Seasonal patterns of leaf gas exchange and water relations in dry rain forest trees of contrasting leaf phenology

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Summary  Diurnal and seasonal patterns of leaf gas exchange and water relations were examined in tree species of contrasting leaf phenology growing in a seasonally dry tropical rain forest in north-eastern Australia. Two drought-deciduous species, Brachychiton australis (Schott and Endl.) A. Terracc. and Cochlospermum gillivraei Benth., and two evergreen species, Alphitonia excelsa (Fenzal) Benth. and Austromyrtus bidwillii (Benth.) Burret, were studied. The deciduous species had higher specific leaf areas and maximum photosynthetic rates per leaf dry mass in the wet season than the evergreens. During the transition from wet season to dry season, total canopy area was reduced by 70–90% in the deciduous species and stomatal conductance ($g_s$) and assimilation rate ($A$) were markedly lower in the remaining leaves. Deciduous species maintained daytime leaf water potentials ($\Psi_L$) at close to or above wet season values by a combination of stomatal regulation and reduction in leaf area. Thus, the timing of leaf drop in deciduous species was not associated with large negative values of daytime $\Psi_L$ (greater than $-1.6$ MPa) or predawn $\Psi_L$ (greater than $-1.0$ MPa). The deciduous species appeared sensitive to small perturbations in soil and leaf water status that signalled the onset of drought. The evergreen species were less sensitive to the onset of drought and $g_s$ values were not significantly lower during the transitional period. In the dry season, the evergreen species maintained their canopies despite increasing water-stress; however, unlike Eucalyptus species from northern Australian savannas, $A$ and $g_s$ were significantly lower than wet season values.

Keywords: CO$_2$ assimilation, deciduous, dry tropical forest, evergreen, stomatal conductance, water potential.

Introduction

Although annual rainfall on the coast of north-eastern Australia is relatively high, the climate of the region is characterized by marked seasonality, with the majority of precipitation occurring during a summer wet season of 3–4 months in duration. Rainfall patterns in the drier lowland areas south of the wet tropics are less predictable than those of the monsoonal climate in far northern Australia, there being greater variation in the timing and duration of the wet and dry seasons (Figure 1). In this region, seasonally dry rain forest communities are fragmented, existing as islands among the dominant sclerophyllous vegetation (Fensham 1995). Tree species...
growing in dry rain forest patches comprise a mix of phenological groups, with deciduous woody taxa accounting for a greater proportion of the community than in complex mesic rain forests that occur in areas of higher rainfall (Gillison 1987).

Studies of seasonally dry tropical forests have revealed differences in the leaf gas exchange characteristics and water relations of co-existing drought-deciduous and evergreen trees (Eamus and Prior 2001). Comparisons of leaf gas exchange and water relations in evergreen and decidual species have been undertaken primarily in the neotropics (e.g., Sobrado 1986, 1993, Goldstein et al. 1989, Medina and Francisco 1994) and in northern Australian savannas (e.g., Myers et al. 1997, Prior et al. 1997, Eamus et al. 1999a). No similar studies have been undertaken in Australian dry rain forest communities.

Sobrado (1993) proposed that drought-deciduous species maximize productivity during the wet season by utilizing more efficient water transport systems, whereas evergreen species maintain more conservative carbon gain (and water loss) over the whole year. However, patterns of leaf gas exchange and water relations do not appear to differ greatly between drought-deciduous species and evergreens during the wet season, with diurnal courses of carbon dioxide (CO₂) assimilation (A), stomatal conductance (gₘ) and leaf water potential (Ψₑ) comparable between the two groups when water availability is high (Sobrado 1986, Goldstein et al. 1989, Olivas and Medina 1992, Myers et al. 1997). With the onset of the dry season, gₘ and Ψₑ decline as accessible soil water decreases and evaporative demand increases. In general, stomata of drought-deciduous species are more sensitive to changes in soil water availability than those of evergreen species, with deciduous species exhibiting greater declines in gₘ than co-existing evergreen species during this period (Myers et al. 1997, Eamus and Prior 2001).

It has been suggested that leaf drop in drought-deciduous species is related to the internal water balance of the plant rather than to direct environmental cues such as photoperiod (Borchert 1980, Sobrado 1993, Machado and Tyree 1994). With the exception of some obligate deciduous species that follow rigid annual patterns of leaf phenology, it is probable that the major determinant of leaf loss in drought-deciduous species is the development of unfavorable water status with seasonal changes in soil water content and evaporative demand (Holbrook et al. 1995). The impact of environmental variation would be modified by endogenous factors such as the rate at which plants can transport water to the canopy, the degree to which water loss from the leaves can be controlled and the tolerance of leaf-level physiological processes to changes in water status.

In this study we investigated seasonal and diurnal patterns of gas exchange and Ψₑ in trees of contrasting leaf phenology growing in a dry rain forest community on the north-eastern coast of Australia. The principal aim of the study was to determine whether deciduous and evergreen species exhibit different responses to the transition from wet season to dry season. We attempted to answer the following questions: (a) do A and gₘ differ between co-occurring deciduous and evergreen species during the wet season; (b) are deciduous species more sensitive to the onset of drought, i.e., is there a more rapid decline in A and gₘ than in evergreens; and (c) is leaf drop in deciduous species associated with a significant decrease in predawn Ψₑ?

Materials and methods

Study site
The study was undertaken in 2000 and 2001 at Many Peaks Range (19°11′S, 145°45′E) on the north-eastern coast of Australia. The climate is characterized by marked inter- and intra-annual variation in rainfall. Mean annual rainfall at the study site is 1100 mm with over 80% of this rainfall usually occurring during the summer wet season (December–March). Annual rainfall differed markedly between the two years of study (Figure 2). Although total rainfall in 2000 (2400 mm) was more than double the long-term mean annual rainfall and rainfall in 2001 was less than half the mean (467 mm), rainfall totals for the two wet seasons during the field study were more similar than annual totals. Rainfall totalled 1517 and 906 mm, respectively, for the 1999–2000 and 2000–2001 wet seasons.
The unusually high rainfall in 2000 was due to Tropical Cyclone Tessa and subsequent heavy rains that occurred in April.

**Plant species**

Two drought-deciduous species, *Brachychiton australis* (Schott and Endl.) A. Terracc. and *Cochlospermum gillivraei* Benth., and two evergreen species, *Alphitonia excelsa* (Fenzel) Benth. and *Austromyrtus bidwillii* (Benth.) Burret were studied. All species are common at the study site although *C. gillivraei* and *A. excelsa* also occur in surrounding savanna vegetation. Three of the study species occurred in open areas that received full sunlight: two deciduous trees, *B. australis* and *C. gillivraei*, and the evergreen *A. excelsa*. The remaining evergreen species, *A. bidwillii*, is a sub-canopy tree.

**Gas exchange, water relations and leaf phenology**

Leaf gas exchange, $\Psi_L$, and canopy area were measured in three seasonal periods: the wet season (November–March), the transition from wet season to dry season (April–June) and the dry season (July–October). Wet and dry season measurements were made in March and August 2000, respectively. However, measurements for the wet to dry transitional period were postponed until May of 2001 because of a tropical cyclone that struck the study site in April 2000. Four replicate trees of each species were selected for study. Measurements were made on one individual of each species per day over four clear, sunny days. Before each field trip, five mature, fully expanded leaves were tagged for gas exchange experiments on each of the 16 trees. All tagged leaves were north facing to maximize exposure to sunlight.

Diurnal patterns of leaf gas exchange parameters and $\Psi_L$ were monitored with measurements made at 0500, 0900, 1100, 1300, 1500 and 1700 h. Carbon dioxide assimilation rate and $g_s$ were measured on the five tagged leaves on each tree with an LCA4 infrared gas analysis (IRGA) system (Analytical Development Corp, Hoddesdon, U.K.). All gas exchange measurements were made in ambient conditions and the leaf temperature, air temperature and photosynthetically active radiation (PAR) at the leaf surface were recorded at each measurement by the LCA4. The leaf to air vapor pressure difference (LAVPD) was calculated from leaf temperature and atmospheric vapor pressure. Concurrent measurements of $\Psi_L$ were made on three similarly displayed leaves from each tree with a Scholander-type pressure chamber (Plant Moisture Stress, Corvallis, OR). An additional series of $\Psi_L$ measurements were made during the late dry season (September 2001).

Total leaf area was estimated in the same individuals used for gas exchange and water relations measurements during each seasonal period. Seasonal changes in leaf area were measured in four replicates of each species by the randomized branch sampling method (Gregoire et al. 1995). Five random pathways were determined by probability sampling for each individual tree. Each pathway commenced at the base of the tree and proceeded acropetally to a terminal branch, which was harvested for measurement of leaf area. Branches harvested from each pathway were taken to the laboratory where the leaf area distal to the branch was measured with a CI-203 leaf area meter (CID, Camas, WA).

**Statistical analysis**

Repeated gas exchange measurements were made on each leaf over the course of the day. This induces a correlation structure between measurements on the same leaf, which was accounted for in the analysis by using linear mixed models, with sampling time within leaf as a random effect. The models were fitted by the restricted maximum likelihood procedure in GenStat (GenStat v.5, VSN International Ltd., Hemel Hamstead, U.K.). The explanatory variables used in the modeling of $A$, $g_s$, and $\Psi_L$ were species and time of day. The relationships between maximum stomatal conductance ($g_{max}$) and predawn leaf water potential ($\Psi_{L,pu}$) were assessed by fitting linear mixed models. Values of $g_{max}$ were log transformed ($\ln(g_{max})$) to homogenize variance. Differences between specific leaf area (SLA) and maximum CO$_2$ assimilation rates ($A_{max}$) on an area and dry mass basis were also examined with linear mixed models.

**Results**

**Seasonal variation in canopy area**

Seasonal variation in canopy area for each species is shown as a percentage of maximum canopy areas measured during the wet season (Figure 3). During the wet to dry transitional period, deciduous species shed the majority of their leaves, with 25% of the canopy remaining for *B. australis* and 9% remaining for *C. gillivraei*. The evergreen species retained a greater proportion (80–95%) of their canopies during the same period. The deciduous species were leafless during the dry season. For the evergreen species, canopy area was lower in *A. excelsa*, which retained roughly 50% of its canopy. Individ-

![Figure 3. Seasonal variation in total canopy area for two evergreen species (Austromyrtus bidwillii and Alphitonia excelsa) and two deciduous species (Brachychiton australis and Cochlospermum gillivraei). Data are shown as percentage of canopy remaining, with all estimates normalized to total canopy area in the wet season. Bars represent standard error (n = 4 trees).](http://heronpublishing.com)
uals of *A. bidwillii* maintained most of their canopies (≈ 80%) throughout the dry season.

**Leaf water potential**

In the wet season, midday $\Psi_L$ remained above −2.0 MPa and $\Psi_{L,pd}$ remained above −0.5 MPa in all species (Figure 4). In the wet to dry transitional period, $\Psi_L$ was lower than those observed in the wet season. During the dry season, $\Psi_L$ decreased considerably in *A. excelsa* after dawn reaching a minimum of −3.9 MPa by midmorning and remaining close to this value for the rest of the day. In the late dry season, values of $\Psi_L$ were between −4.0 and −6.0 MPa for *A. bidwillii* and *A. excelsa*.

**Gas exchange**

In all species, the highest values of $g_s$ occurred in the wet season (Figure 5). The stomatal response to the onset of drought in the wet to dry transition period differed between the species. The deciduous species exhibited significantly lower $g_{max}$ in the wet to dry transition compared with the wet season. In contrast, $g_{max}$ was not significantly different between the wet season and the transitional period for *A. excelsa* or *A. bidwillii*. However, $g_s$ declined in the dry season, remaining below 0.03 mol m$^{-2}$ s$^{-1}$ for the entire day in both evergreen species. There was a significant linear relationship ($P = 0.018$, slope = 1.29, SE = 0.54) between ln($g_{max}$) and changes in soil water status (as inferred from $\Psi_{L,pd}$) in all species. However, there was no significant difference in this relationship between the four species.

Rates of $A$ reflected seasonal and diurnal patterns of $g_s$ (Figure 6). The following basic patterns can be summarized from the data. Maximum assimilation rate occurred in the wet season for all species except in *A. excelsa*, which had a slightly higher assimilation rate in the transition period. During the transitional period, $A$ was significantly lower than in the wet season for the deciduous species, but not for the evergreen species. In the dry season, deciduous species had shed their canopies, whereas $A$ of the evergreen *A. excelsa* was markedly lower than in the wet season or transitional period. In the subcanopy species *A. bidwillii*, $A$ was generally lower in the dry season that in the wet season, even during periods when PAR was saturating.

During the wet season, there was no significant difference in $A_{max}$ on a leaf area basis between evergreen and deciduous species that grew in full sunlight (*A. excelsa*, *B. australis* and *C. gillivraei*). However, deciduous species had higher SLAs than the evergreen species (Table 1) and hence $A_{max}$ per unit dry mass was significantly higher ($P < 0.001$) for the two deciduous species.

**Discussion**

Stomatal conductance and $A$ were greatest for all species in the wet season under conditions of high water availability. This finding is in agreement with the results of other gas exchange studies in seasonally dry tropical forest trees (Unwin and Kriedemann 1990, Hogan et al. 1995, Sobrado 1996, Prior et al. 1997, Eamus et al. 1999). Tropical deciduous trees are predicted to have higher photosynthetic rates than co-existing evergreens during the wet season in order to compensate for the lost opportunity for carbon gain while leafless in the dry season (Eamus 1999). Choat et al. (2005) observed higher rates of sapwood specific and leaf specific hydraulic conductivity in *B. australis* and *C. gillivraei* than in *A. excelsa* and *A. bidwillii*. Thus, higher $A$ could be expected in the deciduous species.

**Figure 4.** Diurnal and seasonal variations in leaf water potential ($\Psi_L$, MPa) for two evergreen species (*Austromyrtus bidwillii* and *Alphitonia excelsa*) and two deciduous species (*Brachychiton australis* and *Cochlospermum gillivraei*). Each value represents the mean of 9–12 measurements (three leaves on each of 3–4 trees). Bars represent the least significant difference (LSD).
species given the positive correlation between hydraulic conductivity and photosynthetic capacity observed for tropical trees (Brodribb and Feild 2000, Brodribb et al. 2002). Nevertheless, we found no clear difference in $A_{\text{max}}$ between evergreen and deciduous species, and a survey of the literature reveals that, on average, evergreen species from seasonally dry forests have higher $A_{\text{max}}$ on a leaf area basis than co-existing deciduous species (cf. Eamus and Prior 2001). However, when $A_{\text{max}}$ is compared on a dry mass rather than on an area basis, it is consistently higher for deciduous species because they generally possess wider, thinner leaves, i.e., they have a higher SLA than evergreens (Prado and DeMoraes 1997, Eamus et al. 1999b, Franco et al. 2005). Our results corroborate these observations (Table 1).

During the transition from the wet season to the dry season, $g_s$ and $A$ dropped significantly in the deciduous species but not in the evergreens. This is consistent with seasonal patterns of $g_s$ and $A$ observed in the deciduous tree species *Terminalia Ferdinandiana*, *Planchonia Careya* and *Cochlospermum fraseri* growing in the savannas of northern Australia (Myers et al. 1997, Eamus et al. 1999a). Thus, deciduous species occurring in both savanna and dry rain forest environments exhibit

![Figure 5](image-url) Diurnal and seasonal variations in stomatal conductance ($g_s$, mol m$^{-2}$ s$^{-1}$) for two evergreen species (*Austromyrtus bidwillii* and *Alphitonia excelsa*) and two deciduous species (*Brachychiton australis* and *Cochlospermum gillivraei*). Each value represents the mean of 15–20 measurements (five leaves on each of 3–4 trees). Bars represent the least significant difference (LSD).

![Figure 6](image-url) Diurnal and seasonal variations in CO$_2$ assimilation rate ($A$, $\mu$mol m$^{-2}$ s$^{-1}$) for two evergreen species (*Austromyrtus bidwillii* and *Alphitonia excelsa*) and two deciduous species (*Brachychiton australis* and *Cochlospermum gillivraei*). Each value represents the mean of 15–20 measurements (five leaves on each of 3–4 trees). Bars represent the least significant difference (LSD).
greater stomatal sensitivity to the onset of seasonal drought than co-existing evergreens. In the dry season, the deciduous species were completely leafless, and A and gs declined significantly in the evergreens. This contrasts with Eucalyptus species occurring in savanna environments, which maintain photosynthetic rates within 10–20% of wet season values despite considerable declines in Ψs (Eamus et al. 1999a). In our study, the reduction in A of evergreen species between the wet and dry season was accompanied by a significant decline in daily minimum Ψs. In the late dry season, ΨL,ps dropped to less than –4.0 MPa in A. excelsa and A. bidwillii, the implication being that these evergreen species have less access to ground water in deeper soil layers than deep-rooted Eucalyptus species.

The seasonal decline in A and gs observed in B. australis and C. gillivraei during the transitional period was accompanied by a 70–90% reduction in leaf area. Stomata of plants in seasonally dry environments have been shown to respond to seasonal increases in LAVPD (Olivares and Medina 1992, Eamus and Prior 2001). Studies of tree species from northern Australian savannas have shown that LAVPD increased from the wet season to the dry season (Duff et al. 1997, Prior et al. 1997). In far northern Australia, daily maximum temperatures in savannas remain above 30 °C throughout the year, whereas atmospheric vapor pressure decreases from the wet to the dry season. As a result, leaf temperatures and LAVPD increase during the dry season. However, in our study, a greater difference in air temperature was observed between the wet and dry seasons and leaf temperatures were generally lower in the dry season. Although the ambient vapor pressure decreased from wet to dry seasons, the decrease in air temperature, and hence leaf temperature, were such that LAVPD changed little between the wet and dry seasons. Because LAVPD was not generally higher for the deciduous species in the transitional period, the reduction in gs was sufficient to lower transpiration and improve water-use efficiency despite higher LAVPD at the onset of the dry season. If LAVPD had been higher in the transitional period, the reduction in stomatal aperture observed for deciduous species may not have decreased transpiration below wet season values.

The effects of leaf age must also be taken into account when assessing seasonal changes in gas exchange behavior of tropical deciduous species. In a study of tree species from a seasonally dry forest in Venezuela, A, E and gs declined in older leaves of deciduous species (Sobrado 1994). Martin et al. (1994) reported that A and gs declined more rapidly with leaf age in deciduous species than in evergreens from a dry forest in Costa Rica. However, gas exchange measurements on older leaves were conducted after the onset of drought in both of these studies, and it is thus difficult to separate the effects of leaf aging from drought. Although older and senescent leaves of deciduous species have been observed to lose stomatal control of water loss (Reich and Borchert 1988), both deciduous species in our study exhibited tight stomatal regulation with the onset of drought.

During the transitional period, deciduous species maintained Ψs at values close to, or above, wet season values by a combination of stomatal control, as shown by reduced gs, and a reduction in the total transpiring leaf surface. Thus, the timing of leaf drop in deciduous species was not associated with large negative values of daytime Ψt (> –1.6 MPa) or ΨL,ps (> –1.0 MPa). This contrasts with the range of water potentials measured in four deciduous tree species in Venezuela in which ΨL,ps declined to around –5.0 MPa just before leaf fall (Sobrado 1993). Other studies have shown that leaf abscission in drought-deciduous species is not always associated with large declines ΨL,ps (Unwin and Kriedemann 1990, Borchert 1994, Duff et al. 1997). It appears that the responses of deciduous species to seasonal drought are highly variable. Although water-storing trees with low wood density such as Cochlospermum are likely to shed their canopies early in the dry season and avoid large decreases in ΨL, other deciduous species, particularly those with higher wood densities, maintain their canopies further into the dry season and tolerate more negative stem and leaf water potentials (Borchert 1994, Chaot et al. 2005).

In our study, gs was sensitive to changes in soil water status as indicated by the significant negative relationship between ΨL,ps and ln(gsmax). A decline in soil water content can effect stomatal closure through increased synthesis of abscisic acid (Davies and Zhang 1991, Thomas and Eamus 1999), or perturbations in leaf water status resulting from xylem cavitation and subsequent loss of hydraulic conductivity (Cochard et al. 2002). Choat et al. (2003, 2005) observed that the deciduous species are more vulnerable to drought-induced embolism than co-occurring evergreen species. The deciduous species

### Table 1 Specific leaf area (SLA) (m² kg⁻¹) and maximum CO₂ assimilation rate (Amax) on a leaf area basis (µmol m⁻² s⁻¹) and dry mass basis (µmol kg⁻¹ s⁻¹) for two evergreen and two deciduous tree species. Within a column, different letters indicate a significant difference for SLA P < 0.001, Amax area basis P = 0.04, and Amax area dry mass basis P < 0.001). Mean standard error of differences is shown in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
<th>SLA (m² kg⁻¹)</th>
<th>Amax (µmol m⁻² s⁻¹)</th>
<th>Amax (µmol kg⁻¹ s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Evergreen</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. bidwillii</td>
<td>11.61 (0.60) a</td>
<td>4.17 (1.58) a</td>
<td>48.45 (19.07) a</td>
</tr>
<tr>
<td>A. excelsa</td>
<td>9.44 (0.60) b</td>
<td>7.19 (1.58) b</td>
<td>67.99 (19.07) a</td>
</tr>
<tr>
<td><strong>Deciduous</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. australis</td>
<td>13.44 (0.60) c</td>
<td>8.85 (1.58) b</td>
<td>118.97 (19.07) b</td>
</tr>
<tr>
<td>C. gillivraei</td>
<td>16.50 (0.60) d</td>
<td>7.02 (1.58) b</td>
<td>115.91 (19.07) b</td>
</tr>
</tbody>
</table>
B. australis and C. gillivraei reached a 50% loss of hydraulic conductivity at xylem water potentials of −3.1 and −1.4 MPa, respectively, whereas the evergreens did not suffer the same loss of hydraulic conductivity until xylem water potential fell below −5.0 MPa (Choat et al. 2003, 2005).

Reduction in \( g_* \) in the deciduous species may have been related to an increasing likelihood of xylem cavitation as soil water availability declined (Jones and Sutherland 1991, Sparks and Black 1999). Several studies have reported a concomitant decline in \( g_* \) with increasing xylem cavitation (Sperry and Pockman 1993, Bond and Kavanagh 1999, Salleo et al. 2000). Some studies have provided evidence of a link between a decline in \( g_* \) and stem and leaf cavitation, indicating that stomata may sense xylem cavitation and regulate water loss in a manner that prevents further decline in leaf and xylem water potential (Nardini and Salleo 2000, Cochard et al. 2002). It is unlikely that catastrophic xylem cavitation in the stem was a causal factor in leaf drop in B. australis or C. gillivraei because predawn and daily minimum \( \Psi_L \) did not fall to values equating to a 50% loss of hydraulic conductivity in either deciduous species. Given that xylem water potential would have been higher than day time \( \Psi_L \), it seems unlikely that stem cavitation would have directly induced leaf drop in these species. This does not rule out the possibility that the decline in \( g_* \) observed during the transitional period was triggered by the initiation of cavitation in branches or other organs such as the leaves (Brodribb and Holbrook 2003).

Conclusions

Our results provide a basis for comparison of deciduous and evergreen species occurring in dry rain forest environments with those occurring in northern Australian savanna habitats and in neotropical seasonally dry forests. The drought-deciduous species B. australis and C. gillivraei had higher SLA and wet-season \( A_{\text{max}} \) per leaf dry mass than two co-existing evergreen species. This is consistent with data showing that tropical deciduous species compensate for shorter leaf life-spans with higher photosynthetic capacity (Eamus and Prior 2001) and with general correlations between leaf life-span and \( A_{\text{max}} \) (Reich et al. 1999). Leaf abscission in the deciduous species was associated with a sharp decline in \( g_* \), but not in \( \Psi_L \), with the onset of drought. The maintenance of high \( \Psi_L \) until the point of leaf abscission in water-storing trees such as Cochlospermum has also been observed in studies in the neo-tropics (Borchert 1994) and in northern Australia (Duff et al. 1997), but not in the deciduous species studied by Sobrado (1993) in a Venezuelan dry forest. These findings emphasize the wide range of responses to seasonal drought within the deciduous guild. The marked dry-season decline in \( g_* \) and \( A \) observed in A. bidwillii and A. excelsa contrasts with seasonal patterns of leaf gas exchange observed in Eucalyptus from savannas in northern Australia (Eamus and Prior 2001), indicating that A. bidwillii and A. excelsa did not have access to deeper ground water resources during the dry season. Although this observation does not agree with the hypothesis of Sobrado (1993) that evergreen species tend to utilize water resources from deeper in the soil profile, studies with stable hydrogen isotopes have shown that many evergreen species in the Brazilian Cerrado (savanna) access water primarily from shallow soil layers (Jackson et al. 1999). Further work involving more taxa is required to increase our understanding of seasonal patterns of water use in perennial woody species from dry rain forests.

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References


