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Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics

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Seasonally dry tropical ecosystems, ranging from savannas to dry forests, occur in the Americas, Africa, India and Australia. They sustain large human populations, determine regional climate, are sites of biological and cultural conservation, and have significant economic value. Evergreen, deciduous and semi and brevi-deciduous trees frequently co-occur. Recent research shows how these various phenological groups respond differently to changes in soil and atmospheric water content. Cost-benefit analyses of evergreen and deciduous species shows how leaves of deciduous species live fast and die young, whereas leaves of evergreen species live slowly but longer.

Seasonally dry ecosystems have periods of plentiful water supply alternating with periods of drought. The impact of these oscillations upon leaf fall and leaf expansion was documented in the early 1990s. Furthermore, studies of crop plants highlighted crop responses to unseasonal drought. However, the response of trees, particularly trees differing in phenology, to predictable seasonal drought (the dry season) has been little studied. There are three main reasons why studies of tree responses to dry seasons are important. First, estimates of annual carbon fluxes to seasonally dry ecosystems, as part of climate change research, requires knowledge of seasonality of tree behaviour. Second, management of water resources in such ecosystems similarly requires understanding of seasonality of tree behaviour. Finally, a complete understanding of any ecosystem cannot be attained if only a fraction of the annual cycle is studied.

Seasonally dry tropical ecosystems

For this review I define seasonally dry forests and woodlands as tropical systems with the following characteristics: ‘a tree canopy that ranges from highly discontinuous, (savannas) to

multi-layered (forest), receiving highly seasonal rainfall. Grasses are frequently, but not always present, and generally dominated by C4 species¹.

Savannas and other seasonally dry ecosystems represent points on a continuum, with rainforest and pure grasslands as the two extremes.

Seasonally dry ecosystems occur naturally in Australia, India, Africa and the Americas and have been generated by human modification in Asia¹. They are important because they sustain large human populations, have biological (genetic) and cultural conservation and economic value (including tourism, pastoral industry and game reserves), and they are significant players in the global carbon and regional water cycles.

Temperature variation between seasons can be large or small, depending upon altitude, distance inland and latitude. In north Australian savannas, which are close to the tropics (12–20 °S) and close to the coast, temperature is uniformly high [January (wet season) maximum and minimum temperatures are 31.8 °C and 24.8 °C, respectively; July (dry season) values are 30.5 °C and 20.0 °C, respectively]. In contrast, at the margins of the tropics or at higher elevations, temperatures can approach freezing and seasonal variations can be 20 °C or more. However, as a general rule, these ecosystems are confined to areas where annual mean air temperature is higher than 20 °C and mean temperature of the coldest month is higher than 13 °C (Ref.1).

Seasonally dry ecosystems have distinct wet and dry seasons. Mean annual rainfall is usually larger than 600 mm and less than 1700 mm with a distinct dry season of between 1 and 7 months duration². Rainfall can be bimodal (central and southern Africa) or uni-modal (north

Africa, Central America and India)¹. Seasonally dry forests and woodlands are distinguished from temperate seasonal climates by the reversal of the association between rainfall and temperature². The dry season can be short (e.g. 1 – 3 months in humid savannas) or long (e.g. 5-8 months in dry savannas)². It is the seasonality of rainfall that has the most significant impact on structure and function of these systems. It determines phenology, growth patterns and physiological behaviour of vegetation. Because of this seasonality of rainfall, soil moisture content peaks in the wet season and minimal is at its lowest by the end of the dry season (Fig. 1a). In the dry season, tree-canopy cover declines, particularly where deciduous trees dominate, and any understorey grass is lost. Soil surface evaporation tends towards zero and consequently atmospheric water vapour pressure deficit (VPD - the difference between how much water vapour the air would hold when saturated and how much water vapour is actually present) increases through the dry season (i.e. relative humidity (RH) declines and evaporative demand increases). VPD increases between morning and afternoon in both wet and dry season (Fig. 1b).

Phenology

African and Indian savannas are mainly deciduous³⁻⁶. In contrast, the Llanos of South America (equivalent of savannas), are dominated by evergreen species^{7,8}, although individual forest patches within the Llanos may be dominated by deciduous species⁹. Dry forests in Thailand can be dominated by evergreen species at high elevations and along streams, or by mixed deciduous or deciduous dipterocarp forest¹⁰. Seasonally dry forests of Costa Rica are also dominated by deciduous species¹¹. In marked contrast, north Australian savannas show no dominance by any single guild. Each of four phenological guilds are approximately equally represented by species number¹². Figure 2 shows the annual pattern of canopy fullness for the

four guilds. Evergreen species retain a full canopy all year and the decline in canopy fullness in the dry season is less than 10%. Deciduous species, in contrast, lose all leaves for at least one but usually two to four months of each year. Semideciduous species, which do not appear to be a major functional group within seasonally dry woodlands and forests elsewhere in the world, lose at least 50% of their leaves every year. Brevi-deciduous differ from semideciduous species in that they never lose more than 50% of their leaves and in some years, when the wet season is large and the dry season short, might lose only a small percentage of their canopy¹².

The majority of leaf flushing frequently occurs before the start of the wet season in Africa, central America, India, Australia and Costa Rica^{3,4,7,13}. This pattern is not universal, however. Flushing can occur at the start of the wet season¹¹, or mid-wet season and in some cases, within the same species, flushing occurs both before and after the start of the wet season¹¹. Peak period of leaf growth can be from early to late dry season¹¹; leaf growth ceases by mid-wet season in most savannas.

Tree water relations

Seasonally dry forests or woodlands have a distinct dry season (when rainfall is essentially zero). This can be between two and seven months long. During this time soil water content declines substantially, especially in the upper three metres. Consequently predawn water potential declines from values close to zero in the wet season to values as low as -2.5 MPa in the dry season^{14,15}, followed by an increase slightly before or after the onset of rain. Predawn water potential (ψ_{pd}) declines for both evergreen and deciduous trees with continuing drought (Fig. 3a). Evergreen species can exhibit a lower (ψ_{pd}) than deciduous species¹⁶, although this is in contrast to a recent study by Medina and Francisco¹⁶ where *Godmania macrocarpa*

(deciduous) maintained a lower leaf water potential (ψ_w) than *Curatella americana* (evergreen). Evergreen species tend to maintain a positive turgor potential to lower values of leaf ψ_w than deciduous species¹⁵⁻¹⁸, thereby allowing them to maintain cellular function at lower soil water potentials than deciduous species.

Deciduous species are drought avoiders because they drop their entire canopy and hence do not transpire at significant rates in the dry season – their foliage thereby avoids drought.

Evergreen species maintain a canopy and transpire. This may be made possible by a root system that accesses deeper layers of soil than deciduous species¹⁹, although there are few detailed studies of root depth of evergreen and deciduous savanna trees. Smaller trees show a larger decline in ψ_{pd} than larger trees during the dry season²⁰ (Fig. 3b). This is because the volume of soil explored by roots of small trees is less than that of large trees²⁰.

Hydraulic architecture – the structure and behaviour of xylem conduits of plants- represents a rapidly expanding field in the study of tropical trees. In the tropics, transpiration rates are usually larger than those of temperate zones because of the large VPD and higher temperatures and solar-radiation loads. Consequently, leaf- specific conductivity (LSC, a good index of the ability of the stem to supply water to leaves) is usually larger in tropical than temperate trees²⁰. This is partly because of a larger Huber values (HV, the ratio of the cross-sectional area of a stem to the leaf area supplied by the stem) of tropical trees. Thus tropical trees invest more in xylem than temperate trees, to support the larger evaporative demand²². Evergreen trees in savannas have larger LSC than deciduous trees^{22,23} so that at the same transpirational flux, the evergreen species requires a smaller gradient of water potential between leaf and soil – an important consideration in the dry season when evaporative demand is very large and upper soil water availability is very low. Vulnerability to cavitation (embolism) is higher in tropical

than temperate trees, a feature that probably results from the requirement to support large transpiration rates²². We are not yet able to compare evergreen and deciduous species in relation to their vulnerability to cavitation.

Daily and seasonal changes in stomatal conductance and photosynthesis

As ψ_{pd} declines, the degree of stomatal opening during the day (i.e. stomatal conductance to water, G_s) declines^{24, 25} (Fig 4a). Not only does the value of the maximum G_s decline, but opening also becomes more confined to the early part of the day when temperature and VPD place smaller demands on transpiration. The decline in G_s in the dry season is both a function of drier soil and increased VPD (or more correctly, LAVPD since it is the gradient of leaf-to-air vapour pressure difference that drives transpiration. With large LAVPDs, transpiration demand exceeds the ability of the plant's hydraulic architecture and soil to supply water to the leaf. Consequently, G_s declines. Interestingly, it appears to be the rate of transpiration and not LAVPD (which drives transpiration) *per se*, that regulates G_s (ref. 26). The mechanism by which transpiration rate regulates stomatal conductance is debated, but presumably reflects changes in the ψ_w gradient within the mesophyll and/or epidermis and guard cells of a leaf. As transpiration increases, supply of water to the guard cells through the epidermis is reduced, which reduces stomatal turgor and hence aperture.

Stomatal sensitivity to LAVPD differs between deciduous and evergreen species¹⁶. Deciduous species have a larger stomatal sensitivity to increasing soil drought than evergreen species, a result attributed to a less elastic cell wall and hence a larger propensity to turgor loss in deciduous compared with evergreen trees¹⁶.

Reduced G_s can limit carbon assimilation (photosynthesis) by reducing the supply of CO_2 to chloroplasts. This certainly occurs in savanna trees and can be observed by the decline in $C_i:C_a$ ratio (the ratio of the concentration of CO_2 inside the leaf to the ratio of the concentration outside the leaf)²⁴ between morning and afternoon in the wet season (Fig 5). However, additional factors, especially in the dry season, reduce photosynthesis *per se* and this results in an increase in $C_i:C_a$ (Fig 5a) because demand for CO_2 (photosynthesis) is reduced more than supply. Similar increases in the $C_i:C_a$ ratio have been interpreted previously as indicative of non-stomatal limitation to assimilation²⁷. Excessive leaf temperatures¹⁵, resulting from reduced transpirational cooling of leaves with lowered G_s and increased supply of ABA to the leaf from the roots, could account for the decline in assimilation.

Photosynthetic rate of mature evergreen trees show only a small declines (15 - 50%) in the dry season, compared with the wet season^{24,28}. Thus, these species maintain a positive carbon balance for each month of the year (Fig. 5b). Semi-deciduous species showed a 25 – 75% decline in assimilation rate per unit leaf area, which, coupled with their 50% or more decline in leaf area, represents a major decline in monthly carbon gain in the dry season. Deciduous species show a 100 % decline in assimilation rate for 2 – 6 months of each year when they are leafless (Fig 5b) (D. Eamus *et al.*, unpublished). This raises an important question – how do evergreen species and deciduous species co-exist when their annual carbon budgets are apparently so different but their life forms so similar? This can be addressed by using a cost-benefit analysis.

Cost-benefit analyses of deciduous and evergreen species

Deciduous trees are leafless for two to seven months of each year. During this time they cannot fix carbon and rely on reserves to support root and shoot respiration. Evergreen trees fix carbon all year. It is not immediately apparent how such different strategies within the same plant form (i.e. trees) can co-exist. Cost-benefit analysis assumes that plant structures have costs and benefits associated with them. Leaves cost a tree to construct and maintain, but the benefit accrued is the carbon fixed throughout the life of the leaf. Leaves on the lower branches of trees often senesce and abscise when light levels get so low that the cost of maintaining those leaves is greater than the benefit of keeping them.

Theoretical considerations have suggested that as leaf longevity increases, leaf construction costs should increase. This is because as longevity increases, the probability of herbivore damage increases, and long-lived leaves should therefore contain more defensive compounds and/or structures. In addition, short lived leaves should be cheaper to construct because the payback interval (the time available to repay construction costs by fixing carbon) is shorter³⁰. A refinement of this argument is that the ratio of construction cost to carbon gain (the cost-benefit ratio) should be correlated with leaf longevity³⁰. Therefore to maximize benefit to a tree, photosynthetic rates of deciduous species should be high, which will require a large investment of nitrogen, whereas to maximize unpalatability and to survive harsh dry season condition, leaves of evergreen species should have relatively low nitrogen contents and be sclerophyllous (i.e. have thick cell walls and resistant to drought and insect attack).

These expectations are usually supported by results. Deciduous trees generally maintain larger nitrogen contents (per unit dry weight) than evergreen species^{17, 31} and consequently maintain a

larger rate of light saturated assimilation^{31,32}. Similarly, the specific leaf area (leaf area divided by leaf dry weight) of evergreen species is generally smaller than that of deciduous species^{29,31,32}, reflecting the more sclerophyllous nature of evergreen leaves.

Maximum construction costs were larger in evergreen than deciduous species in a study of Australian savannas³³. This result is supported by theoretical considerations but is in contrast to work in other savannas where leaves of deciduous species have higher construction costs^{34,35}. This contradiction between results is probably because Australian savannas, which are Eucalypt dominated, are more sclerophyllous and have a higher oil (and hence heat of combustion) content than evergreen species elsewhere.

In a detailed study of seven co-occurring *Piper* species in a tall evergreen rainforest in Mexico, the cost:benefit ratio was correlated with leaf life-span³⁰ (Fig.6) a result in close agreement with that from a study in north Australia³³ (Fig. 6). 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.

Future directions and conclusion

Several important questions face savanna ecophysiologicalists. First, what is the actual distribution of roots of evergreen, deciduous and semi and brevi-deciduous species? This is important for two reasons.

- An assessment of the standing biomass of savanna trees is required in many countries in international agreements for carbon budgeting after the Kyoto agreement in relation to climate change. The largest gap in our biomass estimates concerns the amount of roots present in different ecosystems and their rate of turnover.
- Groundwater represents an important resource for an increasing number of people in arid and semi-arid lands. The sustainable use of these resources requires some estimate of the degree of utilization of groundwater by vegetation. A key item of information required to assess this is the distribution of tree roots.

A second significant challenge facing savanna ecophysiologicalists is to be able to quantify the diurnal and seasonal patterns of CO₂ and water vapour fluxes to and from savannas at the regional scale. This will require a multidisciplinary team incorporating physiologists, GIS (geographic information services) and RS (remote sensing) personnel and ecologists. Only then will regional-scale estimates of the behaviour of savannas be possible. It is at the catchment and regional scale that owners and managers of land require information for sustainable development of savannas.

Finally, a comparison of the vulnerability of evergreen and deciduous species to xylem embolism is required. It is likely that this has a role in determining phenology, timing of phenological events, and as a limiting factor in tree growth and behaviour. in savannas. Recent

work in temperate systems suggest that embolism and hydraulic architecture may be of fundamental importance in tree behaviour and phenology^{10,34,35}.

In conclusion, evergreen and deciduous species generally differ in several fundamental ways, including differences in leaf life-span, assimilation rate and cost-benefit ratio (Table 1). Such differences contribute to a partitioning of resources between species of differing phenology, thereby reducing competition for those resources.

Table 1. General features of evergreen and deciduous species^a.

	Deciduous	Evergreen
Leaf life-span	Short	Long
Leaf nitrogen content	High	Low
Specific leaf area	Large	Small
Assimilation rate (per unit dry weight)	Large	Small
Cost – benefit ratio	Large	Small
Rooting depth	Shallow ?	Deep ?

^a Results compiled from refs. 24, 29, 32, 33.

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Figures

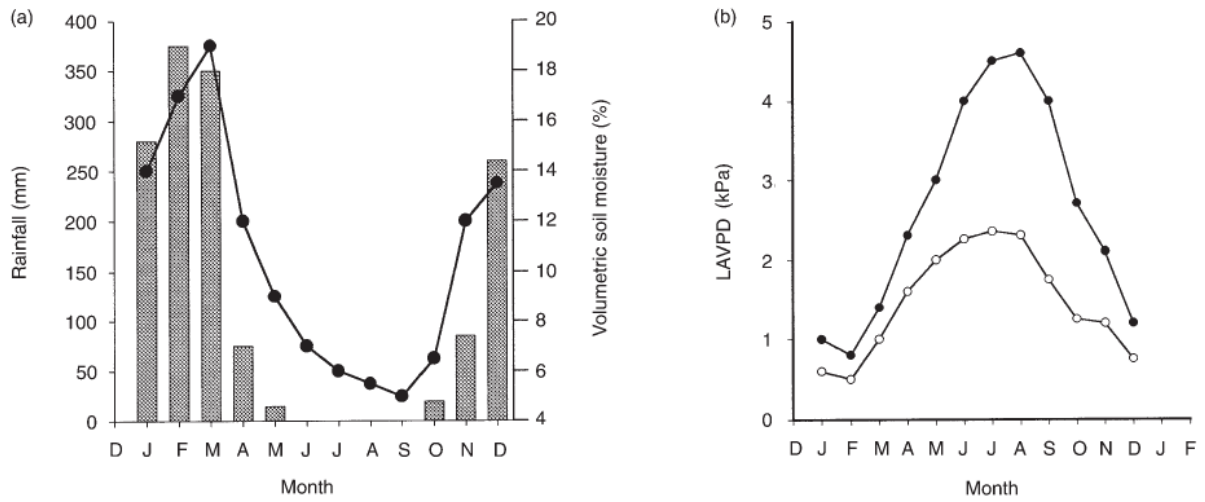


Fig. 1. (a) Rainfall (bars) is bimodal in many savannas, with a distinct dry season between the start and end of the wet season. Once rains have ceased, percentage soil moisture (●), especially in the upper 1 m, declines substantially because of transpiration by trees and percolation to deeper layers. *Re-drawn, with permission from Ref. 16.* (b) Leaf-to-air vapour pressure difference increases from morning (●) through to the afternoon (○) in both wet and dry seasons, but the increase is largest in the dry season (April-October).

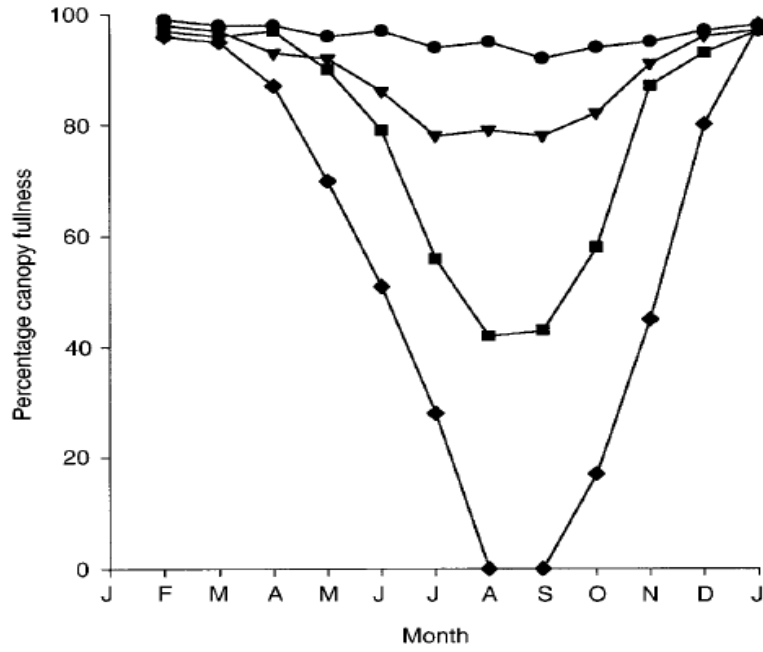


Fig. 2. Annual pattern of canopy fullness for four phenological guilds in north Australian savannas: evergreen (●); brevi-deciduous (τ); semi-deciduous (v) and deciduous (υ). The four guilds are present in equal numbers in Australian savannas but not elsewhere. The dry season extends from April to October. *Re-drawn with permission from Ref. 11.*

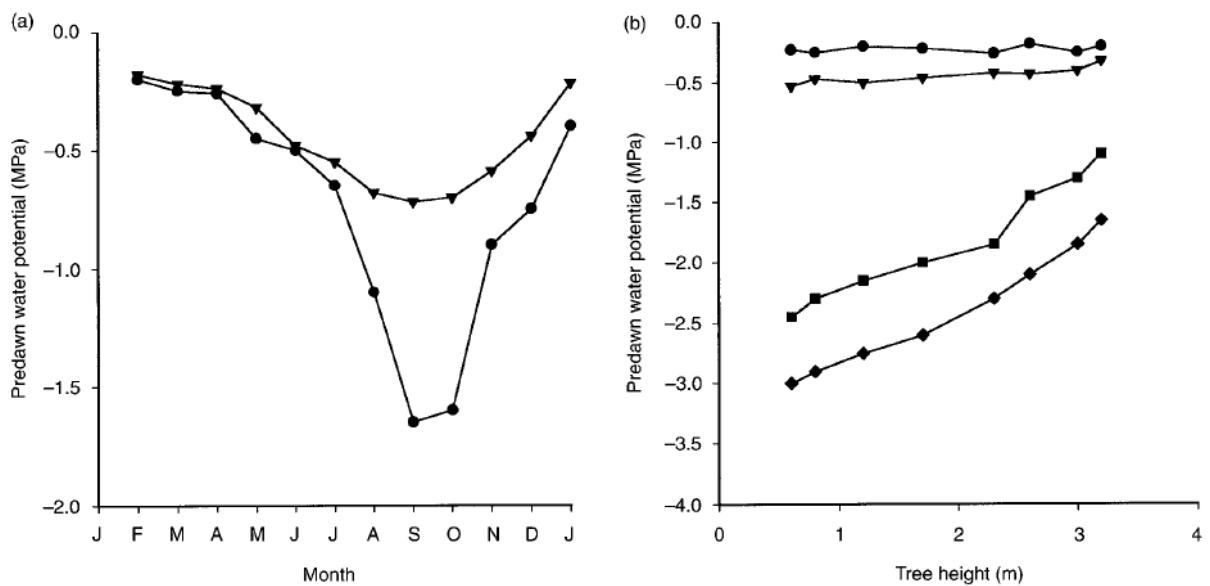


Fig. 3. (a) Predawn water potential declines from a high value in the wet season (Nov- April) to a low value in the dry season (May – Oct). Deciduous trees (τ) can maintain higher values than evergreens (λ) in some savannas, but not all. *Re-drawn with permission from Ref. 16.* (b) Taller trees have a more extensive root system than shorter trees. Therefore shorter trees tend to show larger declines in pre-dawn water potential as the dry season progresses. Key: λ December; τ May; ν September \cup October. *Re-drawn with permission from Ref. 20.*

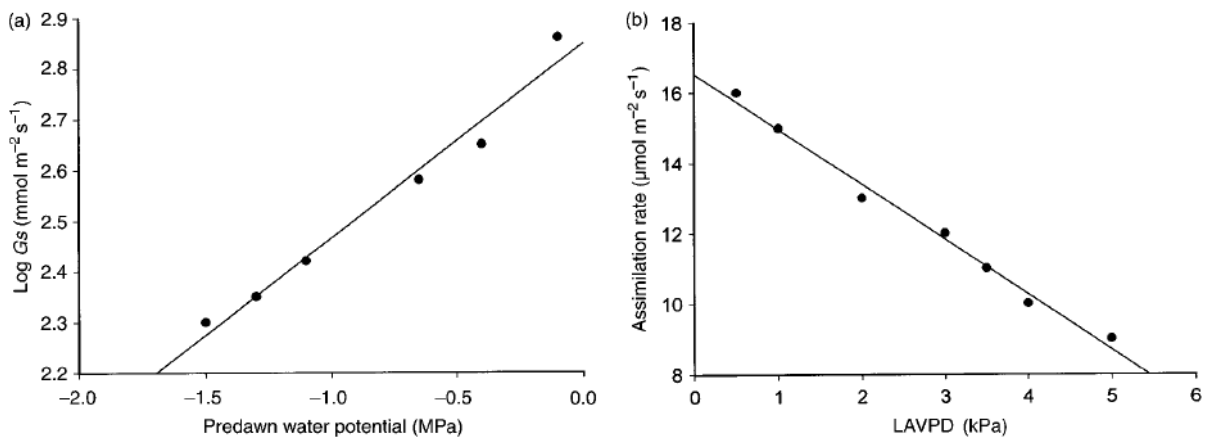


Fig. 4. (a) As pre-dawn water potential declines, water availability for transpiration declines. Therefore stomatal conductance (Gs) declines to reduce transpiration. The semi-log plot linearises the logarithmic decline in Gs. (b) As leaf-to-air vapour pressure difference (LAVPD) increases, evaporative demand increases. Photosynthesis declines because stomata close at high values of LAVPD. In addition, leaf temperature can become supra-optimal for photosynthesis. *Both figures re-drawn from Ref. 15.*

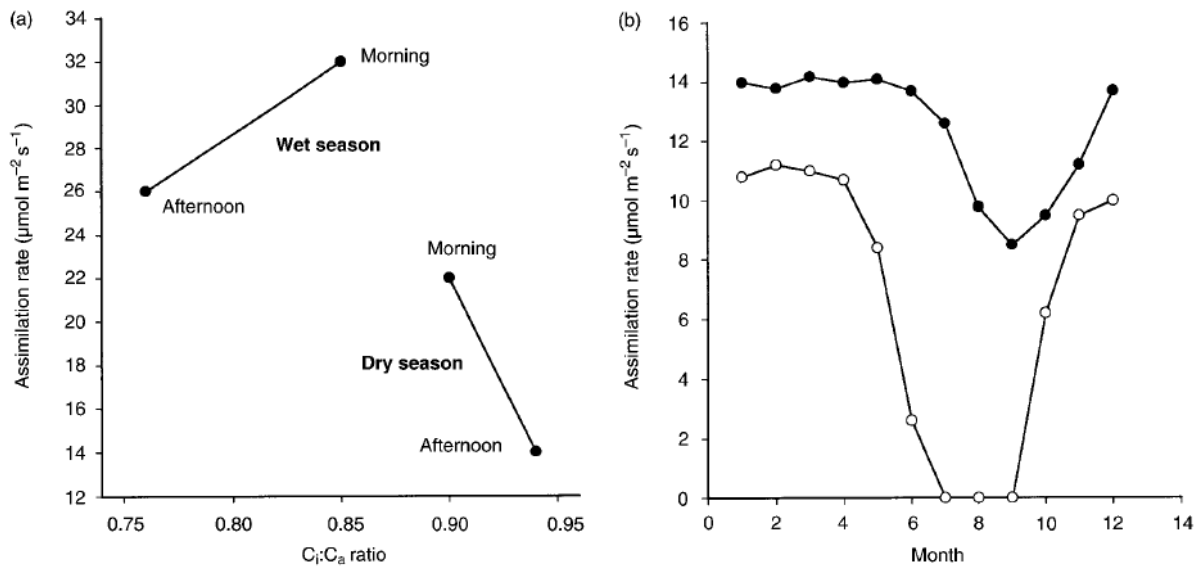


Fig. 5. (a) Carbon assimilation rate between morning and afternoon in the wet season and dry-season of the wet-dry tropics of Australia as a function of the ratio of the concentration of CO_2 inside a leaf to the concentration outside ($C_i:C_a$). If stomatal closure accounts for all of the decline in carbon assimilation rate with increasing LAVPD, the C_i/C_a ratio declines because supply of CO_2 becomes limiting. If carbon assimilation *per se* is affected more than stomatal conductance, the $C_i:C_a$ ratio can increase despite assimilation decreasing, as observed in the dry season. *Re-drawn with permission from Ref. 20.* (b) Evergreen trees (λ) maintain carbon assimilation throughout the dry season by using deep stores of water. Deciduous trees (O) lose their canopy and so only photosynthesize for seven to nine months of the year. *Re-drawn with permission from Ref. 24.*

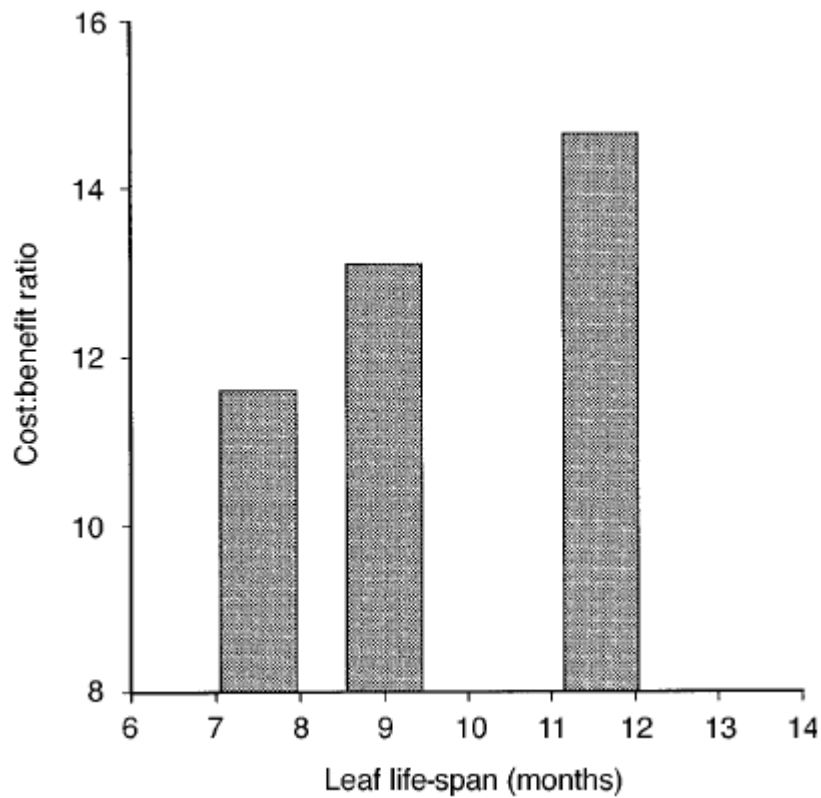


Figure 6. As leaf life-span (months) increases the cost:benefit ratio increases. Short-lived leaves of deciduous species have a higher assimilation rate (per unit dry weight) than longer lived leaves of evergreen species, but leaves of evergreen species have a longer payback interval.