

# Ecophysiology of Trees of Seasonally Dry Tropics: Comparisons among Phenologies

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## I. INTRODUCTION

The subject matter of this review is the seasonally dry tropical and subtropical woodlands and forests of the world. We follow Specht (1981) in differentiating woodland (typically <30% canopy cover) from forest (typically >30% cover) on the basis of percentage canopy cover but clearly discrete boundaries do not exist. The definition of a dry season is more problematic. However, we propose that a dry season has two attributes. First, it is a predictable annual event, and second, in the driest 3 months of

the year, less than 10% of annual precipitation occurs and typically less than 25 mm per month falls. In few sites does absolutely no rainfall occur in the dry season, if a sufficiently long (a century or more) time average is taken.

Seasonally dry tropical areas are occupied largely by savanna, but also include areas of dry forest in which grasses are mostly absent. Savannas are here defined as:

tropical or sub-tropical biomes with a tall (>30 cm) continuous grass understorey during the wet season and a discontinuous tree canopy. Grasses are usually dominated by those with the C<sub>4</sub> photosynthetic pathway. Rainfall is highly seasonal, with the wettest period occurring during the warmest months.

Dry tropical forests and savanna vegetation types occupy far greater total areas worldwide than does wet tropical rainforest (Olivares and Medina, 1992; Murphy and Lugo, 1995). These seasonally dry tropical areas are distinguished from wet tropical areas by a marked dry period that occurs each year. This means that closed forest canopies do not develop, except in small areas where topographic factors lead to permanently high soil moisture content, and which are thus not truly dry. Conversely, shallow and freely draining soils can also support savannas in the middle of areas otherwise covered in rainforest. This clearly illustrates the importance of soil water availability over the year, rather than rainfall alone, as a determinant of vegetation structure in seasonally dry systems. Seasonally dry tropical areas do, however, have a reliable and pronounced wet season, which distinguishes them from deserts.

Rather than become embroiled in semantic discussion as to the definition of savannas, we must accept that savannas represent a region along a continuum extending from desert at one extreme to tall closed rainforest at the other, with subtle shifts and mergers occurring at boundaries. Vegetation units occur as segments of continua, not as distinct separate units (Murphy and Lugo, 1995).

The co-existence of trees and grasses constitutes perhaps the most striking feature of savannas; this has been reviewed by Scholes and Archer (1997). These authors conclude that traditional simple models based on separation in rooting depth of trees and grasses are inadequate, and that the effects of browsers, grazers and fires on tree recruitment must be considered. In many parts of the world, savanna reverts to woodland in the absence of fire or other disturbance. Thus the distinction between savanna and dry tropical forest or woodland is somewhat arbitrary. In both biomes, trees must contend with seasonal drought and high temperatures, to which conditions they can be expected to share similar physiological responses.

Structurally, seasonally dry woodlands contain a seasonal grass understorey. Typically three layers of vegetation (grass, understorey herbs and forbs, overstorey dispersed tree layer) occur. Epiphytes and vines are absent. In seasonally dry forests, the grass layer and epiphytes are absent, but vines can be present. The upper canopy can vary between <3 m height for shrublands, to <10 m for low woodlands, to >30 m for tall forests.

Savannas are important for several reasons, including their conservation (genetic) and cultural values, their economic value (tourism, pastoral/beef industry, agriculture) and their aesthetic value, among others. They support an increasing number of people globally. They are also major determinants of regional climate and have a significant role to play in regional water balances and global carbon cycles. Any attempt at sustainable resource management within savannas and any attempt at modelling savanna functioning at the landscape scale requires knowledge about the behaviour of savanna trees, particularly in relation to water and carbon fluxes. The aim of this chapter is to provide a review of what is known about the ecophysiology of trees in seasonally dry woody ecosystems. In particular, we shall compare and contrast daily and seasonal patterns of behaviour of different phenological guilds; this approach provides a unifying conceptual framework within which to consider tree ecophysiology. Savannas form an extensive but not exclusive reference ecosystem throughout this chapter. Where relevant and possible, comparative values for temperate or wet tropical ecosystems are presented. We focus on water and carbon dioxide (CO<sub>2</sub>) fluxes and related ecophysiology for the following reasons: first, seasonally dry forests are subject to regular and predictable annual drought, which is a major determinant of ecosystem structure and function. Temperature and light are generally not limiting to the functioning of these systems. Second, carbon influx and attendant processes are coupled to water availability and drive all downstream processes.

## **A. Distribution and Climate of Seasonally Dry Tropics**

Native savannas occupy large areas of Africa and Australia, as well as parts of Central and South America. Savannas that have arisen because of human activity can be found in India and other parts of Asia. Savannas often have regional names, including the 'miombo' woodland of Angola and Zambia, the 'cerrado' and 'caatinga' of Brazil and the 'llanos' of Venezuela and Colombia. Bushveld and thornveld of southern Africa are also seasonally dry woodlands. Dry woodlands of the 'chaco' occur in the west of Central America and in the Amazon lowlands. Seasonally dry forests include dipterocarp forest in Thailand, and dry deciduous forests in Mexico and Venezuela.

In most savannas, mean annual temperatures are higher than 20°C, although at higher elevations in Brazil and East Africa mean annual temperatures can be lower than this. The mean temperature of the coldest month is generally higher than 12°C, although occasional values of 4°C have been recorded in eastern Australia (Archibald, 1995). Savannas that are close to the equator and/or close to the coast have small fluctuations in mean temperature between wet and dry seasons, but savannas at the margins of the tropics or at higher elevations experience larger temperature fluctuations and frosts may occur occasionally. Mean temperatures are higher than 20°C for each month in most savannas.

Rainfall is highly seasonal, with distinct wet and dry seasons. Rainfall can be bi-modal (Central and Southern Africa) or uni-modal (Central America, India, Australia) and usually lies in the range 250–2000 mm yr<sup>-1</sup>. In Africa and Australia, less than 25 mm total rain falls during the dry season, while in Guianan savannas, rainfall in the 'dry season' can exceed 200 mm (Archibald, 1995). Savannas are distinguished from temperate seasonal climates by the reversal of the association between rainfall and temperature.

Soil and atmospheric water content are coupled to seasonality of rainfall. In the wet season water can be supra-abundant and flooding may occur. This contrasts with very dry surface soils (upper 0.5 m) during the dry season. Soil water potential in the upper soil profile can decline from zero (wet season) to -3.5 MPa or lower (Goldstein *et al.*, 1986; Holbrook *et al.*, 1995; Franco *et al.*, 1996) (see section III). In a west African humid savanna gravimetric soil water content varied between 0.18 g g<sup>-1</sup> at 2 m depth and 0.10 g g<sup>-1</sup> in the top 10 cm in the wet season and between 0.12 g g<sup>-1</sup> at 1.6 m and 0.01 g g<sup>-1</sup> in the top 10 cm in the dry season (Le Roux *et al.*, 1995). There may also be large seasonal fluctuations in depth to groundwater. In northern Australia, depth to groundwater increases over the dry season by up to 12 m in north Australia (Cook *et al.*, 1998). Vapour pressure deficit (VPD) here ranges between 0.4–0.8 kPa in the wet season and 0.5–2.5 kPa in the dry season (Duff *et al.*, 1997), similar to values recorded in a west African humid savanna (Le Roux and Bariac, 1998). VPD peaks between midday and mid-afternoon, declining thereafter.

Because solar radiation loads are high all year, potential evaporation rates are approximately 7 mm day<sup>-1</sup> in north Australia, and 1600 mm yr<sup>-1</sup> for miombo of equatorial Africa (Menaut *et al.*, 1995). Similarly, in the caatinga of Brazil, potential evaporation is generally above 2000 mm yr<sup>-1</sup> (Sampaio, 1995, calculated evaporation to be 1.6–5.3 mm day<sup>-1</sup> for Brazilian caatinga).

Generally, in savannas, the ratio of annual potential evapotranspiration to annual rainfall is between 1.2 and 1.8 (Murphy and Lugo, 1995;

Sampaio, 1995), but this is highly seasonal. In the wet season, rainfall can exceed potential evapotranspiration, but in the dry season the reverse is true.

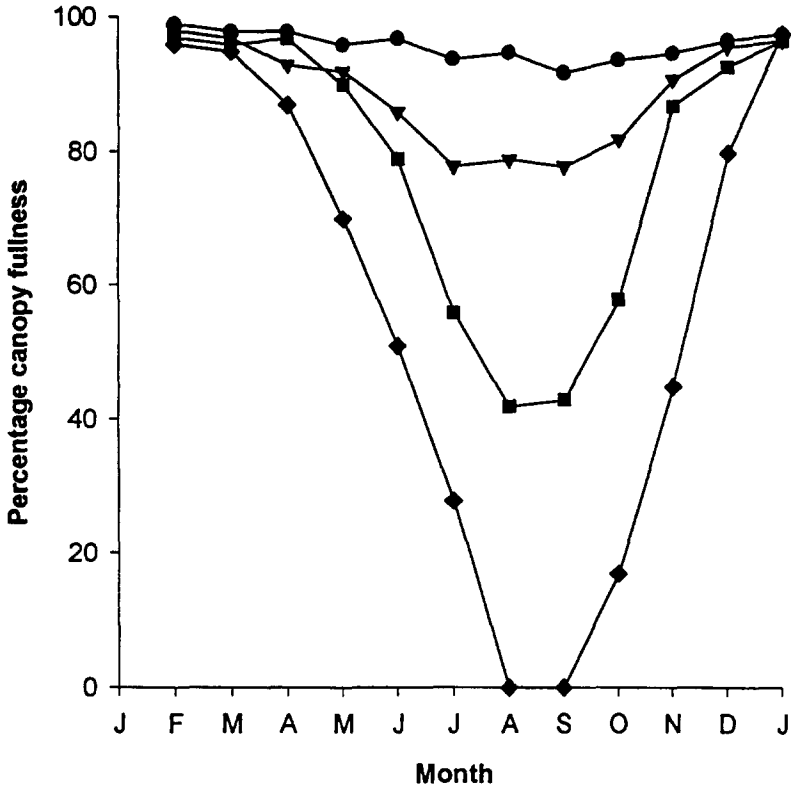
## II. PHENOLOGY

### A. Phenological Guilds

Woody species of savannas may be evergreen, deciduous or semi-deciduous. There is considerable variation, at ecosystem-level, in the relative proportions of these guilds. African and Indian savannas are dominated by deciduous species (Menaut and Cesar, 1979; Shukla and Ramakrishnan, 1982; Chidumayo, 1990; Yadava, 1990). In contrast, the llanos savannas of South America are dominated by evergreen species (Monasterio and Sarmiento, 1976; Sarmiento *et al.*, 1985), although individual patches may be dominated by semi-deciduous or deciduous species (Medina, 1982). Similarly, seasonally dry forests of Costa Rica are dominated by semi-deciduous or deciduous species (Borchert, 1994a). Venezuelan tropical dry forests are dominated by deciduous species, with a few evergreen species also present (Sobrado, 1997).

Australian savannas differ from other savannas in having an approximately equal number of species (but not standing biomass; evergreens dominate in terms of biomass) in each of four phenological guilds (Williams *et al.*, 1997b; Figure 1). Deciduous species lose all of their leaves every year for 1–3 months in north Australian savannas, or longer where the dry season is particularly long (Williams *et al.*, 1997b). Evergreens retain all, or almost all, of their canopy, throughout the year. Semi-deciduous species lose more than 50% of their canopy each year, while brevi-deciduous species lose between 10 and 50% of their canopy each year, but this is very dependent on the length and magnitude of the wet season (Williams *et al.*, 1997b). Although 50% of species are deciduous or semi-deciduous in Australian savannas, the evergreen species account for approximately 90% of the projected canopy cover. Consequently during the dry season total tree canopy cover declines by only approximately 15%.

Within Australia deciduous species have mainly pantropical affinities (Bowman *et al.*, 1988) and are generally broad-leaved. Curiously, the abundance of deciduous species declines along a gradient of declining rainfall from coastal north Australia to inland central Australia (Egan and Williams, 1995; Williams *et al.*, 1996). This is in contrast to tropical forests and savannas on other continents, where the proportion of deciduous species increases as dry season severity increases (Reich, 1995). This is presumably a function of the extremely high degree of



**Fig. 1.** Four phenological guilds are recognized in Australian savannas (Williams *et al.*, 1997). Evergreen species (●) retain an almost full canopy all year; brevideciduous species (▼) never lose more than 50% of their canopy, the amount lost depending on the duration of the wet season; semi-deciduous species (■) lose more than 50% of their leaves every year; deciduous species (◆) are leafless for at least 2 months every year. Re-drawn from Williams *et al.* (1997).

dominance by Acacias and Eucalypts (which are sclerophyllous and predominantly evergreen; Ashton and Attiwell, 1994; Gill, 1994) throughout Australia, including its savanna areas.

## B. Environmental Control of Leaf Flushing

Leaf fall in tropical forests and savannas usually peaks in the dry season (Wright and Cornejo, 1990; van Schaik *et al.*, 1993; Sun *et al.*, 1996). By contrast, there is considerable inter-annual, inter-site and inter-specific variation in the timing of leaf flushing. In Costa Rican dry forest, rehydration of stems always preceded leaf flushing or flowering (Borchert, 1994a).

Many trees rehydrated soon after leaf shedding, which allowed leaf flushing to occur during the dry season. Deciduous lightwood and softwood trees generally fell into this category, while deciduous hardwood trees, which desiccated strongly, remained bare to the end of the dry season. Evergreen trees exchanged most leaves during the dry season (Borchert, 1994c). Medina and Francisco (1994) observed that, in a Venezuelan savanna, leaf exchange in *Curatella americana* (evergreen) occurs in the middle of the dry season, but in *Godmania macrocarpa* (deciduous) leaf flushing occurs at the start of the wet season.

The cause of such variation in timing and intensity of leaf phenophases has been much debated (Reich, 1995; Wright, 1996). Day length (Opler *et al.*, 1976; Bullock and Solis-Magallanes, 1990), temperature (Specht, 1986), vapour pressure deficit (Wright and Cornejo, 1990; Duff *et al.*, 1997) and irradiance (Wright and van Schaik, 1994; Wright, 1996) have all been identified as environmental cues controlling leaf fall and leaf flush. However, Reich and Borchert (1982, 1984), Borchert (1991, 1994a,b) and Reich (1995) strongly argue for endogenous whole-plant control that is subject to environmental perturbation.

Wright and Cornejo (1990) showed little impact on leaf fall of a 2-year irrigation experiment in the field – only four of 29 species showed delayed leaf fall after irrigating in the dry season to extend the wet season. In contrast, in a Costa Rican study, Borchert (1994b) observed that leaf flushing was initiated in *Tabebuia ochracea* within 1 week of irrigation. In the savannas of northern Australia, a dry season irrigation experiment (Myers *et al.*, 1998) showed that leaf flushing of a common deciduous species (*Terminalia ferdinandiana*) occurred significantly earlier (by 4 weeks) in response to increased soil water availability. Flushing was initiated within 10 days of irrigation starting. Furthermore, the decline in canopy cover associated with the onset of the subsequent dry season was delayed by 2 weeks in the irrigated plots. For a second species (*Planchonia careya*), Myers *et al.* (1998) found that the attainment of full canopy was significantly earlier in the irrigated plots, but high inter-tree variation masked any differences in timing of leaf flushing or initial canopy decline. In contrast to these results, there was little impact of irrigation on canopy cover or timing of leaf flushing in evergreen species, although leaf lifespan was increased (Myers *et al.*, 1998). This supports the view that evergreens, postulated as having deeper roots and therefore having access to deeper reserves of water in the dry season, are able to maintain an almost completely full canopy in the dry and avoid drought (Sobrado, 1986; Nepstad *et al.*, 1994; Myers *et al.*, 1997). However, the inverse argument – that deciduous trees are facultatively deciduous and lose leaves in response to soil drying – appears to be poorly supported. Both species studied shed leaves at the start of the dry season despite irrigation maintaining a high soil

water availability, and one species – *Planchonia* – showed little response in terms of leaf flushing to dry season irrigation. Therefore, within the same phenological grouping, leaf fall and leaf flush appear to be under the control of different mechanisms.

Leaf fall in deciduous species occurs early in the dry season because of a depletion of water stored in the tree (Reich and Borchert, 1984; Borchert, 1994a; Reich, 1995). When the canopy is reduced or absent for a sufficient time, stems rehydrate and leaf flush can be initiated. This can explain why leaf flush is frequently initiated prior to rains (but generally after VPD starts to decline; Duff *et al.*, 1997). The patterns of change in stem diameter in the Myers *et al.* (1998) study are consistent with this hypothesis.

The interaction between wood density and groundwater availability may also have a role to play in determining phenology and species distribution (Borchert, 1994c). As stemwood density increases, water content, and hence potential for water storage, declines linearly (Borchert, 1994c). In Costa Rica, deciduous hardwoods on sites with little access to groundwater have low stemwood water contents and little potential for storage. Leaf drop occurs early in the dry season and there is minimal stem rehydration during the dry season after leaf drop. Consequently, leaf flush does not occur until after the onset of significant rains and rehydration. In contrast, deciduous lightwoods and deciduous softwoods have a high storage capacity. In both cases, leaf initiation occurs in the dry season after stems rehydrate. However, full stem expansion and leaf growth often only occur after heavy rains (Borchert, 1994c). Thus it is the elimination of water deficits within the tree that initiates leaf flush, and not an environmental cue such as day length or temperature.

### III. TREE WATER RELATIONS

#### A. Foliar Water Potential

Water availability is a key factor in determining savanna structure and function (Scholes and Walker, 1995). As water availability increases, tree height and tree density increase so that standing biomass increases. Trees, being perennial, must survive the 2- to 8-month dry season and must either avoid (deciduous) or tolerate (evergreen) this drought. Given the extent and diversity of savannas/dry tropical forests worldwide, there have been relatively few detailed studies of seasonal patterns of tree water status in these biomes (Le Roux and Bariac, 1998).

Pre-dawn leaf water potential ( $\Psi_{pd}$ ) has been used extensively as a surrogate measure of soil water availability (Sala *et al.*, 1981; Le Roux and Bariac, 1998). This use is based upon the assumptions that (a) rehydration of leaves occurs rapidly enough for leaf water potential

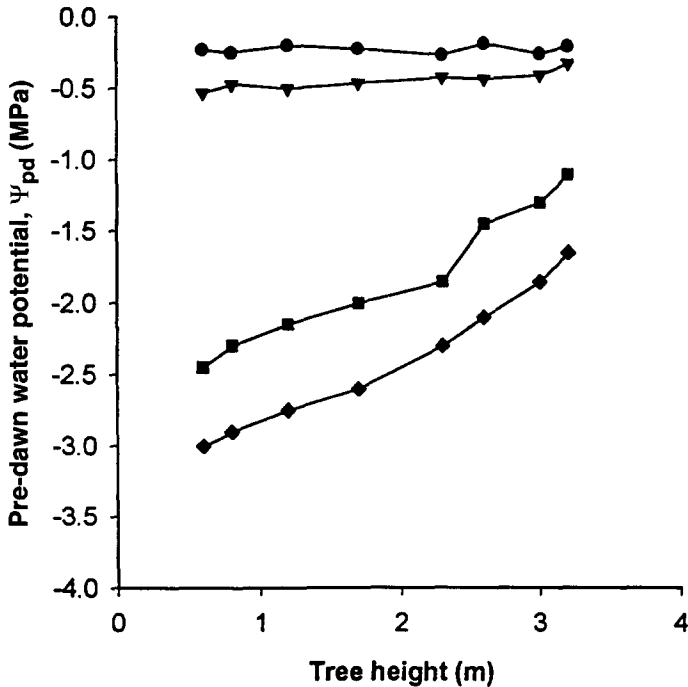


pre-sunrise to equal that of the soil–root interface; and (b) there is some relationship between the proportion of roots at various depths (and hence soil water contents) and the final equilibrium water potential attained by the leaf; and (c) that lateral heterogeneity of soil water content does not prevent the use of bulk soil moisture content as a suitable explanatory variable for plant water status (Ameglio and Archer, 1996).

Pre-dawn leaf water potential is high in the wet season and declines as the dry season progresses. This decline is both a function of declining soil moisture content and declining atmospheric water content (increasing leaf-to-air vapour pressure deficit). In a study of eight species of a north Australian savanna,  $\Psi_{pd}$  of mature (10–15 m tall) trees varied between  $-0.02$  MPa in the wet season and  $-1.5$  MPa in the dry season (Duff *et al.*, 1997). For smaller trees, the decline in  $\Psi_{pd}$  was larger such that dry season minima were as low as  $-2.5$  MPa (Prior *et al.*, 1997a). Interestingly, in a detailed study of *Eucalyptus tetrodonra* (one of the two canopy dominants that account for  $>80\%$  of standing biomass in these savannas), the impact of the dry season upon tree water status decreased as tree height increased (Prior and Eamus, 1999). Thus, as soil and atmospheric water content declined from the wet to the dry season,  $\Psi_{pd}$  declined and the slope of the relationship between tree height and  $\Psi_{pd}$  increased (Figure 2). Such a response demonstrates the importance of rooting volume in maintaining favourable plant water status as water content of surface soil decreases.

The decline in  $\Psi_{pd}$  through the dry season is also reflected in the decline in midday leaf water potential. As soil water potential declined from close to zero in the wet season to  $-2.0$  MPa in the top 30 cm of soil in the Brazilian cerrado, leaf water potentials declined to  $-2.5$  MPa (Franco, 1998). Similarly midday leaf water potentials declined to  $-3.0$  MPa in smaller trees and  $-2.5$  MPa in tall trees (Myers *et al.*, 1997; Prior *et al.*, 1997a,b; ) in a northern Australian savanna. In an upland savanna in Costa Rica, Borchert (1994a,b) observed leaf water potentials as low as  $-4.0$  MPa.

Similar patterns of seasonal leaf water potential have been observed in savannas around the world. Medina and Francisco (1994) showed that, in a Venezuelan savanna, the highest leaf water potential (close to zero; collected at sunrise) declined from  $-0.1$  MPa in the wet season to  $-0.8$  MPa in the dry season in young *Curatella americana* leaves and from  $-0.3$  MPa to  $-1.2$  MPa in *Godmania macrocarpa* leaves. Similarly, midday values declined from  $-0.5$  to  $1.2$  MPa and from  $-1.4$  to  $-2.5$  MPa for the two species, respectively. Goldstein *et al.* (1986) showed seasonal declines in leaf water potential for four tree species growing in a South American savanna of approximately  $1.0$  MPa. Seasonal minimum leaf



**Fig. 2.** Tree height influences the extent of the dry-season decline in water status of *Eucalyptus tetrodonta*. Short (young) trees suffer the most. Measurement made in: ●, May (early dry season); ▼, June; ■, August; ◆, October (late dry season). Re-drawn from Prior and Eamus (1999).

water potentials in 38 Costa Rican dry forests ranged from  $-0.8$  MPa to less than  $-4.0$  MPa (Borchert, 1994b).

The oft-stated view that soil water potentials of less than (more negative than)  $-1.5$  MPa represent the 'wilting point' of plants, i.e. represent the limit of plant available water, is clearly untenable within the savanna environment. Even pre-dawn leaf water potential can be as low as this and leaves still have open stomata and photosynthesize as leaf water potential declines through the day (see below).

Seasonal declines in leaf water potential are the result of declines in both soil and atmospheric water content resulting from marked seasonality of rainfall and vapour pressure deficit. However, the documentation of such declines gives no conceptual framework within which to interpret between-species variation. The next section attempts to interpret such differences in the context of contrasting phenologies.

## 1. Phenological Comparisons of Seasonal Changes in Water Potential

In Venezuelan dry tropical forest,  $\Psi_{pd}$  values declined at the end of the wet season in both evergreen and deciduous species (Sobrado, 1986). The decline was more rapid in the deciduous species, which shed their leaves in the mid dry season. The evergreen species attained the same  $\Psi_{pd}$  ( $-2.8$  MPa) about 2 months later (Sobrado, 1986). Evergreen trees in the wetter Venezuelan llanos showed only slight seasonality in pre-dawn and midday leaf water potentials (Sarmiento *et al.*, 1985; Goldstein and Sarmiento, 1987).

The lowest  $\Psi_{pd}$  recorded for saplings of the deciduous Australian savanna tree, *Terminalia ferdinandiana*, was  $-1.18$  MPa, at the start of leaf shedding in the early dry season (Prior *et al.*, 1997b). At the same time,  $\Psi_{pd}$  of co-occurring evergreen *Eucalyptus tetrodonta* saplings was  $-0.48$  MPa, and this continued to decrease to a minimum of  $-2.45$  MPa late in the dry season (Prior *et al.*, 1997a). Thus the evergreen species was both better able to extract water from drying soil (possibly by having deeper roots) and to retain functional leaves at lower  $\Psi_{pd}$  than was the deciduous species. In mature trees also,  $\Psi_{pd}$  in the early dry season tended to be lower in deciduous and semi-deciduous species than in evergreen species (Myers *et al.*, 1997).

Different patterns of water uptake and water relations can occur within a genus within a phenological guild. In a study of two deciduous shrub species in a West African humid savanna, Le Roux and Bariac (1998) observed that two co-occurring species exhibited marked differences in the magnitude of the dry-season decline in minimum leaf water potential. Furthermore, the relationship between water content of the upper 60 cm of soil and leaf water potential differed significantly. Pre-dawn and midday leaf water potentials of *Cussonia barteri* were not correlated with water content of the 0–60 cm profile and when the water potential of this layer was below  $-1.5$  MPa the  $\Psi_{pd}$  was only  $-0.5$  MPa. In contrast, *Crossopteryx febrifuga* showed significant declines in leaf water potential as the upper soil profile dried and pre-dawn and midday leaf water potentials were lower for this species than for *Cuss. barteri*. Clearly *Cuss. barteri* was accessing deeper water than was *Cross. febrifuga*. Similarly, in Costa Rican dry forest, there was a variety of seasonal responses in water relations within deciduous species. Seasonal minimum leaf water potentials were lowest in deciduous hardwood trees (average of  $-3.7$  MPa), highest in deciduous lightwoods ( $-1.5$  MPa) and intermediate in deciduous softwoods ( $-2.5$  MPa), evergreen softwoods ( $-2.5$  MPa) and evergreen lightwoods ( $-2.0$  MPa) (Borchert, 1994c). Pelaez *et al.* (1994) showed a similar result, which highlights the caution required in characterizing water use on the basis of phenology alone.

## B. Solute Potential and Osmotic Adjustment

The ability to maintain turgor as cell water content and leaf water potential decrease can contribute to drought tolerance (Morgan, 1984). High turgor maintenance capacity is associated with low osmotic potentials and a large difference between osmotic potentials at full turgor ( $\pi_{100}$ ) and the turgor loss point ( $\pi_0$ ) (Jones and Turner, 1978). Solute accumulation in response to water stress is termed 'osmotic adjustment' (often erroneously called 'osmoregulation') and involves an increase in the number of solute molecules per cell rather than a decrease in the amount of water in the cell (Munns, 1988). A decrease in osmotic potential at full turgor is evidence of osmotic adjustment (Morgan, 1984). However, a passive increase in cellular solute concentration resulting from loss of water can also help maintain positive turgor during drought stress (Evans *et al.*, 1992).

Osmotic potentials were lower in woody species from Venezuelan dry forest (annual rainfall 900 mm) (Sobrado, 1986) than those from Venezuelan savanna (annual rainfall 1300 mm) (Goldstein *et al.*, 1987), northern Australian savanna (annual rainfall 1650 mm) (Myers *et al.*, 1997; Prior and Eamus, 1999) or Guinean savanna (annual rainfall 1200 mm) (Le Roux and Bariac, 1998). These low osmotic potentials enable leaves to maintain turgor at the low leaf water potentials prevailing in this dry environment.

The osmotic potential of *Crossopteryx febrifuga* was significantly lower than that of *Cussonia barteri*, a co-occurring shrub of a West African humid savanna (Le Roux and Bariac, 1998). In addition, as the leaves dried during the dry season, a passive increase in solute concentration (resulting from reduced water content rather than active solute accumulation) was observed only in *Crossopteryx febrifuga*. The association of a lower solute potential and osmotic accumulation with water uptake from the upper soil profile are entirely consistent.

Drought-induced osmotic adjustment has been demonstrated in a wide range of species (Morgan, 1984), including saplings of the Australian savanna trees *E. tetradonta* and *T. ferdinandiana* (Table 1). This osmotic adjustment enabled the saplings to maintain positive turgor overnight throughout the year, although they probably lost turgor during the day at the end of the dry season (Prior and Eamus, 1999). By contrast, osmotic adjustment was not detected in mature trees of these or five other Australian savanna species (Myers *et al.*, 1997). However,  $\Psi_{pd}$  was higher throughout the year than the wet season value of  $\pi_0$ , so that osmotic adjustment was not necessary for overnight recovery of turgor during the dry season (Myers *et al.*, 1997; Table 1).

Osmotic adjustment did not occur in Venezuelan evergreen savanna trees during the dry season (Goldstein and Sarmiento, 1987), but there

**Table 1**  
Comparison of some water relations parameters for species from Mediterranean and seasonally dry tropical environments

Species	$\Psi_{pd}$				$\pi_{t0}$				$\pi_{t100}$				Comments	Reference		
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry			OA	
Seasonally dry tropical forest/savanna species																
<i>Allosyncarpia ternata</i>	-0.5	-1.6	-2.46	-2.82	-2.17	-2.48	0.31								Dry hilltop site, Australia	9
<i>Allosyncarpia ternata</i>	-0.3	-0.1	-2.23	-2.29	-2.08	-2.08	0								Wet ravine floor	9
<i>Eucalyptus miniata</i>	-0.2	-0.8	-1.98	-2.08	-1.81	-1.83	0.02								Australian savanna, mature, evergreen	5
<i>Eucalyptus terodonta</i>	-0.1	-0.8	-2.06	-2.13	-1.83	-1.93	0.10									
<i>Erythrophloeum chlorostachys</i>	-0.2	-1.1	-2.13	-2.37	-1.95	-2.23	0.28								Australian savanna, mature, semi-deciduous	5
<i>Xanthostemon paradoxus</i>	-0.1	-1.2	-1.69	-1.77	-1.39	-1.50	0.11									
<i>Eucalyptus clavigera</i>	-0.2	-0.6	-2.60	-2.70	-2.16	-2.29	0.13								Australian savanna, mature, deciduous	5
<i>Planchonia careya</i>	-0.1	-0.7	-1.73	-1.83	-1.62	-1.58	-									
<i>Terminalia Ferdinandiana</i>	-0.1	-0.9	-1.8	-1.72	-1.54	-1.48	-								Australian savanna, sapling, evergreen	6
<i>Eucalyptus terodonta</i>	-0.2	-2.5	-1.75	-2.80	-1.33	-2.25	0.92									
<i>Terminalia Ferdinandiana</i>	-0.1	-1.2	-1.32	-1.58	-1.18	-1.39	0.21								Venezuelan dry forest; 1 tree and 2 shrubs pre-dawn $\pi$ , not $\pi_{t0}$ , but similar water content so values comparable	8
3 evergreen spp.	-1.2	-3.0	-3.1	-3.1	-4.4	-4.4	1.3									
3 deciduous spp.	-0.6	-2.8	-1.5	-1.5	-3.1	-3.1	1.2								Venezuelan dry forest; 2 trees and 1 vine pre-dawn $\pi$ , not $\pi_{t0}$ estimated OA adjusted for change in H <sub>2</sub> O content	8
<i>Byrsonima crassifolia</i>	-0.25	-0.6		-1.5											Evergreen tree of Venezuelan savanna	7
<i>Curatella americana</i>	-0.45	-0.7		-2.8												
<i>Bowditchia virilandes</i>	-0.3	-0.8		-1.4											Guinean deciduous shrubs	2
<i>Caesarea sylvestris</i>	-0.35	-1.2		-2.3												
<i>Cussonia barteri</i>	-0.2	-0.7	-1.37	-1.72	-1.00	-1.15	0.15									
<i>Crotophyerx febrifuga</i>	-0.2	-0.7	-1.73	-2.17	-1.44	-1.67	0.23									

Table 1 (Continued)

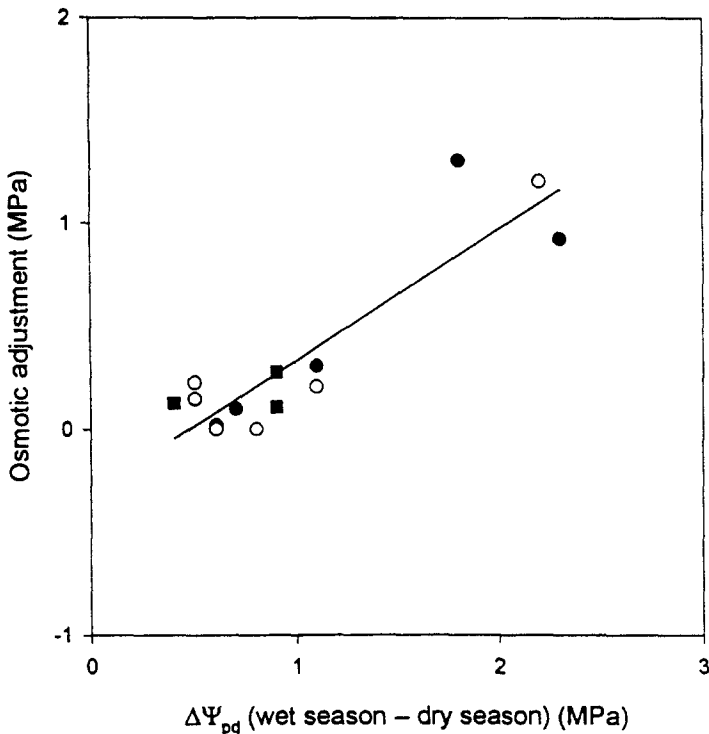
Species	$\Psi_{pd}$		$\pi_0$		$\pi_{100}$		OA	Comments	Reference
	Wet	Dry	Wet	Dry	Wet	Dry			
Species from Mediterranean environments									
<i>Quercus dumosa</i>	-0.1	-1.1	-2.2	-3.1	0.9		}	Evergreen, chaparral	1
<i>Ceanothus greggii</i>	-0.1	-2.7	-2.1	-3.1	1.0				
<i>Arctostaphylos glandulosa</i>	-0.3	-1.7	-2.3	-2.9	0.6				
<i>Eucalyptus behriana</i>		-3.5	-1.63	-1.93	0.30			Evergreen, seedlings	4
<i>Eucalyptus behriana</i>	-2.6	-4.5	-2.8	-3.7	0.9			Mature	3
<i>Eucalyptus microcarpa</i>		-3.6	-1.72	-1.98	0.26			Evergreen, seedlings	4
<i>Eucalyptus microcarpa</i>	-1.8	-4.0	-2.8	-3.5	0.7			Mature	3
<i>Eucalyptus polyanthemos</i>		-3.6	-1.63	-2.14	0.51			Evergreen, seedlings	4

Note:  $\Psi_{pd}$  is pre-dawn leaf water potential,  $\pi_0$  is osmotic potential at turgor loss point,  $\pi_{100}$  is osmotic potential at full turgor, and OA is osmotic adjustment, all in MPa. Deciduous species do not have leaves during the driest time of year, therefore dry season measurements presented here are the minimum values when leaves were present, and were generally not made at the same time as the dry season measurements on evergreen species.

References: 1, Bowman and Roberts (1985); 2, Le Roux and Bariat (1998); 3, Myers and Neales (1984); 4, Myers and Neales (1986); 5, Myers *et al.* (1977); 6, Prior and Eamus (1999); 7, Sarmiento *et al.* (1985); 8, Sobrado (1986); 9, Fordyce *et al.* (1997).

was little seasonality in leaf water potentials and minimum leaf water potential was almost always higher than  $\pi_0$  (Sarmiento *et al.*, 1985). However, in Venezuelan seasonally dry tropical forests, which receive less rainfall than the savanna areas,  $\Psi_{pd}$  values fell to about  $-3.0$  MPa in both evergreen and deciduous species. Pre-dawn turgor was always positive owing to a concomitant decrease in leaf osmotic potential (Sobrado, 1986).

For a range of woody species from seasonal tropical environments on three continents, the extent of osmotic adjustment has been found to be proportional to the decrease in  $\Psi_{pd}$  between the wet and dry periods and independent of leaf phenology (Figure 3). In other words, osmotic adjustment is proportional to the degree of stress experienced by the leaf tissue.



**Fig. 3.** The degree of osmotic adjustment increases as the difference between wet and dry season pre-dawn water potential ( $\Delta\Psi_{pd}$ ) increases, regardless of phenological guild. Data are from Myers *et al.* (1997), Prior and Eamus (1999), Sobrado (1986), Le Roux and Bariac (1998) and Fordyce *et al.* (1997). Closed circles represent evergreen species, closed squares are semi-deciduous species, and open circles are deciduous species.

## C. Hydraulic Properties and Water Transport

Plants balance their root growth, internal water transport capabilities and stomatal behaviour such that they maintain positive carbon assimilation while preventing leaf desiccation. Large xylem vessels are efficient at transporting water but are generally more susceptible to blockage by air (embolism) during water stress, compared to small vessels. There is a trade-off between efficiency and security of the water transport system (Tyree and Sperry, 1989; Tyree *et al.*, 1994; see below).

There are several recent reviews of hydraulic conductivity, hydraulic architecture and xylem embolism (Tyree and Sperry, 1989; Tyree and Ewers, 1991; Tyree *et al.*, 1994), including one on hydraulic architecture of tropical plants (Tyree and Ewers, 1996). Most studies, however, have been conducted on temperate species or tropical rainforest trees. Trees from seasonally dry systems have been relatively neglected.

Xylem conduits consist of tracheids in conifers and vessels in angiosperms. Conduits vary greatly in diameter, and even more in length (Tyree *et al.*, 1994). Typically, tracheids are 1–3 mm in length, while vessels are 0.1–10 m long. In flowing to the leaves of a tree, water passes through many conduits. Movement between conduits requires passage through the pores of pit membranes. (Note that a pit membrane is not a semi-permeable phospholipid bilayer membrane as is found in living cells, but rather a middle lamella with a very thin layer of primary wall on either side. Xylem pit membranes are not metabolically active.)

### 1. *Wood Anatomy of Conifers and Diffuse-Porous and Ring-Porous Trees*

Differences in wood anatomy between ring-porous, diffuse-porous and coniferous trees affect their hydraulic characteristics. Most tropical trees are angiosperms, but conifers are found in Southeast Asia, Australia and New Guinea, especially in montane rainforests and seasonally dry areas (Whitmore, 1985). Coniferous xylem, with numerous small tracheids, has a relatively low conductivity and is less vulnerable to embolism than xylem of angiosperm trees (Tyree and Ewers, 1991; Wang *et al.*, 1992). Smaller vessels of diffuse-porous wood are less conductive and less vulnerable than large-diameter vessels of earlywood in ring-porous species.

Ring-porous wood contains growth rings demarcated by much longer, wider vessels in earlywood (formed in spring) than in latewood (formed in summer/autumn) (Carlquist, 1988). Ring-porous trees generally contain between one and four, sometimes as many as 12, rings in the sapwood, compared with 20–100 rings for diffuse-porous and up to 150–200 for conifers (Ewers and Cruiziat, 1991). In ring-porous temperate trees, the wide



earlywood vessels that conduct most of the sap embolize during autumn, while the much less conductive (and 'safer') latewood vessels function for several years (Zimmermann, 1983; Cochard and Tyree, 1990; Lo Gullo *et al.*, 1995). Whether some drought-deciduous tropical trees function similarly has not been reported.

Many temperate Northern Hemisphere trees are easily classified as either ring-porous or diffuse-porous, but trees from other areas, such as the tropics and temperate areas of the Southern Hemisphere, often are not. For example, Ingle and Dadswell (1953a) stated that no eucalypts are ring-porous, but in some species vessels are markedly wider in earlywood than in latewood, and Carlquist (1988) considers these to be ring-porous. In addition, maximum vessel length often exceeds 1 m in various *Eucalyptus* species (Skene and Balodis, 1968; Franks *et al.*, 1995), including *E. tetradonta* (L.D. Prior, unpublished data), a dominant tree over large areas of north Australian savanna. Maximum vessel lengths in American diffuse-porous species are generally less than 60 cm, with most vessels being less than 10 cm long (Zimmermann and Jeje, 1981). We therefore need to be cautious in applying generalizations based on Northern Hemisphere diffuse-porous species to tropical and Southern Hemisphere species.

## 2. Hydraulic Conductance and Conductivity

Hydraulic conductance ( $L_p$ ) is defined as flow rate per pressure *difference*. The value of  $L_p$  is obtained from the relationship between sap flow rate ( $Q$ ) and the driving force, which is the water potential difference between the root ( $\Psi_R$ ) and the leaf ( $\Psi_L$ ) (note that these include a gravitational component):

$$L_p = Q/(\Psi_R - \Psi_L) \quad (1)$$

Leaf water potential is averaged over an adequate sample of transpiring leaves. Root water potential is assumed to stay constant throughout the day, and may be approximated by the value of pre-dawn leaf water potential. This relationship applies under steady-state conditions, when transpiration and uptake are equal. During transient conditions, there is also a capacitance (storage) component, but this is usually small compared with water uptake (Moreshet *et al.*, 1990; Tyree *et al.* 1991; Goldstein *et al.*, 1998).

Hydraulic conductance (and conductivity, see below) values are usually scaled to sapwood area (or stem cross-sectional area) and/or to leaf area. Generally, hydraulic conductance (leaf area basis) is higher in species with high transpiration rates (Figure 4). Values for woody plants from a range of environments are shown in Table 2. The patchiness of the data

**Table 2**  
 Hydraulic conductance of whole trees or shrubs from a range of environments. Values are scaled to sapwood area  
 ( $\text{g m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ ) and/or leaf area ( $\text{mg m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ )

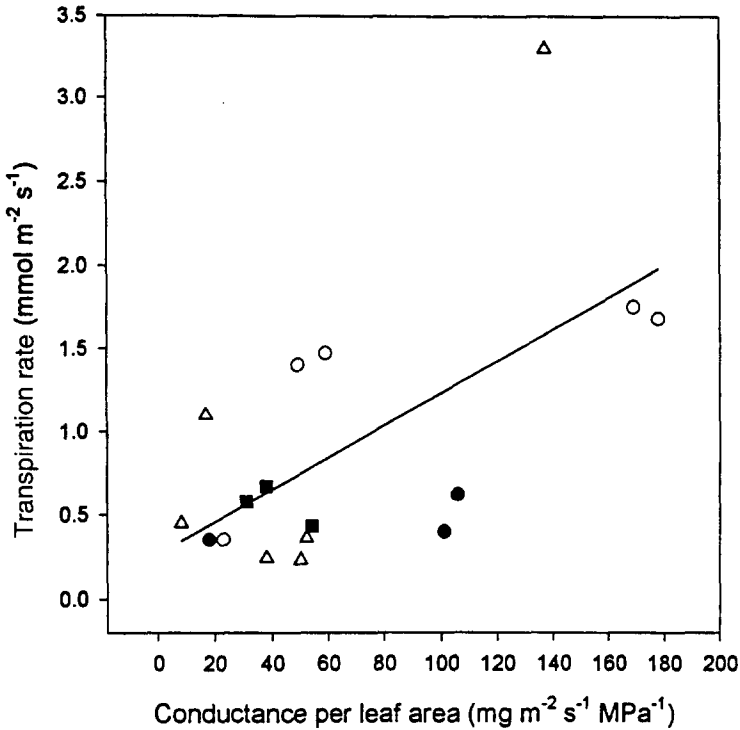
Species	Hydraulic conductance				Comments	Method	Reference
	Sapwood area basis		Leaf area basis				
	Well-watered	Droughted	Well-watered	Droughted			
Conifers							
<i>Abies bornmulleriana</i>	67	20	21		Saplings	S	7
<i>Juniperus virginiana</i>			8.1			P	4
<i>Larix</i> sp.			6.5			S	17
<i>Picea abies</i>	61	13				S	17
<i>Picea abies</i>	56	3				S	7
<i>Picea sitchensis</i>			17	17		S	19
<i>Pinus pinaster</i>	72					S	9
<i>Pinus pinaster</i>	100					S	7
<i>Pinus pinaster</i>	115					S	11
<i>Pinus sylvestris</i>	31 (average)					S	10
<i>Pinus sylvestris</i>	34		50	23		S	8
<i>Pinus sylvestris</i>	66		38			P	18
<i>Pinus sylvestris</i>			52			P	18
<i>Pinus sylvestris</i>			137	89		S	9
Temperate shrubs							
<i>Disyllum lepidotum</i>			126	54	Evergreen	P	14
<i>Dodonea viscosa</i>			72	45	} Evergreen, xerophytic	P	14
<i>Hibiscus glaber</i>			171	99		P	14
<i>Larrea tridentata</i>			65	24		P	12
<i>Ligustrum micranthum</i>			117	54		P	14
<i>Wikstroemia pseudoretusa</i>			114	54	Semi-deciduous	P	14

Table 2 (Continued)

Temperate angiosperm trees							
<i>Juglans nigra</i>		256				P	4
<i>Quercus alba</i>		117				P	4
<i>Quercus marilandica</i>		36		9		P	16
<i>Quercus petraea</i>	18-61					S	1
<i>Quercus petraea</i>	63					S	2
<i>Quercus petraea</i>	13-61			9		S	3
<i>Quercus rubra</i>		31				P	16
Tropical rainforest trees							
<i>Cecropia insignis</i>		169				S	13
<i>Cecropia obtusifolia</i>		49				S	13
<i>Coccoloba manzanillensis</i>		59				S	13
<i>Miconia argentea</i>		178				S	13
<i>Palicourea guianensis</i>		23				S	13
Trees of savannas/seasonal tropical forests							
<i>Bursera crassifolia</i>		101				S	5
<i>Curatella americana</i>		106				S	5
<i>Eucalyptus terrodonta</i>		18		9		S	15
<i>Cecropia longipes</i>	40					S	6
<i>Ficus insipida</i>				26		S	6
<i>Luehea seemannii</i>				53		S	6
<i>Cochlospermum vitifolium</i>				27		S	6
<i>Genipa caruto</i>		38				S	5
<i>Terminalia ferdinandiana</i>		54				S	5
<i>Anacardium excelsum</i>	125	31				S	15
<i>Spondias mombin</i>				4		S	6
						Brevi-deciduous; abnormally wet dry season	
				29		Facultatively deciduous; abnormally wet dry season	6

Note: Method refers to whether transpiration was measured using sap flow sensors (S) or scaled up from porometry measurement (P); these may produce an overestimate of transpiration and therefore conductance).

References: 1. Bréda *et al.* (1993); 2. Bréda *et al.* (1995); 3. Cochar *et al.* (1996); 4. Ginter-Whitehouse *et al.* (1983); 5. Goldstein *et al.* (1989); 6. Goldstein *et al.* (1998); 7. Granier *et al.* (1989); 8. Irvine *et al.* (1998); 9. Jackson *et al.* (1995b); 10. Loustau and Granier (1995); 11. Loustau *et al.* (1996); 12. Meinzer *et al.* (1988); 13. Meinzer *et al.* (1995); 14. Mishio (1992); 15. Prior (1997); 16. Reich and Hinckley (1989); 17. Schulze *et al.* (1985); 18. Whitehead *et al.* (1984); 19. Lu *et al.* (1996).



**Fig. 4.** Transpiration rate increases with increasing hydraulic conductance (expressed per unit leaf area) of stems. Triangles represent conifers; open circles are rainforest species; closed circles are evergreen savanna species; closed squares are deciduous savanna trees; and open squares are temperate trees.

and different methods used to determine transpiration make it difficult to draw generalizations about the different groups of plants. For example, there are few values for temperate trees other than *Quercus* spp., and some of these were derived from scaled-up porometry data. However, conductance does tend to be lower in trees from seasonally dry tropical areas than in tropical rainforest gap species. This is probably a reflection of the larger, year-round, availability of water in rainforests. There are few consistent differences between conductance in evergreen compared with deciduous tropical species. It may not be valid to include deciduous trees measured by Goldstein *et al.* (1998) in the comparison, since measurements were made in the dry season and may be much lower than wet season values.

Hydraulic conductivity ( $k_h$ ) is defined as the flow rate per pressure gradient ( $\Delta\Psi_w/l$ , where  $\Delta\Psi_w$  is the difference in water potential between two points in the plant, and  $l$  is path length). This can be written:

$$k_h = Ql/\Delta\Psi_w \quad (2)$$

where  $Q$  = flow rate ( $\text{ml s}^{-1}$ ).

In order to scale for size, conductivity measurements may be divided by leaf area (often termed 'leaf specific conductivity'), or by stem or sapwood cross-sectional area ('specific conductivity'). However, in the SI system the term 'specific' is reserved to describe a value per unit mass, so we will refer to conductivity (leaf area basis), ( $k_l$ ), and conductivity (sapwood area basis), ( $k_s$ ).

Hydraulic conductivity of a cylinder is proportional to the fourth power of its radius (Poiseuille's law). The  $k_h$  of trunks, stems and branches is therefore largely determined by the number and size distribution of xylem conduits, but is also modified by properties of the inter-conduit pit membranes, which add to the resistance of the system (Tyree and Sperry, 1989). Actual conductivities of different species range between 20% and 100% of the theoretical maximum  $k_h$  (Tyree and Ewers, 1991).

Hydraulic conductivity values for stem segments from a range of woody species are shown in Table 3. Vines and lianas generally have the highest conductivity values, followed by tropical shrubs and rainforest trees, with conifers and savanna trees having the lowest values (these aspects will be discussed further in section III.C.8). Values of  $k_l$  and  $k_s$  were lower in savanna than rainforest trees, probably because high soil water availability enables rainforest trees to maintain high rates of transpiration throughout the year, whereas soil water is more limited in savannas during the dry season.

A study of four deciduous and two evergreen trees from Venezuelan dry forest found that the maximum  $k_h$  of the drought-deciduous species was 2–6 times that of the evergreen species, but was severely reduced at leaf fall (Sobrado, 1993; Table 3). Another study of 20 tropical vine and tree species also found that, within these two growth forms, deciduous plants generally had higher  $k_s$  values than did evergreen plants (Gartner, 1991; Table 3). These findings are consistent with surveys showing that plants of xeric habitats or those active in the dry season tend to have smaller diameter vessels and tracheids than those from more mesic sites and those active in wetter seasons (Carlquist and Hoekman, 1985 – cited by Gartner *et al.*, 1990). By contrast, Goldstein *et al.* (1987) found that the  $k_l$  of stem segments and the conductance of whole trees from Venezuelan savanna was substantially higher in two evergreen than two deciduous species. However, these evergreen species maintain high water potentials throughout the dry season, and it has been suggested that they have extensive root systems that allow them access to subsoil water (Goldstein *et al.*, 1987), as well as effective stomatal control of transpiration (Sobrado, 1996). The large  $k_l$  values in the evergreen species were largely due to a high ratio

**Table 3**  
Hydraulic parameters of stem segments from trees, shrubs and lianas from a range of environments

Species	HV $\times 10^4$	$k_1 \times 10^3$	$k_s$	DBH (mm)	Comments	Ref.
<b>Conifers</b>						
<i>Abies balsamea</i>	2.8	0.34	1.35	15		3
<i>Thuja occidentalis</i>	0.4	0.069	1.7	15		3
<i>Tsuga canadensis</i>	1.1	0.12	1.1	15		3
<b>Temperate angiosperm trees</b>						
<i>Acer saccharum</i>	1.5	0.5	2.5	15	Diffuse-porous	3
<i>Betula papyrifera</i>		0.74			Diffuse-porous	3
<i>Populus angustifolia</i>	2.1	1.04	3.9	15	Diffuse-porous	3
<i>Populus balsamifera</i>	2.5	0.75	3.0	15	Diffuse-porous	3
<i>Populus deltoides</i>	2.9	1.01	4.8	15	Diffuse-porous	3
<i>Populus grandidentata</i>		0.62			Diffuse-porous	3
<i>Eucalyptus grandis</i>	4	2.5	6.5	15-30	Diffuse-porous, evergreen	8
<b>Tropical vines and lianas</b>						
<i>Aristolochia taliscana</i>			41	3-20	Evergreen	1
<i>Adenocalymma inundatum</i>			1.5	3-20	Brevi-deciduous	1
<i>Combretum fruticosum</i>			17	3-20	Deciduous	1
<i>Dieterlea fusiformis</i>			88	3-20	Deciduous	1
<i>Entadopsis polystachya</i>			210	3-20	Deciduous	1
<i>Gaudichaudia mcvaughii</i>			20	3-20	Deciduous	1
<i>Gouania rosei</i>			110	3-20	Deciduous	1
<i>Ipomoea bracteata</i>			32	3-20	Deciduous	1
<i>Paddiflora juliana</i>			40	3-20	Deciduous	1
<i>Serjania brachycarpa</i>			9	3-20	Deciduous	1
<i>Bauhinia fassoglenis</i>	0.14	11	171			3
<i>Bauhinia vahii</i>	0.24	6.8	35			3
<b>Tropical shrubs</b>						
<i>Bauhinia aculeata</i>	1.58	6.2	7			3
<i>Bauhinia galpinii</i>	0.6	5.8	11			3
<b>Tropical rainforest trees</b>						
<i>Bauhinia blakeana</i>	1.2	11	14			3
<i>Bauhinia variegata</i>	0.94	12.3	15			3
<i>Ochroma pyramidale</i>	10	2.0	2.1	45	Evergreen	3
<i>Pseudobombax septenatum</i>	12	1.8	1.6	45	Deciduous	3
<i>Schefflera morotoni</i>	20	4.5	2.2	45		3
<i>Ficus dugandii</i>	6.1	5.2	14	15		3
<i>Ficus glabrata</i>	2.2	2.1	11	15		3
<i>Ficus yoponensis</i>	2.0	2.3	14	15		3
<i>Ficus citrifolia</i>	2.2	1.5	7.9	15	Hemi-epiphyte	3
<i>Ficus colubrinae</i>	1.8	2.3	34	15	Hemi-epiphyte	3
<i>Ficus obtusifolia</i>	1.8	2.2	17	15	Hemi-epiphyte	3
<i>Ficus pertusa</i>	1.0	0.66	7.3	15	Hemi-epiphyte	3
<i>Clusia uvitana</i>	1.4	0.15	1.1	15	CAM-hemi-epiphyte	3

Table 3 (Continued)

Species	HV $\times 10^4$	$k_1 \times 10^3$	$k_s$	DBH (mm)	Comments	Ref.
Trees of savannas/seasonal tropical forests						
<i>Eucalyptus miniata</i>	3.2	0.67	2.2	3.2	Evergreen	4
<i>Eucalyptus tetradonta</i>	1.8	0.59	3.1	3.1	Evergreen	4
<i>Byrsonima crassifolia</i>	4.5	0.41	0.91	11	Evergreen	2
<i>Curatella americana</i>	3.1	0.13	0.43	11	Evergreen	2
<i>Curatella americana</i>	1.55	0.23	1.5	5.0	Evergreen	6
<i>Capparis indica</i>			1.0	3-20	Evergreen	1
<i>Capparis aristiguetae</i>	1.2	0.026	0.23	4.4	Evergreen	5
<i>Capparis aristiguetae</i>	2.1	0.016	0.09	5.7	Evergreen	7
<i>Morisonia americana</i>	1.1	0.025	0.23	4.4	Evergreen	5
<i>Morisonia americana</i>	2.8	0.035	0.14	6.1	Evergreen	7
<i>Beureria cumanensis</i>	1.11	0.066	0.50	4.3	Deciduous	5
<i>Beureria cumanensis</i>	2.94	0.100	0.41	4.3	Deciduous	7
<i>Coursetia arborea</i>	0.77	0.098	1.50	4.4	Deciduous	5
<i>Coursetia arborea</i>	0.81	0.092	1.26	3.0	Deciduous	7
<i>Lonchocarpus dipteroneurus</i>	0.50	0.065	1.31	4.3	Deciduous	5
<i>Lonchocarpus dipteroneurus</i>	0.88	0.096	0.98	3.8	Deciduous	7
<i>Pithecellobium dulce</i>	0.68	0.048	0.59	4.4	Deciduous	5
<i>Pithecellobium dulce</i>	1.53	0.071	0.54	3.5	Deciduous	7
<i>Cochlospermum vitifolium</i>	0.79	0.027	0.35	11	Deciduous	2
<i>Genipa caruto</i>	1.06	0.056	0.52	11	Deciduous	2
<i>Caesalpinia eriostachys</i>			1.8	3-20	Deciduous	1
<i>Cnidoscolus spinosus</i>			2.7	3-20	Deciduous	1
<i>Cordia alliodora</i>			2.6	3-20	Deciduous	1
<i>Guapira</i> sp.			1.7	3-20	Deciduous	1
<i>Heliocarpus pallidus</i>			5	3-20	Deciduous	1
<i>Ipomoea wolcottiana</i>			2.2	3-20	Deciduous	1
<i>Psidium sartorianum</i>			1.2	3-20	Deciduous	1
<i>Ruprechtia fusca</i>			2.4	3-20	Deciduous	1
<i>Spondias purpurea</i>			2.7	3-20	Deciduous	1

Note: HV (Huber value,  $\text{m}^2$  xylem cross-sectional area/ $\text{m}^2$  leaf area). Units for  $k_1$  and  $k_s$  are  $\text{kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1}$ . Stem diameter at breast height (DBH, mm) is presented since hydraulic parameters change according to DBH (Patino *et al.*, 1995). Data for many species have been normalized to a stem diameter of 15 mm or 45 mm (Patino *et al.*, 1995). Where available, Huber values have sometimes been used to convert between  $k_s$  and  $k_1$ .

References: 1, Gartner (1991); 2, Goldstein *et al.* (1987); 3, Patino *et al.* (1995, and references contained therein); 4, L.D. Prior (unpublished); 5, Sobrado (1993); 6, Sobrado (1996); 7, Sobrado (1997); 8, Van der Willigen and Pammenter (1998).

of cross-sectional area of conducting tissue to total leaf area (Goldstein *et al.*, 1987). Goldstein *et al.* (1987) suggested that an efficient water transport system is required to keep pace with high transpiration rates during the dry season without causing an excessive drop in leaf water potential. However, such a strategy of maintaining high leaf water potential by facilitating large flows of water requires a large and reliable supply of accessible water to avoid extreme soil water deficits. Only the most favoured microsites within savanna landscapes could support such trees.

### 3. Water Storage Capacitance

Water storage capacitance is defined as the mass of water that can be extracted per MPa change in water potential of the tissue, either per unit volume or per unit dry mass (Tyree and Ewers, 1996). This topic has been reviewed by Holbrook *et al.* (1995).

Large leaf and stem water capacitances could substantially reduce the maximum rate of water uptake by the roots during the morning, and spread the period of water uptake over more hours in the diurnal cycle. Internally stored water could allow stomata to stay open for longer each day, enhancing carbon uptake. The range in wood density (0.15–1.1 g cm<sup>-3</sup>) and hence in stem water storage capacity is much greater among tropical trees than among temperate trees (0.4–0.8 g cm<sup>-3</sup>) (Borchert, 1994c). Calculations of diurnal water storage and release showed that stem and leaf water storage contributed, respectively, 16% and 5% of daily transpiration in *Thuja occidentalis*, 14% and 3% in *Acer saccharum* and only <0.5% and 2% in *Schefflera morotoni*. The contribution was low for *Schefflera* because there was a very narrow diurnal range in stem water potential (Tyree and Ewers, 1991). In five tree species from a seasonally dry tropical forest, diurnal water storage capacity ranged between 9% and 15% of total daily water use (Goldstein *et al.*, 1998). The contribution was proportionally larger in large trees, and could partially compensate for decreases in hydraulic conductivity with tree size (Goldstein *et al.*, 1998). Stem storage of water is likely to have a significant role in phenology (Borchert, 1994a; Holbrook *et al.*, 1995; see above).

### 4. Xylem Embolism

Xylem conduits are prone to embolism because xylem sap is under tension, typically between -1 and -2 MPa (Tyree and Sperry, 1989), or lower in species adapted to arid conditions. This means that water must remain liquid at pressures considerably below its vapour pressure. Cavitation must be prevented if continuity of the water column is to be maintained.

Emboli may occur as a result of drought or freezing. The mechanisms are different for the two stresses (Sperry and Pockman, 1993). Since most savannas and seasonally dry tropical forests rarely experience freezing temperatures, this review will concentrate on drought-induced embolism.

Drought-induced cavitation in xylem occurs through air-seeding (Sperry and Tyree, 1988, 1990; Cochard *et al.*, 1992; Jarbeau *et al.*, 1995; Pockman *et al.*, 1995; Sperry *et al.*, 1996). Air does not easily penetrate the pores of a wet membrane, but will do so if the pores are large enough and there is a sufficient pressure difference between the two sides of the membrane. The



critical pore diameter ( $d$ ) or pressure difference ( $\Delta P$ ) can be approximated from a simplified version of the capillarity equation (Zimmermann, 1983):

$$d \times \Delta P \approx 0.3 \quad (3)$$

where  $d$  is measured in  $\mu\text{m}$  and  $\Delta P$  in MPa. Air-seeding occurs first through the largest pores in the conduit wall, which are located in the inter-conduit membranes. The maximum pressure difference to which an inter-conduit membrane could be exposed occurs if a neighbouring vessel becomes air-filled, for example because of mechanical injury or insect damage. The pressure in the air-filled conduit is then atmospheric (approximately 0.1 MPa), compared with that in the functional vessel (Zimmermann, 1983) of approximately  $-1$  to  $-3$  MPa.

A safe pit membrane (i.e. resistant to propagation of air) has narrow pores, but also needs to be strong enough to resist substantial pressure differences without rupturing. Vulnerability to cavitation depends not only on the diameter of pit membrane pores, but also on conduit length. Long conduits have a larger contact surface between cavitating conduits and those that are still functioning, and the consequences of them failing are worse than for short conduits (Lo Gullo *et al.*, 1995).

### 5. Vulnerability Curves

The relationship between loss of hydraulic conductivity and the xylem water potential that induced the loss of conductivity is shown in a vulnerability curve (Figure 5 provides examples using two tree species from seasonally dry forests in Venezuela).

Values of xylem water potential corresponding to a 50% loss of conductivity for temperate trees range between  $-1.2$  MPa in *Populus deltoides* (Tyree *et al.*, 1992) and  $-11$  MPa in *Ceanothus megacarpus* (Kolb and Davis, 1994). For Bornean rainforest trees, values were between  $-0.18$  MPa in *Xerospermum laevigatum* and  $-6.3$  MPa in *Homalium moultonii*, but were less than  $-1.0$  MPa for most species (Tyree *et al.*, 1998).

In the evergreen savanna tree *Curatella americana*, 50% of hydraulic conductivity was lost at  $-1.5$  MPa (Figure 5). This species appears able to access subsoil water and maintains high leaf water potentials throughout the year (Sobrado, 1996). Another two evergreen tree species from Venezuelan dry forest lost 50% of conductance at about  $-2.4$  MPa, compared with  $-1.65$ ,  $-1.77$ ,  $-2.42$  and  $-3.82$  MPa for four deciduous species (Sobrado, 1997). Thus there is considerable overlap for the two phenological guilds, and we need data from more species, and from more areas (especially trees from African and Australian savannas), before we can

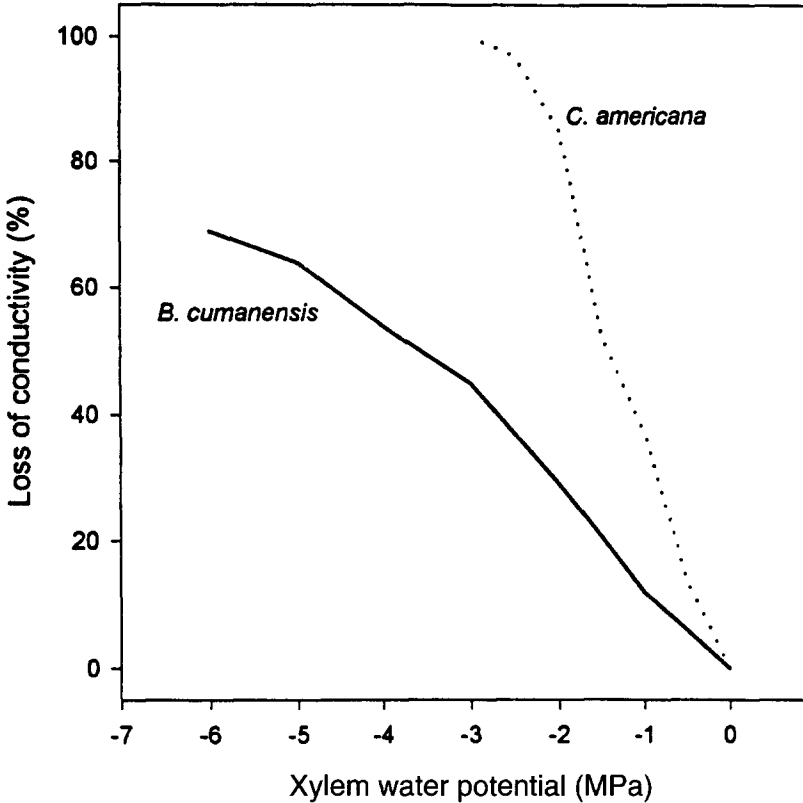


Fig. 5. As xylem water potential declines, the percentage embolism for the tree species *Curatella americana* and *Beureria cumanensis* increases. Re-drawn from Sobrado (1996).

draw conclusions about possible differences in vulnerability between evergreen and deciduous trees. We also do not know whether xylem embolism is involved in the process of leaf shedding by drought-deciduous trees. Dry season leaf water potentials were much lower in four deciduous than in two evergreen tree species (Sobrado, 1993), so that extent of embolism would vary, even when vulnerability curves are similar.

In general, the vulnerability of species correlates with the xylem pressures they experience in the field (Tyree and Sperry, 1989). For tropical tree species, xylem water potentials that cause 50% loss of conductivity are least negative in dipterocarp forest (high soil water-holding capacity), slightly lower and more variable in heath forest (low soil water-holding capacity, and subject to occasional drought), and most negative in tropical, seasonally dry forest or savannas (Figure 6; Tyree *et al.*, 1998). Tyree *et al.* (1998) suggest that other mechanisms, such as stomatal control to avoid

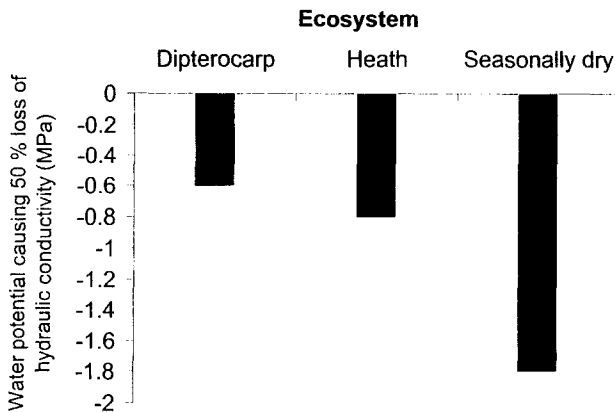
embolism-inducing xylem tensions, are cost-effective adaptations against occasional drought, but that the resulting reduction in productivity places a greater premium on resistance to embolism when drought is annual and predictable.

### 6. Trade-off between 'Safety' and 'Efficiency' of Xylem

The features that make xylem safe – short vessels (or tracheids), separated by a thick, strong pit membrane with narrow pores – also add to its resistance. Additionally, within an individual tree, conduit size and size of pores in the pit membrane are correlated, so that large vessels are more vulnerable to cavitation than small ones (Tyree and Sperry, 1989; Sperry and Saliendra, 1994; Alder *et al.*, 1996). There is a trade-off between safety and efficiency of xylem.

The relationship between conduit diameter and size of pit membrane pores does not necessarily hold between species. For a range of 57 trees from widely varying environments, Tyree *et al.* (1994) found there was a weak but statistically significant correlation between conduit diameter and xylem potential at which 50% of hydraulic conductivity is lost. This contrasts with freezing-induced embolism, for which the correlation was very strong. Nonetheless, Tyree *et al.* (1994) concluded that wet, warm environments tend to favour species with wide conduits, whereas cold or dry environments tend to favour species with narrow conduits.

Studies of wood characteristics of tropical trees give results consistent with these expectations. Wood from 19 species of a very dry Venezuelan



**Fig. 6.** Xylem water potential causing 50% loss of hydraulic conductivity decreases from dipterocarp, through heathland to seasonally dry forests/savannas. Re-drawn from Tyree *et al.* (1998).

forest had features that would contribute to hydraulic safety, such as numerous grouped vessels of narrow, short vessel elements (vessel length was not examined), and very small inter-vessel pits (Lindorf, 1994). Wide vessels were found in only one species, *Acacia tortuosa*, which can obtain water from deep within the soil profile. In Mexican deciduous forest, there was more diversity in vessel diameter categories, and a good representation of medium-sized and moderately large vessels was found (Barajas-Morales, 1985, cited in Lindorf, 1994). In trees of a Venezuelan cloud forest, wide vessels predominated, but mean vessel diameter was smaller than in the Mexican deciduous forest (Perez Mogollon, 1989, cited in Lindorf, 1994). This probably reflects the fact that xylem of drought-deciduous trees usually transports water only when water is readily available.

### 7. *Recovery from Embolism*

Embolized conduits may become functional again through bubble dissolution. In a few species, refilling of xylem conduits may also occur when gas is expelled from very dry branches, where the ends of conduits are exposed to the air through open vessels or dry pit membranes (Yang and Tyree, 1992). Xylem conductivity can recover from embolism when xylem pressure is positive, or at pressures only slightly below atmospheric (Yang and Tyree, 1992).

Root pressures can be effective in repairing embolism in herbaceous plants, but embolism reversal in tall trees is more problematic (Tyree and Sperry, 1989). Among tropical plants, positive xylem pressures have been detected in only eight taxa, and only in a fern and three grass species were these sufficient to refill embolized conduits throughout the shoots. None of 29 species of dicotyledonous vines exhibited root pressures that would be adequate to refill embolized vessels in canopy stems (Tyree and Ewers, 1996).

Temperate ring-porous trees rely on production of new earlywood vessels each spring, rather than refilling embolized vessels. It is not known whether deciduous savanna trees can refill embolized xylem vessels during the early wet season or whether they produce new xylem that only functions until the next dry season. We do not even know to what extent embolism occurs in most drought-deciduous trees (see section IX).

### 8. *Hydraulic Architecture*

'Hydraulic architecture' describes how the hydraulic conductivity of the xylem in various parts of a tree is related to the leaf area it must supply (Zimmermann, 1978). By investigating hydraulic architecture, we can

predict how much water can be conducted to various parts of a tree, the resulting water potentials and pressure gradients at varying levels of transpirational flow, how vulnerable the tree will be to embolism, and where embolism is most likely to occur.

About one half of a tree's resistance is located in the root system (Running, 1980; Moreshet *et al.*, 1990; Tyree *et al.*, 1995, 1998), the other half in the shoot. Generally,  $k_1$  for minor branches is 10 to 1000 times lower than for major branches (Tyree and Sperry, 1989). Since the pressure gradient ( $\Delta\Psi_w/l$ ) in the stem is equivalent to transpirational flux density divided by  $k_1$ , most of the water potential drop in the shoot xylem occurs in small branches, twigs and petioles. Nodal areas also present a distinct hydraulic constriction, with conductivity through junctions often half that of the branch itself (Zimmermann, 1978). In addition,  $k_h$  of leaf blades is very low, and there are presumably large gradients in water potential within them (Yang and Tyree, 1994).

Hydraulic resistance was much higher in leaves of evergreen than in deciduous trees of Venezuelan dry tropical forest (Sobrado, 1997/98). Leaves contributed 92–96% of total resistance of shoots (3–5 mm diameter) from evergreen trees, but only 69–76% of total resistance of shoots from deciduous trees. Such resistances were calculated to cause a drop in water potential across a leaf of 1.0–1.7 MPa in deciduous species and 1.8–1.9 MPa in evergreen species (Sobrado, 1997/98). These results are consistent with those of Borchert (1994b), who found greater differences in water potential between leaves and stems in evergreen (*c.* 1.2 MPa) than deciduous (*c.* 0.1–1.0 MPa) trees.

Vessel size and  $k_1$  decrease from base to apex, where water potentials are always more negative (Zimmermann, 1978; Patino *et al.*, 1995; Tyree and Ewers, 1996). This may also apply to root systems: in the proteaceous shrub *Banksia prionotes*,  $k_s$ , decreased 5- to 20-fold from the base to the top of sinker roots, so that absolute conductance was relatively constant along its length, despite a 10- to 15-fold decrease in cross-sectional area (Pate *et al.*, 1995). The relatively high conductivities of the trunk and main stem means that the absolute conductance per unit leaf area of some woody species is nearly independent of plant size (Yang and Tyree, 1994).

The Huber value is defined as the sapwood cross-sectional area (or sometimes the stem cross-sectional area) divided by the leaf area distal to the segment. It is a measure of the investment of stem tissue per unit leaf area supplied (Tyree and Ewers, 1991). Obviously the Huber value will change seasonally in deciduous species, so it is important to measure it when leaf area is maximal. Conductivity (leaf area basis) is the product of the Huber value and  $k_s$  (Tyree and Ewers, 1991). Thus, plants may compensate for a low  $k_s$  by having a higher Huber value (Pallardy, 1989). This can happen within a species; for example, *Toxicodendron diversilobum*

grows as a vine when support is present, but as a shrub when support is absent. Narrow stems of supported plants had lower Huber values (xylem transverse area/leaf area), but wider vessels and higher  $k_s$ , than those of unsupported plants (Gartner, 1991).

In tropical dry forests of Venezuela, the Huber value was higher in stems of six evergreen and one drought-deciduous tree than in stems of the remaining five deciduous trees (Goldstein *et al.*, 1987; Sobrado, 1997). Lianas have very wide vessels and high  $k_s$  but relatively small sapwood areas and low Huber values (Table 3; Tyree and Ewers, 1996). They have very little heartwood and rely on external plants or objects for mechanical support (Tyree and Ewers, 1996).

Zimmermann's (1978) 'segmentation hypothesis' states that during periods of severe drought, water potentials will always be lowest in the most peripheral parts of the tree, and this is where embolism will first occur, provided vulnerability of these parts is similar or greater. Leaves and twigs will be sacrificed first, protecting the vital main stem and major branches. This has been demonstrated in several temperate species (Tyree *et al.*, 1991, 1993), but not in tropical trees.

It can be useful to integrate the factors affecting the balance between water potential gradient and transpiration in plants into an explicit equation. Sap flow rate,  $Q$ , can be expressed as

$$Q = E \times A_1 \quad (4)$$

where  $E$  is the transpiration rate and  $A_1$  is the leaf area. From Pearcy *et al.* (1989),

$$E = G_s D \quad (5)$$

where  $G_s$  is stomatal conductance and  $D$  is leaf-to-air vapour pressure deficit (expressed as a mole fraction).

The conductivity per unit sapwood area,  $k_s$ , is defined by

$$k_s = k_h / A_s$$

where  $k_h$  is hydraulic conductivity and  $A_s$  is the sapwood cross-sectional area. We can therefore rewrite (2) as

$$k_s A_s = G_s D A_1 / \Delta \Psi_w \quad (6)$$

Whitehead (1998) hypothesized that trees growing in conditions of different evaporative demand will adjust  $G_s$ ,  $k_s$ ,  $A_s$  or  $A_1$  as a result of a homeostatic response to maintain the water potential gradient within

narrow limits. Thus, two stands of *Pinus sylvestris* growing under different conditions (Mencuccini and Grace, 1995) exhibited a lower ratio of foliage area to sapwood cross-sectional area at warmer, drier sites than at cooler wetter sites. Trees of northern Australian savannas also appear to maintain fairly constant water potential gradients between roots and leaves throughout the year, despite large seasonal variations in soil and atmospheric water availability. Assuming mean water potential of fine roots is equivalent to pre-dawn leaf water potential, water potential difference between roots and leaves of *Eucalyptus tetrodonta* trees was 1.7 MPa and 1.6 MPa in the late wet season and the late dry season, respectively (Myers *et al.*, 1997). For saplings, these values were 1.3 MPa and 1.6 MPa, respectively (Prior *et al.*, 1997a). Decreased stomatal conductance prevented development of excessive leaf water potential differences.

### 9. Seasonal Decreases in Hydraulic Conductance

Drought-induced changes in whole-tree hydraulic conductance have been demonstrated in conifers, temperate trees and shrubs and in one study of a savanna evergreen tree (Table 2). In addition, many studies have found seasonal changes in embolism in stems of woody plants (see section III.C.9(d)), but this is only one of many possible reasons for a decrease in hydraulic conductance of whole trees. These reasons include:

(a) *Decrease in leaf area.* A decrease in leaf area will lead to a decline in flow for a particular pressure difference, and therefore a lower absolute hydraulic conductance, as well as a lower apparent  $k_s$ . Hydraulic conductance may also decline on a leaf area basis, since lower leaves on a branch, and lower branches on a tree, are often shed first, giving a longer average pathway for water to travel. This would depend on the hydraulic architecture of the tree, and the location of the major resistances to water flow.

Fully deciduous savanna trees represent an extreme case. These trees shed all their leaves during the dry season, so there is no flow of water and zero conductance. It may be argued that this is simply due to sealing of the xylem vessels during petiole abscission, and that the stem of the tree retains a high conductance. Whether this is so could be tested by measuring flow that occurs after cutting the tips off branches and imposing a pressure gradient on the tree, for example with a high-pressure flowmeter such as described by Tyree *et al.* (1995). Even evergreen savanna trees lose some leaf area during the dry season (Williams *et al.*, 1997b; O'Grady *et al.*, 1999), and a consequent decrease in hydraulic conductance would be expected. This especially applies to saplings and smaller trees (Prior *et al.*, 1997a; Williams *et al.*, 1997b).

(b) *Death of roots.* Loss of roots would reduce hydraulic conductance of the whole tree, as well as its apparent  $k_s$  and  $k_l$ . Species may differ in production and turnover of fine roots, and how active these remain during drought. Many trees produce fine roots in response to rain, and these fine roots may die during periods of drought (D. Bowman, personal communication).

(c) *Decrease in sapwood cross-sectional area.* It is theoretically possible that heartwood formation (possibly following embolism) occurs at the inner edge of sapwood during the dry season, and likely that sapwood formation primarily occurs during the early wet season. This would decrease the area of sapwood and thus hydraulic conductance and  $k_l$ .

Several trees in Bornean dipterocarp and heath forests had smaller hydroactive areas during the dry period than during the wet period (Becker, 1996), and the probable emboli in this inner part of the sapwood may lead to heartwood development. However, the proportion of sapwood in mature *E. tetradonta* trees (common in northern Australian savannas, and relatively insensitive to drought) was constant throughout the dry season (A.P. O'Grady, unpublished data). In this species, trunk expansion and leaf flushing occurred through to the end of the dry season (Myers *et al.*, 1998), probably indicating formation of new xylem during most of the dry season.

(d) *Decrease in efficiency of sapwood in conducting water ( $k_s$ ), which may be due to xylem embolism.* Blockage of xylem vessels by air or plugging with tyloses, gums, suberization or lignification (Zimmermann, 1983) reduces hydraulic conductance. For example, in several *Quercus* spp., earlywood vessels are completely blocked by tyloses within a year of their formation (Cochard and Tyree, 1990). Other changes may occur in xylem conduits. For example, conifers may experience irreversible loss of conductivity when dried to very low water potentials, probably as the result of sealing of the inter-tracheid torus (Sperry and Tyree, 1990). Older xylem vessels may also be selectively embolized as a result of increases in permeability of their inter-vessel pits to air; this increased permeability is associated with degradation of the pit membrane, and may be a step in initiating heartwood formation (Sperry *et al.*, 1991).

Seasonal changes do occur in the degree of embolism in woody plants. In several temperate Northern Hemisphere trees xylem embolism of 20–50% has been measured during summer, compared with freezing-induced embolism of 80–90% during winter (Cochard and Tyree, 1990; Tognetti and Borghetti, 1994; Magnani and Borghetti, 1995). In California, xylem embolism was 48% at the beginning of summer and 78% at the end in the facultatively deciduous shrub *Salvia mellifera*, compared with only 12%



and 17% at the beginning and end of summer, respectively, in the evergreen *Ceanothus megacarpus* (Kolb and Davis, 1994).

Sobrado (1997) studied embolism in four drought-deciduous and two evergreen species of a Venezuelan tropical dry forest. In deciduous species, loss of conductivity due to embolism in terminal branches ranged between 8% and 19% during the wet season, increasing to 38–79% during the dry season. By contrast, in the evergreen species it was between 30% and 35% during the wet season, and between 40% and 48% during the dry season. In an earlier study, Sobrado (1993) found that, during the dry season, wood water content in drought-deciduous species declined and the minimum value was recorded when leaf fall was complete. At this time, the volumetric fraction of gas increased, indicating air entry into xylem vessels. In contrast, wood water content and volume of gas did not change significantly through the year in evergreen species (Sobrado, 1993). Differences in extent of embolism between deciduous and evergreen species were attributed to differences in root depth and water availability (Sobrado, 1997).

It is not clear what role, if any, is played by embolism formation in inducing leaf fall in deciduous species. In Venezuelan dry forest, leaf fall in deciduous trees coincided with a decrease in water content of terminal branches, but usually occurred before any marked increase in gas volume (Sobrado, 1993). In these species,  $\Psi_{pd}$  values fell to about  $-2.8$  MPa (Sobrado, 1986), and dry-season embolism was between 38% and 79%. However, in two deciduous species of northern Australian savannas, water potentials of terminal twigs did not fall below  $-1.5$  MPa (Duff *et al.*, 1997) and, from vulnerability curves of other species, there is unlikely to be extensive embolism in these species. It has not been possible to measure directly embolism in these species because the sapwood contains an exudate that partially blocks xylem after a cut is made (Prior, 1997; D. Thomas, personal communication). There was a wide range of seasonal minimum stem water potentials ( $-1.5$  to  $< -4$  MPa) in deciduous trees in a Costa Rican dry forest, implying there may be varying degrees of embolism in stems of different species (Borchert, 1994b). The three deciduous hardwoods all had minimum stem water potentials around  $-4$  MPa, so embolism in this group is likely to be substantial unless they are very resistant.

(e) *Changes in hydraulic conductance at soil–root interface.* Hydraulic conductance may vary with transpiration rate, and the site of variability appears to be the root (Koide, 1985). Passioura and Munns (1984) found that hydraulic conductance of barley and lupin plants may vary diurnally, and independently of transpiration rate. When water flows into an intact root system, to reach the xylem it must cross the root epidermis, the cortex,

and then the endodermis. Direct control of hydraulic conductance is exerted at the living membranes within the root. Root hydraulic conductance is influenced by root age (Lopez and Nobel, 1991), temperature (Radin, 1990; Lopez and Nobel, 1991) and abscisic acid (ABA) (Eamus *et al.*, 1995). It is thus possible the plant can exert some short- to medium-term control of water uptake by changing the hydraulic conductance of the root system via effects of ABA on root membranes.

Since we rarely measure root water potential directly, but rather infer it from soil water potential or  $\Psi_{pd}$ , changes in hydraulic conductance at the soil-root interface will cause changes in apparent hydraulic conductance of the whole tree. Increases in soil-to-root conductances in drying soil have often been attributed to poor contact between root and soil. However, there is evidence that solutes accumulate either in the root or just outside it, creating large osmotic pressures, that give the appearance of an interfacial resistance (Stirzaker and Passioura, 1996).

Large seasonal changes in soil water content are characteristic of savannas. Savanna trees are therefore likely to experience seasonal changes in hydraulic conductance between the bulk soil and the root, as well as between the root surface and the xylem. O'Grady *et al.* (1999), studying savanna trees in north Australia, suggest that hysteresis in the transpiration versus vapour pressure deficit curve may be partially attributed to decreases in soil hydraulic conductance at the soil-root interface. Williams *et al.* (1998), in a study of seasonal variation of evapotranspiration from a Brazilian rainforest, concluded that soil and root hydraulic resistance increased during the dry season, causing a decline in evapotranspiration.

#### IV. ROOT DISTRIBUTION

Evergreen trees tolerate periods of six or more months without significant rainfall and maintain a full canopy. In addition, stomatal conductance and photosynthesis, although reduced during the dry season, remain higher than would be expected *a priori* from consideration of the seasonality of water availability alone (see below). Indeed, transpiration rates per tree can be the same in the dry season as the wet season in some systems (O'Grady *et al.*, 1999). Clearly, uptake of water by roots must occur throughout the dry season, despite the water table falling to depths of 5–20 m.

Direct observation of roots has been made at depths of  $\geq 60$  m in the Kalahari (Jennings, 1974). Stone and Kalisz (1991) report roots to depths of  $>20$  m in 11 tree species, while in the Sonoran Desert, USA, tree roots to depths of  $\geq 50$  m have been found (Phillips, 1963). Trees generally have

roots to greater depths than shrubs or grasses (Canadell *et al.*, 1996). In a review of 290 observations, covering 253 species in 11 biomes, Canadell *et al.* (1996) show that boreal forest, croplands, temperate deciduous forests and tundra have very shallow rooting depths (<5.0 m). Temperate coniferous forest, temperate grassland and tropical deciduous forest have intermediate root depths (<10 m), and deserts, sclerophyllous shrubland and forest, tropical evergreen forest and tropical grassland and savannas have deep roots (>15 m). As may be expected, plants from arid environments, or from environments with a seasonal rainfall, showed the deepest rooting. Sclerophyllous trees, especially Eucalypts, may have particularly deep roots. Furthermore, tap roots, which are specialized for deep growth, are present in 75% of tropical trees (Canadell *et al.*, 1996). The presence of hardpans, rocky strata and compact clay layers are not impenetrable barriers to root growth (Canadell *et al.*, 1996). Macro-pores and channels, through cracking and dissolution of material, and acid digestion by acids released by roots, allow deep penetration through very hard layers. This is further evidenced by the fact that percolation of water through such hard layers occurs faster than predicted from a knowledge of the hydraulic conductivity of non-fractured layers.

In a second major review of 200 data sets, Vogt *et al.* (1996) show that there were no significant or consistent patterns for above- and below-ground biomass accumulated across different climatic forest types. Soil organic matter varied significantly according to soil chemistry – for example, ultisols and oxisols had high total living and dead organic matter accumulations, especially in cold or tropical regions. Of particular note was the observation that deciduous forests tended to accumulate less above-ground (and total, and thus by difference, less root biomass) biomass than evergreen and semi-deciduous forests growing on the same soil series (Vogt *et al.*, 1996). This supports the view that deciduous species have a smaller rooting volume (and by inference smaller root biomass) than evergreen species (Sobrado, 1986).

Analyses in the 1980s showed that fine root biomass and production in the cold temperate zone could be accounted for by variation in mean annual temperature, the ratio of mean annual temperature to annual precipitation, and soil nitrogen (N) dynamics/pool size. More recent analyses show that different variables are able to account for different amounts of variation in fine root biomass in different climates and forest types (Vogt *et al.*, 1996). Climatic variables could not account for any variation in fine root biomass in deciduous species. However, soil nutrient dynamics did account for much of the variation in deciduous species fine root biomass. In the evergreen species, climatic (e.g. mean annual temperature, mean annual precipitation) and soil nutrient status (e.g. litterfall N/P ratio, soil Ca content) are significant variables accounting for

differences in fine root biomass. Precipitation explains a low proportion of variation in fine root biomass in boreal and cold temperate zones but where N, P or K availability limit growth (such as in savannas), root biomass is strongly correlated with N, P or K transfer from litterfall to soil. In tropical broadleaf deciduous forest, the ratio of N/P in litterfall can explain 99% of variation in fine root net primary productivity (Vogt *et al.*, 1996). Precipitation may often not correlate well with root dynamics because this does not take into account soil storage capacity. Factors that determine the amount of fine roots present are poor predictors of the amount of fine roots produced per year (Vogt *et al.*, 1996).

In a West African humid savanna, Mordelet *et al.* (1997) observed that both tree and grass roots were mostly confined to the top 20 cm of soil, with a peak of tree root biomass at 10 cm. Similarly, Castellanos *et al.* (1991) show that approximately 65% of all roots in a dry deciduous tropical forest in Mexico occur in the top 20 cm of soil. Seghieri (1995) showed that in a Cameroon savanna, tree root profiles were mostly confined to the upper 40 cm with only a small number of deeper tap roots penetrating to 1.5 m or more (the limit of the excavation). *Parkia biglobosa*, a tree indigenous to most of the savannas of west Africa, maintains 60% of its root biomass in the top 20 cm of soil (Tomlinson *et al.*, 1998). However, as with the majority of such studies, only shallow (<100 cm) excavations were made. Therefore it is difficult to assess how much root material was deeper. It is pertinent to note that in many studies (Seghieri, 1995; Smit and Rethman, 1998; Tomlinson *et al.*, 1998) there are significant numbers of coarse roots (>1 cm diameter) at 50–150 cm depth. It is likely that these roots proliferate at a depth similar to that observed for jarrah (Kimber, 1974). Furthermore it is clear that for semi-deciduous, brevi-deciduous and evergreen species, which transpire throughout the dry season, there must be substantial root biomass at much greater depths to account for the water transpired in the dry season. Thus Cook *et al.* (1998) have shown that significant amounts of roots in a north Australian savanna must reach depths of 6 m to supply the water requirements of the dominant evergreens in the dry season. Carbon *et al.* (1980) have shown that roots of *Eucalyptus marginata* (jarrah) extend to 20 m in dry sclerophyll forests in Australia. Of particular interest is the observation that roots of jarrah appear to be bimodal – with peaks of root biomass occurring at shallow (less than 1 m depth) and deeper depths (14–15 m; Kimber, 1974). Such a distribution is likely to occur where capillary rise and a permanent groundwater reservoir exist. Seghieri (1995) and D. Eamus, X. Chen, A.P. O'Grady, G. Kelley and L. Hutley (unpublished observations) note that many savanna tree species have a 'double' root system, that is, shallow lateral roots (less than 50 cm depth) and a number of deep tap roots going many metres

down. Using a novel lithium chloride tracer, Haase *et al.* (1996) show water uptake in a seasonally dry Mediterranean from depths of 28 m.

Savanna soils are patchy with respect to nutrient availability, both spatially and temporally. This patchiness is reflected in root distribution. Thus Mordelet *et al.* (1997) show root density is far higher in nitrogen-rich areas (close to termite mounds and close to root stumps) than in nitrogen-poor areas. Lateral roots can extend 10–20 m away from the trunk, or three to six times the radius of the crown (Mordelet *et al.*, 1996; Tomlinson *et al.*, 1998). Fine root biomass usually peaks in the wet season and declines in the dry season (Visalakshi, 1994; Sundarapandian and Swamy, 1996), presumably a reflection both of declines in soil water availability and hence nutrient availability. Root distribution is also a function of soil type. Seghieri (1995) has shown that soil depth and drainage characteristics determine the depth and pattern of root distribution in a Cameroon savanna. Fine and coarse root distribution can differ (Smit and Rethman, 1998). Thus 66% of fine roots were found in the first 40 cm of soil but coarse roots were essentially absent in the first 20 cm with a peak distribution between 20 and 60 cm (Smit and Rethman, 1998). In the 80–100 cm depth, coarse roots accounted for 75% of root biomass.

Hydraulic lift, whereby a few deep large roots move water up the soil profile during the night, followed by re-uptake during the day by shallow roots in the upper profile (Caldwell *et al.*, 1998), could theoretically support dry season transpiration. In a study of Kenyan and west Australian seasonally dry ecosystems, Burgess *et al.* (1998) show that hydraulic lift and reverse hydraulic lift occur. Before rains occur, flow of water in lateral roots of *Grevillea robusta* was negative (that is, away from the trunk towards root tips) at night and positive (towards the leaves) when transpiration demand was high (midday). This was taken as evidence of hydraulic lift. Significant water flow at night occurred through lateral roots even when flow through the trunk was negligible, indicating stem recharge and reverse hydraulic lift. These results were confirmed in *Eucalyptus camaldulensis* in Western Australia (Burgess *et al.*, 1998). After rain, lateral roots appeared to supply water from the upper wet profile into the deeper dry profile. Water flow in shallow lateral roots and deep tap roots was strongly and inversely correlated. Therefore roots were redistributing water along gradients of soil water potential and this flow was not simply to recharge root stores (Burgess *et al.*, 1998). Such data do not support the recent controversial interpretations of water transport in plants (Pockman *et al.*, 1995; Milburn, 1996). It remains to be seen whether such redistribution of water both up and down the soil profile is a common phenomenon in seasonally dry ecosystems.

## A. Isotopic Signatures and Root Water Uptake

Direct determination of below-ground processes is difficult to achieve. Seasonally dry tropical forests are particularly difficult to study because of high temperatures, the presence of lateritic hardpans in soils and high species diversity. Stable isotope analyses of soil and plant water can be used to investigate partitioning of water resources between different plant functional groups (Ehleringer *et al.*, 1993). However, the majority of such studies have been in temperate zones, partially because of poor differences in isotope signatures of different rainfall events in the wet season. Jackson *et al.* (1995a) have shown that while lake and stream hydrogen isotope composition (deuterium content,  $\delta D$  ‰) were similar to the weighted mean of annual precipitation, evaporation of soil water from the surface resulted in enrichment of heavy isotopes of hydrogen and oxygen. Most importantly, drought-deciduous species had higher xylem  $\delta D$  values than evergreen species. This was because deciduous species were accessing water from shallower soils than evergreen species. Further support of this conclusion was obtained from the relationship between pre-dawn xylem water potential and xylem water  $\delta D$ . Deciduous species exhibited higher  $\delta D$  values than evergreen species but also more negative pre-dawn potentials, as expected from their shallower roots. In addition, evergreen shrubs and small trees exhibited  $\delta D$  values resembling those of deciduous trees, a result ascribed to their short stature and hence presumably more shallow roots (Jackson *et al.*, 1995a).

Le Roux *et al.* (1995) also used isotopic analyses of soil and xylem water in a West African humid savanna. In this study there were very few woody roots below 1.2 m and the majority of both grass and shrub roots occurred in the top 60 cm. The isotopic signature of stem water showed that both grasses and shrubs utilized water in the upper 30 cm. Le Roux *et al.* (1995) conclude that there is very little partitioning of water resources between shrubs and grasses in this system, that is, competition for water occurs. It should be noted that the shrubs in this study were deciduous. In contrast, at the same site, Le Roux and Bariac (1998) showed partitioning of water resources between two deciduous shrubs.

Age and season influence the depth of water uptake in cool savanna in Arizona (Weltzin and McPherson, 1997). Trees and saplings extract water all year from deep soil, and young seedlings extract water from a shallower depth than grasses and older saplings. This pattern may enhance germination and very early establishment of seedlings (Weltzin and McPherson, 1997). As the dry season progresses, extraction of water occurs from deeper and deeper soil.

## V. GAS EXCHANGE

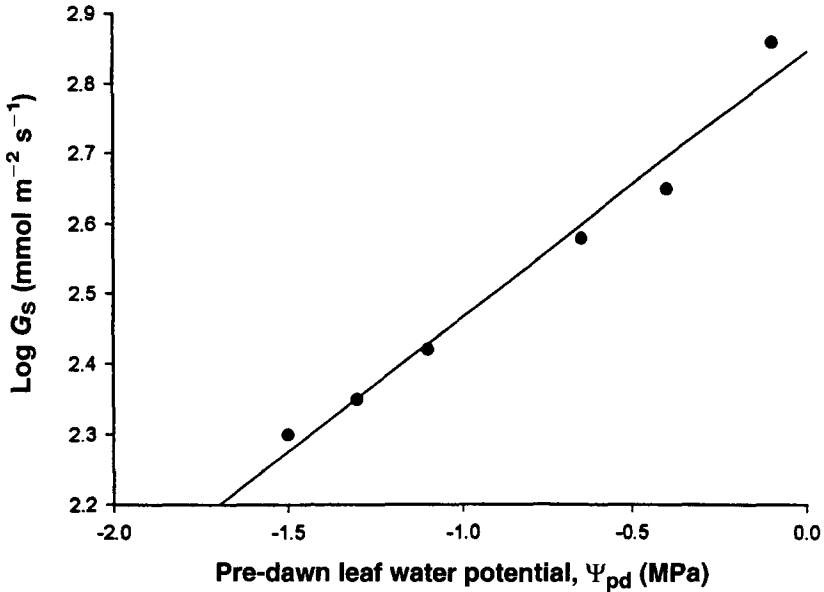
### A. Stomatal Conductance and Transpiration

#### 1. Stomatal Behaviour and Responses to the Environment

Stomata are the pores through which  $\text{CO}_2$  and  $\text{H}_2\text{O}$  diffuse into and out of leaves. Stomatal aperture is affected by both internal controls, which include root and leaf water status, abscisic acid (ABA) levels in xylem and leaf, and leaf internal  $\text{CO}_2$  concentration, and external factors, which include light flux density, temperature, and soil and atmospheric water content (Eamus, 1999). Within savannas the major determinants of stomatal aperture (apart from normal diurnal patterns of opening and closing imposed by day/night transitions) are soil and atmospheric water content and temperature (Martin *et al.*, 1994; Pitman, 1996; Eamus and Cole, 1997; Prior *et al.*, 1997a; Franco, 1998). Most studies have found that stomatal conductance ( $G_s$ ) is larger in the wet season than the dry season, and larger in the morning than the afternoon, especially in the dry season (Martin *et al.*, 1994; Hogan *et al.*, 1995; Pitman, 1996; Eamus and Cole, 1997; Prior *et al.*, 1997a,b; Franco, 1998). Midday depressions of  $G_s$  are also evident in a range of species in both wet and dry seasons (Schulze *et al.*, 1980; Meinzer *et al.*, 1993; Fordyce *et al.*, 1997).

It is possible to distinguish two causes for these patterns, one long-term and one short-term. First, there is the seasonal impact of changes in soil water content. As soil water availability declines as the dry season progresses,  $\Psi_{\text{pd}}$  also declines (Duff *et al.*, 1997; Myers *et al.*, 1997; Franco, 1998). Maximum  $G_s$  and  $\Psi_{\text{pd}}$  are negatively and linearly or curvilinearly correlated (Figure 7; Reich and Hinckley, 1989; Pitman, 1996; Fordyce *et al.*, 1997; Myers *et al.*, 1997; Prior *et al.*, 1997a,b). Second, there is a daily and seasonal response of stomata to the increasing leaf-to-air vapour pressure difference (LAVPD) that occurs diurnally and seasonally (see below).

There are two mechanisms coupling soil water availability and  $G_s$ . First, drying soils cause increased synthesis of ABA in roots and subsequent transport in the transpiration stream to leaves, where stomata close in response to increased supply of ABA (Gowing *et al.*, 1993; Loewenstein and Pallardy, 1998; Thomas and Eamus, 1999). Foliar and xylem ABA contents are correlated with  $G_s$  (Gowing *et al.*, 1993; Thomas and Eamus, 1999). Second, as soil water availability declines, the water column in the xylem is put under increasing tension and xylem cavitation can occur (see section V.C). Declines in stem hydraulic conductivity as pre-dawn leaf potential declined have been observed in *Eucalyptus tetradonta*, an evergreen tree of north Australian savannas (Thomas and Eamus, 1999), and in several other tree species (Franks *et al.*, 1995; Williams *et al.*, 1997a).



**Fig. 7.** As the dry season progresses,  $\Psi_{pd}$  declines and consequently stomatal conductance ( $G_s$ ) declines in a range of north Australian savanna species. Re-drawn from Eamus and Cole (1997).

Similarly a reduction in stem hydraulic conductivity can reduce  $G_s$  (Sperry and Pockman, 1993). It is possible that increased embolism and decreased stem hydraulic conductivity as pre-dawn water potential declines through the dry season is a simple mechanism by which  $G_s$  can be simultaneously coupled to a decline in both soil and atmospheric water content (Thomas and Eamus, 1999). However, this is not readily reversible and is unlikely to account for diurnal patterns of stomatal behaviour.

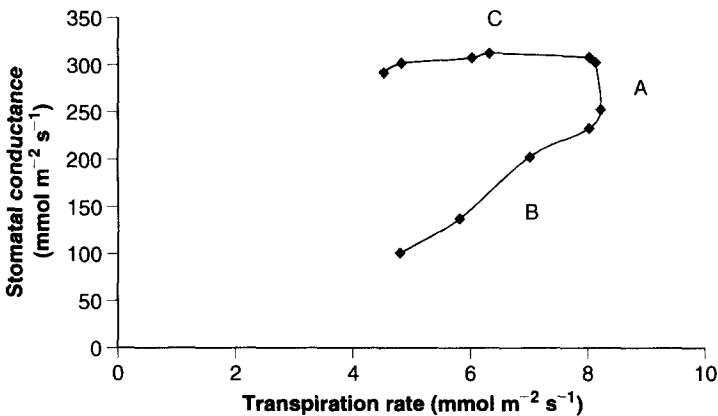
A cause of the decline in  $G_s$  observed between morning and afternoon and wet and dry seasons is increased LAVPD. Stomata close as LAVPD increases, and LAVPD increases between morning and afternoon and between wet and dry seasons. Stomatal conductance may decline linearly or log-linearly as LAVPD increases (Olivares and Medina, 1992; Verhoef *et al.*, 1996; Eamus and Cole, 1997; Prior *et al.*, 1997b; Thomas and Eamus, 1999). Meinzer *et al.* (1997) showed there were strong, species-specific correlations between  $G_s$  and vapour pressure difference from leaf to boundary layer, but not from leaf-to-bulk air vapour pressure difference. Most importantly, the relationship between canopy conductance and leaf-to-bulk air vapour pressure difference for the four species studied collapsed to one relationship describing all species when canopy conductance



was normalized by the ratio of leaf area to sapwood area (approximately equivalent to the inverse of the Huber value; see section III.C.8).

The response function of stomata to increasing LAVPD varies with plant water status (Prior *et al.*, 1997a; Thomas and Eamus, 1999). The slope of the relationship between  $\log G_s$  and LAVPD increased between mid-wet season and early dry season in *E. tetradonta* saplings in a north Australian savanna. During this period pre-dawn water potential declined from  $> -0.5$  MPa to between  $-0.5$  and  $-1.5$  MPa (Prior *et al.*, 1997a). Similarly, Thomas and Eamus (1999) showed that drought increased stomatal sensitivity to LAVPD, possibly through a change in the ratio of leaf area to root biomass.

Declines in  $G_s$  as soil or atmospheric water content decline may not always be sufficient to reduce transpiration (Monteith, 1995). In well-watered plants there are three response regions in the relationship between  $G_s$  and transpiration rate ( $E$ ; Figure 8). Note that in Figure 8, the data points in region C were obtained for low values of LAVPD, in region A, moderate values of LAVPD were imposed, and for region C, large values of LAVPD were imposed. As one moves along the line joining the points from region C to B, LAVPD is increasing in steps of approximately 0.5 kPa. In region C, which is obtained for low values of LAVPD,  $E$  is not regulated by stomata and, as LAVPD increases,  $E$  increases approximately proportionally. This is made possible by the fact that the hydraulic architecture of the plant is sufficient to supply water at rates that support



**Fig. 8.** Stomatal conductance ( $G_s$ ) shows three response regions to increasing transpiration rate. In region C  $G_s$  is unresponsive to increasing transpiration rate; in region A it decreases slightly while  $E$  remains constant, and in region B it declines significantly, causing  $E$  to decline substantially also. Reproduced from Thomas and Eamus (1999).

this value of  $E$ . In region A, at intermediate values of LAVPD, a transition occurs in stomatal responses such that aperture declines in proportion to increasing LAVPD and  $E$  is constant. At larger values of LAVPD, stomata respond in a 'feedforward' manner (see Farquhar and Cowan, 1977; Thomas and Eamus, 1999) such that  $E$  declines with increasing LAVPD. Thomas and Eamus (1999) have shown that, as drought develops in *E. tetradonta*, region C is lost first, then region A, so that eventually the entire response of  $G_s$  to increasing LAVPD is confined to region B. There is, therefore, an interaction between plant water status and LAVPD in determining stomatal responses to LAVPD.

Pitman (1996) studied stomatal behaviour of *Hopea ferrea*, an evergreen canopy emergent of tropical dry evergreen forests in Thailand. He adopted the empirical approach of Jarvis (1976) to model responses of  $G_s$  to changes in light flux density, temperature, soil water potential and LAVPD, and determined the sensitivity of  $G_s$  to changes in these variables. Good agreement between the modelled and observed values of  $G_s$  were obtained for periods of high and low soil water availability. He concluded that light flux density was the major determinant of  $G_s$ , followed by soil water potential. Unlike most other studies, he found little response of  $G_s$  to LAVPD. However, there are two reasons for this anomaly. First, the range of LAVPD experienced was very small (<2.0 kPa). It is likely that, had a larger range of LAVPD been used, a response for  $G_s$  would have been observed (Thomas and Eamus, 1999). Second, he pooled all the data that were collected between 06.00 and 18.30 h. During this time there are significant changes in light flux density, LAVPD and temperature. If only data from 10.00 to 15.00 h had been used, when temperature and light flux density are more consistent, a response to LAVPD may have been observed.

Some patterns of differential sensitivity of stomata of evergreen and deciduous species to changes in  $\Psi_{pd}$  and LAVPD have been noted. Stomata were more sensitive to declining  $\Psi_{pd}$  in deciduous trees than in evergreen trees (Myers *et al.*, 1997). This pattern possibly reflects the fact that leaves of evergreen species must tolerate lower  $\Psi_{pd}$  than leaves of deciduous trees during the dry season, and that to gain the benefit of maintaining leaves in the dry season requires the stomata to remain open as  $\Psi_{pd}$  declines. By contrast, stomatal sensitivity to increasing LAVPD may be greater in evergreen than in deciduous species (Myers *et al.*, 1997). This may reflect the fact that deciduous trees maintain leaves only during the wet season when LAVPDs are low. In addition, payback time (leaf lifespan) for deciduous leaves to fix carbon is relatively short, and they may compensate by having stomata that can remain open as much as possible in the wet season by being relatively insensitive to LAVPD.

## 2. Coupling of Transpiration to Atmospheric Conditions

Transpiration can be a major pathway for the discharge of groundwater. Global demand for clean water and hence utilization of groundwater increases annually. The sustainable management of groundwater resources requires knowledge of the role of vegetation in catchment hydrology.

*A priori* reasoning suggests that water use by trees should decline in the dry season because (a) water availability in the upper soil profile declines in the dry season; (b)  $G_s$  is lower in the dry season than in the wet season (see above); and (c) there is a decline in leaf area per tree. This decline can be 100% for deciduous trees and up to 30% for evergreen trees (Williams *et al.*, 1997b). Leaf-scale measurements support this *a priori* reasoning. Sobrado (1996) observed a decline in transpiration rate,  $E$ , of up to 50% in an evergreen tree in Venezuelan savanna while Prior *et al.* (1997a,b) observed a 40–70% decline in transpiration between wet and dry seasons. However, in these cases,  $E$  was calculated from leaf-scale measurements of  $G_s$  using portable porometers. Such measurements routinely overestimate  $E$  by up to 10-fold (Mulkey *et al.*, 1996) and do not take into account seasonal changes in leaf area per tree, the influence of the boundary layer on  $E$  and within-canopy variation in microclimate and hence  $E$  from leaves. Partitioning of the control of transpiration into stomatal and boundary layer conductances show the importance of the boundary layer (Meinzer *et al.*, 1997). Leaf-scale estimates of  $E$  can be significantly improved if the LAVPD of the boundary layer, rather than the bulk air, is used to calculate  $E$  (Meinzer *et al.*, 1997).

There are few estimates of whole-tree water use in savannas or dry tropical forests (but see section D below). For example, a recent review of 52 studies presented data for a range of tropical rainforest species but no savanna species (Wullschleger *et al.*, 1998). Transpiration of several species of tropical tree, measured using sapflow techniques during an unusually wet dry season in Panama, ranged from 0.6 to 2.8 mmol m<sup>-2</sup> s<sup>-1</sup> (Meinzer *et al.*, 1997). Unfortunately seasonal patterns were not shown.

In contrast to estimates of  $E$  derived from leaf-scale measurements, measurements based on sapflow techniques of whole-tree water use by evergreens showed little variation between seasons (O'Grady *et al.*, 1999). There are several reasons for this unexpected result. First, the proportional decline in leaf area per tree is equal to the proportional increase in LAVPD between the wet and dry season. Second, storage of water in the top 6 m of soil is sufficient to account for the rate of water use in the dry season (Cook *et al.*, 1998) and therefore water availability is not limiting  $E$  despite a very dry upper 1 m soil profile. Finally, stomata of many species of tree do not close sufficiently to prevent increased  $E$  as LAVPD increased (see above), except when drought stress is experienced or

LAVPD is very large. In aerodynamically rough canopies (such as open forests and woodlands),  $E$  should be closely coupled to LAVPD if soil water is not limiting (Jarvis and McNaughton, 1986).

O'Grady *et al.* (1999) showed there was no difference in rate of transpiration per leaf area between two species of evergreens. This conclusion can be extended to five species in the savannas of north Australia (A.P. O'Grady, personal communication). Similarly, Meinzer *et al.* (1997) concluded that transpiration rates, when normalized by branch-specific ratio of leaf area to sapwood area (inverse of Huber value), did not differ between four contrasting species in a tropical Panamanian forest. Similarly, Andrade *et al.* (1998) showed that stomatal conductance in five disparate tree species growing in a seasonally dry forest responded similarly to variation in total soil-tree hydraulic conductance. These results suggest that large-scale modelling of water use by savanna vegetation may not require excessively large numbers of measurements of large numbers of species. It is likely that water use per sapwood area of savanna vegetation, on a large scale, does not differ between species, and only varies with time of day, season, stand density and soil characteristics, all of which can be measured remotely. It is also likely, at the canopy scale, that canopy conductance responses to LAVPD are essentially species independent (Granier *et al.*, 1996; Meinzer *et al.*, 1997).

The relative effects of stomatal conductance and boundary layer conductance can be evaluated from the dimensionless decoupling coefficient,  $\Omega$ . A high value (close to 1) of  $\Omega$  indicates that boundary layer conductance is low, and that changes in  $G_s$  have little effect on transpiration, so that transpiration is mostly determined by radiation. A low value (close to zero) indicates that transpiration varies almost in direct proportion to  $G_s$ . In Panamanian lowland tropical forest,  $G_s$  was often equal to or larger than boundary conductance so that  $E$  was strongly uncoupled from the bulk atmospheric VPD (Meinzer *et al.*, 1995, 1997). Here  $\Omega$  ranged from 0.82 to 0.9. In a number of broadleaf tropical forests, estimates of  $\Omega$  varied between 0.6 and 0.9, while in small individuals of forest gap pioneers in Panama,  $\Omega$  was about 0.6–0.8 (Meinzer *et al.*, 1995, 1997). These systems have a relatively high LAI ( $\geq 2$ ). This compares with values of around 0.1 for needle-leaved, aerodynamically rough coniferous trees (Jarvis and McNaughton, 1986). In savannas, with well-spaced trees, relatively low canopy density, and small rather than large leaves,  $\Omega$  is likely to be low ( $<0.5$ ) because the ratio of canopy conductance to boundary layer conductance is low. It is also likely that dry-season values of  $\Omega$  will be lower than wet-season values because of the decline in average stomatal conductance in the dry season.

San Jose *et al.* (1998) showed that  $\Omega$  varied between 0.03 and 0.58 over a typical non-rainy wet season day in the Orinoco Llanos of Venezuela, and

this variability was because of changes in the ratio of aerodynamic conductance to surface conductance over the day. The low values of  $\Omega$  show that transpiration is well coupled to atmospheric VPD and that changes in both stomatal conductance and VPD do have a large impact on transpiration rate. Similarly, Miranda *et al.* (1997) estimate values of  $\Omega$  of 0.32 and 0.17 in the wet and dry seasons, respectively. They also conclude that there is significant control of transpiration through stomatal aperture.

For a closed canopy of a cultivated grass (*Brachiara decumbens*) in the Orinoco Llanos of Venezuela, evapotranspiration flux density was mainly driven by net radiation, particularly when net radiation exceeded  $400 \text{ W m}^{-2}$  (San Jose *et al.*, 1998a). Such poor coupling of canopy transpiration to atmospheric VPD is to be expected for short, closed canopies (Jarvis and McNaughton, 1986).

In a number of ecosystems, stomata behave in a manner to ensure that vapour phase conductance and hydraulic (liquid phase) conductance are balanced. Consequently leaf water potential is maintained within narrow limits, despite significant changes in soil and atmospheric water content (Kuppers, 1984; Sperry and Pockman, 1993; Meinzer *et al.*, 1995). It appears likely that these principles also apply to savannas.

## B. Hysteresis in $G_s$ and Transpiration

Hysteresis in stomatal behaviour in leaf-scale studies in the lab has been observed for the past 30 years. In temperate zones, hysteresis has been observed in the relationship between sapflux and leaf water potential in *Eucalyptus marginata* trees of Western Australia and in cool-temperate wetland species (Takagi *et al.*, 1998). However, only recently has hysteresis been observed in tropical, seasonally dry vegetation. Pitman (1996) observed hysteresis in the relationship between  $G_s$  and three environmental variables, namely, solar irradiance, temperature and VPD. The degree of hysteresis was largest for all three variables when soil moisture content was largest. This is in contrast to the data of O'Grady *et al.* (1999), who showed that the degree of hysteresis between transpiration rate and LAVPD was largest in the dry season. Hysteresis in transpiration and LAVPD (and hence the behaviour of stomata) is likely to be caused by (a) the decline in the contribution of water stored in the stem with time during the day; (b) the decline in soil-root-leaf hydraulic conductivity with time during the day; or (c) a combination of (a) and (b). The cause of the disparity between Pitman's and O'Grady's data remains unknown, but differences in the contribution of water stored in the stem may contribute. Water stored in stems of trees in a tropical seasonal Panamanian forest accounted for 9–15% of daily water transpired (Goldstein *et al.*, 1998). This

stored water regulated the water status of leaves that were exposed to large diurnal variation in evaporative demand (Goldstein *et al.*, 1998). In addition, the rate of change of LAVPD may differ between Pitman's and O'Grady's sites. Such differences were able to account for day-to-day differences in the degree of hysteresis in cool-temperate wetland trees (Takagi *et al.*, 1998).

### C. Photosynthesis

An understanding of the carbon cycle of ecosystems is fundamental to the complete understanding of the functioning of any ecosystem. In addition the Kyoto protocol requires governments, as signatories, to quantify the amount of carbon in and moving through major ecosystems. An important step in this quantification is an understanding of the photosynthetic characteristics of an ecosystem, including information on patterns of daily and seasonal change in C assimilation.

#### 1. Daily and Seasonal Patterns of C Assimilation

Assimilation rates of savanna species are larger in the wet season than in the dry season, and in the dry season assimilation rates are usually larger in the morning than in the afternoon (Hogan *et al.*, 1995; Le Roux and Mordelet, 1995; Sobrado, 1996; Eamus and Cole, 1997; Prior *et al.*, 1997a; Franco, 1998). Such behaviour is a function of declining soil water content, supra-optimal leaf temperature and increasing LAVPD. (Stomatal responses to humidity should be considered in relation to LAVPD since this, rather than VPD, provides the driving force for water loss from leaves. Leaf temperature is frequently higher than air temperature, especially when stomatal conductance is low and transpirational cooling reduced. At such times, LAVPD can be considerably higher than VPD.)

As soil or atmospheric water content declines, stomatal conductance is reduced (see section V.A, above). This will limit assimilation by reducing the supply of CO<sub>2</sub> to chloroplasts. This was demonstrated in four Australian savanna species by the decline in the ratio of CO<sub>2</sub> concentration inside the leaf ( $C_i$ ) to the CO<sub>2</sub> concentration of ambient air outside the leaf ( $C_a$ ) between morning and afternoon in the wet season (Eamus and Cole, 1997). Such changes in  $C_i/C_a$  ratio are indicative of non-stomatal limitations to photosynthesis (Lauer and Boyer, 1992). However, additional factors, especially in the dry season, can reduce photosynthetic rate independently of reduced stomatal conductance. Leaf temperature can become supra-optimal for photosynthesis, particularly when soil water availability is low and transpirational cooling is reduced (Prior *et al.*, 1997a). In saplings of the savanna tree *Eucalyptus tetrodonta*, high leaf

temperatures at the end of the dry season could account for a 16% decline in assimilation rates in the afternoon compared with the morning, independent of changes in  $C_i$  (Prior *et al.*, 1997a). Similarly, Sharkey (1984) has shown that high transpiration rates *per se* are able to reduce photosynthesis independently of stomatal conductance.

Midday depression of assimilation occurs in many species, especially those subject to any combination of high temperature, high radiation loads and low atmospheric and soil water content, as commonly occurs in seasonally dry ecosystems (Fordyce *et al.*, 1997; Pathre *et al.*, 1998). Causes of such a decline include feedback inhibition of assimilation through carbohydrate accumulation (Foyer, 1988), photoinhibition (Correia *et al.*, 1990; Prior, 1997), decreased carboxylation efficiency (Demming-Adams *et al.*, 1989) and increased LAVPD (Cowan and Farquhar, 1977; Fordyce *et al.*, 1997). However, it is apparent that there is an interaction between temperature, LAVPD and photosynthetic photo flux density (PPFD) such that a high value of any two can significantly reduce assimilation rate. At low LAVPD, temperature appears to be the least significant factor in causing a decline in assimilation, and low LAVPD can significantly reduce the impact of high PPFD (Pathre *et al.*, 1998). Thus LAVPD appears to be the dominant factor in causing midday declines in assimilation. Most, but not all, of this decline can be explained by the influence of reduced  $G_s$  on  $CO_2$  supply.

Leaf age influences assimilation rate. Old leaves tend to have a reduced capacity for photosynthetic carbon gain and also have a reduced ability to regulate water loss (Reich, 1984; Reich and Borchert, 1988). In a study of *Curatella americana*, an evergreen tree of Venezuela, assimilation rates were lowest in young expanding leaves and in old mature or senescing leaves (Sobrado, 1996). Interestingly, foliar nitrogen concentrations declined approximately linearly as leaves aged and specific leaf area (SLA; leaf area/dry weight,  $m^2 g^{-1}$ ) also decreased with leaf age. Consequently there was not a simple clear relationship between assimilation rate and foliar nitrogen content (mass basis). Loss of nitrogen with leaf age is a common response before senescence and is a principal cause of the decrease in photosynthetic capacity observed in older leaves. Increased  $C_i/C_a$  ratio with declining assimilation rate provides strong evidence that a decreased biochemical capacity for photosynthesis occurs as leaves age (Martin *et al.*, 1994).

Assimilation rate and stomatal conductance declined more rapidly with leaf age in deciduous species compared to evergreen species in 18 species of Costa Rican tropical deciduous forest (Martin *et al.*, 1994). For deciduous species, the decline in photosynthetic rate of deciduous leaves was attributed both to leaf age (senescence) and the onset of drought. There was little evidence of an age-related decline in photosynthetic rate

for evergreen species, especially those growing on moist sites, in the early dry season (Martin *et al.*, 1994). Specific leaf area decreases with leaf age (Sobrado, 1996; Prior, 1997) and Martin *et al.* (1994) expressed all assimilation data on a leaf area basis. Therefore the differences in photosynthetic rate between old and young leaves observed by Martin *et al.* (1994) may underestimate differences in photosynthetic rate expressed on a dry weight basis. These results support the conclusions of Reich *et al.* (1991), who showed that age-related decline in assimilation rate was more pronounced in short-lived (i.e. deciduous) leaves than in long-lived leaves.

The season during which leaves expand may influence their photosynthetic and stomatal performance. Leaves that flush and expand at the end of the wet season experience conditions of high light flux density and large LAVPD, in contrast to leaves that flush and expand in the late dry/early wet. Long-lived leaves will experience the full range of environmental conditions and therefore leaf-scale adaptations (e.g. differences in SLA; N content) will be small, in contrast to short-lived leaves, where one population may experience predominantly dry season conditions and another population experience wet season conditions. Consequently leaf-scale adaptations are larger in short-lived species (Kitajima *et al.*, 1997). Thus Kitajima *et al.* (1997) observed that photosynthetic rate (expressed on an area basis) of leaves emerging in the late wet season (measured in the dry season) was larger than that of leaves emerging in the early wet and measured in the wet season. Furthermore, the difference between these two populations of leaves increased as leaf lifespan decreased. Differences in SLA were able to account for these differences. Allocation of N per unit dry mass did not differ between populations of leaves. It is pertinent to note that this is the only study in which the rate of light-saturated assimilation is larger in the dry season than in the wet season and it remains to be seen whether such seasonal differences in leaf characteristics are a common phenomenon.

Stomatal sensitivity to LAVPD, of leaves that developed in the dry season, was significantly larger than for those that developed in the wet season (Thomas and Eamus, 1999). Leaves of two tropical grasses, exposed to different levels of atmospheric water content during development, similarly differed in stomatal sensitivity to LAVPD (Kawamitsu *et al.*, 1993).

## 2. Phenological Comparisons

In both tropical and temperate environments, deciduous species have a larger photosynthetic rate per unit dry weight than evergreen species (Chabot and Hicks, 1982; Reich *et al.*, 1992; Prado and De Moraes, 1997; Eamus and Prichard, 1998; Table 4). However, because deciduous species



Table 4

A summary of some of the recently published data for light-saturated assimilation rate ( $A_{\max}$ , expressed on a dry weight or area basis), specific leaf area (SLA) and foliar nitrogen content for a number of deciduous (Decid), semi-deciduous (SD), evergreen (E'green) and unknown phenology (?) species of seasonally dry woodlands and forests. Data are for wet season periods

Species	Type	$A_{\max}$ ( $\mu\text{mol g}^{-1} \text{s}^{-1}$ )	SLA ( $\text{m}^2 \text{g}^{-1}$ ) $\times 10^{-1}$	$A_{\max}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	N content ( $\text{mg g}^{-1}$ )	Reference
<i>Calycophyllum candidissimum</i>	Decid			4		Martin <i>et al.</i> (1994)
<i>Cordia alliodora</i>	Decid			6		Martin <i>et al.</i> (1994)
<i>Guazuma ulmifolia</i>	Decid			5		Martin <i>et al.</i> (1994)
<i>Luehea candida</i>	Decid			5		Martin <i>et al.</i> (1994)
<i>Myrospermum</i>	Decid			8		Martin <i>et al.</i> (1994)
<i>Apeiba tibourbou</i>	Decid			1		Martin <i>et al.</i> (1994)
<i>Astronium graveolens</i>	Decid			2		Martin <i>et al.</i> (1994)
<i>Tabebuia ochracea</i>	Decid			0.3		Martin <i>et al.</i> (1994)
<i>Cassia emarginata</i>	Decid			3		Martin <i>et al.</i> (1994)
<i>Tabebuia rosea</i>	Decid			2.7		Martin <i>et al.</i> (1994)
<i>Jacquinia pungens</i>	Decid			11		Martin <i>et al.</i> (1994)
<i>Pseudobombax septenatum</i>	Decid	0.0103	0.13493	8		Hogan <i>et al.</i> (1995)
<i>Godmania macrocarpa</i>	Decid	0.0083	0.18		23.6	Medina and Francisco (1994)
<i>Cochlospermum fraseri</i>	Decid	0.0199	0.24676		17.7	Eamus <i>et al.</i> (1999b)
<i>Planchonia careya</i>	Decid	0.0101	0.10908		13.5	Eamus <i>et al.</i> (1999b)
<i>Terminalia ferdinandiana</i>	Decid	0.0102	0.10914		13.6	Eamus <i>et al.</i> (1999b)
<i>Erythrophloeum chlorostachys</i>	SD	0.0109	0.14824		22	Eamus <i>et al.</i> (1999b)
<i>Eucalyptus clavifera</i>	SD	0.0072	0.0864		10.4	Eamus <i>et al.</i> (1999b)
<i>Xanthospermum paradoxus</i>	SD	0.0125	0.14875		11	Eamus <i>et al.</i> (1999b)
<i>Humboldtdiella arborea</i>	Decid	0.0268	0.185		3.15	Sobrado (1991)
<i>Mansoa verrucifera</i>	Decid	0.0175	0.103		2.71	Sobrado (1991)
<i>Lonchocarpus dipiperoneurus</i>	Decid	0.0242	0.227		4.08	Sobrado (1991)
<i>Beureria cumanensis</i>	Decid	0.0116	0.115		2.87	Sobrado (1991)
<i>Pithecellobium dulce</i>	Decid	0.0151	0.134		2.59	Sobrado (1991)
<i>P. ligustrinum</i>	Decid	0.0154	0.142		3.5	Sobrado (1991)
<i>Planchonia careya</i>	Decid	0.00904	0.1264		12	Eamus and Prichard (1998)
<i>Terminalia ferdinandiana</i>	Decid	0.0107	0.1613		15.8	Eamus and Prichard (1998)
<i>Terminalia ferdinandiana</i>	Decid	0.0175	0.1925		12.2	Prior <i>et al.</i> (1997b)
<b>Mean for deciduous</b>		<b>0.014</b> $\pm 0.001136$	<b>0.15</b> $\pm 0.0107$	<b>4.7</b> $\pm 0.92$	<b>10.67</b> $\pm 1.75$	



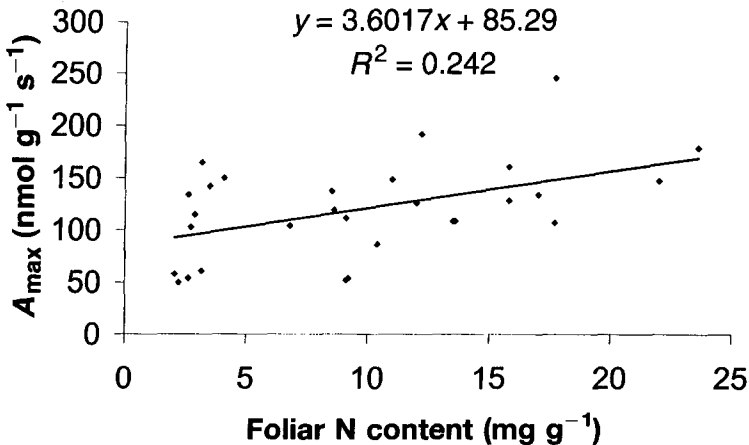
Table 4 (Continued)

Species	Type	$A_{\max}$ ( $\mu\text{ mol g}^{-1} \text{ s}^{-1}$ )	SLA ( $\text{m}^2 \text{ g}^{-1}$ ) $\times 10^{-1}$	$A_{\max}$ ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ )	N content ( $\text{mg g}^{-1}$ )	Reference
<i>Aegiphyla lhotkiana</i>	?	0.008333	0.078	9.4		Prado <i>et al.</i> (1997)
<i>Amnora coriacea</i>	?	0.006711	0.0624	9.3		Prado <i>et al.</i> (1997)
<i>Aspidosperma tomentosum</i>	?	0.007092	0.0723	10.2		Prado <i>et al.</i> (1997)
<i>Bauhinia holophylla</i>	?	0.006993	0.0727	10.4		Prado <i>et al.</i> (1997)
<i>Bowdichia virgiloides</i>	?	0.005952	0.0548	9.2		Prado <i>et al.</i> (1997)
<i>Campomanesia aromatica</i>	?	0.006711	0.0705	10.65		Prado <i>et al.</i> (1997)
<i>Caryocar brasiliense</i>	?	0.008475	0.0797	9.4		Prado <i>et al.</i> (1997)
<i>Connarus suberosus</i>	?	0.006711	0.0819	12.2		Prado <i>et al.</i> (1997)
<i>Davilla rugosa</i>	?	0.006024	0.0615	10.2		Prado <i>et al.</i> (1997)
<i>Didymopanax vinosum</i>	?	0.006757	0.1189	17.6		Prado <i>et al.</i> (1997)
<i>Duguetia furfuracea</i>	?	0.005988	0.0581	9.7		Prado <i>et al.</i> (1997)
<i>Gochnatia floribunda</i>	?	0.005952	0.0964	16.2		Prado <i>et al.</i> (1997)
<i>Kielmeyera coriacea</i>	?	0.004878	0.0512	10.5		Prado <i>et al.</i> (1997)
<i>Miconia albicans</i>	?	0.006536	0.0843	12.9		Prado <i>et al.</i> (1997)
<i>Miconia ligustroides</i>	?	0.007634	0.1069	14		Prado <i>et al.</i> (1997)
<i>Piptocarpha rotundifolia</i>	?	0.00625	0.1331	12.3		Prado <i>et al.</i> (1997)
<i>Qualea dichotoma</i>	?	0.006993	0.0762	10.9		Prado <i>et al.</i> (1997)
<i>Syrax camporum</i>	?	0.004762	0.0386	8.1		Prado <i>et al.</i> (1997)
<i>Tibouchina stenocarpa</i>	?	0.007353	0.1456	19.8		Prado <i>et al.</i> (1997)
<i>Tocoyena formosa</i>	?	0.006329	0.0411	6.5		Prado <i>et al.</i> (1997)

have thinner leaves than evergreen species, and there is less leaf tissue per unit leaf area (i.e. SLA is larger; Sobrado, 1991; Medina and Francisco, 1994; Reich *et al.*, 1995; Prado and De Moraes, 1997; Eamus and Prichard, 1998), photosynthetic rates per unit leaf area may be similar or lower in deciduous than evergreen species (Medina, 1984; Sarmiento *et al.*, 1985; Goldstein *et al.*, 1989; Prado and De Moraes, 1997; Eamus and Prichard, 1998).

The larger photosynthetic rate per unit dry weight of deciduous species results from a larger total investment in leaf N content in deciduous species (Medina and Francisco, 1994; Kitajima *et al.*, 1997; Prado and De Moraes, 1997; Eamus and Prichard, 1998; Table 4). A linear relationship between leaf N content (area or mass basis) and the rate of light-saturated photosynthesis,  $A_{\max}$  (area or mass basis), is generally observed (Evans, 1989; Reich *et al.*, 1992, 1994, 1995). Figure 9 shows that, for a range of tree species from a range of seasonally dry ecosystems, N content (mass basis) increases linearly with  $A_{\max}$ , with no clear distinction between evergreen and deciduous species. The slope of the relationship for seasonally dry ecosystems (3.6) is within the range observed in a diverse range of natural ecosystems (slope 0.8–20; Reich *et al.*, 1991, 1992, 1994).

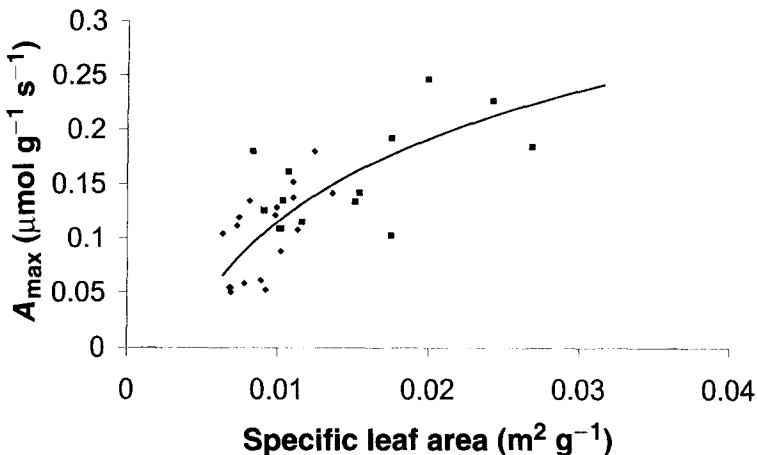
Nitrogen content (mass basis) increases with increasing SLA (Poorter and Evans, 1998). Consequently the assimilation rate ( $A$ ) increases with



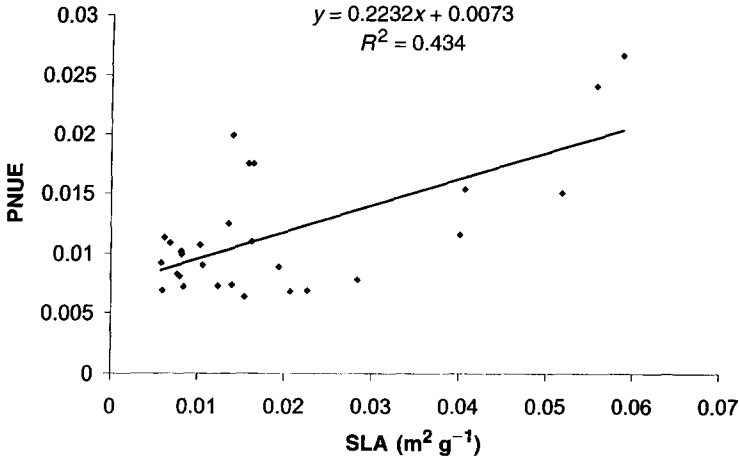
**Fig. 9.** There is a significant increase in light-saturated assimilation rate ( $A_{\max}$ ) as foliar N content increases. Data from Coomes and Grubb (1998), Hogan *et al.* (1995), Medina and Francisco (1994), Prior *et al.* (1997a,b), Prado and De Moraes (1997), Eamus *et al.* (1999b), Sobrado (1991, 1996), Eamus and Prichard (1998) and Fordyce *et al.* (1997).

increasing SLA. In an analysis of a range of tree species from several seasonally dry ecosystems, deciduous and evergreen trees occur at opposite ends of a single relationship (Figure 10; Table 4) between maximum assimilation rate and SLA. The slope of the relationship describing the log-log plot of assimilation and SLA (0.86) is similar to that observed in a diverse range of ecosystems (Reich *et al.*, 1992, 1994; Reich and Walters, 1994).

The ratio of  $A_{\max}$  to N content (both on a mass basis, known as photosynthetic nitrogen use efficiency, PNUE; Poorter and Evans, 1998) varies according to soil nutrient availability (Reich *et al.*, 1995), life-form (Field and Mooney, 1986) and phenologies (Sobrado, 1991; Medina and Francisco, 1994). Assimilation rate increases with increasing investment of N in photosynthetic apparatus (Evans, 1989; Medina and Francisco, 1994; Figure 9). Photosynthetic nitrogen use efficiency also increases with SLA (Poorter and Evans, 1998; Figure 11). However, there appears to be no consistent pattern of PNUE for deciduous and evergreen species. In a detailed study of PNUE for deciduous and evergreen species in southern Wisconsin, USA, Reich *et al.* (1995) observed that the slope of the relationship between photosynthesis and foliar N content (mass or area basis) was larger in broad-leaved deciduous species



**Fig. 10.** There is a significant increase in light-saturated assimilation rate ( $A_{\max}$ ) as specific leaf area (SLA) increases. Data from Coomes and Grubb (1998), Hogan *et al.* (1995), Medina and Francisco (1994), Prior *et al.* (1997a,b), Prado and De Moraes (1997), Eamus *et al.* (1999b), Sobrado (1991, 1996), Eamus and Prichard (1998) and Fordyce *et al.* (1997). Evergreen (diamonds) and deciduous (squares) species tend to occur at opposite ends of the regression.



**Fig. 11.** There is a significant increase in photosynthetic nitrogen use efficiency (PNUE) as specific leaf area (SLA) increases. Data from Coomes and Grubb (1998), Hogan *et al.* (1995), Medina and Francisco (1994), Prior *et al.* (1997a,b), Prado and De Moraes (1997), Eamus *et al.* (1999b), Sobrado (1991, 1996), Eamus and Prichard (1998) and Fordyce *et al.* (1997).

than in needle-leaved evergreens. They concluded that species with long leaf lifespans and low SLA tend to have lower  $A_{\max}$  per unit leaf N (lower PNUE). In contrast, a single regression described the relationship for both deciduous and evergreen species in a study of north Australian savanna species (Eamus *et al.*, 1999b). Different slopes between deciduous, broadleaf and evergreen coniferous species arose because the conifers were found on, and were adapted to, nutrient-depleted soils, whereas the deciduous species were growing on nutrient-rich soils (Reich *et al.*, 1995). In the north Australian study, evergreen and deciduous species co-occur and do not occupy locations differing in nutrient availability, consequently the same relationship between  $A_{\max}$  and N was observed (Eamus and Prichard, 1998). Similar variability exists within two Venezuelan studies. Photosynthetic nitrogen use efficiency was higher in the dominant deciduous species on a Venezuelan savanna (Sobrado, 1991) but in central Venezuela, PNUE was lower in deciduous species than in evergreen (Medina and Francisco, 1994). It is likely that local conditions (soil nutrient and water availability, micro-climate) are more important determinants of PNUE than phenology. In a plot of PNUE against SLA, deciduous and evergreen species occur on the same line (Figure 11).

## D. Relationships between Carbon Gain and Water Loss

### 1. Instantaneous Transpiration Efficiency

The ratio of instantaneous assimilation rate to transpiration rate yields the instantaneous transpiration efficiency (ITE; often mistakenly referred to as water-use-efficiency (WUE); Eamus, 1991). A large ITE represents an optimization response in water-limited environments.

Eamus *et al.* (1999a) found that instantaneous transpiration efficiency in eight evergreen, semi-deciduous and deciduous species in a northern Australian savanna was largest in the dry season, and lower in the wet season or after initial rains at the end of the dry season (Eamus *et al.*, 1999a). Similarly, ITE in the Venezuelan evergreen *Curatella americana* was higher in the dry than in the wet season, particularly in old leaves (Sobrado, 1996).

In northern Australia, in saplings of both *Eucalyptus tetrodonta* (evergreen) and *Terminalia ferdinandiana* (deciduous), ITE was higher in the transitional periods (when  $\Psi_{pd}$  values were between  $-0.5$  and  $-1.5$  MPa) than during the wet season (Prior *et al.*, 1997a,b). During the driest period ( $\Psi_{pd} < -1.5$  MPa), when only the evergreen species had leaves, ITE was the same as in the transitional period in the morning, but declined markedly in the afternoon. This was due to both very high leaf temperatures (supra-optimal for photosynthesis) and high LAVPDs. Interestingly, stomata were most responsive to LAVPD during the transitional period. During the wet season, LAVPDs were uniformly low, and  $G_s$  high, while during the late dry season,  $G_s$  was consistently low due to severe soil drought. During the wet season, ITE was similar for both species, but was lower in the deciduous species during the transition periods, when leaves had started to senesce.

Drought stress may also lead to decreases in ITE. For *Acacia auriculiformis* in northern Australia, ITE decreased markedly between the mid-wet and the dry seasons, mostly due to large increases in LAVPD causing large increases in transpiration (Cole, 1994). Similarly, Franco (1998) showed that the decrease in  $G_s$  of an evergreen tree in a Brazilian savanna in the dry season was smaller than the decrease in  $A$ , consequently ITE declined. Part of the reason for this was the differential impact of leaf age on  $G_s$  and  $A$ . As leaves age ITE generally declines because the ability of stomata to regulate water loss is lost to a larger extent than the ability to fix carbon (Reich and Borchert, 1988; Martin *et al.*, 1994; Franco, 1998). In addition, leaf ageing usually coincides with increasing LAVPD, and hence greater transpirational loss for a given  $G_s$ .

Some studies have found higher ITE in deciduous than in evergreen species (Sobrado, 1991; Medina and Francisco, 1994; Eamus and Prichard, 1998), but others have found ITE to be similar for both

phenological guilds (Goldstein *et al.*, 1989; Martin *et al.*, 1994; Prior *et al.*, 1997a,b; Eamus *et al.*, 1999a). High ITE represents an optimization response of resource use in water-limiting environments. Evergreen woody species may be less limited by water availability (Myers *et al.*, 1997) because of extensive and deep root systems that provide water for plant use during the dry season, whereas deciduous woody species have shallower roots (Canadell *et al.*, 1996). It could also be argued that for most of the time that deciduous trees photosynthesize, conditions are wet and there is little need to optimize water use.

Higher ITE in deciduous trees is not consistent with the predictions of Lloyd and Farquhar (1994), who propose that species with short-lived leaves should have a larger  $\delta E/\delta A$  (and hence a lower ITE) than species with longer-lived leaves ( $\delta E/\delta A$  is the marginal unit water cost of plant carbon gain (see Thomas *et al.*, 1999a,b), calculated as the ratio of the slopes of  $E$  against  $G_s$  to  $A$  against  $G_s$ ; see section VIII.D). A central feature of the Lloyd and Farquhar (1994) analyses, apart from the assumption that stomata optimize their behaviour, was the use of  $C_i : C_a$  ratio to calculate  $\delta E/\delta A$ . It has been extensively shown that the  $C_i : C_a$  ratio can decrease with increasing LAVPD if the proportional closure of stomata is larger than that of the decline in assimilation, but it can also increase if the opposite occurs (Eamus and Cole, 1997; Prior *et al.*, 1997a). Therefore the use of the  $C_i : C_a$  ratio as an indicator of optimal behaviour of stomata may lead to errors in savanna systems.

## 2. Isotope Discrimination

Instantaneous leaf-scale values may not truly reflect whole-plant leaf lifespan water use efficiency (WUE). In contrast,  $^{13}\text{C}$  leaf discrimination values – which show the extent to which leaves discriminate against the heavy ( $^{13}\text{C}$ ) isotope of carbon – may more accurately represent leaf WUE over the lifetime of the leaf (Farquhar *et al.*, 1989). In an early study of  $^{13}\text{C}$  leaf discrimination values, Goldstein *et al.* (1989) found no significant differences in  $\delta^{13}\text{C}$  (the ratio of  $^{13}\text{C}$  to  $^{12}\text{C}$  compared with an international standard) between five evergreen and three deciduous species of a Venezuelan llanos. Typical  $\delta^{13}\text{C}$  ranged between  $-26.74$  and  $-30.23\%$ . Similarly they could find no significant differences in ITE.

Medina and Francisco (1994) showed that, for two species of savanna trees,  $\delta^{13}\text{C}$  values tended to increase (become less negative) as the dry season progressed. An increase in  $\delta^{13}\text{C}$  values is indicative of a larger WUE of the leaves. Furthermore, young leaves showed consistently larger WUE than old leaves, a result in agreement with those of Martin *et al.* (1994).



In a recent study across a rainfall gradient (from 1800 mm yr<sup>-1</sup> to 216 mm yr<sup>-1</sup>) in northern Australia, Schulze *et al.* (1998) observed no trend in community carbon isotope discrimination ( $\Delta$ , which is negatively related to WUE; see Farquhar *et al.*, 1989) as annual rainfall decreased from 1800 mm to 450 mm. However, as rainfall declined further,  $\Delta$  decreased (WUE increased). This contrasts with the results of Stewart *et al.* (1989), who observed linearly declining  $\Delta$  as rainfall decreased from 1700 mm to 350 mm. Unfortunately Stewart *et al.* (1989) pooled data for trees and shrubs, so this study is not directly comparable with that of Schulze *et al.* (1998).

Deciduous trees have a larger SLA and a larger N concentration than evergreen trees (Sobrado, 1991; Reich *et al.*, 1995; Eamus and Prichard, 1998; Schulze *et al.*, 1998). Nitrogen, SLA and assimilation are tightly linked and an expectation that this would be reflected in  $\Delta$  was partially supported (Schulze *et al.*, 1998). Carbon isotope discrimination increased with increasing N content (mass basis) and increasing SLA. Clearly, deciduous trees have high SLA and high N content (mass basis). These features support a high assimilation rate, which requires a large stomatal conductance to support a large CO<sub>2</sub> influx. Consequently the transpiration rate tends to be large and WUE may potentially be low (and consequently  $\Delta$  is large).

### 3. Optimization Theory

Cowan and Farquhar (1977) proposed that stomata behave in a manner such that the sensitivities of the rates of transpiration ( $E$ ) and C assimilation ( $A$ ) to changes in conductance ( $G_s$ ) (i.e.  $(\delta E/\delta G)/(\delta A/\delta G)$ ) remain constant. This occurs if the marginal unit water cost of carbon gain ( $\delta E/\delta A$ ) is a constant (Cowan and Farquhar, 1977). Several tests of this theory have shown  $\delta E/\delta A$  to be reasonably constant over a day or two (Mooney and Chu, 1983; Williams, 1983; Lloyd, 1991; Berninger and Hari, 1993). However, several data sets reveal significant variation in  $\delta E/\delta A$  (Grieu *et al.*, 1988; Guehl *et al.*, 1991). Savannas represent a highly pertinent environment within which to test optimization theories because of the occurrence of very large annual fluctuations in soil and atmospheric water content.

Lloyd and Farquhar (1994), using a simplified method for calculating  $\delta E/\delta A$ , observed that biomes with consistently high water availability had a good linear relationship between inferred  $\delta E/\delta A$  and mean LAVPD experienced during photosynthesis. Thus, tropical forests, drought-deciduous forests, temperate evergreen forests, mangroves and tundra all fell on the same line (Lloyd and Farquhar, 1994). However, in biomes where evaporative demand is high and water availability is periodic

(savannas, seasonal forests), a high  $\delta E/\delta A$  (non-conservative water use;  $\delta E/\delta A > 1000$ ) is the most successful strategy to adopt. When evaporative demand is high and water availability is episodic, a low  $\delta E/\delta A$  (conservative water use) is the optimal strategy. Plants with a rapid phenological development but short payback interval (i.e. deciduous trees in savannas) are predicted to have a less conservative strategy for water use (larger  $\delta E/\delta A$ ) while plants with a slower phenological development over a longer period (evergreen species) should have a more conservative strategy for water use (smaller  $\delta E/\delta A$ ) (Lloyd and Farquhar, 1994). Givnish (1986) has also proposed that absolute values of  $\delta E/\delta A$  are associated with the hydraulic conductivity of the plant.

There has been only one study of stomatal optimization theory of savanna species (Thomas *et al.*, 1999a,b). Several important features were apparent in this study. First, stomata did not behave in a manner that optimized  $\delta E/\delta A$  when either LAVPD or soil moisture content was varied. As LAVPD increased,  $\delta E/\delta A$  increased in all five species studied. Species occurring in more xeric conditions tended to show larger changes in  $\delta E/\delta A$  than species growing in more mesic environments. The most deciduous species tended to have a smaller value of  $\delta E/\delta A$  than the most evergreen species, in contradiction to the prediction by Lloyd and Farquhar (1994). However, the analyses of Lloyd and Farquhar (1994) assume that  $\delta E/\delta A$  is constant, an assumption shown to be invalid (Thomas and Eamus, 1999).

As drought developed,  $\Psi_{pd}$  declined and  $G_s$  declined log-linearly (Thomas and Eamus, 1999). In addition,  $\delta E/\delta A$  declined substantially. Furthermore, the rate of increase of  $\delta E/\delta A$  as LAVPD increased was reduced as drought progressed (Thomas and Eamus, 1999). This decline in the rate of increase of  $\delta E/\delta A$  presumably reflects a more conservative use of soil water as this availability declines and evaporative demand (LAVPD) increases.

## **E. Canopy- and Landscape-Scale CO<sub>2</sub> and H<sub>2</sub>O Exchange Rates**

### *1. Canopy Scale*

Catchment- and regional-scale predictions of carbon and water fluxes require estimates of canopy-scale exchanges. Three methodologies may provide these estimates. First, canopy-scale fluxes of water can be assessed using sapflow measurements of individual trees followed by scaling up (Cook *et al.*, 1998; O'Grady *et al.*, 1999). Second, eddy covariance or Bowen ratio techniques (Grace *et al.*, 1995; San Jose *et al.*, 1998b; Tenhunen *et al.*, 1998) can be applied to CO<sub>2</sub> and water fluxes. Finally,

remotely sensed information using aircraft or satellite-mounted sensors can provide estimates of regional temperature and evapotranspiration (Running *et al.*, 1989; Brunet *et al.*, 1991), woodland and forest tree density and leaf area index, rates of photosynthesis, canopy chlorophyll and N contents, and other parameters (Field *et al.*, 1994). Synthetic aperture radar data have been used for measurements of vegetation classification and for structural attributes of savanna woodlands (Ahmad *et al.*, 1998).

Tropical forests in southwest Amazonia experience a mild, short dry season (Grace *et al.*, 1995). Peak assimilation rates (expressed per unit ground area) measured using eddy covariance techniques were typically  $15 \mu\text{mol m}^{-2} \text{s}^{-1}$  in light-saturated conditions, a value remarkably close to values obtained from leaf-scale measurements of seasonally dry forests (see section V.C.1). Similarly bulk stomatal conductance of the canopy ranged from 0.4 to  $1.0 \text{ mol m}^{-2} \text{ s}^{-1}$ , in agreement with leaf-scale measurements of seasonally dry forests.

Two field studies in the Amazon forest showed minimal variation in assimilation rate between seasons (Grace *et al.*, 1995, 1996), although recent modelling suggests that reductions in dry season gas fluxes can occur in response to changes in soil water content and soil-root hydraulic resistance (Williams *et al.*, 1997b). However, the degree of seasonality is small for their site because the dry season is short and the site receives frequent but low-intensity rainfall. In contrast, Miranda *et al.* (1997) observed large seasonal changes in gas exchange characteristics in nearby cerrado vegetation, where seasonality is much more pronounced. Thus canopy exchange rates (expressed per unit ground area) were 12 and  $4 \mu\text{mol m}^{-2} \text{ s}^{-1}$  in the wet and dry season, respectively, and LAI decreased from 1 to 0.4. Apparent ecosystem quantum efficiency declined from wet to dry season (from  $68 \text{ mol photon (mol C)}^{-1}$  to  $77 \text{ mol photon (mol C)}^{-1}$ ). These values are considerably higher than comparable values for mixed deciduous hardwood forests in the USA (Wofsy *et al.*, 1994), Brazilian rainforest (Grace *et al.*, 1995) or *Nothofagus* forest of New Zealand (Hollinger *et al.*, 1994). This is probably a function of the high degree of sclerophylly (Miranda *et al.*, 1997). There was no influence of season upon the relationship between  $C_i : C_a$  ratio and VPD (Miranda *et al.*, 1997), in contrast to many leaf-scale studies (see section V.C.1). In the wet season, the cerrado vegetation was a net sink for  $\text{CO}_2$  but for a brief period in the dry season it was a net source.

Verhoef *et al.* (1996) measured fluxes of  $\text{CO}_2$  and  $\text{H}_2\text{O}$  over a deciduous savanna in Niger, west Africa, from the end of the wet season through to the middle of the dry season. Leaf stomatal conductance (measured with a porometer) declined after the cessation of rains as soil and atmospheric water content declined (see section V.A.1). Transpirational  $\text{H}_2\text{O}$  and photosynthetic  $\text{CO}_2$  flux from/to the canopy showed peak values of

about  $6 \text{ mmol m}^{-2} \text{ s}^{-1}$  and  $10 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , respectively, shortly after the end of the wet season. Over the subsequent 15 days as  $G_s$  declined, transpiration and photosynthesis declined by 50%. Photosynthetic  $\text{CO}_2$  flux linearly increased with increasing leaf-scale  $G_s$ , indicating a low  $\Omega$  value for this sparsely wooded ( $\text{LAI} = 0.32$ ) and low-lying ( $< 3 \text{ m}$ ) savanna. This study showed that both VPD and soil moisture determined transpiration and rates of photosynthesis. Canopy quantum yield and maximum rates of photosynthesis declined with decreasing soil and atmospheric water content (Verhoef *et al.*, 1996). Similar results were obtained by Monteny *et al.* (1997) for a similar site, where peak assimilation rates were approximately  $12 \mu\text{mol m}^{-2} \text{ s}^{-1}$ . Declines in soil moisture after the end of the wet season resulted in a rapid decline in quantum yield and light-saturated rates of photosynthesis. Monteny *et al.* estimated that grasses represented 65% of the total evapotranspiration and that, as soil water content declined, more sensible heat was transferred to the atmosphere so that leaf temperature became supra-optimal for photosynthesis.

Half-hourly estimates of instantaneous transpiration use efficiency (ITE) of the Sahelian savanna declined curvilinearly as VPD increased (Verhoef *et al.*, 1996). The clear relationship between VPD and ITE suggests that  $\text{CO}_2$  fluxes can be predicted from a knowledge of VPD and  $E$  only (Verhoef *et al.*, 1996). Interestingly, on a daily time frame, ITE was a linear function of VPD (and also soil water content), rather than a curvilinear function of VPD as observed when half-hourly averages were used. This is probably because of hysteresis in the response of  $G_s$  to VPD.

A comparison of eddy covariance measurements of  $\text{CO}_2$  flux and model outputs for a Sahelian savanna in Niger, west Africa (Hanan *et al.*, 1998), showed coefficients of determination of 0.8 when literature-based values for quantum yield and Rubisco (ribulose biphosphate carboxylase) capacity were used in the model. However, when seasonal changes in these physiological parameters was accounted for, the coefficient of determination increased to 0.93. Physiological parameters controlling photosynthesis were highly seasonal, in contrast to the Jarvis functions used to describe  $G_s$  (Hanan and Prince, 1997). It was observed that, during the short wet season (100 days), peak rates of photosynthesis were as high as in more mesic ecosystems, but annual carbon sequestration was small because LAI was very low and the wet season was short. Thus leaf area duration ( $\text{LAI} \times \text{duration}$ ) and annual photosynthetic carbon uptake appear to be correlated (Hanan *et al.*, 1998).

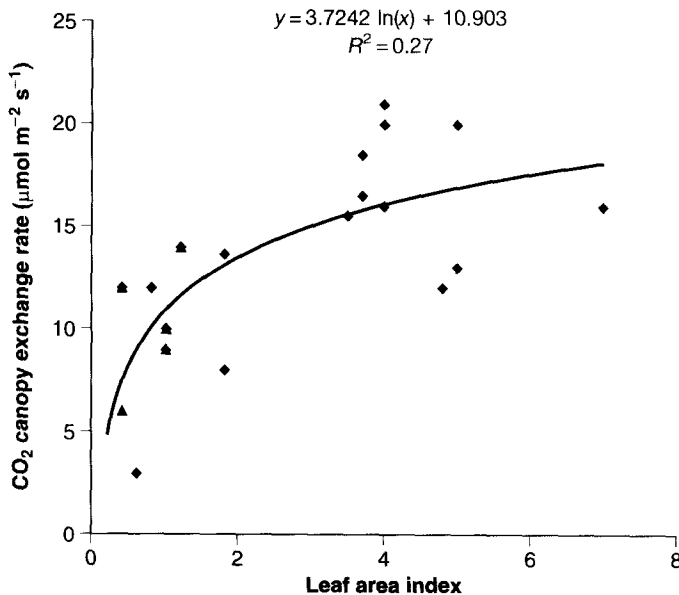
The patchy distribution of shrubs and trees of savannas introduces significant heterogeneity into spatial distributions of radiation, momentum and gas fluxes (Tuzet *et al.*, 1997). Such spatial (and temporal, given the

seasonality of soil water availability) variability must be accounted for in canopy-scale measures of water and CO<sub>2</sub> fluxes.

Tuzet *et al.* (1997) and D. Eamus, X. Chen, G. Kelley, A.P. O'Grady and L. Hutley (unpublished observations of roots in Northern Territory savannas) have shown that the partitioning of water and CO<sub>2</sub> fluxes between the woody and grass components of the vegetation varies according to soil water content. In the wet season, grasses can dominate total water and CO<sub>2</sub> flux, but trees and shrubs dominate in the dry season. Similarly the partitioning of available energy between sensible heat and evaporation varies between seasons such that in the wet season sensible heat and evaporation are approximately equal but in the dry season sensible heat exceeds evaporation (Miranda *et al.*, 1997).

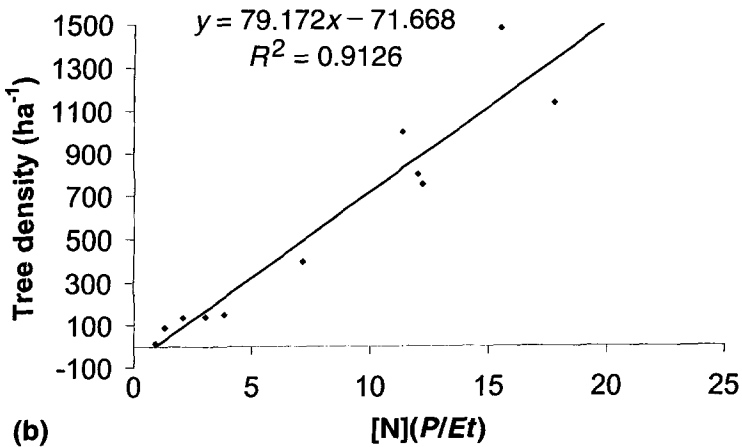
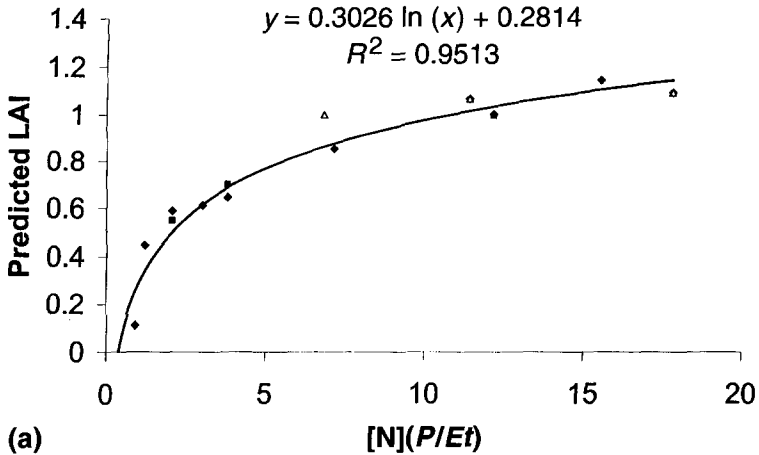
## F. Scaling Up to Landscapes

There is a significant relationship between LAI and canopy CO<sub>2</sub> exchange rate for a number of ecosystems (Figure 12). It is noteworthy that the few savanna sites that have been studied fit the same line as sites with LAI of



**Fig. 12.** As leaf area index (LAI) increases, the rate of CO<sub>2</sub> flux to the canopy increases. The diamonds are data from a wide range of ecosystems, and the triangles are savanna sites. The data have been taken from a wide range of sources.

over 6. Given the simple relationship between (foliar N content (mass basis))  $\times P/Et$  and LAI (Figure 13; equation from Baldocchi and Meyers, 1998), it is clear that canopy  $CO_2$  exchange rate can be predicted from a knowledge of foliar N content (mass basis) and the ratio of precipitation to annual equilibrium evaporation, since:



**Fig. 13.** Along a rainfall gradient of approximately 1600mm, there is a clear relationship between either (a) leaf area index and  $[N](P/Et)$  or (b) tree density and  $[N](P/Et)$ , where  $[N]$  is the foliar N content,  $P$  is the precipitation,  $Et$  is the potential evaporation. For Figure 13(a) data are recalculated from Schulze *et al.* (1998) (diamonds), Bowman (1996) (squares) and O'Grady *et al.* (1999) (triangles).

$$\text{CO}_2 \text{ flux} = 3.72 \times \ln(\text{LAI}) + 10.9$$

and

$$\text{LAI} = 0.3026 \times \ln([\text{N}]/\text{Et}) + 0.2814$$

Therefore

$$\text{CO}_2 \text{ flux} = 3.72 \times \ln(0.30 \times \ln([\text{N}]/\text{Et}) + 0.2814) + 10.9$$

This equation yields a prediction of peak growing season  $\text{CO}_2$  flux for canopies over a large range of  $[\text{N}]/\text{Et}$  values, including those exhibited by seasonally dry woodlands and forests (Figure 13).

Savannas cover a land surface of approximately  $15 \times 10^{12} \text{ m}^2$  (Miranda *et al.*, 1997). If we add xerophytic woodlands and other tropical seasonally dry ecosystems, the total land area covered is about  $25 \times 10^{12} \text{ m}^2$  (IPCC, 1995). Using eddy covariance data recently obtained during the wet, early dry and late dry seasons (Eamus *et al.*, 2001) and integrated for net 24-hr total carbon fluxes, we obtained total annual C sequestration of  $0.75 \text{ t ha}^{-1} \text{ yr}^{-1}$  (or  $6.2 \text{ mol C m}^{-2} \text{ yr}^{-1}$ ). This compares well with  $0.32 \text{ t ha}^{-1} \text{ yr}^{-1}$  for a Sahelian fallow savanna (Hanan *et al.*, 1998) and  $2\text{--}5 \text{ t ha}^{-1} \text{ yr}^{-1}$  for temperate deciduous forests (Goulden *et al.*, 1996; Greco and Baldocchi, 1996). Clearly, seasonally dry forests represent globally significant sites of C exchange between the atmosphere and vegetation.

## VI. COST-BENEFIT ANALYSES FOR LEAVES OF SAVANNA TREES

### A. Theory

Leaves incur a cost in their construction and also in their maintenance. Construction costs are the sum of all the carbon and energy utilized in producing a net gain in dry weight, including carbon incorporated into biomass and carbohydrate consumed to produce ATP and reductant for biosynthetic processes and transport processes (Chiariello *et al.*, 1989). The benefit to the plant of a leaf is clearly the carbon fixed in photosynthesis. *A priori* reasoning suggests that a leaf should return more investment to the plant than it costs to construct and maintain it.

Construction costs of leaves can be calculated from detailed investigations of biochemical pathways utilized during construction of the principal components of leaves (Penning de Vries, 1975). Alternatively, elemental analyses of the major components of biomass can be undertaken

(McDermitt and Loomis, 1981). Such analyses are very labour and equipment intensive. Merino *et al.* (1982) used growth and CO<sub>2</sub> exchange analyses to calculate construction costs, but this method is also slow and can be difficult in some environments. Measurements of organic nitrogen content, ash-free heat of combustion and ash content are required to determine the construction cost, for which the equation developed by Williams *et al.* (1987) is often used:

$$C = \{(0.06968 H_c - 0.065)(1 - A) + [(kN/14.0067)(180.15/24)]\}/0.89$$

where C is the construction cost (g glucose equivalents (g dry wt)<sup>-1</sup>); H<sub>c</sub> is the ash-free heat of combustion (kJ g<sup>-1</sup>); A is the ash content (g ash g<sup>-1</sup>); N is the total Kjeldahl nitrogen (g N (g dry wt)<sup>-1</sup>); and k is a factor that has the value +5 when N is imported as nitrate into the plant, giving the maximum construction costs, or -3 when N is imported as ammonia, giving minimum costs.

Maintenance costs (g glucose equivalents (g dry wt)<sup>-1</sup> day<sup>-1</sup>) are calculated following Merino *et al.* (1984), using biochemical pathway analyses. The following maintenance coefficients are used:

Fat	0.0425 g g <sup>-1</sup>
Protein	0.028 g g <sup>-1</sup> (minimum), 0.053 g g <sup>-1</sup> (maximum)
Ash	0.06 g g <sup>-1</sup> (minimum), 0.01 g g <sup>-1</sup> (maximum)

Maintenance costs of leaves include all processes requiring energy but not resulting in a net increase in dry matter, such as maintenance of ion gradients across lipid membranes and turnover of organic compounds (Chiariello *et al.*, 1989). Maintenance costs can be calculated from ash, lipid and protein contents of leaves and their maintenance coefficients (Merino *et al.*, 1984).

Williams *et al.* (1987) utilized the concept of glucose as equivalent energy units to modify the calculation of construction costs developed by Penning de Vries (1975). A comparison of the biochemical approach, the elemental analyses approach, the growth and CO<sub>2</sub> gas exchange method and the heat of combustion method showed good agreement (Merino *et al.*, 1982; Williams *et al.*, 1987). The heat of combustion method is faster and less costly than the alternative methodologies.

## B. Phenological Comparisons

Heat of combustion is higher in leaves of evergreen than deciduous species (Sobrado, 1991; Eamus and Prichard, 1998). The heat of combustion of leaves is positively related to the glucose equivalent (GE) (McDermitt and



Loomis, 1981), and therefore GE provides a measure of the amount of glucose required to provide the carbon and electrons contained in the leaf (Williams *et al.*, 1987). Since a high heat of combustion means a high energy storage of biomass, leaves of evergreen species must have a higher energy storage of biomass than those of deciduous species. This is a result of the higher degree of sclerophylly and larger investment in secondary defence compounds in evergreen species.

Heat of combustion provides an estimate of construction costs of leaves (McDermitt and Loomis, 1981). A high lipid content of leaves is associated with high construction costs (Merino *et al.*, 1984), and lipid content has been found to be significantly higher in evergreen than in deciduous species. These characteristics explain the higher foliar construction cost of evergreen species. High lipid content may be associated with defensive compounds in evergreen leaves and the smaller cells (and hence proportionally more cell wall material) of sclerophyllous evergreen species.

Poorter (1994) has concluded that there is very little evidence for differences in construction costs between deciduous and evergreen species. Similarly, within tree species, Merino (1987) found no difference in construction costs between evergreen and deciduous species. However, Eamus and Prichard (1998) found construction costs of evergreen species to be larger than those of deciduous or semi-deciduous species. This is in contrast to results obtained in other studies (Merino *et al.*, 1982, 1984; Williams *et al.*, 1987). However, from a theoretical consideration, construction costs of leaves of evergreen species should be higher than those of deciduous species because of the smaller cells, thicker cell walls and hence larger proportion of structural material in long-lived evergreen species (Orians and Solbrig, 1977; Chabot and Hicks, 1982; Williams *et al.*, 1989). Longer-lived leaves are also more likely to be subject to herbivore attack than short-lived leaves (Reich *et al.*, 1992). Consequently, investment in secondary compounds for defence may be higher in leaves of evergreen trees than in those of deciduous trees. This may also contribute to the larger leaf construction costs of evergreen species (Reich *et al.*, 1992). The results presented by Eamus and Prichard (1998) support the hypothesis that leaf construction costs are correlated with lifespan.

In a detailed study of seven co-occurring *Piper* species in a tall evergreen rainforest in Mexico, the ratio of cost to benefit was correlated with leaf lifespan, a result in close agreement with that found in a study conducted in north Australia (Williams *et al.*, 1989). It is clear that deciduous and evergreen species have adopted alternative survival strategies. Deciduous species invest large amounts of nitrogen in leaves to support a very large assimilation rate each day of the wet season when soil water is freely available. Their short-lived leaves fix large amounts of carbon for a short time. Evergreen species do not invest large amounts of nitrogen into

their leaves, and assimilation rates are consequently lower, but they fix carbon for 12 months and hence the return to the tree occurs over a longer time.

Maintenance costs of leaves are significantly higher for deciduous compared to evergreen species (Merino *et al.*, 1982, 1984; Sobrado, 1991). Low maintenance costs are associated with long-lived sclerophyllous leaves (Merino *et al.*, 1984). The higher foliar nitrogen content of deciduous species suggests a higher protein content, which is expensive to maintain due to protein turnover. Thus the high  $A_{\max}$  of leaves of deciduous species is expensive to maintain because of the amount of enzymes involved in photosynthesis. The higher lipid content of leaves of evergreen species was more than offset by the higher nitrogen (hence protein) and ash content of leaves of deciduous species, thereby making the maintenance costs of leaves of deciduous trees higher than that of leaves of evergreen trees.

### **C. Leaf Lifespan as Determinant of Leaf Characteristics**

On average, deciduous trees have shorter leaf lifespans than evergreen trees. It is also clear that, as leaf lifespan increases, several leaf attributes change. Maximum assimilation rate (on a dry weight basis), foliar N content, SLA and maximum stomatal conductance, all decline with increasing leaf lifespan for a large range of environments, including seasonally dry environments (Figures 9–11; Reich *et al.*, 1992, 1994; Eamus and Prichard, 1998). Because assimilation rate is highly dependent on N content, and possibly a single universal relationship exists for this (Reich *et al.*, 1992), the observation that evergreen trees exhibit lower assimilation rates, larger SLA and lower stomatal conductance is attributed to their longer leaf lifespan. It is also likely that deciduous species with relatively long-lived leaves (9–10 months) will have attributes more closely resembling those of evergreen species with relatively short leaf lifespans (12–24 months) than those of deciduous species with very short leaf lifespans (<6 months) (Reich *et al.*, 1992). Given the relationships between leaf lifespan, relative growth rate and leaf-mass ratio (the ratio of leaf mass to whole plant mass) and forest production efficiency (Reich *et al.*, 1992), it is clear that leaf lifespan is an important integrator of plant, canopy and forest function. We must concur with Reich *et al.* (1992) that evergreen and deciduous are two ends of a gradient of leaf lifespan. Furthermore, within seasonally dry forests, evergreen species can have relatively short leaf lifespans (Williams *et al.*, 1997b) and thus have leaf attributes more similar to deciduous species than to evergreens with leaf lifespans of two or more years. We would suggest that it is likely that stand-level canopy production efficiency is a function of weighted average canopy leaf lifespan.

## VII. LARGE-SCALE STRUCTURE AND FUNCTION

Composition, structure and dynamics of savannas depend primarily on plant available moisture (PAM) and plant available nutrients (PAN), with fire and herbivory as secondary determinants (Walker and Langridge, 1997). If an adequate model of savanna structure and function can be developed using the PAM/PAN concept, it is likely that predictions will be possible for all savanna sites concerning functional attributes (e.g. productivity, transpiration rates) (Walker and Langridge, 1997).

Walker and Langridge (1997) and Williams *et al.* (1996) showed that variation in structural and compositional attributes of tropical savannas (tree height, percentage tree cover, tree basal area, deciduous tree richness, woody species richness, total leaf biomass) can be well described by knowledge of the PAM/PAN attributes. Plant available moisture is determined by both the amount of water available to a plant and the duration of availability. PAM is thus a function of root depth, soil characteristics and the distribution of rainfall in time. Plant available nutrients can, to a large extent, be estimated from measurements of soil depth, soil texture and available calcium, magnesium, potassium and phosphorus (Walker and Langridge, 1997). However, as Walker and Langridge (1997) acknowledge, the availability of soil data (depth, water-holding characteristics, nutrient exchange properties) is frequently limited. Williams *et al.* (1996) used percentage clay content as a surrogate measure of PAN, which greatly simplified data acquisition.

An alternative approach to estimate the productivity of seasonally dry tropical areas may be to use a simple global empirical scaling index such as that developed by Baldocchi and Meyers (1998) for boreal and temperate systems and tropical evergreen systems. For these systems, LAI could be predicted from knowledge of annual potential evaporation, annual precipitation and foliar N content. Leaf area index determines the maximum potential for carbon and water fluxes to and from canopies. Leaf area index is also highly correlated with a range of ecologically significant variables, including net primary productivity, site water balance and annual temperature (Waring and Schlesinger, 1985; Neilson, 1995). It is apparent that, for a range of seasonally dry forests, there is a significant relationship between (foliar N content  $\times P/Et$ ) and LAI or tree density (Figure 13). Thus, for the savannas of north Australia, covering a rainfall gradient of almost 1500 mm, and for other sites in Africa, tree density (which is highly correlated with leaf area and stem volume) or LAI can be predicted ( $r^2 > 0.9$ ) from the following equation (Baldocchi and Meyers, 1998):

$$\text{tree density} = [\text{N}] P/Et$$

where  $[N]$  is foliar N content in  $\text{mg g}^{-1}$ ,  $P$  is the annual precipitation and  $Et$  is the annual equilibrium evaporation.

Foliar N content provides at least a simple and crude estimate of nutrient availability, while the term  $P/Et$  is a surrogate measure of water availability. The  $[N]P/Et$  relationship for tree density and LAI may be easier to use than the PAM/PAN model since the data required are far more widely available.

## VIII. CONCLUSIONS AND FUTURE DIRECTIONS

Seasonally dry forests represent an important class of vegetation globally. Unlike most temperate systems, temperature and light availability are infrequently limiting for productivity. However, water can be very limiting for a significant part of the year (2–8 months) in the majority, but not all, seasonally dry woodlands and forests (O'Grady *et al.*, 1999).

Deciduous and evergreen species represent two ends of a continuum of leaf lifespan. Useful comparisons can be made between the strategies employed by these two extremes. Thus cost–benefit analyses of maintenance and construction costs reveal significant differences in the trade-off between nitrogen invested, assimilation of carbon, SLA and leaf lifespan. Species with short-lived leaves exhibit a suite of related characteristics (see Table 5), including high N investment, high SLA and a high rate of light-saturated assimilation. However, it is true to say that a deciduous tree with a leaf lifespan of 9 months probably has more in common with an evergreen tree with a leaf lifespan of 12 months than with a deciduous tree with a leaf lifespan of 3 months.

Because of their open canopy and low  $\Omega$  values, the rates of leaf- and canopy-scale  $\text{CO}_2$  assimilation in seasonally dry forests are broadly comparable, this is not the case in rainforests, coniferous forests and other closed-canopy forests, where  $\Omega$  is much larger. The rate of canopy  $\text{CO}_2$  uptake by seasonally dry forests is also comparable to that of many other woodlands and forests where LAI ranged from 2 to 6. This seems surprising, given the low soil nutrient content and low LAI of seasonally dry systems. It also raises the question – why have a closed forest canopy with a high LAI ( $>3$ ) if canopy  $\text{CO}_2$  exchange rates are not proportionally larger?

Leaf area index and tree density, which are major determinants of ecosystem productivity and water use, can be predicted with surprising ease from knowledge of foliar N content and the ratio of rainfall to equilibrium evaporation rate. It remains to be seen whether such relationships continue as more data are published. However, this simple

**Table 5**  
A summary of some of the characteristics associated with deciduous and evergreen phenologies in seasonally dry woodlands and forests

Attribute	Deciduous	Evergreen
Specific leaf area	High	Low
N content per unit dry wt	High	Low
$A_{\max}$ (wt basis)	High	Low
Leaf longevity	Low	High
Construction costs	Low	High
Maintenance costs	High	Low
Cost-benefit ratio	Low	High
Decline in leaf water potential between wet and dry season	Larger and faster	Smaller and slower
Resistance to water flow in stem or leaf	Small	Large
Huber value	Small	Large
Embolism during the dry season	Larger or smaller	Smaller or larger
Root depth	Shallower	Deeper

relationship may prove useful when attempting to estimate ecosystem productivity and C balances.

During the 1980s and early 1990s there were many leaf-scale studies of different species in seasonally dry ecosystems. Such studies highlighted the differences between species in assimilation rate, SLA, transpiration rate and other variables. However, more recent studies, at leaf, tree and canopy scale, suggest that similarities are more important than differences. O'Grady *et al.* (1999) has shown that transpiration rate can be estimated with suitable precision for any tree species from a single relationship between DBH (diameter at breast height), leaf area and transpiration rate. Similarly Meinzer *et al.* (1997) show that stomatal responses to VPD of a number of species are essentially identical. These data suggest that modelling of the savanna ecosystem function will not require large numbers of leaf- and species-scale measurements.

As in most environments, below-ground processes are not so well understood as above-ground ones. Most statements about rooting depths for savanna evergreen and deciduous trees are based on circumstantial evidence, such as  $\Psi_{pd}$  values (e.g. Myers *et al.*, 1997; Prior *et al.*, 1997a) or anecdotal evidence or unspecified sources (e.g. Olivares and Medina,

1992). There are few published studies of rooting depth or distribution, and fewer still of seasonal growth patterns. How does a deep-rooted tree cope with seasonal water-table fluctuations of up to 10 m, as can occur in northern Australian savannas? Do fine roots die as the saturated zone rises to surround them? If not, how do they survive this inundation? How many deep roots are needed to supply the tree's water requirements during the dry season?

Functional wood anatomy of tropical species needs further investigation. Are there generalized differences between the wood of evergreen and deciduous species? Does xylem embolism play a role in leaf abscission in some deciduous species? In those species that are extensively embolized, is xylem refilled, or is new xylem produced?

Comparisons between winter-deciduous, drought-deciduous and evergreen species may allow us to separate characteristics of deciduousness *per se* from what may be responses to a cold, nutrient-rich environment or a tropical environment with a marked dry season. So far, relationships between leaf lifespan and specific assimilation rates, SLA and leaf N content appear to hold for both tropical and temperate environments.

There have been many generalizations about differences between tropical evergreen and deciduous species. Most have been based on a very limited number of species comparisons (2–6) from only one environment. Which of these hold from a global perspective? There is a wide diversity in characteristics of deciduous trees. Some deciduous trees are leafless for a mere week or two, others for 4 months or more. With such a range in leaf phenological characteristics within the deciduous habit, it is not surprising that there is a corresponding diversity in physiological behaviour.

Briefly-deciduous trees are not leafless long enough to avoid drought, and their leaves may have an average lifespan equal to or longer than that of some evergreen leaves. These deciduous trees may share with evergreen trees similar adaptations to seasonal drought, such as deep roots, low solute potentials and capacity for osmotic adjustment, and effective stomatal control of transpiration.

Some deciduous species (e.g. fully deciduous species of northern Australia; Duff *et al.*, 1997; Myers *et al.*, 1997) shed their leaves while water potentials are still high, whereas others (e.g. from Venezuelan dry forest; Sobrado, 1996) are severely dehydrated before leaf loss occurs. In some species, leaf flush occurs during the dry season, whereas leaves of other species do not flush until after rain falls.

It is clear that the future of ecophysiological research, in all large ecosystems, will require input from multidisciplinary teams, including plant physiologists, ecophysiologicalists, hydrologists, micro-meteorologists, remote sensors and modellers. The challenge for tropical ecosystem

research is to conduct long-term, detailed, year-long studies, as opposed to short field campaigns during the most 'apparently active' growth period.

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