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A cost-benefit analysis of leaves of eight Australian savanna tree species of differing leaf life-span

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Abstract

Cost-benefit analyses of foliar construction and maintenance costs and of carbon assimilation of leaves of differing life-span were conducted using two evergreen, three semi-deciduous, and three deciduous tree species of savannas of north Australia. Rates of radiant-energy-saturated CO_2 assimilation (P_{max}) and dark respiration were measured and leaves were analysed for total nitrogen, fat, and ash concentrations, and for heat of combustion. Specific leaf area, and leaf N and ash contents were significantly lower in longer-lived leaves (evergreen) than shorter-lived leaves (deciduous) species. Leaves of evergreen species also had significantly higher heat of combustion and lower crude fat content than leaves of deciduous species. On a leaf area basis, P_{max} was highest in leaves of evergreen species, but on a leaf dry mass basis it was highest in leaves of deciduous species. P_{max} and total Kjeldahl N content were linearly correlated across all eight species, and foliar N content was higher in leaves of deciduous than evergreen species. Leaf construction cost was significantly higher and maintenance costs were lower for leaves of evergreen than deciduous species. Maintenance and construction costs were linearly related to each other across all species. Leaves of evergreen species had a higher cost-benefit ratio compared to leaves of deciduous species but with longer lived leaves, the payback interval was longer in evergreen than deciduous species. These results support the hypotheses that longer lived leaves are more expensive to construct than short-lived leaves, and that a higher investment of N into short-lived leaves occurs which supports a higher P_{max} over a shorter payback interval.

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Abbreviations: GE, glucose equivalents per dry mass; P_{max}, rate of radiant energy-saturated assimilation; PAR, photosynthetically active radiation; SLA, specific leaf area; TKN, total Kjeldahl nitrogen.

Additional keywords: ash; deciduous and evergreen trees; fat; heat of combustion; maintenance and construction costs; nitrogen content; photosynthetic rate; specific leaf area.

Introduction

Savannas consist of a discontinuous upper layer of trees above a continuous layer of grasses (Huntley and Walker 1985) and are a significant global biome. Within Australia they cover approximately 25 % of the continent. Despite an apparent structural simplicity, species diversity can be high (Bowman *et al.* 1991). Tropical savannas are characterised by highly seasonal rainfall; approximately 93 % of average annual rain falls during 6 months of the year in the 'Top End' of the Northern Territory of Australia (Duff *et al.* 1997). Such seasonality may significantly impact upon physiology and phenology of trees.

There are four phenological guilds present amongst woody species of north Australian savannas: evergreen, brevi-deciduous, semi-deciduous, and deciduous (Williams *et al.* 1997). A full canopy is maintained all year and leaf turnover is continuous in evergreen species; brevi-deciduous species have a brief reduction of canopy area but this reduction is never more than 50 % and does not occur every year; semi-deciduous species exhibit a reduction in canopy area every year of 50 % or more; deciduous species are leafless for at least one month every year (Williams *et al.* 1997). Each guild is represented in approximately equal proportions of species and such an even distribution of species across phenologies is unusual within savannas. Evergreen species dominate South American savannas (Monasterio and Sarmiento 1976, Medina and Silva 1990); deciduous species dominate African and Indian savannas (Chidumayo 1990, Yadava 1990), and in tropical dry forests of Venezuela, deciduous species dominate (Sobrado 1991).

Cost-benefit analyses allow quantification and comparison of the costs and benefits of various structures or strategies employed by plants of differing plant form or phenology. For foliar cost-benefit analysis, construction and maintenance costs of leaves are compared with the benefit accrued in terms of carbon fixation. Construction costs can be calculated from investigations of the biochemical pathways involved in construction of the major components of biomass (Penning de Vries 1975). From detailed analyses of the biosynthetic pathways utilised, the quantity of glucose required to supply carbon skeletons, ATP, and NADPH can be calculated. Alternatively, an elemental analysis of the major components of biomass (McDermitt and Loomis 1981) can be undertaken, whereby leaf composition is determined and the carbon requirements determined. Both of these approaches are extremely labour and equipment intensive (Prichard 1996). Merino *et al.* (1982) used growth and CO_2 exchange analyses for calculation of construction costs. This approach is based upon the fact that leaf construction requires the metabolism of saccharides to supply energy for synthetic processes but also requires saccharide input for the synthesis of structural components. Such measurements are slow and can be difficult to make in tropical field environments.

Construction costs of leaves account for the carbon or energy required to produce a net gain in dry mass, including carbon actually incorporated into new biomass by assimilation and any saccharide metabolised to produce ATP and NADPH/NADH for biosynthetic processes, transport processes, and nutrient uptake and reduction (Chiariello *et al.* 1989). Construction cost is calculated from organic nitrogen content, ash-free heat of combustion, and ash content of leaves (Merino 1987, Williams *et al.* 1987, Sobrado 1991). Glucose provides electrons for oxidative biochemical pathways and is also considered the starting material for the synthesis of carbon skeletons (McDermitt and Loomis 1981), hence the use of the term glucose equivalent (GE) as a unit of energy for the plant.

The concept of glucose as equivalent energy units for construction costs, developed by Penning de Vries (1975), was extended by Williams *et al.* (1987) but they used heat of combustion, ash content, and tissue organic nitrogen costs for the calculation of construction costs. A comparison of the biochemical and elemental analysis approaches, the growth and CO_2 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.

Maintenance costs of leaves include all the processes requiring energy but not resulting in a net increase in dry matter, such as maintenance of ion gradients and turnover of macromolecules such as proteins and membranes (Chiariello *et al.* 1989). Thus maintenance costs can be calculated from knowledge of ash, lipid, and protein contents of leaves and their respective maintenance coefficients (Merino *et al.* 1984). Maintenance also includes the processes of physiological adaptation that maintain cells as active units in a changing environment (Penning de Vries 1975), but this is a conceptual feature that is difficult to measure in short time periods.

Coefficients for requirements of maintaining plant biomass were proposed by Penning de Vries (1975) and modified by Merino *et al.* (1984). Maintenance costs of leaves include all processes that consume energy but which do not directly result in carbon gain. Poorter (1994) states that there is hardly any evidence to support the view that species with long-lived leaves have higher construction costs than species with a shorter leaf life-span, despite there being theoretical reasons for believing such a relationship exists (Williams *et al.* 1989, Reich *et al.* 1992). Consequently this paper addresses several questions that together culminate in answering the question – is there a relationship between cost-benefit relationships and phenology? Thus we ask: do species of differing phenologies have different rates of radiant energy-saturated assimilation and can this be related to foliar nitrogen contents? Is the P_{max}/N relationship the same for deciduous and evergreen savanna species? Can a cost-benefit analysis of construction and maintenance costs and assimilation be applied to the dominant evergreen, semi-deciduous, and deciduous species of a north Australian savanna? Do deciduous and evergreen species differ in their cost-benefit relationships? We also tested the hypothesis that evergreen trees invest more heavily in the construction of longer-lived leaves but the rate of return of fixed carbon is smaller (per unit dry mass invested in leaf) whilst deciduous species, with short-lived leaves invest more nitrogen into their leaves, thereby maintaining a larger P_{max} over the shorter lifespan of the leaf.

Materials and methods

Study site and plants: The study was carried out at Solar Village (12°37'S, 131°10'E) 35 km south-east of Darwin, in the Northern Territory of Australia. Vegetation is open forest (sensu Specht 1981) dominated by *Eucalyptus tetrodonta* (F. Muell) and *E. miniata* (Cunn. *ex* Schauer) with sub-canopy dominants mostly comprised of *Erythrophleum chlorostachys* (F. Muell.) Baillon, *Xanthostemon paradoxus* (F. Muell.), and *Terminalia ferdinandiana* (Excell). Perennial and some annual grasses (*Sorghum, Chrysopogon, Ericahne* spp.) are present in the understorey. Rainfall is approximately 1600 mm per annum, 90 % of which falls in the months December-March (the wet season). Temperatures are high all year with mean monthly max/min temperatures of 31.8/24.8 °C in the wet season and 30.5/20.0 °C in the dry season. Seasonal variations in micro-climate, water relations, and phenology of trees at this site have been described in detail by Duff *et al.* (1997), Myers *et al.* (1997), and Williams *et al.* (1997).

Eight species were chosen to represent the dominant (in terms of standing biomass) evergreen, semi-deciduous, and deciduous species and to complement the studies of Williams *et al.* (1997), Myers *et al.* (1997), and Prior *et al.* (1997a,b). Three deciduous species (*Planchonia careya, Terminalia ferdinandiana, Cochlospermum fraseri*), three semi-deciduous species (*Erythrophleum chlorostachys, Xanthostemon paradoxus, Eucalyptus clavigera*), and two evergreen species (*Eucalyptus tetrodonta, E. miniata*) were chosen for analyses.

Field measurements: Between 5 and 7 replicate trees per species were sampled for P_{max}, specific leaf area (SLA), total Kjeldahl nitrogen (TKN), crude fat, ash and ash-free heat of combustion (see below). Trees were between 4 and 7 m tall. Scaffolding was used to access the upper canopies.

Assimilation rate: P_{max} was measured with a *Li-Cor 6200* portable photosynthesis unit (*Li-Cor Instruments*, Nebraska, USA). Three leaves from each of seven trees were measured in the morning (between 09:00 and 12:00 h under saturating irradiance (PAR > 1000 μmol m^{-2} s^{-1}) of February/March when assimilation rate is highest in this environment (Eamus and Cole 1997, Prior *et al.* 1997a,b). Fully expanded, healthy leaves were selected from the upper canopy of each tree.

Foliar nitrogen, fat, and ash contents: After measuring P_{max} the same leaves plus several additional leaves, similar in size and location on the branch, were removed and stored in damp plastic bags until return to the laboratory (typically 2-4 h). Leaf area was determined using a *Delta-T* leaf area meter (*Delta-T Devices*, Cambridge, England). Leaves were then dried in an oven at 70 °C to constant mass. Dried leaves were ground to pass through a 2 mm mesh screen in a hammer mill *5657* (*Retsch,* Haan, Germany) and then further ground in a mechanical mortar and pestle.

All chemical analyses were performed in duplicate for each leaf sample. TKN in a 0.2 g sample was determined using a micro-Kjeldahl method (Helrich 1990). Digests were performed with concentrated sulphuric acid on block digesters. Initial block temperature was 160 °C which was ramped up to 390 °C in 60 min and held at that temperature for 2 h. Quantitative analyses were performed by flow injection analysis (*Lachat Instruments QuikChem* method *13-107-06-2-D*). Crude protein was calculated as the product of TKN and 6.25 (AOAC 1990).

Crude fat was measured gravimetrically following diethyl ether extraction using Soxhlet extraction glassware (Helrich 1990). Samples of 1 g were extracted in 70 cm^3 diethyl ether and duplicates yielded less than 2 % variation. A stearic acid standard determined extraction efficiency.

Ash content was determined after combustion to a white-grey end-point at 500 °C for 3 h. Pre-heated (to remove moisture) crucibles were weighed immediately prior to addition of ground, dried leaf material. Following the combustion, crucibles were cooled in a desiccator.

Heat of combustion was measured using a *1421* semi-micro bomb calorimeter (*Parr Instruments*, Illinois, USA) using 0.2 g samples. Benzoic acid pellets were used to calibrate the bomb. Ash-free heat of combustion was calculated by converting the heat of combustion on a total dry mass basis to the corresponding ash-free mass.

Calculation of costs: Construction costs were calculated from the equation given in Williams *et al.* (1987):

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

where C = construction costs [kg(glucose equivalent) kg^{-1}(DM)], H_c = ash-free heat of combustion [MJ kg^{-1}], A = ash content [kg(ash) kg^{-1}], N = total Kjeldahl nitrogen [kg(N) kg^{-1}(DM)], k = +5 when N is imported as nitrate into the plant, giving the maximum construction costs, or k = -3 when N is imported as ammonia, giving minimum costs.

Maintenance costs [kg(GE) kg^{-1}(DM) d^{-1}] were calculated following Merino *et al.* (1984), using biochemical pathway analyses. The following maintenance coefficients were used: fat: 0.0425 kg kg^{-1}; protein: 0.028 kg kg^{-1} (minimum), 0.053 kg kg^{-1} (maximum); ash: 0.060 kg kg^{-1} (minimum), 0.010 kg kg^{-1} (maximum).

Statistical analyses were performed on *Systat* Software. Differences in construction costs and maintenance costs, P_{max}, ash and N contents, and heat of combustion were analysed between species using nested ANOVA. Where significant differences were found, Tukey's pairwise comparison of means was applied. ANOVA was also used to compare the means of pooled species within the three phenological guilds. A significance value of 0.05 or less was used throughout.

Results

The ash, fat, and N concentration of leaves of deciduous species was significantly larger than that of the semi-deciduous species, which in turn was larger than that of

Table 1. Fat, ash, and nitrogen contents, heat of combustion, and specific leaf area (SLA) (± SE) for the three phenological guilds (D - deciduous, S - semideciduous, E - evergreen) examined in savanna species of northern Australia. Means followed by a different letter within a column are significantly different ($p<0.05$).

		Ash [g kg^{-1}]	Fat [g kg^{-1}]	Heat of comb. [MJ kg^{-1}]	N [g kg^{-1}]	SLA [m^2 kg^{-1}]
Cochlospermum fraseri	D	67.0±0.4	49.2±2.2	21.75±0.32	17.7±0.9	19.98±0.85
Planchonia careya	D	40.1±2.1	38.5±4.7	21.62±0.34	13.5±1.0	10.14±0.36
Terminalia ferdinandiana	D	46.9±1.3	59.5±0.9	19.81±1.02	13.6±5.0	10.16±0.30
Erythrophleum chlorostachys	S	22.7±1.6	44.6±8.0	22.30±0.49	22.0±4.0	10.94±0.26
Eucalyptus clavigera	S	42.1±4.8	45.5±6.7	21.87±0.28	10.4±2.0	7.15±0.22
Xanthostemon parodoxus	S	43.8±1.0	41.5±3.0	19.62±0.14	11.0±1.0	12.50±1.31
Eucalyptus miniata	E	23.5±2.1	46.9±3.6	22.20±0.22	17.0±5.0	8.07±0.22
Eucalyptus tetrodonta	E	33.5±3.6	33.0±3.3	21.67±0.12	9.1±1.0	7.25±0.31
Deciduous		51.3^a	49.1^a	20.94^a	14.9^a	13.43^a
Semi-deciduous		34.2^b	43.9^b	21.26^a	14.6^a	10.20^b
Evergreen		32.2^c	39.9^c	21.90^b	13.0^b	7.66^c

the evergreen species (Table 1). Similarly the SLA of leaves increased from evergreen through semi-deciduous to deciduous species. In contrast, the heat of combustion declined from evergreen through semi-deciduous to deciduous species (Table 1).

Maximum construction costs expressed on a leaf area or dry mass basis increased from deciduous through semi-deciduous to evergreen species (Table 2). In contrast, maximum maintenance costs either increased from deciduous to evergreen phenological groups when expressed on a leaf area basis or decreased when expressed on a leaf dry mass basis (Table 2).

P_{max} expressed on an area basis was largest in the evergreen species and declined through semi-deciduous and deciduous species. This trend was reversed when P_{max} was expressed on a dry mass basis (Table 3). P_{max} was linearly related to foliar N content (Fig. 1) with all species showing the same relationship. Construction costs

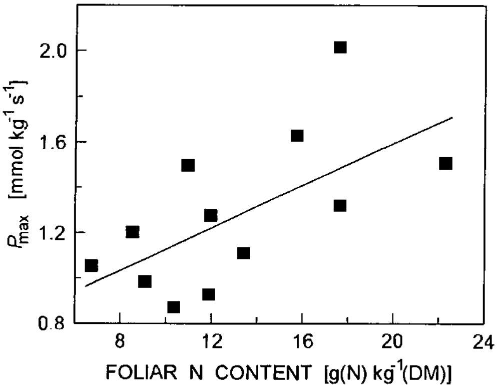

Fig. 1. Maximum photosynthetic rate (P_{max}) increased with increasing foliar nitrogen content in 8 savanna tree species. Regression equation is: P_{max} = 0.0055(N content) + 0.052; $p < 0.05$.

were linearly correlated to maintenance costs for all species (Fig. 2).

Table 2. A summary of construction and maintenance costs (±SE) of 8 tree species of Australian savannas, expressed on leaf dry mass and leaf area bases. For abbreviations see Table 1.

		Construction cost		Maintenance cost	
		[kg kg^{-1}]	[g m^{-2}]	[g kg^{-1} d^{-1}]	[g m^{-2} d^{-1}]
Cochlospermum fraseri	D	1.590±0.029	79.50±1.44	9.70±2.90	0.490±0.147
Planchonia careya	D	1.600±0.023	157.40±2.24	6.60±0.57	0.650±0.056
Terminalia ferdinandiana	D	1.520±0.021	149.60±0.74	7.10±0.86	0.690±0.070
Erythrophleum chlorostachys	S	1.660±0.049	151.70±4.44	9.70±0.86	0.880±0.079
Eucalyptus clavigera	S	1.580±0.050	220.80±7.05	5.90±0.64	0.820±0.089
Xanthostemon parodoxus	S	1.440±0.012	114.60±1.00	5.80±0.15	0.460±0.012
Eucalyptus miniata	E	1.660±0.084	206.00±1.05	7.70±0.81	0.950±0.101
Eucalyptus tetrodonta	E	1.610±0.023	222.50±3.15	5.70±0.29	0.650±0.041
Deciduous		1.56^{a}	129.0^{a}	7.80^{a}	0.610^{a}
Semi-deciduous		1.56^{a}	162.4^{b}	7.10^{b}	0.720^{b}
Evergreen		1.64^{c}	214.3^{c}	6.70^{c}	0.610^{a}

The cost-benefit ratio defined as the ratio of construction costs to P_{max} (Sobrado 1991) increased from deciduous (11.6) through semi-deciduous (13.1) to evergreen (14.7) species when expressed on a leaf dry mass basis.

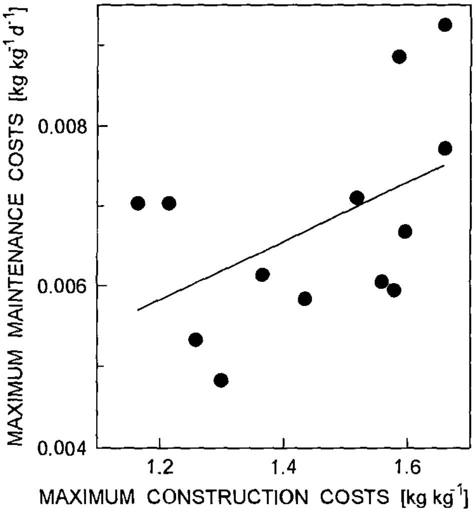

Fig. 2. Linear correlation between construction and maintenance costs across 8 savanna tree species. Regression equation is: Maintenance costs = 0.0033(construction costs) + 0.002; $p<0.05$.

Discussion

Different phenological guilds differ in average leaf lifespan. Approximate leaf life spans are 12 months for evergreen and 9 months for deciduous species (Williams *et al.* 1997, Myers *et al.* 1998). Thus evergreen species are able to fix carbon all year

Table 3. A summary of assimilation rate (±SE) and cost/benefit ratio of eight tree species of Australian savannas. P_{max} - maximum photosynthetic rate; for other abbreviations see Table 1.

		P_{max}		Cost/benefit ratio
		[μmol m^{-2} s^{-1}]	[nmol g^{-1} s^{-1}]	[g s μmol^{-1}]
Cochlospermum fraseri	D	12.4±0.5	248±10	6.60
Planchonia careya	D	10.8±0.7	110±7	14.55
Terminalia ferdinandiana	D	10.7±0.6	109±6	13.93
Erythrophleum chlorostachys	S	13.6±0.7	149±5	11.17
Eucalyptus clavigera	S	12.0±0.5	86±5	18.41
Xanthostemon parodoxus	S	11.9±0.5	149±6	9.70
Eucalyptus miniata	E	116.6±0.1	131±8	12.72
Eucalyptus tetrodonta	E	15.3±0.7	100±5	16.60
Deciduous		11.3^{a}	160^{a}	11.60^{a}
Semi-deciduous		12.5^{b}	128^{b}	13.10^{b}
Evergreen		16.0^{c}	116^{b}	14.65^{b}

whilst deciduous species cannot (Prior *et al.* 1997a,b), as long as access to water remains sufficient for stomatal opening during the dry season (Prior *et al.* 1997b). It is not immediately apparent, therefore, how deciduous species (and semi-deciduous species which lose more than half of their canopy most years) remain competitive with evergreen species in the same environment. Cost-benefit analysis is one means of assessing the relative benefits of competing phenological strategies. Construction costs include construction of cell walls, membranes, and other materials (Chiariello *et al.* 1989) whilst maintenance costs include turnover of proteins, membranes, and other materials, and the maintenance of ionic gradients (Penning de Vries 1975).

Nitrogen contents of deciduous species were larger than those of semi-deciduous and evergreen species (Table 2), as has been observed previously (Medina 1984, Sarmiento *et al.* 1985, Reich *et al.* 1992, 1995). The relatively low N content observed in the present study is consistent with the low nutrient status of the highly weathered and leached soils of tropical Australia.

On a leaf area basis, P_{max} was significantly larger in evergreen species than in semi-deciduous or deciduous species. However, this was because the SLA of evergreen species was significantly smaller than that of the other two groups. Thus the same leaf area of a deciduous species contains less leaf mass than the same area of an evergreen species. Similar results have been obtained previously (Chabot and Hicks 1982, Sarmiento *et al.* 1985, Reich *et al.* 1992). The larger P_{max} of the deciduous species on a dry mass basis was supported by the larger foliar N content of deciduous species. Linear relations between foliar N and P_{max} are generally observed (Evans 1987, Givnish 1988) because of the large amount of N invested in photosynthetic apparatus.

Reich *et al.* (1992, 1995) showed that the relationship (on an area basis) between N content and P_{max} differed between species having different leaf life spans; they related this to differences in nutrient status of soils on which conifers, evergreen and deciduous broadleaves were found in their study. In our study, the different phenological guilds co-exist on the same substrate and therefore the relationship between P_{max} and N content may be expected to be the same for all species, as was observed (Fig. 1).

Nitrogen and ash contents of leaves of deciduous trees were higher than in evergreen species. Similarly, Chabot and Hicks (1982) observed that deciduous species have a higher ash content than evergreen species. This may result from the larger stomatal conductance of deciduous trees which finally results in a large flux of water, and hence nutrients, to the leaves (Masle *et al.* 1992).

Heat of combustion was higher in evergreen than deciduous and semi-deciduous species, as has been observed by Sobrado (1991). This larger heat of combustion reveals a higher energy content of the leaf, which means a higher energy of storage in evergreen leaves. This is further reflected in the larger construction costs of evergreen species (Table 2). Large lipid contents of leaves correlate well with the cost of construction (McDermitt and Loomis 1981, Merino *et al.* 1984). The fat content of evergreen species was lower than that of deciduous and semi-deciduous species, despite the larger heat of combustion. The larger heat of combustion reflects the accumulation of aromatic oils in the two eucalypt species.

Construction costs determined in our study were within the typical range for leaves (Griffin 1994, Poorter 1994). Poorter (1994) concluded that there was very little evidence for differences in construction costs between deciduous and evergreen species. Similarly, Merino (1987) found no difference in construction costs between evergreen and deciduous tree species. In the present study, construction costs of evergreen species were larger than those of deciduous or semi-deciduous species. This is in contrast to results of Merino *et al.* (1982, 1984) and 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 subject to herbivore attack than short-lived leaves (Reich *et al.* 1992). Consequent investment in secondary compounds for defense may be higher in leaves of evergreen than deciduous trees. This may also contribute to the larger leaf construction costs of evergreen species (Reich *et al.* 1992). Our present results support the hypothesis that leaf construction costs are correlated with life span.

Maintenance costs were higher for leaves of deciduous than evergreen species, on a dry mass basis. Low maintenance costs are generally associated with longer lived foliage which is often sclerophyllous and has a high structural component and low turnover rate (Merino *et al.* 1982, 1984, Sobrado 1991). The high N and fat contents of deciduous leaves presumably reflect high protein and lipid contents, which unlike cell walls have a high rate of turnover.

Cost-benefit ratio can be defined as the ratio between investment (construction costs) and potential payback (P_{max}) (Sobrado 1991). This ratio was largest in the evergreen species which supports the hypothesis that leaf life span is correlated with cost-benefit ratio (Williams *et al.* 1989, Sobrado 1991). Evergreen trees invested less N into their foliage per unit dry mass, which supported a lower P_{max}, than deciduous or semi-deciduous species. However, maintenance costs were lower and most importantly the pay-back interval for each leaf was approximately 70 % longer in evergreen than deciduous species. Thus the higher cost-benefit ratio of evergreen trees is made possible only by the longer time available for carbon fixation in these leaves.

An alternative approach to the cost-benefit ratio calculated above (suggested by an anonymous referee of the ms.) is to calculate the profit, that is, ratio of return (in amount of carbon fixed) after removing respiratory losses which account for maintenance costs, to investment (in amount of carbon) in constructing the leaf. Thus:

Profit = [(amount of C fixed per d - amount of C respired per d)×(payback interval)]/(amount of C invested in constructing the leaf)

This analysis has the merit of explicitly taking into account the relative payback interval of different species and also expresses investment and return in the same units. In the following calculation we assume the following: (*1*) the maximum rate of radiant energy-saturated assimilation is proportional to the total amount of C fixed in a day by the leaf; (*2*) long and short-lived leaves experience the same irradiance (which is probably true in savannas of north Australia where trees are spaced apart and the canopies of adjacent trees do not overlap); and (*3*) the rate of respiration is a fixed proportion of P_{max} (see Givnish 1988) and set at 8 %. Using the equation above and setting leaf life-span as 360 and 270 d for evergreen and deciduous species, respectively (Myers *et al.* 1998), and converting construction costs to kg(C) kg^{-1} rather than kg(glucose equivalent) kg^{-1} and assuming a 10 h day, profit becomes 2.45×10^4 % for evergreen and 2.70×10^4 for deciduous species. This is a very large number because the leaves (which account for about 1 % of the total tree biomass in this ecosystem) must support the growth and respiration requirements of the entire tree.

The profit is larger for deciduous species, a similar conclusion to that based on the previous cost-benefit analyses (which is calculated using the inverse relationship between cost and return as that used in calculating profit), where the cost-benefit ratio was larger for evergreen species. The profits of the two extreme phenologies are not as different as perhaps may have been expected. We conclude that this may partially explain why the evergreen and deciduous species do not exclude each other from the savannas of north Australia. Because the profit margin is similar for the two phenologies, no single phenology is able to completely exclude the other. We have not calculated the profit for semi-deciduous species because we do not have reliable average leaf life-spans. Finally, we suggest that evergreen and deciduous species do not compete for water in this seasonally arid environment. In the wet season, water is supra-abundant, and therefore not limiting. In the dry season, deciduous species drop all of their leaves and therefore do not access deep water used by evergreen species. Because the species do not compete for water, co-existence of these extremes of phenological behaviour is allowed.

In conclusion, the P_{max} per unit leaf dry mass invested in foliage of deciduous species of north Australian savanna species is higher than that of evergreen species.

This higher P_{max} results from the larger N investment in deciduous leaves. In addition, the construction costs per unit dry mass are considerably smaller in deciduous species, and consequently the cost-benefit ratio of evergreen trees is larger than that of deciduous and semi-deciduous species. The hypothesis that longer lived foliage has larger construction costs is supported. The pay-back interval for evergreen trees is larger than for deciduous and semi-deciduous species, and thus the larger cost-benefit ratio is produced by the longer time for carbon fixation per leaf.

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