partial canonical correspondence analysis are shown in Figure 1. Here as in Cochrane et al. [1985], we have divided the forest vegetation into three types; “evergreen,” “semievergreen,” and “seasonally dry” following the broad definition of Eyre [1963]. Semievergreen forest is considered to consist of a mixture of evergreen and deciduous trees, whereas seasonally dry forests consist mainly of species which lose all their leaves in the dry season. Within the savanna biome, we have di-

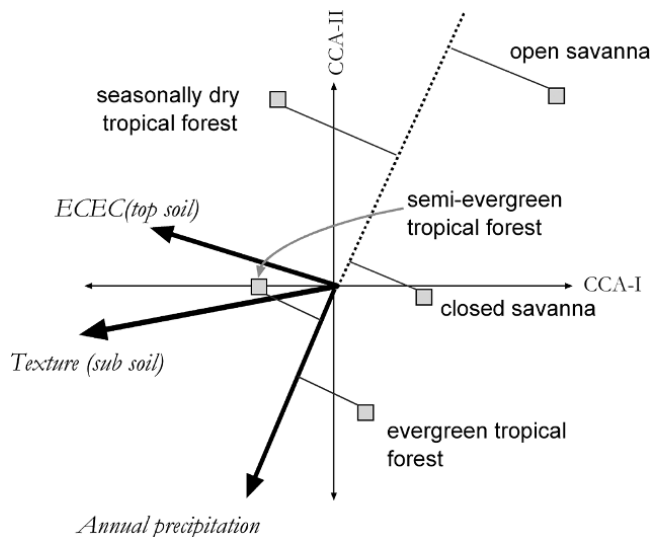


Figure 1. Partial canonical correspondence analysis of Amazonian vegetation types in terms of climate and soil properties. The arrow for soil texture (right to left) goes from fine (clay) to coarse (sand) textured soils, with topsoil being defined as 0.0- to 0.2-m depth and subsoil as 0.21- to 0.50-m depth. For more details, see section 2.3.

vided vegetation into “closed” and “open: on the basis of woodiness: “open” savannas being grassland with or without scattered trees and shrubs (*campo limpo*, *campo sujo*, and *campo cerrado*) and “closed” savannas consisting of the tree savanna and woodland forms commonly referred to as *cerrado* (*sensu strictu*) and *cerradão*. To remove any spatial autocorrelation structures in the data, latitude and longitude of the centers of the various polygons describing the various different landforms within Amazonia within Cochrane et al. [1985] have been taken as covariates [Legendre and Legendre, 1998].

Figure 1 uses “Type 2 Scaling” [ter Braak, 1994; Legendre and Legendre, 1998], where the distances among the various centroids approximate their chi-square distances in the ordination space. The ranking of any vegetation type along any environmental variable consists of projecting (at right angle) those vegetation type centroids onto the arrow representing that variable. This gives an approximation for the weighted average for the vegetation type with respect to environmental variables and, as an aid, is shown explicitly for annual precipitation. The three environmental/edaphic variables shown have been chosen from a group of 26 taken from Cochrane et al. [1985] and New et al. [2000] using forward selection [ter Braak and Šmilauer, 2002] and together account for 0.38 of the variation. In addition to annual precipitation, the other two variables that emerge as important are the

effective cation capacity of the topsoil (ECEC) and subsoil texture, both these parameters coming from *Cochrane et al.* [1985]. In the work of *Cochrane et al.* [1985], “topsoil” is defined as soil from 0.00–0.20 m depth and “subsoil” as soil from 0.21–0.50 m depth.

Figure 1 suggests that although precipitation amount is a key environmental variable influencing vegetation distributions across Amazonia, soil fertility and texture are also important. In particular, the distribution of closed savanna versus semievergreen tropical forest seems to be controlled as much by topsoil ECEC and subsoil texture as by precipitation and with seasonally dry tropical forest also being associated with fertile soils as well as a lower than average precipitation. This confirms and, to some extent, formalizes many of the statements in sections 2.1 and 2.2. For example, where soils are unusually infertile and/or subsoils are coarsely textured, savanna type vegetation can occur, even when precipitations are reasonably high. Likewise, the main differentiation between seasonally dry tropical forests and savanna vegetation types is soil fertility. The key question which we try to answer in this chapter is to what extent these differences in “niche optima” are reflected by differences in plant physiological characteristics for these various vegetation types.

3. PHYSIOLOGY OF FOREST AND SAVANNA VEGETATION

3.1. Structural Aspects

The amount and distribution of biomass for any vegetation type provides a first indication of both physiological strategy and likely limitations on plant function imposed by soil and/or environment. For example, with the Amazonian tropical forest biome as a whole, there is a clear tendency for aboveground biomass (AGB) to decline with increasing dry season length [*Malhi et al.*, 2006; *Saatchi et al.*, 2007, 2009]. This suggests that either carbon resources for growth become more limiting as dry season length increases or that an increased allocation of carbon belowground occurs as precipitation declines [*Cairns et al.*, 1997; *Mokany et al.*, 2006]. A third possibility is that more severe soil water deficits for the driest forests result in higher long-term rates of mortality (i.e., an increased frequency disturbance regime) as has recently been suggested by *Quesada et al.* [2009a]. Although there is not enough evidence yet to clearly differentiate these three possibilities, generally speaking, root:shoot ratios are higher for seasonally dry-deciduous forests than for evergreen tropical forests [*Fittkau and Klinge*, 1973; *Murphy and Lugo*, 1986; *Castellanos et al.*, 1991; *Jipp et al.*, 1998; *Mokany et al.*, 2006], and it is clear that significant variations in root:shoot between forest and cerrado exist. For

example, *Mokany et al.* [2006] cite globally average root:shoot ratios of 0.24 and 0.64 for tropical forest and savanna, respectively, and this is consistent with the very high belowground biomass values of up to 53 Mg DW ha⁻¹ found by *Castro and Kaufmann* [1998] for cerrado vegetation near Brasilia. This occurred despite a relatively low AGB of about 17 Mg DW ha⁻¹. That AGB value may be an underestimate, however, because an allometric equation suitable for forest as opposed to savanna trees was used. Nevertheless, even when more appropriate calculations are applied [*Abdala et al.*, 1998], AGB for dense cerrado vegetation still only amounts to 20–40 Mg DW ha⁻¹ [*Haridasan*, 2000; *Quesada et al.*, 2008].

Although belowground biomass values for Amazonian evergreen forests are typically less than for woody cerrado vegetation, 20–40 Mg DW ha⁻¹ [*Jipp et al.*, 1998; *Metcalf et al.*, 2007], aboveground biomass values are much higher, typically 200–300 Mg DW ha⁻¹ [*Malhi et al.*, 2006; *Saatchi et al.*, 2007]. Although it is tempting to account for these differences in root:shoot solely in terms of physiological adjustments associated with the large differences in soil water regime, which may be characteristic of the two biome types (section 4.1), low rates of soil fertility (sections 3.6 and 4.2) and the characteristic fire regime of savanna ecosystems, itself associated with the presence of grasses [*Miranda et al.*, 2002], may also be important. Studies with seedlings, in particular, have shown higher root:shoot ratios for savanna as opposed to forest species [*Paulilo and Felipe*, 1998; *Hoffmann et al.*, 2004]. This allows for greater belowground carbohydrate reserves to be present for young savanna trees, thus facilitating a more rapid growth recovery after fire than is the case for those from the forest [*Hoffmann et al.*, 2004]. Savanna trees often also have additional physiological and anatomical characteristics associated with fire resistance, such as unusually thick bark [*Gignoux et al.*, 1997] and an ability to resprout from dormant or adventitious buds [*Hoffmann and Moreira*, 2002].

3.2. Leaf Area and Light Interception

Tropical forests have among the highest leaf areas per unit ground area (leaf area index (LAI)) of any biome [*Asner et al.*, 2003] with values for Amazonia typically ranging from 4 to 8 [*McWilliam et al.*, 1993; *Carswell et al.*, 2002], significantly greater than cerrado vegetation for which the peak LAI (trees and grasses) typically varies from less than 1 to around 2.5 [*Miranda et al.*, 1997; *Hoffmann et al.*, 2005a].

Quantitative, in situ observations of the timing of leaf production are difficult given the height of most tropical forest canopies, but qualitative and anecdotal observations suggest that new leaf production often occurs in the dry season [*van*

Schaik et al., 1993; *Goulden et al.*, 2004]. Satellite observations have confirmed dry season leaf flushing, showing increases in both normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI) late in the dry season [*Potter et al.*, 2001; *Huete et al.*, 2006; *Xiao et al.*, 2006]. *Myneni et al.* [2007] used the Moderate Resolution Imaging Spectroradiometer (MODIS) LAI product to infer that leaf out creates a large, transient increase in Amazonian forest LAI during the dry season and subsequent decrease in the wet season. However, an alternative hypothesis, that tropical forests simply exchange leaves in the dry season, and LAI remains nearly constant or is reduced during this exchange [*Goulden et al.*, 2004], remains viable. For example, it is not clear that the MODIS LAI product fully accounts for the increased NIR reflectance by young leaves [*Roberts et al.*, 1998], and this raises the possibility that the observed dry season increases in NDVI and EVI are simply a result of seasonal shifts in mean leaf age and leaf level spectral reflectance. The few in situ time series observations of LAI that have been reported are either ambiguous or too short to fully address this issue [*Carswell et al.*, 2002; *Asner et al.*, 2004], and longer-term, in situ observations of LAI are still needed for evergreen and semideciduous forest. The issue of seasonality in cerrado and seasonally dry tropical forest is more certain.

Both cerrado trees and seasonal dry tropical forest show the expected seasonality of LAI with significantly lower values in the dry season than in the wet [*Vourlitis et al.*, 2004; *Hoffmann et al.*, 2005a, 2005b], though with many cerrado trees beginning a new flush of vegetative growth prior to the wet season commencing [*Lenz and Klink*, 2006]. Cerrado grasses and herbs show sharp reductions in green leaf biomass/LAI toward the end of the wet season with commensurate increases in the amount of dead material present [*Miranda et al.*, 1997; *Santos et al.*, 2003; *Hoffmann et al.*, 2005a; *Quesada et al.*, 2008].

3.3. Nutrients and Leaf Structure

Although with a high LAI, nutrient contents of the leaves of tropical forest and trees can be surprisingly low compared to trees of the temperate zone, this being especially the case for phosphorus [*Reich and Oleksyn*, 2004], but only on highly weathered and infertile ferralsol and Acrisol/Alisol soils. (Here we use the new World Reference Base (WRB) for Soil Resources classification system [*IUSS Working Group WRB*, 2006]. For the soils of the Amazon Basin, equivalences with the USDA system are given by *Quesada et al.* [2009b].) Such soils are typical of eastern Amazonia and for some forests on the Guinean and Brazilian shields [*Quesada et al.*, 2009b] with the forests growing on them typically

having foliar phosphorus of $\sim 0.6 \text{ mg g}^{-1} \text{ DW}$ [*Townsend et al.*, 2007; *Fyllas et al.*, 2009]. In western Amazonia (and generally closer to the Andes), soils are generally younger and more fertile and with the forests there having higher levels of available soil phosphorus [*Quesada et al.*, 2009c], also reflected in significantly higher foliar phosphorus concentrations, typically $1.0\text{--}1.6 \text{ mg g}^{-1} \text{ DW}$ [*Fyllas et al.*, 2009]. This reduction in soil phosphorus availability as soils age is consistent with soil pedogenic theory [*Walker and Syers*, 1976], with *Quesada et al.* [2009a] showing that the higher productivity of forests in western Amazonia [*Malhi et al.*, 2004] is almost certainly attributable to higher levels of available phosphorus being present there. This is consistent with phosphorus being a key determinant of tropical forest productivity, as was first suggested by *Vitousek* [1984].

Despite these differences in foliar phosphorus concentration, foliar nitrogen concentrations of Amazonian forests are much less variable, being comparable to temperate zone forests [*Reich and Oleksyn*, 2004], typically averaging $25 \text{ mg g}^{-1} \text{ DW}$, although values may be only half of that on white sand (arenosol) or podzol soils [*Fyllas et al.*, 2009]. These relatively high foliar nitrogen contents are consistent with the notion that nitrogen may be available in excess for many tropical forests [*Martinelli et al.*, 1999] with the lower [N] for forests growing on white sand soils, also being consistent with the idea that nitrogen may indeed be limiting for these systems as indicated by plant and soil $^{15}\text{N}/^{14}\text{N}$ ratios [*Martinelli et al.*, 1999; *Mardegan et al.*, 2008; *Quesada et al.*, 2009c] and the dominance of ectomycorrhizal associations for the trees growing there [*Alexander and Lee*, 2005]. Despite the abundance of leguminous trees in Amazonia, it now appears that many of these do not fix nitrogen, even though they clearly have this ability [*Nardoto et al.*, 2008] (see also section 4.2).

Most recently, *Davidson et al.* [2007] have suggested that the nitrogen availability in terrestrial ecosystems can be ephemeral and eventually disrupted by disturbance; thus, periods of low nutrient availability might arise, for instance, due to limited litter decomposition during the dry season [*Saleska et al.*, 2003], even though on longer-term timescales nitrogen may still be relatively abundant. The observations by *Davidson et al.* [2007] rely on a study carried out in a forest succession following agricultural abandonment in eastern Amazonia using biogeochemical and isotopic parameters, and the patterns of nitrogen and phosphorus cycling, during the succession over decadal time scales, are considered to be compared to nitrogen and phosphorus cycling patterns during primary succession as soils age over thousands and millions of years.

When compared to tropical forests, cerrado trees tend to have significantly lower foliar nitrogen and phosphorus

concentrations (dry weight basis) [Franco, 2002; Hoffmann *et al.*, 2005b], with foliar nitrogen concentrations for both C3 and C4 grass species even lower [Miranda *et al.*, 1997]. Although not known at this stage, it seems reasonable to assume that, as is the case elsewhere [Prior *et al.*, 2004], leaves of dry-deciduous forests within Amazonia would be both thinner (i.e., higher specific leaf area (SLA)) and with higher foliar nutrient contents, consistent with their tendency to occur on more fertile soils (section 2.3).

3.4. Leaf Photosynthetic Characteristics

Compared to broadleaf temperate zone tree species, photosynthetic rates of tropical forest and savanna species are relatively low, typically ranging from 5 to 15 $\mu\text{mol m}^{-2} \text{s}^{-1}$ [Medina and Klinge, 1982; Franco, 2002; Carsewell *et al.*, 2002; Domingues *et al.*, 2005; Franco *et al.*, 2005; Miranda *et al.*, 2005; Domingues *et al.*, 2007]. As pointed out by Meir *et al.* [2002], such low rates occur, despite foliar nitrogen concentrations being similar to temperate zone broadleaf tree species whose photosynthetic rates are typically significantly higher, 25–40 $\mu\text{mol m}^{-2} \text{s}^{-1}$; a result confirmed and expanded by the recent global survey of Kattge *et al.* [2008], who showed that this effect (i.e., low photosynthetic rate per unit leaf nitrogen for tropical tree species) was most pronounced for trees growing on the relatively infertile ferralsol soils. As there is also now increasing evidence that plants growing on such soils generally have lower foliar phosphorus concentrations than those growing on more fertile soils and with this occurring despite similar foliar N concentrations [Townsend *et al.*, 2007; Fyllas *et al.*, 2009], this raises the interesting possibility that phosphorus rather than nitrogen may limit photosynthetic rates on such soils. Nevertheless, even on these characteristically phosphorus-poor soils, some analyses have continued to concentrate solely on nitrogen as the underlying nutrient limiting photosynthesis [e.g., Coste *et al.*, 2005; Domingues *et al.*, 2005], even though it is well documented that phosphorus rather than nitrogen can limit photosynthetic rates under some circumstances [Brookes *et al.*, 1984; Campbell and Sage, 2006].

Considerable differences between species in photosynthetic rates can be observed for both savanna and forest [Reich *et al.*, 1994; Prado and De Moraes, 1997; Turner, 2001]. For example, a simple literature survey has shown that forest trees leaves of “shade-intolerant” trees typically have higher photosynthetic rates than “light demanders” (trees that can tolerate shade, but require light to express their true growth potential), which in turn are higher than “shade-tolerant” plants [Turner, 2001]. Likewise, deciduous tropical trees tend to have higher photosynthetic rates than their evergreen counterparts in both the cerrado [Prado and De

Moraes, 1997; Franco *et al.*, 2005] and elsewhere [Sobrado, 1991; Prior *et al.*, 2004]. Such differences are readily accountable for in terms of physiological trade-offs associated with differing growth strategies [Turner, 2001] and are considered in more detail in section 3.6.

Despite their low foliar nitrogen contents (section 3.2), tropical C4 grasses are typically capable of higher photosynthetic rates than their C3 counterparts [Pearcy and Ehleringer, 1984; Anten *et al.*, 1998] and with massively higher photosynthetic nitrogen and phosphorus use efficiencies; for a summary, see discussion section of Mantlana *et al.* [2008a]. Although not yet measured for cerrado grasses to our knowledge, a simple comparison can be made of leaf level gas exchange and nutrient data of Domingues *et al.* [2005] for semievergreen tropical forest with that of Anten *et al.* [1998] for a C4 grass (*Hypharrhenia rufa*) growing in a central Venezuelan savanna. The highest foliar [N] observed for *H. rufa* was about 50 mmol m^{-2} , this being associated with net CO_2 assimilation rate of around 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$. By contrast, none of the forest leaves studied by Domingues *et al.* [2005] had [N] less than 70 mmol m^{-2} with these leaves having net CO_2 assimilation rates of less than 5 $\mu\text{mol m}^{-2} \text{s}^{-1}$. From what little we currently know, cerrado trees seem to be intermediate between these two contrasts but, not unexpectedly, much closer to forest trees. For example, from the study of Franco *et al.* [2005], the lowest foliar [N] reported was around 120 mmol m^{-2} with these leaves having net CO_2 assimilation rates of approximately 10 $\mu\text{mol m}^{-2} \text{s}^{-1}$. These differences are considered in more detail in section 3.6.

Seasonal variations in photosynthetic capacity for either forest or savanna trees have yet to be studied in any great detail, although Domingues [2005] reported little evidence of reduced photosynthetic capacities during the dry season for trees growing in a semievergreen forest near Santarém. By contrast, Miranda *et al.* [2005] observed significant reductions in maximum photosynthetic capacities during the dry season for several species growing in a semideciduous (transitional) forest near Sinop, and Franco [1998] and Franco *et al.* [2005] also reported reduced photosynthetic rates for cerrado tree species during the dry season. These differences between biomes are also being reflected in the strong seasonality of stand level carbon fluxes considered in section 4.2.

3.5. Plant Water Relations

Much work done over the last 10 years as part of the LBA project has confirmed earlier observations of Nepstad *et al.* [1994] and Hodnett *et al.* [1995, 1996] that water uptake from considerable soil depths during the dry season allows for the continued functioning of the semievergreen forests

of eastern and southwestern Amazonia. In particular, *Jipp et al.* [1998] and *Bruno et al.* [2006] demonstrated significant water uptake at depth during the dry season, with the latter study also showing significant water uptake at depths greater than 10 m for such forests.

Work by *Oliveira et al.* [2005a, 2005b] has also shown that some forest trees growing in such seasonal environments are capable of hydraulic redistribution: that is, the nocturnal transfer of water from moist to dry regions of the soil profile, with this distribution being upward in the dry season (i.e., from moister soil at depth to the drier layers closer to the surface) with flow occurring in the opposite direction in the wet season (i.e., from moist surface layers to dryer subsurface layers). This can be interpreted as an indication that plants growing in such regions may utilize hydraulic redistribution to help alleviate drought stress during dry periods by creating a readily available pool of water in the superficial soil where most of the trees' fine roots are located. Nevertheless, questions remain. For example, as pointed out by *Ludwig et al.* [2004], interplant competition can reduce the facilitative effects of hydraulic lift, as it is not only the plants investing in deep roots and allowing the uplift of water that are likely to benefit from the increased water availability of soil water close to the surface. Thus, it might be expected that not all trees growing in such an environment would exhibit such a phenomenon, with some species simply being "parasitic" users of the upper layer soil water transferred from depth by others. Hydraulic lift has also been observed to occur for some cerrado species during the dry season [*Scholz et al.*, 2002; *Moreira et al.*, 2003] with that study also showing that smaller seedlings growing near the larger trees actually transporting the water also had access to the water made available through hydraulic lift. Similarly, it is also clear that cerrado trees can extract water from depth during the dry season, at least when growing on deep and highly weathered ferralsol soils [*Jackson et al.*, 1999; *Oliveira et al.*, 2005a, 2005b; *Quesada et al.*, 2008]. Nevertheless, *Dawson et al.* [2007] have observed, for several plant species growing under different climate conditions, that many plants still transpire at night, especially when slight soil water deficits happen or immediately after a rain event, consistent with isotopic data discussed in section 4.3. If the night transpiration exists, it would reduce the efficacy of the hydraulic lift or hydraulic distribution processes; but as discussed by *Goldstein et al.* [2008], nocturnal transpiration, as observed for cerrado trees by *Bucci et al.* [2004], may be an adaptive trait allowing enhanced nutrient uptake from nutrient-poor savanna soils. This picture was further clarified by *Scholz et al.* [2008] who noted that the occurrence of reverse sap flow for deciduous and brevideciduous cerrado species during the dry season was consistent with hydraulic lift, but that evergreen species

did not exhibit a similar reverse flow. Moreover, consistent with their ability to carry out hydraulic lift, the deciduous and brevideciduous species had both shallow and deep roots (i.e., dimorphic root systems), whereas the evergreen species had mostly deep roots only. Evidence was also found that deciduous and brevideciduous cerrado species may utilize more water for processes such as nocturnal transpiration. The picture that emerges then, is that, for cerrado species, there is a trade-off between year-round access to nutrients in the upper soils (the integrity of surface roots for deciduous and brevideciduous species being maintained through hydraulic lift) versus a greater access to deeper and more reliable water during the dry season for evergreen species.

Lee et al. [2005] observed during the Amazonian dry season that when forest plants are allowed to redistribute soil water through hydraulic lift, photosynthesis and transpiration rates were significantly increased. According to these authors, the hydraulic redistribution increases the dry season transpiration by 40% over Amazonia, establishing a direct link between plant root functioning and climate.

Despite this clear ability of both forest and savanna trees to utilize water from considerable soil depth during the dry season, this being potentially aided by hydraulic lift at least for some species, semievergreen forest trees utilizing such deep water still show clear evidence of the effects of soil water deficits during the dry season as evidenced by significantly more negative midday leaf water potentials [*Domingues*, 2005; *Fisher et al.*, 2006]. By contrast, only relatively minor differences in midday leaf water potentials between wet and dry season are observed for cerrado trees [*Meinzer et al.*, 1999; *Bucci et al.*, 2005; *Franco et al.*, 2005; *Goldstein et al.*, 2008]. Presumably, these differences arise as a consequence of the different phenological patterns observed for the two vegetation types, as even evergreen cerrado trees lose some of their leaves in the dry season [*Hoffmann et al.*, 2005a], allowing for leaf-specific hydraulic conductances (conductance for water flow from soil to leaf expressed per unit leaf area) to be maintained or even increased during the dry season [*Bucci et al.*, 2005]. As pointed out by *Bucci et al.* [2005], this apparent "isohydric" behavior (tendency for leaf-water potentials to remain constant during the day and across seasons) is also facilitated by strong stomatal responses in leaf-to-air water vapor mole fraction differences (D) in cerrado trees, as was also reported by *Miranda et al.* [1997] and *Meinzer et al.* [1999]. Similarly, *Naves-Barbiero et al.* [2000] showed a strong stomatal control of transpiration for two evergreen species from different vegetation types in the Brazilian cerrado. Although sometimes construed as being indicative of some "mechanistic" stomatal response [*Williams et al.*, 1998], a recent analysis of stomatal and whole plant hydraulics suggests "isohydric

controls” of leaf water potential may actually be much more apparent than real [Buckley, 2005].

From the above discussion, significantly more negative leaf water potentials for trees growing in semievergreen forests during the dry season can be interpreted as a consequence of the leaf area of such trees not declining during the dry season (see section 4.5). Second, there is also some evidence from leaf exchange experiments of Domingues [2005] that for some plant species growing on a deep and highly weathered ferralsol near Santarém, stomata are relatively insensitive to changes in leaf-to-air water vapor mole fraction deficit, suggesting a much less tight control of transpiration rates by stomata than is the case for the cerrado. Carswell *et al.* [2002] also observed that canopy conductances for a semievergreen forest growing on a deeply weathered ferralsol at Caxiuanã were actually higher in the dry season than the wet season. This was despite higher D during the dry season.

By contrast, working in the Rebio Jarú semievergreen forest site in southwest Amazonia, strong stomatal responses to D have been observed at both the individual leaf [McWilliam *et al.*, 1996] and whole canopy level [Grace *et al.*, 1998]. McWilliam *et al.* [1996] also observed that leaf water potentials tended to be similar or even less negative during the dry season than for the wet season at this site, a result also reported for late-stage canopy trees growing in French Guiana [Bonal *et al.*, 2000a]. Examining the relationship between stand level latent heat fluxes (λE) and net radiation (R_n), Hasler and Avissar [2007] also noted that, as would be expected from the above, proportionally greater reductions in the $\lambda E/R_n$ occurred for the Rebio Jarú site compared to the Santarém and Caxiuanã sites, attributing this to shallower rooting depths at the former. Although this is conceivably also the case for the French Guiana site mentioned above [Bonal *et al.*, 2000b], water extraction during the dry season certainly occurs at depths beyond 2.4 m for this site [Bonal *et al.*, 2008] and below at least 3.4 m for Rebio Jarú [Negrón Juárez *et al.*, 2007].

In conclusion, where soils are old and weathered, they are almost invariably also deep [Quesada *et al.*, 2009c], and this means that for much of Amazonia, both forest and savanna species have access to water at depths greater than 3.0 m. This allows for continual woody plant functioning through the dry season, but for cerrado, where this dry season is of a longer duration than for semievergreen or evergreen forest, significant reductions in leaf area also occur. For both forest and savanna, there is good evidence for hydraulic lift occurring, at least for deciduous and brevideciduous species, this facilitating continued functioning of surface roots throughout the dry season.

It would also be interesting to see if other characteristics, for example, the presence of xylem pits, which are geneti-

cally associated and thought to influence the ease of transport of water [Jansen *et al.*, 2004], are also characteristic of the cerrado and dry deciduous forest species found in the drier environments, as there is now good evidence that species-dependent differences in drought sensitivity are important in shaping species distributions along rainfall gradients [Engelbrecht *et al.*, 2007].

Unfortunately, little attention seems to have been paid to the water relations and physiological functioning of cerrado grasses, but it is clear from studies on other continents that considerable reductions in stomatal conductance occur during the dry season as a consequence of dramatic reductions in soil water availability and much higher leaf-to-air vapor pressure differences [e.g., Mantlana *et al.*, 2008b].

3.6. Integration of Physiological Characteristics and Fundamental Trade-Offs

It is now well established that plant physiological characteristics do not vary independently of each other. But rather, they tend to covary in a systematic manner in accordance with what is often considered a multivariate ecological “strategy” dimension [Westoby *et al.*, 2002]. Although the underlying source of such variation is often considered to be solely genetic, arising as difference in phylogenetic background [e.g., Wright *et al.*, 2006; Swendon and Enquist, 2007], it is also clear for tropical trees that even within a given species, systematic and significant variations occur according to growth conditions [Patino *et al.*, 2009] and that the nature of the covariation between key plant physiological attributes varies according to the underlying cause of any contrasts in characteristics observed [Fyllas *et al.*, 2009].

Indeed, analyzing 1040 individual trees positioned in 63 plots across Amazonia, Fyllas *et al.* [2009] found some foliar characteristics, such as SLA, [C], [N], and [Mg], to be highly constrained by the taxonomic affiliation of tree species but others, such as [P], [K], [Ca] and $\delta^{13}\text{C}$, to be more strongly influenced by site growing conditions. By removing the environmental contribution to trait variation, they found that intrinsic values of most trait pairs coordinate, although different species (characterized by different trait suites) were found at discrete locations along a common axis of coordination. Species that tend to occupy higher fertility soils, such as those that typically occur in the western part of the Amazon Basin [Quesada *et al.*, 2009b], are characterized by intrinsically higher SLA and have an intrinsically higher [N], [P], [K], [Mg], and $\delta^{13}\text{C}$ than their lower fertility counterparts, generally occurring on the more heavily weathered soils toward the east. Despite this consistency, different scaling patterns were observed between low and high fertility

sites showing that, for Amazonian trees, trait interrelationships are substantially modified by growth environment. Soil fertility was found to be the most important environmental influence, affecting all leaf nutrient concentrations and $\delta^{13}\text{C}$ composition and increasing SLA.

One of the longest established correlations is between photosynthetic capacity and stomatal conductance [Wong *et al.*, 1979], and here Amazonian forest trees are no exception [McWilliam *et al.*, 1996; Carswell *et al.*, 2000; Domingues *et al.*, 2005, 2007]. Nevertheless, as outlined in section 3.3, what is still unclear though is the extent to which nitrogen, as opposed to phosphorus, constitutes the key limiting nutrient for photosynthetic activity.

As for other plant species [Wright *et al.*, 2004], SLA of tropical trees tends to scale positively with photosynthetic capacity (dry weight basis) and with dry weight-based foliar nitrogen phosphorus concentrations when measured [Prado and De Moraes, 1997; Franco *et al.*, 2005; Domingues *et al.*, 2005], although Hoffmann *et al.* [2005b] showed that even when controlling for phylogenetic differences and going in similar environments, savanna trees tended to have lower SLA and higher N/P ratios than their rainforest counterparts, the opposite result to that seen when comparing across biomes (section 3.3). As is discussed in section 5, this suggests that nitrogen may be intrinsically more limiting in savanna than in rainforest environments.

It might also be expected that the lower SLA typical of evergreen savanna trees (section 3.2) would be associated with a longer leaf life time, on average, than is the case for evergreen tropical forest trees, although this has not yet been established. Nevertheless, as expected from theory [Givnish, 2002], it is now well documented that deciduous savanna trees tend to have higher SLA and higher photosynthetic rates and/or nitrogen contents when expressed on a dry weight basis [Prado and De Moraes, 1997; Franco *et al.*, 2005], and such a distinction presumably also exists for tropical forest trees, both within and across forest types.

Although deciduous leaves tend to have higher photosynthetic rates on a dry weight basis than do evergreen leaves, photosynthetic rates on an area basis are typically lower [Prado and De Moraes, 1997; Prior *et al.*, 2003; Franco *et al.*, 2005] and, because of their shorter lifetime, generally result in a lower return on their carbon and nutrient investment than do evergreen leaves [Chabot and Hicks, 1982; Givnish, 2002]. Thus, the dominance of evergreen trees in the cerrado vegetation with relatively long-lived sclerophyllous type leaves can best be interpreted as a possible adaptation to the low soil nutrient status [Franco, 2002] with, as discussed in section 3.5, deciduous cerrado trees saving water through dry season leaf losses and with a greater emphasis on high rates of nutrient uptake through the presence of dimorphic

root systems with the integrity of nutrient-acquiring surface roots maintained throughout the dry season.

As well as there being an intercorrelation between the various leaf traits as discussed above, correlations with whole plant hydraulic parameters can also be expected to exist. For example, deciduous trees in both forest and savanna typically have higher specific hydraulic conductivities (conductance to water flow per unit stem cross-sectional area, K_S) than do their evergreen counterparts [Sobrado, 1993; Choat *et al.*, 2005], and these should be associated with lower wood densities, D_w [Hacke *et al.*, 2001] and an increased susceptibility to xylem cavitation [Sobrado, 1997]. Leaf specific conductivities, K_L , such as those that can also be estimated from measurements of transpiration rate and leaf/soil water potentials [Mencuccini, 2003] can be expressed as $K_L = K_S A_L/A_S$, where A_L/A_S represents the leaf area per unit twig cross-sectional area (the inverse of the so called “Huber value”), and working for a range of trees from a semievergreen forest in Panama, Santiago *et al.* [2004] found an excellent correlation between K_L and leaf level photosynthetic rates, but no correlation between photosynthetic rate and leaf nitrogen concentrations. Unfortunately, they did not test for leaf phosphorus concentrations, as was also the case for the study of Meinzer *et al.* [2008] who, also working in Panama, further showed that, despite K_L and photosynthetic capacity per unit leaf nitrogen both declining with increasing branch wood density, A_L/A_S and leaf nitrogen also simultaneously increased. Also, this increase in A_L/A_S and nitrogen was not sufficient to offset the costs of producing denser wood, also with the increased A_L/A_S and presumably higher photosynthetic capacity considered to exacerbate the negative effect of increasing wood density on branch hydraulic and leaf water status. Meinzer *et al.* [2008] did, however, find that, across the range of species examined, SLA declined sharply with increasing wood density. As discussed above, this would be expected to result in a greater longevity for leaves of high wood density species, a factor which also needs to be taken into account in the calculation of any carbon-related trade-offs.

Although it is generally theorized that a low wood density and a high SLA with associated higher nutrient contents of a dry weight basis should all be generally associated with higher rates of tropical tree growth [Wright *et al.*, 2006; Poorter *et al.*, 2008], strong negative correlation between these two traits, as reported by Meinzer *et al.* [2008], for Panamanian forest species, and also by Bucci *et al.* [2004], for cerrado trees, has not always been observed [Wright *et al.*, 2006]. This is perhaps a consequence of differences between studies in the methods of wood density determination, with studies across different sites also being complicated by the fact that wood density seems to be a more “plastic” trait

than may have been appreciated up until now [Patino *et al.*, 2009]. Moreover, when comparing across sites, it is important to note that the genetically dependent trait interrelationships between SLA and leaf nutrient concentrations may be substantially modified in accordance with variations in soil fertility [Fyllas *et al.*, 2009].

As detailed in section 3.1, one would also expect increased allocation belowground in response to both increased soil water deficits and low soil nutrient status. Working with long-term nitrogen and phosphorus fertilization in the cerrado, Bucci *et al.* [2006] observed a decline in midday leaf water potential for woody species. These authors argued that those species apparently have the capacity to exploit changes in nutrient availability by allocating resources to maximize carbon gain and enhance growth, with cost of increased allocation to leaf area relative to water transport capacity considered to have resulted in a higher total water loss per plant and a decrease in minimum leaf water potentials.

4. PHYSIOLOGY AT THE STAND LEVEL SCALE

4.1. Geographical Variations

The pioneering work on Amazonian soils of Sombroek [1966] in Brazil, Cochrane [1973] in Bolivia, and Sanchez and Buol [1974] in Peru was soon followed by large scale studies such as RADAMBRASIL, which when integrated together revealed considerable variations in the soil types of Amazonia [Sombroek, 1984, 2000; Cochrane *et al.*, 1985], a recent summary of which is provided by Quesada *et al.* [2009b]. In short, these studies reveal a large-scale gradient in soil fertility running broadly from northeast to southwest, with soils becoming considerably more fertile as one approaches the Andes. As has also been pointed out by Quesada *et al.* [2009c], it is not only soil fertility that changes, but also soil physical conditions, with the prevalence of shallower soils with more potential physical constraints on plant productivity also increasing toward the Andes.

Superimposed upon this gradient in soil physical characteristics is a second large-scale gradient in rainfall, which increases more or less from the southeast to the northwest [Malhi and Wright, 2004]. Given that these two large gradients are key drivers of plant physiological processes varying more or less orthogonally, it is not surprising that large-scale variations in plant physiological processes occur, with broad-scale changes in stand level wood density, tree dynamics, and aboveground growth rates all associated with soil fertility variations [Baker *et al.*, 2004a, 2004b; Malhi *et al.*, 2004; Phillips *et al.*, 2004; Quesada *et al.*, 2009a]. The variations in both soil and stand characteristics are also associated with variations in plot level nutrient status with fo-

liar concentrations of phosphorus, in particular, being much higher in the faster growing forests of western Amazonia [Fyllas *et al.*, 2009]. Nevertheless, direct causal linkages remain to be firmly established. For example, as has already been discussed by Malhi *et al.* [2004], effects of soil fertility on aboveground forest net primary productivity (NPP) could be due to nutrient effect differences in allocation above- and belowground or, alternatively, to higher rates of ecosystem photosynthesis (often referred to as gross primary productivity (GPP)) associated with the higher soil fertilities in western Amazonia. We currently lack the necessary ecosystem and leaf level physiological measurements to allow these different possibilities to be considered. However, examining detailed measurements of above- and belowground productivities for 10 Amazonian forests across a range of different soil types, Aragão *et al.* [2009] found no differences between the fraction of NPP allocated above- versus belowground. This suggests that a higher GPP, perhaps associated with the higher foliar phosphorus for western Amazonian forests discussed above [Fyllas *et al.*, 2009], may be the main driver for the geographical differences in wood productivity. This is also suggested by the strong relationship between wood productivity and the appropriate measures of soil available phosphorus [Quesada *et al.*, 2009a].

4.2. Seasonal Patterns

Several dendrometer data sets of tree stem diameter change at monthly resolution have been published for Amazonian forest. Most of these records indicate that stem increment is comparatively large in the wet season and small in the dry season [Vieira *et al.*, 2004; Rice *et al.*, 2004; Goulden *et al.*, 2004]. This pattern might be attributable to a reduction in wood production with drought stress or even to changes in stem water content, though a more detailed examination indicates increased diameter increment at the end of the dry season that often precedes the onset of heavy rain. Consequently, the seasonality of wood growth may be associated with factors such as the production of new xylem associated with leaf flushing, rather than the direct effects of drought. Such observations also imply that the seasonal patterns of tropical forest-atmosphere exchange do not solely reflect the direct effect of the physical environment on physiology and that many tropical trees follow genetically programmed phenological patterns [van Schaik *et al.*, 1993; Goulden *et al.*, 2004].

In situ observations of the seasonality of root production are extraordinarily difficult measurements given the depth of root penetration in tropical forest [Nepstad *et al.*, 1994; Bruno *et al.*, 2006], although first advances are now being made in this respect, at least for surface roots. For forests

growing on reasonably high clay content soils, *Silver et al.* [2005] and *Jiménez et al.* [2009] found maximum rates of fine root growth during the wet season, although *Jiménez et al.* [2009] observed the opposite pattern for a forest in the relatively high precipitation Colombian Amazon region growing on a podzol soil. They attributed the lack of fine root growth observed during the wet season for this forest to waterlogging, a consequence of the high rainfall and an impermeable ortsteinic horizon (a horizon consisting of cemented sesquioxides and organic matter; see *IUSS Working Group WRB* [2006]) in this case located at about 1.1-m soil depth [*Quesada et al.*, 2009b].

Several micrometeorological records of CO₂ and water vapor exchange were collected during LBA, building on the earlier work of *Grace et al.* [1995] in Rondônia, *Malhi et al.* [1998] near Manaus, and the ABRACOS project [*Gash et al.*, 1996]. As is discussed in detail elsewhere [*da Rocha et al.*, this volume; *Saleska et al.*, this volume], seasonal patterns of daytime gross CO₂ uptake (canopy photosynthesis) and canopy conductance to water vapor vary from forest to forest. Some researchers have reported that canopy photosynthesis and canopy conductance decrease in the dry season [*Malhi et al.*, 1998, 2002; *Vourlitis et al.*, 2004], while other researchers have reported that canopy photosynthesis remains nearly constant year round [*Carswell et al.*, 2002; *Araujo et al.*, 2002; *Saleska et al.*, 2003] or increases moderately toward the end of the dry season [*Goulden et al.*, 2004; *da Rocha et al.*, 2004]. In a broad sense, these results are consistent with the leaf level observations mentioned in sections 3.3 and 3.4. That is to say, there seems little evidence of direct water stress effects on either photosynthetic capacity or stomatal conductances for such forests. Nevertheless, differences exist, which probably reflect contrasts between sites or years, though the controls on tropical forest seasonality and physiological activity remain poorly understood. Progress toward a more mechanistic understanding of seasonality requires that researchers (1) draw a clear distinction between seasonal changes that are genetically programmed and those that are a direct effect of limitations imposed by the physical environment on physiology, and between the proximate and ultimate causes of seasonal activity [*van Schaik et al.*, 1993]; (2) recognize that the controls on plant activity observed at interannual time scales may not apply to seasonal time scales; and (3) recognize the diversity of tropical forest and the possibility that the controls on tropical forest seasonality may differ from forest to forest, or year to year.

As is also considered in more detail by *Phillips et al.* [2009], there is, however, evidence that extreme drought directly impacts tropical forest production. *Nepstad et al.* [2002] reported that prolonged rainfall exclusion from an evergreen

forest decreased primary production and increased large tree mortality. Satellite observations combined with the CASA model suggest a decrease in NPP during dry El Niño periods [*Potter et al.*, 2001]. It appears that many tropical forests growing on the deeper soils avoid drought stress during average rainfall years and that seasonal patterns observed largely reflect genetically programmed phenological patterns. On the other hand, it appears likely that more severe dry periods deleteriously impact tropical forest NPP and GPP by exerting a direct effect on physiology. The challenge for researchers is to quantitatively model and predict the point at which a drought becomes so severe that it results in plant mortality [*Phillips et al.*, 2009] with a potential lasting impact on land-atmosphere exchange and vegetation structure.

In contrast to semievergreen and evergreen forests, transitional (semideciduous) forest and cerrado vegetation show marked seasonalities in both LAI and surface fluxes [*Miranda et al.*, 1997; *Santos et al.*, 2004; *Vourlitis et al.*, 2004], these also being associated with large changes in soil water status [*Quesada et al.*, 2004, 2008] and consistent with the leaf level results reported in sections 3.2, 3.3, and 3.4. Also consistent with the idea that hydraulic lift can serve to maintain the integrity and function of the surface roots of deciduous and brevideciduous savanna trees during the dry season, *Quesada et al.* [2008] found that, almost immediately upon the commencement of wet season rains, the main region of cerrado ecosystem level root water uptake shifted from depths greater than 2.0 m to the upper soil surface layers.

4.3. Insights From Isotopes

Stable isotopes can provide good integrative measurements of variations in nutrient, water cycling, and assimilation capacity in terrestrial ecosystems, for example, allowing a determination of the relative contributions of C3 trees versus C4 grasses to the productivity of savanna ecosystems [*Lloyd et al.*, 2008]. According to *Ometto et al.* [2006], the isotope ratio data for three distinct regions in the forested region of Amazonia are consistent with the current understanding of the roles of light, water availability, recycling of soil-respired CO₂ and also consistent with the understanding that an open nitrogen cycle can lead to high $\delta^{15}\text{N}$ values, despite a significant number of legumes in the vegetation, and as already mentioned (section 3.3), the relatively negative $\delta^{15}\text{N}$ of plants and soil for white sand forests in Amazonia provides some strong indications that these forests may be nitrogen rather than phosphorus limited. Although *Nardoto* [2005] observed an inverse correlation of the $\delta^{15}\text{N}$ with the length of the dry season for nonwhite sand forests, suggesting more open N cycling as one goes to more humid regions of

Amazonia, an alternative hypothesis accounting for variations in $\delta^{15}\text{N}$ across the full spectrum of Amazonian forests was put forward by *Quesada et al.* [2009c]. They argued that as soils age on geological time scales, phosphorus becomes progressively more limiting and nitrogen progressively more in excess (increasing soil and plant $\delta^{15}\text{N}$) and with the structural and physiological characteristics of the vegetation also changing, there being a tendency toward species with slower potential growth rates, lower intrinsic SLA and nutrient requirements, and higher levels of structural defenses on older more heavily weathered soils (see also section 3.6). During this phase of ecosystem development, leaf and soil $\delta^{15}\text{N}$ progressively increases, this reflecting continual losses of nitrogen from the ecosystem. Nevertheless, eventually a point is reached where nitrogen, rather than phosphorus, becomes limiting for plant productivity. This is hypothesized to arise primarily as a consequence of changes in leaf litter chemistry with high levels of tannins and lignin in leaves of slow growing species inhibiting enzymes involved in nitrogen mineralization, though with several other factors also involved. In support of their theory, *Quesada et al.* [2009c] noted that not only are unusually negative $\delta^{15}\text{N}$ observed on the arenosols and podzols, but that they also occur for forests on the most heavily weathered ferralsol and Acrisol soil types.

Bustamante et al. [2004] found a wide range of variations in cerrado tree foliar $\delta^{15}\text{N}$, which they related to differences between tree species and individuals in nitrogen uptake characteristics, precipitation seasonality, fire frequency, also observing that in contrast to the forest, many cerrado Fabaceae species seem to be actively fixing atmospheric N_2 . Nevertheless, even for non- N_2 -fixers, $\delta^{15}\text{N}$ was, on average, significantly less than is observed for Amazonian forest species growing on similar soils [*Nardoto, 2005; Nardoto et al., 2008*]. This supports the general view that cerrado productivity may be nitrogen rather than phosphorus limited [*Bustamante et al., 2006*].

Water cycling in plant and ecosystems can also be approached using the stable isotope signature for the oxygen on the water molecule enclosed in these compartments and fluxes within. Distinct pattern in anatomical structure of various plant species in Amazonia results in complex pathways of water flow within a leaf causing large differences in the diel fluctuation of the oxygen isotope ratios ($\delta^{18}\text{O}$) in the leaf water [*Lai et al., 2008*]. The implications of these findings for regional water and carbon balance are related to the isotopic signal of the ecosystem-respired CO_2 [*Ometto et al., 2005*] and to the terrestrial contribution to the seasonal fluctuations in the $\delta^{18}\text{O}$ of atmospheric CO_2 [*Friedli et al., 1987*]. According to *Lai et al.* [2008], the leaf water turnover calculated for nighttime was consistently 2–10 times greater

than those during daytime. This prolonged turnover time is the reason for the considerable nonsteady state effect on the leaf water $\delta^{18}\text{O}$ enrichment at night [*Cernusak et al., 2002*]. Lower isotopic $\delta^{18}\text{O}$ on leaf water compared to stem (soil) water in understory plants suggests exchange of leaf water with vapor water [*Lai et al., 2008*], which might be an important contributor to the water balance in environment under high humidity and plants with open stomata (J. Berry, personal communication, 2007). Water uptake by leaves was also observed in a controlled dry-out experiment in Brazilian Amazonia by *Cardinot* [2007]. Furthermore, *Doughty et al.* [2006] have recently proposed that the photosynthesis gas exchange in 65% of studied species in Brazilian Amazonia function under circadian rhythms once they have closed stomata and photosynthetic rates during the night, even under continuous and constant light, and resuming the active gas exchange during the normally light period.

The importance of lianas for the ecology of the tropical forest has been pointed out elsewhere. Usually ignored in forest inventories, lianas exert an important ecological effect in the forest representing, for instance, less than 5% of the forest biomass, but 40% of leaf productivity [*Phillips et al., 2002*]. According to *Ometto et al.* [2006], the lianas tend to show higher $\delta^{13}\text{C}$ values and lower ratios of intercellular to ambient CO_2 concentration, suggesting that this group is more conservative in its water use, in agreement with relatively lower stomatal conductance when compared to upper canopy tree species [*Domingues et al., 2007*]. Lianas tend to have the highest leaf water turnover time due to their relatively smaller conductances. Grasses and shrubs in the pasture have significantly lower turnover time at night compared to the overstory trees and lianas in the forest, which contributes to the relatively smaller nonsteady state leaf water enrichment [*Lai et al., 2008*].

5. CONCLUDING COMMENTS AND SYNTHESIS

As outlined in the introduction, one main aim of this review was to investigate the extent to which contrasts in the physiology of the various vegetation types found across Amazonia were correlated with broad-scale patterns of their distributions. We have been partially successful in this respect. For example, it has been concluded that semievergreen forests can persist despite an extended dry season through the ability to develop roots and transport water from considerable soil depths (section 3.4). Likewise, from Figure 1, we can also reasonably conclude that this is facilitated by the presence of clay-rich, yet well-drained, subsoils in these areas, also with relatively high water-holding capacities [*Quesada et al., 2009a, 2009c*] effectively allowing high amounts of wet season rainfall to be stored in the soil profile

and utilized during the dry season. The importance of this should not be underestimated. For example, although generally more fertile, many soils of western Amazonia have physical restrictions present at depths shallower than 2 m [Quesada *et al.*, 2009c]. Were such soils to exist in eastern or southern Amazonia, where, even in forested areas, the rainfall is generally much less than in the western part of the basin [Malhi and Wright, 2004], it is highly unlikely that semievergreen forest could exist. Similarly, as is summarized in section 3.5, the strong presence of evergreen trees in the cerrado is most likely also a consequence of their ability to extract water from considerable depths during the dry season. This can occur because, although most cerrado soils are old, strongly weathered and thus infertile, as a consequence of this extreme weathering, they are also very deep and with good water-holding characteristics. In section 3.5, it was also noted that deciduous and brevideciduous trees also coexist with evergreen trees; this coexistence being possible through their employment of an alternative ecophysiological strategy, namely, a reduction in water requirements through having a leafless period in the dry season. This allows a greater allocation of resources toward the presence of surface roots, which, in turn, allows for higher rates of nutrient uptake to occur: Such high nutrient uptake rates being required to support the deciduous habit.

In similarly low rainfall regions where soils are more fertile, but also more shallow, and with a lower water-holding capability, the evergreen habit would not be favored, this probably being the main factor defining the distribution of drought-deciduous forests as the dominant vegetation type in lower rainfall regions, where more fertile soils occur (sections 2.2 and 2.3).

Other ecophysiological characteristics related to different growth environments across Amazonia have also been noted. For example, the species which occupy the more fertile forests of western Amazonia have intrinsically higher requirements for nutrients, higher SLA, and lower wood densities than their slower growing counterparts in eastern Amazonia (sections 3.3 and 3.6). Moreover, foliar nutrient concentrations, especially nitrogen, seem to be lower for cerrado trees than for (semi) evergreen forest trees in eastern Amazonia (section 3.3), with this also being associated with variations in other leaf properties such as SLA and leaf longevity. Indeed, as is summarized in section 4.3, evidence from $\delta^{15}\text{N}$ studies strongly suggests, in contrast to most Amazonian forests, that the productivity of cerrado trees and grasses is nitrogen limited.

How can such a stark contrast between two ecosystems occur? Overall, there does not seem to be any great difference between eastern Amazonian cerrado and forest soils, both often being rather infertile but with good water-holding

characteristics [Motta *et al.*, 2002; Quesada *et al.*, 2009b]. Nevertheless, as is outlined by Bustamante *et al.* [2006] and Nardoto *et al.* [2006], slow rates of nitrogen mineralization during the dry season and significant fire-associated losses of nitrogen could both be contributing factors to the apparent low nitrogen availability of cerrado as opposed to forest ecosystems in Amazonia.

Yet we suspect that is not the whole story. It seems quite likely that the physiological characteristics of cerrado trees and grasses also contribute to maintaining a low nitrogen status ecosystem through mechanisms similar to that outlined as giving rise to eventual nitrogen limitation for the oldest forest ecosystems in section 4.3. That is to say, associated with the sclerophyllous characteristics of the leaves of (in particular, evergreen) cerrado trees, namely, a low SLA and low nutrient contents (section 3.3), are also relatively high levels of lignin and phenols [Varanda *et al.*, 1997], which should themselves serve to impose significant constraints on nitrogen mineralization. As discussed by Quesada *et al.* [2009c], this would occur through nitrogen being incorporated into the lignin fraction of the litter during humification and through the direct inhibition of enzymes involved in nitrogen mineralization by high levels of tannins, lignin, and associated compounds. This, along with factors such as fire [Miranda *et al.*, 2002] probably serves to make the cerrado ecosystem, to some extent, self-sustaining, and this provides one explanation as to why the last expansion of cerrado into previously forested areas during the brief dry episode of the Holocene has not been reversed, with Amazonian forests apparently failing to regain their original area, even though rainfall has apparently returned to previous levels over the last few thousand years [Ledru, 1993].

These general ideas are illustrated in Plate 1, when it is suggested that the vegetation changes associated with any spatial or temporal variation in precipitation should depend fundamentally on soil characteristics, as well as the precipitation regime itself. For the forest areas in western Amazonia, consisting of relatively fertile but often shallow soils, it is suggested that, at reduced precipitation regimes, high nutrient-requiring drought-deciduous forest should prevail. On the other hand, for eastern Amazonia, where soils are often old and extremely weathered and infertile, they are also often deep and thus capable of storing considerable amounts of water. This favors evergreen cerrado-type species with low nutrient requirements but also capable of extracting water from depth and maintaining their leaves over the dry season. Also shown in Plate 1 is a feedback loop, representing effects of leaf sclerophyllous physiological properties and also potentially fire (as discussed in the paragraph above) in maintaining a savanna-type ecosystem through a tightening of the nitrogen cycle.

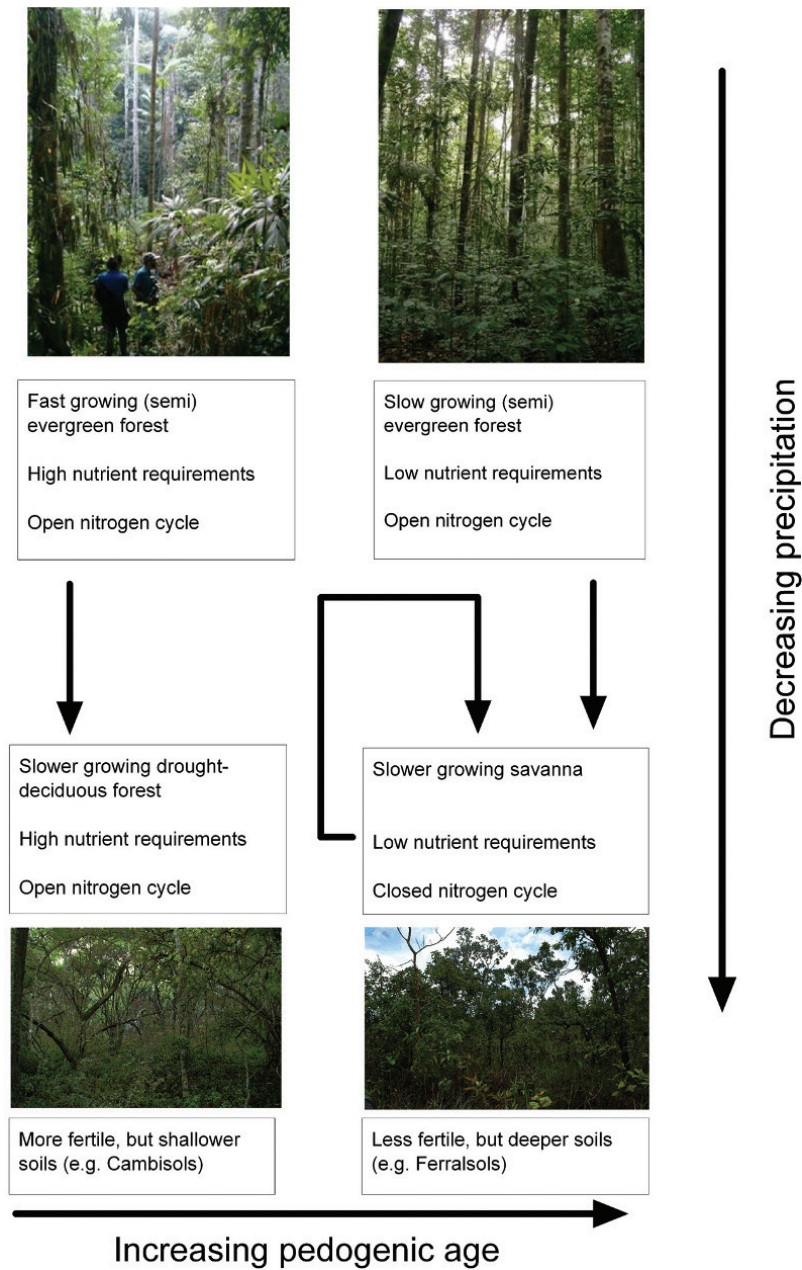


Plate 1. Proposed scheme for transitions between forest and savanna vegetation types as affected by soil age and precipitation. As is described in the text, the feedback loop for savanna (cerrado) vegetation represents a closure of the whole ecosystem nitrogen cycle initiated through the physiological characteristics of woody and herbaceous savanna species as well as fire. (top left) Evergreen forest in southwest Amazonia (Porongaba, Brazil). (top right) Semievergreen forest in eastern Amazonia (Caixuana, Brazil). (bottom left) Drought-deciduous (Chiquitano) forest in southern Amazonia (Tucavaca, Bolivia). (bottom right) Cerrado in southern Amazonia (Los Fierros, Bolivia). Photos credits: T. Baker (Brazil) and J. Lloyd (Bolivia).

Of course, much more work has to be done to validate and/or develop upon this general scheme. Nevertheless, understanding the interactions between precipitation regime and soil chemical and physical characteristics in influencing Amazonian vegetation structure and function will be of considerable importance in understanding and predicting effects of climate change on Amazonia, especially if significant declines in precipitation occur as predicted by some Global Climate Models [see Marengo *et al.*, this volume]. For example, according to Malhi *et al.* [2009], any future reduction in precipitation in eastern Amazonia, as a consequence of climate change, should give rise to drought-deciduous forest rather than cerrado. We disagree: this is because much of the forest in the areas predicted to be most severely affected by drought are in the southeastern part of the basin [Salazar *et al.*, 2007] where nutrient-poor but deep ferralsol and Acrisol soils dominate [Quesada *et al.*, 2009b]. According to our understanding, and as shown in Plate 1, we consider it much more likely that the semievergreen forests there would undergo a direct transition to an evergreen-dominated cerrado-type vegetation. On the other hand, should southwestern Amazonia be most affected by future declines in precipitation as was the case for the 2005 Amazon drought [Phillips *et al.*, 2009], then it is more likely that the fast-growing and dynamic forests situated there would transform to drought-deciduous forest, the soils of this part of Amazonia typically being rather fertile, but also often of limited depth and thus also of a much lower water-holding capability [Quesada *et al.*, 2009b].

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