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Near-ground solar radiation along the grassland–forest continuum: Tall-tree canopy architecture imposes only muted trends and heterogeneity

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Abstract Solar radiation directly and indirectly drives a variety of ecosystem processes. Our aim was to evaluate how tree canopy architecture affects near-ground, incoming solar radiation along gradients of increasing tree cover, referred to as the grassland–forest continuum. We evaluated a common type of canopy architecture: tall trees that generally have their lowest level of foliage high above, rather than close to the ground as is often the case for shorter trees. We used hemispherical photographs to estimate near-ground solar radiation using the metric of Direct Site Factor (DSF) on four sites in north Queensland, Australia that formed a grassland–forest continuum with tree canopy cover ranging from 0% to 71%. Three of the four sites had tall *Eucalyptus* trees with foliage several metres above the ground. We found that: (i) mean DSF exceeded >70% of the potential maximum for all sites, including the site with highest canopy cover; (ii) DSF variance was not highly sensitive to canopy coverage; and (iii) mean DSF for canopy locations beneath trees was not significantly lower than for adjacent intercanopy locations. Simulations that hypothetically placed Australian sites with tall tree canopies at other latitude–longitude locations demonstrated that differences in DSF were mostly due to canopy architecture, not specific site location effects. Our findings suggest that tall trees that have their lowest foliage many metres above the ground and have lower foliar density only weakly affect patterns of near-ground solar radiation along the grassland–forest continuum. This markedly contrasts with the strong effect that shorter trees with foliage near the ground have on near-ground solar radiation patterns along the continuum. This consequence of differential tree canopy architecture will fundamentally affect other ecosystem properties and may explain differential emphases that have been placed on canopy–intercanopy heterogeneity in diverse global ecosystem types that lie within the grassland–forest continuum.

Key words: Australia, energy balance, *Eucalyptus*, field, savanna, shading, woodland.

INTRODUCTION

A commonly used descriptor of vegetation at a site is the amount of canopy coverage by woody plants – trees and shrubs. This coverage, and its height, differentiates grasslands, shrublands, savannas, woodlands and forests (Coffin & Urban 1993; Belsky & Canham 1994; Anderson *et al.* 1999; Breshears & Barnes 1999; Breshears 2006). Indeed, a large portion of the terrestrial biosphere can be viewed as a continuum of increasing cover by woody plants spanning a gradient from grassland with no woody cover to forests with complete canopy cover. This gradient is referred to as the grassland–forest continuum (Breshears & Barnes 1999; Martens *et al.* 2000; House *et al.* 2003; Breshears 2006). The amount and patchiness of tree cover (or, where appropriate, shrub cover) at a site not only helps determine vegetation type, but also determines many landscape processes and ecosystem attributes related to the dynamics of energy, water and biogeochemistry (e.g. Belsky *et al.* 1989; Vetaas 1992; Scholes & Archer 1997; Klopatek *et al.* 1998; Hibbard *et al.* 2003; Ludwig *et al.* 2005; Breshears 2006) and affects biodiversity (e.g., Ludwig *et al.* 2000).

One of the most direct ways that tree canopies modify the environment is through the shading patterns or mosaics that they produce. The areas beneath tree canopies often receive substantially less near-ground solar radiation than the intercanopy patches between trees (Breshears *et al.* 1997; McPherson 1997). For example, differences in near-ground solar radiation translate into distinct patterns of soil temperature (Breshears *et al.* 1998), which in turn affects soil evaporation (Breshears *et al.* 1998) and soil respiration (Klopatek *et al.* 1998; Murphy *et al.* 1998).

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Shading patterns depend on numerous factors, including the amount of tree canopy cover and the branching pattern and foliar density of the canopy (Martens *et al.* 2000). Tree canopy height, especially the height of the lower canopy also affects shading. The spatial pattern of trees at a site and site location (latitude, longitude, altitude) can also affect shading.

Simulations of different patterns of tree canopy structure have sought to find general trends in near-ground solar radiation (Martens *et al.* 2000). Studies to date have focused on sites with shorter trees with dense canopies. Findings support several hypothesized trends about how near-ground solar radiation varies as tree canopy cover varies from 0% to nearly 100%, such as how mean solar radiation decreases linearly with increases in tree cover when tree height is held constant. Two key questions still need to be explored: (i) how is near-ground solar radiation affected by taller trees with less dense canopies, especially for where the lowest height of the canopy is farther above the ground than for shorter trees, and (ii) how this radiation is affected at the canopy–intercanopy patch (within site) scale.

Based on previous related studies that consider how the density and height of trees influence near-ground solar radiation and its spatial variation at a plot (Martens *et al.* 2000), we hypothesize that (i) mean near-ground solar radiation decreases in a sigmoidal fashion as lower-canopy height increases with increasing tree canopy cover and (ii) mean near-ground solar radiation decreases with increasing canopy cover for both canopy and intercanopy patches but the point of equal variance between canopy and intercanopy patch types occurs at an intermediate amount of tree cover, which is less than 50%. These two hypotheses provide a useful framework for evaluating general trends across the grassland–forest continuum.

Tree canopy simulation studies to date (Martens *et al.* 2000) treated tree canopies as ellipses, such that foliage extended down to near the ground surface (Fig. 1). However, many tropical savanna and woodland trees, such as species of *Eucalyptus* (e.g. Gillison 1994), have tall canopies (>10 m) with foliage limited to the upper portion of the tree (Fig. 1). Because incoming near-ground solar radiation is determined in large part by solar angles other than from directly above, these two contrasting tree architectures are likely to produce different patterns of near-ground solar radiation. Differences in near-ground solar radiation would be expected even if foliar density between the lower and upper heights was similar for contrasting tree architectures and could be further amplified if taller trees also had a lower foliar density, as might be expected.

The second characteristic of tree canopy architecture among various sites that requires further consideration is the location of the site itself, particularly with respect to both latitude and direction (northern *vs.* southern hemisphere). Solar radiation patterns for the tropics differ from those in temperate regions with respect to temporally dependent solar angles. The hypothesized trends discussed above are based on simulations for mid-latitudes (~35°) of the northern hemisphere (Martens *et al.* 2000). Are these trends also applicable to other latitudes, including the southern hemisphere?

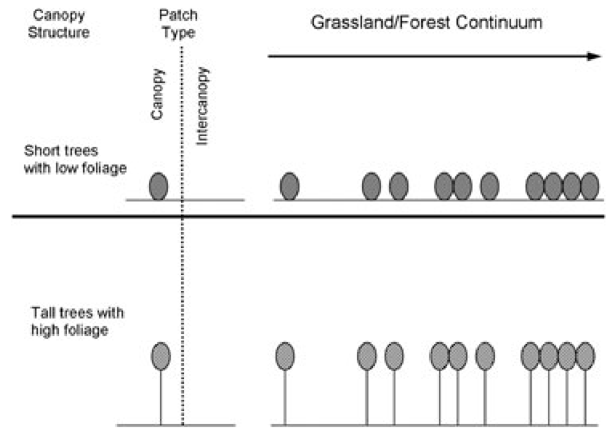

Fig. 1. Individual trees with two architectures and associated gradients along the grassland–forest continuum for trees with lower foliage near the ground and taller trees with lower foliage far (several metres) above the ground.

Our overall aim was to evaluate how patterns of near-ground solar radiation varied along a grassland–forest continuum, especially for taller trees where the lower limit of canopy foliage is several metres above the ground (hereafter referred to as tall trees-foliage). Our specific aims were (i) to evaluate trends in site-scale means and variances of incoming near-ground solar radiation for tall trees-foliage with tree canopy cover spanning the grassland–forest continuum, (ii) to evaluate trends in patch–scale heterogeneity for canopy patches *versus* intercanopy patches; and (iii) to compare and evaluate differences in near-ground solar radiation between sites with an intermediate amount of tree cover for tall trees with high foliage *versus* short trees with low foliage.

Our goal was to provide a better understanding of how shading affects attributes along the grassland–forest continuum, which comprises a significantly large fraction of the terrestrial biosphere. Our approach was to use hemispherical photography (Rich 1990). Many approaches exist for estimating overall light attenuation in tree canopies (e.g. Gates 1980; Terborgh 1985; Kucharik *et al.* 1999; Eagelson 2002; Geiger *et al.* 2003), but do not explicitly assess spatial variation. Additional modelling approaches evaluate surface radiation trends using canopy surfaces (e.g. Hetrick *et al.* 1993; Rich *et al.* 1995). Our approach differs from these latter approaches in that hemispherical photos capture variations in canopy architecture.

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We discuss our findings in the context of savannas and other ecosystems that are intermediate within the grassland–forest continuum with respect to the role that tree canopy architecture might play on determining spatial variation in solar radiation and associated responses.

STUDY SITE

Our study site was located along Rocky Creek, 5 km northwest of Tolga in north Queensland, Australia (17.20°S, 45.43°E; elevation 720 m; Fig. 2). We positioned four 100-m transects within the study site. Transects were within 0.8 km of each other and were 75–200 m west of Rocky Creek (Table S1). The surrounding topography was relatively flat, with slopes of 3% or less. Transects were oriented along the general contour. Effects of nearby topography on incoming solar radiation were largely negligible and were limited to minor effects of a low ridge about 2 km west of the study site.

Transects varied in amount of tree canopy, which ranged from 0% to 71%, and ground cover, which ranged from 86% to 100%. The vegetation was dry sclerophyll woodland or mixed eucalypt woodland with the most common canopy trees being narrow-leaved ironbark (*Eucalptus crebra*) and white gum (*Eucalyptus platyphylla*; Tracey 1982). The grass layer was dominated by perennial kangaroo grass (*Themeda triandra*). Charring on the base of ironbark trees (up to 2 m) indicated that the grass layer occasionally burns (about every 3–5 years). There was no evidence of cattle or horse grazing on the study site, although some wallaby droppings were observed. The four transects were located on the same soil type, described as clay loams formed from old, very strongly weathered basaltic lavas (Laffan 1988).

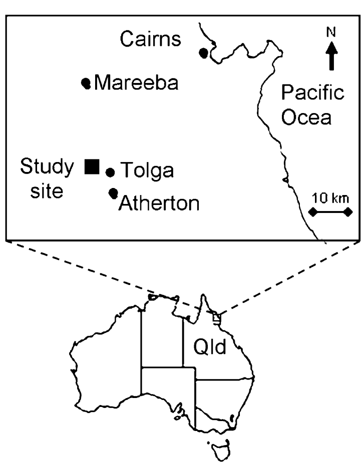

Fig. 2. Study site location in northern Queensland, Australia.

We compared our results with those from another woodland, the Mesita del Buey site in northern New Mexico, USA (34.30°N, 106.27°W, 2140 m) where estimates of near-ground solar radiation have been obtained previously (Breshears *et al.* 1997) and where simulations have been conducted, leading to general grassland–forest continuum hypotheses (Martens *et al.* 2000; Breshears 2006). The Mesita del Buey site is a semiarid piñon–juniper woodland (dominated by *Pinus edulis* Engelm. and *Juniperus monosperma* Sarg.) with nearly 50% tree canopy cover (Padien & Lajtha 1992; Breshears *et al.* 1997; Martens *et al.* 2000). Canopy height based on a mean of all trees over 1 m tall was reported as 2.6 m (Martens *et al.* 2000) but is 6 m tall based on the mean for the taller of the two co-dominant species (*P. edulis*) and nearly 8 m tall based on the 90th percentile of that species (Martens *et al.* 1997).

METHODS

Vegetation cover and foliar density

We measured tree canopy cover using the line-intercept method by estimating (0.5-m resolution) where a 10-m high pole entered and exited canopy along a 100-m tape (Table S2). The pole was held vertical using a 'bubble' level. The maximum height of each tree canopy was also estimated (0.5-m resolution) using the 10-m pole. The height of the bottom edge of canopy foliage where it first entered and exited the line-transect was also recorded. Tree canopies that overlapped were treated as a contiguous single canopy and only a single pair of lower foliage height estimates was recorded. The line-intercept method was also used to estimate (0.1-m resolution) ground cover in five categories: perennial grass patches, mixed perennial grass–shrub patches, bare soil, litter and logs.

We subsequently estimated canopy volume for use in estimating average foliar density at the Rocky Creek transects, which we then compared with the results from Mesita del Buey. For each tree whose canopy intersected our 100-m transect lines, we measured two canopy widths (one parallel to the line, the other perpendicular) and the tree trunk diameter at 1.3 m (d.b.h.). We calculated the canopy volumes of each tree as a prolate spheroid (an ellipse rotated about its major axis). Foliar density for eucalypt trees at the Rocky Creek transects was based on our measurements of canopy volume and on published foliar data for similar eucalypt species (Prior *et al.* 2004; Cook *et al.* 2005).

Hemispherical photos

We estimated the effect of tree canopies on incoming solar radiation using hemispherical photography.

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Hemispherical photographs capture the geometry of sky obstructions due to plant canopies and can be used to evaluate shading via obstruction by the canopy for all relevant sun angles for a period of interest. In contrast to other approaches for estimating near-ground solar radiation, hemispherical photographs require acquisition of site-specific photos rather than simply a site Digital Elevation Model. Hemispherical photographs capture the full range of surrounding geometry associated with canopy architecture, thereby enabling more robust assessment of site microclimate (Rich 1989; Rich *et al.* 1999).

We obtained hemispherical digital photographs using Delta T's system (Burwell, UK), which uses a Nikon Coolpix 5400 digital camera with a FC-E9 Fisheye lens; field of view is 190° and lens equation coefficients were those recommended by Delta T (a1 = 0.642700, a2 = 0.034600, a3 = –0.024491). Camera settings were also those recommended by the manufacturer (manual SLM5-UM-1.0), which were 'white balance' = auto, 'metering' = matrix, 'image adjustment' = normal, 'saturation' = normal, 'image sharpening' = normal, 'lens' = normal, 'focus' = auto-single autofocus, 'zoom' = off, 'speedlight control' = internal and external active, 'flash exposure compensation' = –2.0 EV and 'flash' = anytime. The exposure was set to auto for all photos. The camera was mounted on a self-levelling mount as described by the manufacturer and placed on a tripod that was collapsed to function as a monopod. All photos were taken at a height of 1 m.

Photos were acquired between 26 and 28 June 2005 during overcast conditions and at dusk so that sky conditions were uniform for subsequent digitizing. Photos were taken every 3 m along each transect beginning at 0 m and ending at 99 m (Table S3). Images were processed using Delta T's Hemi-view software. Conditions were generally very similar for the photos, such that an image threshold of 125 in the HemiView software was applied to the majority of the images. When a different threshold was deemed appropriate, two analysts evaluated multiple optional thresholds and agreed on the threshold yielding results most consistent with those for other images that were processed using the default value. Our analysis does not account for phenological changes associated with wet *versus* dry season but these are expected to be relatively minor (e.g. leaf area in *Eucalyptus tetrodonta*, a species similar to those at our study site, differs by only ~6% between wet and dry seasons; Prior *et al.* 2003, 2004).

Site factor simulations

We used Delta T's HemiView software (HemiView 2.1, Delta-T Devices, Cambridge, UK; Rich *et al.* 1999) to estimate various site factors using the photos from the four Rocky Creek transects. Here, we focused on the annual Direct Site Factor (DSF) metric, which is the fractional amount of annual direct beam radiation that is able to penetrate the canopy, in this case, to 1 m above ground (hereafter referred to as near-ground). This metric is directly related to other ecosystem water and energy processes, such as surface heating, evaporation and respiration (Bonan 2002). Sun and zenith angles were calculated as (Gates 1980; Rich 1989; Rich *et al.* 1999):

$$\beta = \arcsin(\sin ø \cdot \sin \delta + \cos ø \cdot \cos \delta \cdot \cos h), \text{ and}$$

$$\alpha = 2 \arctan((\cos \delta \cdot \sin h)/ (\cos ø \cdot \sin \delta - \sin ø \cdot \cos \delta \cdot \cos h - \cos \beta)),$$

where β is the elevation angle (the compliment of the zenith angle), ø is the latitude, δ is the solar declination for a given date, h is the hour angle, and α is the azimuth angle. Path length for a ray varies with secant of the zenith angle for angles greater than 80°:

$$S_\theta = S_0 \Gamma^{m(\theta)},$$

where S_θ is the radiation flux from direct sunlight when the sun is at a given zenith angle θ, S_0 is the radiation flux outside the atmosphere, Γ is the atmospheric transmittance, and metres is the optical air mass.

Our primary set of analyses of the hemiphotos used the actual latitude, longitude and elevation for the Rocky Creek study site. In addition, we wanted to assess the magnitude of location *versus* canopy structure effects on the differences in mean transect DSF between a transect with intermediate cover, tall trees, and tropical and southern hemisphere latitude at Rocky Creek (17.20°S) and a similar site with intermediate cover, short trees and mid- and northern hemisphere latitude. To do so, we reanalysed the Rocky Creek photos from the Medium cover transect using location information for the Mesita del Buey site (34.30°N); declination remained at Rocky Creek values so that the orientation of canopy structure was held constant relative to true north. To further partition the causes of location effects of hemisphere *versus* other location attributes on site DSF, the Rocky Creek photos were run a third time at the same location as the Mesita del Buey site, but this time set in the southern hemisphere (that is 34.30°S instead of 34.30°N); again declination remained at Rocky Creek values so that the orientation of canopy structure was held constant relative to true north. Differences in mean site DSF from these three runs were used to estimate how much of the site DSF difference between the actual Rocky Creek Medium cover site and the actual Mesita del Buey site, both of which had nearly equal amounts of tree canopy cover at about 50%, were associated with canopy architecture effects, and with locational effects as partitioned between a hemisphere effect and a latitude magnitude, longitude and altitude effect.

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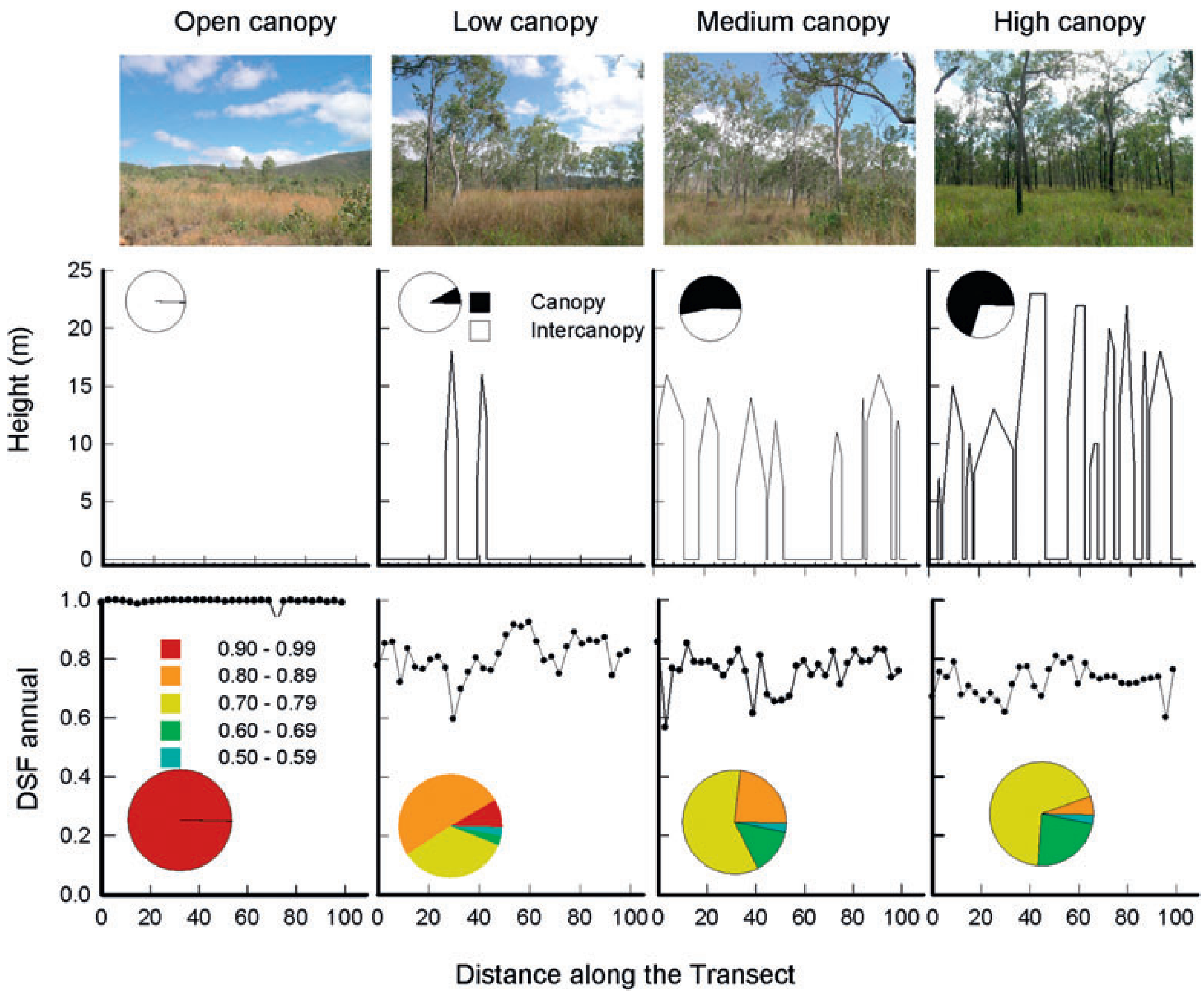

Fig. 3. Study sites spanning the grassland–forest continuum from no to high tree canopy coverage (open, low, medium, high; left to right, top row); height and spatial patterns of canopy coverage (middle row) and associated amounts of tree canopy coverage (pie diagrams, middle row); and fraction of annual near-ground solar radiation estimated as the Direct Site Factor (DSF) along each transect (bottom row) and associated distributions of DSF in five categories (0.5 to 1.0 by 0.1 intervals) (pie diagrams, bottom row).

RESULTS

Grassland–forest continuum trends

The four study transects spanned the grassland–forest continuum from 0% to 71% tree cover, with 0% tree cover and no canopy patches on the Open (grassland) transect, 9% and 2 canopy patches along the Low cover transect, 52% and 8 canopy patches along the Medium cover transect, and 71% and 11 canopy patches along the High cover transect (Fig. 3). Mean tree height across the Low, Medium and High cover transects was 15.3 m (standard deviation = 4.3 m), and mean height to lower edge of foliage across those transects was 10.4 m (standard deviation = 4.1 m).

The four transects varied in mean DSF – the fractional amount of annual direct beam radiation able to penetrate the canopy – and as expected, the mean decreased with canopy cover: 99.3% (standard deviation = 1.2%) for the Open transect, 80.9% (6.8%) for the Low cover transect, 76.0% (6.8%) for the Medium cover transect, and 72.2 (5.0%) for the High cover transect. The distribution of DSF values among 3-m point locations along transects shifted markedly. All the 3-m points along the Open transect had DSF > 90%. In contrast, most of the Low cover transect points had DSF of 80–89%, the Medium site had mostly DSF of 70–79%, and the High cover had mostly DSF of 60–69% (Fig. 3, bottom row). Mean site DSF remained above 70% for all four sites along the grassland–forest continuum and exhibited the sharpest decrease between 0% and 9% tree canopy cover (Fig. 4A). Site variance in DSF among locations was greater at the two intermediate values of cover

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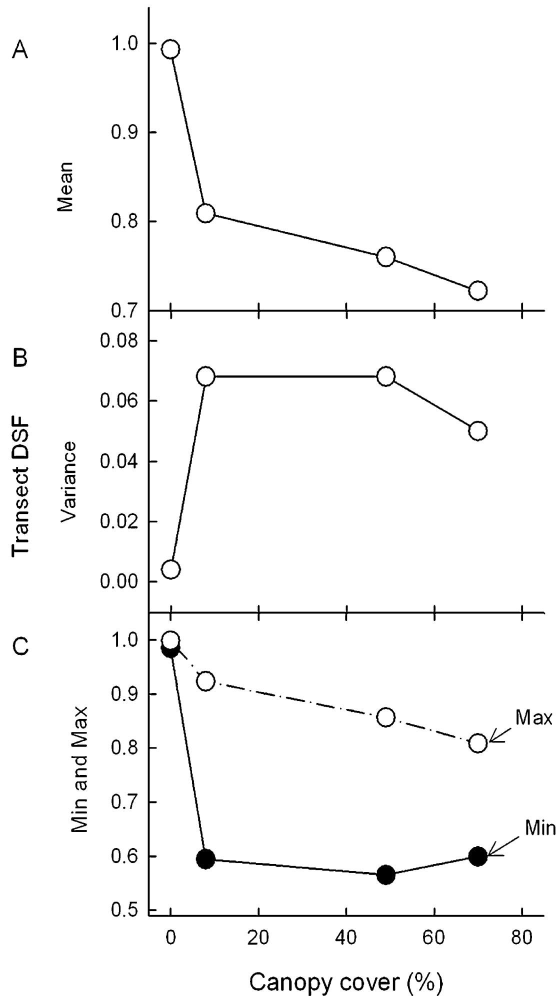

Fig. 4. Fraction of near-ground solar radiation, measured as the Direct Site Factor (DSF), for sites along a grassland–forest continuum of increasing woody plant canopy coverage for site (A) mean, (B) variance and (C) minimum (min) and maximum (max).

(9% and 52%) than at either end of the grassland–forest continuum (0% or 71%), as expected (Fig. 4B); site maximum DSF decreased with cover whereas site minimum DSF dropped off as cover increased from the Open to Low cover site and then remained relatively constant (Fig. 4C).

Canopy and intercanopy patch–scale trends

Canopy locations – those locations estimated to be directly below tree canopies – did not have a significantly lower mean DSF than intercanopy locations for any of the transects with tree cover (Low, Medium and High; Fig. 5A; there are no canopy locations on the Open transect); the magnitude of the mean canopy DSF was slightly lower than that for the corresponding intercanopy mean for each transect but theses differences were not significant. When evaluated with respect to canopy cover in the context of the grassland–forest continuum, mean intercanopy DSF remained relatively stable from 9% to 71% canopy cover. Variance in the canopy patches exceeded that in the intercanopy patches for all three sites with tree cover, and the difference was least for the High cover site (Fig. 5B).

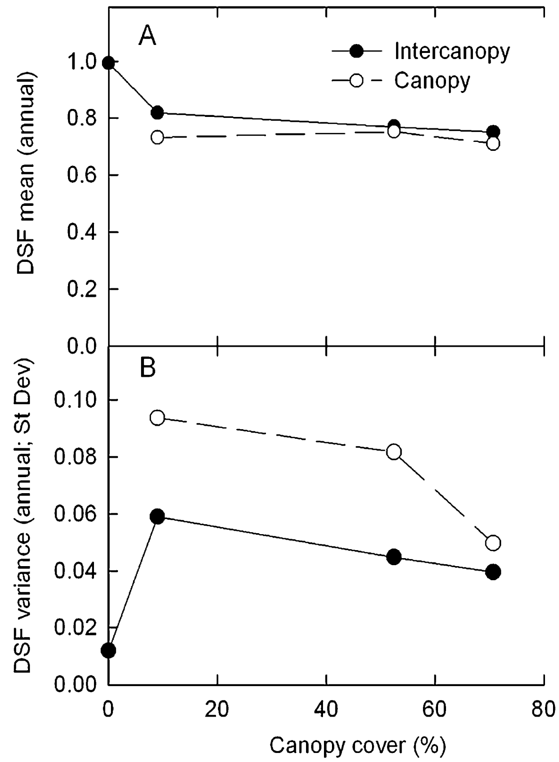

Fig. 5. Fraction of near-ground solar radiation, measured as the Direct Site Factor (DSF), for sites along a grassland–forest continuum of increasing woody plant canopy coverage for locations beneath tree canopies and in intercanopies for (A) mean and (B) variance.

Comparisons for intermediate amounts of tree cover

Cover at the Rocky Creek Medium site (52%) was similar in amount to that at Mesita del Buey (50%), and the two sites differed in both canopy architecture (height, height to lower foliage, foliar density) and in location. The two sites had starkly different patterns of DSF along transect locations (Fig. 6A). Note that both sites had locations receiving about 85% maximum DSF, but the Rocky Creek site had minimum DSF values of about 55% whereas the Mesita del Buey site reached minimum DSF values of nearly 10%. Consequently, the Rocky Creek Medium site mean DSF was much greater than that for Mesita del Buey (76% *vs.* 51% respectively).

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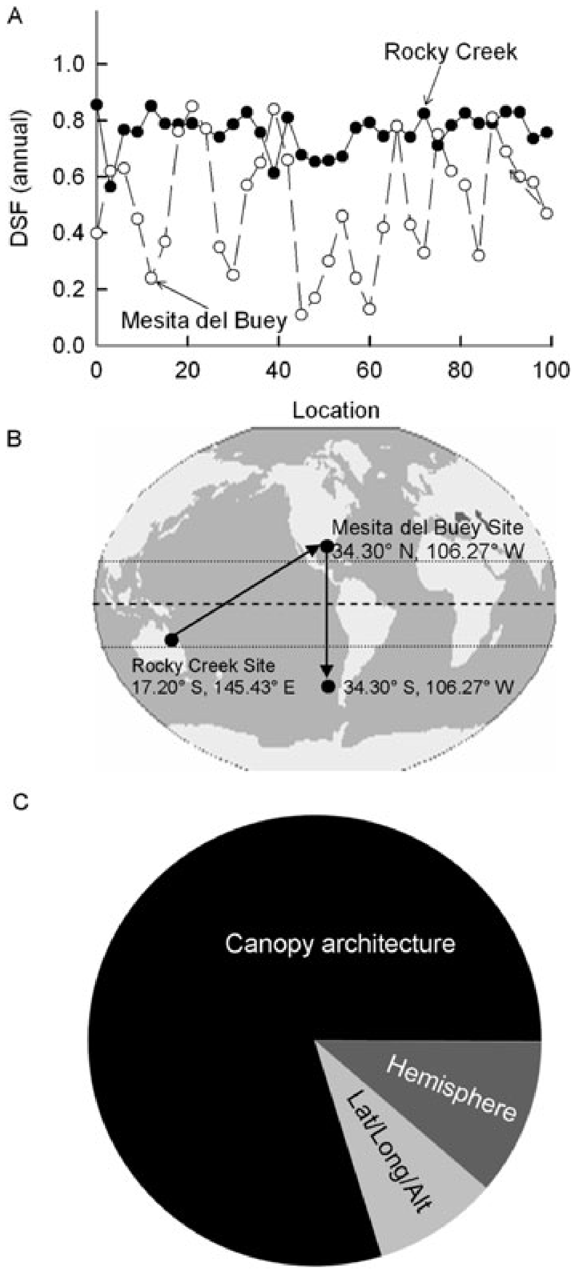

Fig. 6. (A) Comparison of fraction of annual near-ground solar radiation, measured as the Direct Site Factor (DSF) for two sites with ~50% tree cover: one with tall trees with lower foliage several metres above the ground (Rocky Creek Medium site, Queensland, Australia; this study) and one with shorter trees with foliage near the ground (Mesita del Buey, New Mexico, USA; from Breshears *et al.* 1997). (B) Simulations estimating DSF with trees from the Rocky Creek Medium site at the actual location in Queensland, at the Mesita del Buey location in the USA, and at a comparable location to Mesita del Buey located in the southern hemisphere. (C) Relative contributions of canopy architecture, hemisphere and other locational attributes (latitude, longitude, altitude) to the differences in mean DSF between the two sites with ~50% canopy cover presented in A.

Because cover was similar between these two sites, differences in mean site DSF were evaluated in the context of locational *versus* canopy structural differences. For re-estimated DSF for the Rocky Creek Medium cover site, hemiphotos placed at the northern hemisphere latitude of the Mesita del Buey site, and at this site's equivalent latitude in the southern hemisphere (Fig. 6B), resulted in site DSF means that approached those for the Mesita del Buey site mean. Based on the changes in site mean DSF from these simulations, we estimated that more than three quarters of the difference appears to be due to canopy architecture (Fig. 6C), which included differences in overall tree height, height to the bottom of the canopy, and foliar density. Foliar density for trees on the Rocky Creek site, which were eucalypts, was 0.40, compared with 1.1 for junipers on the Mesita del Buey site (Martens *et al.* 2000). The remaining difference appeared to be split nearly equally between the effect of hemisphere and other locational effects related to a magnitude of latitude, longitude and altitude effect.

DISCUSSION

Grassland–forest continuum trends

Our findings provide insights into general trends for how near-ground solar radiation, measured as a direct site factor or DSF, varies along the grassland continuum for tall trees that have canopies of low-density foliage many metres above the ground. We found that only a small percentage of tree canopy cover (<10%) was sufficient to reduce mean site DSF to about 80% relative to 100% for an open field site with no canopy cover. Yet increasing tree cover further up to 72% cover only reduced mean site DSF to 72% of the maximum for an open site. We found that variance was greater for intermediate values of canopy cover, but there was not a well-defined peak, with DSF variances for our Rocky Creek sites being about equal for 9% and 51% canopy covers.

Our findings are consistent with the results and hypotheses of Martens *et al.* (2000) in that (i) mean near-ground solar radiation decreases with increasing tree canopy cover, and (ii) site variance peaks at an intermediate value of canopy cover. However, our findings contrast with the results and hypotheses of Martens *et al.* in that: (i) mean near-ground solar radiation decreased rapidly and non-linearly with tree cover; (ii) variance for site DSF as a function of canopy cover was relatively flat for very tall trees with foliage well above the ground; and (iii) DSF variance was high at a low canopy cover whereas Martens *et al.* found a distinct peak in the variance curve at a higher value of canopy cover for a site with shorter trees having foliage near the ground surface.

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Canopy and intercanopy patch–scale trends

The differences in the mean and variance in near-ground solar radiation as a function of ground cover for a site can be further understood in the context of canopy and intercanopy patterns. In contrast to previously studied USA ecosystems with shorter trees having dense foliage near the ground (Breshears *et al.* 1997), we found that means for near-ground solar radiation were not significantly less for locations under tall trees with less dense canopies *versus* intercanopies. Further, patch–scale (canopy–intercanopy) variances were higher for USA sites dominated by short trees with low canopies of dense foliage compared with the lower patch–scale variances for the Australian savanna sites characterized by tall trees with high open canopies.

The different findings for the Australian *versus* USA studies can be attributed to different sun angle–canopy architecture relationships involving an interaction of tree height, height to lower foliage and foliar density. Hemispherical photography is an ideal way to evaluate these canopy effects as opposed to labour-intensive spatially mapping of vegetation surrounding each point of interest.

Comparisons for intermediate amounts of tree cover

Our findings also provide insights into the relative role of location *versus* canopy architecture in determining differences in mean near-ground solar radiation for sites of similar cover (~50% in this case). We found that location explained about 20% of the difference in the mean site DSF between the Rocky Creek Medium cover site and the Mesita del Buey site. Nearly half of this locational effect was due simply to the differences in the dynamics of being in the southern *versus* the northern hemisphere at the same location. The other half of the locational effect was due to a combination of the difference in magnitude of latitude (17.2° *vs.* 34.3°), longitude (45.43°E *vs.* 106.27°W) and altitude (720 m *vs.* 2140 m), of which latitude is likely to be the most important component.

Note that latitude places the Rocky Creek site within the tropics whereas the Mesita del Buey site is temperate. A key consequence for sites within the tropics is that sun angle varies greatly through the year. The sun passes directly overhead the Rocky Creek site twice a year on its path to the Tropic of Capricorn. This tends to dampen any canopy–intercanopy near-ground solar radiation heterogeneity compared with more temperate sites. The sun angle is always southerly at Mesita del Buey and there will always be shady patches on the north side of low, dense tree canopies (Breshears *et al.* 1997).

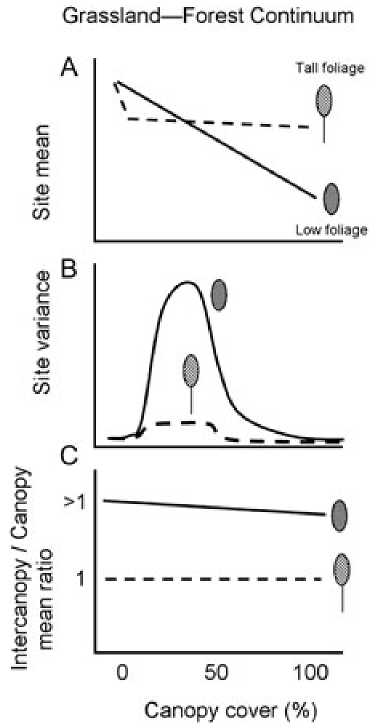

Fig. 7. Hypothesized relationships for near-ground solar radiation along grassland–forest gradients for short trees with lower foliage near the ground *versus* taller trees with foliage above (several m) the ground, for (A) mean, (B) variance, (C) canopy/intercanopy ratio.

Further, we found that mean site near-ground solar radiation was high and variance was low for sites with tall trees with high canopies with sparser foliage. The net result of this is less heterogeneity at the patch–scale. As noted above, as trees become taller, they have a disproportionately wider influence on the inter-canopy patches adjacent to them. Simultaneously, if the lower height of foliage increases with tree height, then as trees become taller, they have a diminishing influence on the canopy patches beneath them.

Synthesis and broader implications

Our analyses quantify a strong effect of tree canopy architecture on near-ground solar radiation along the grassland–forest continuum that builds on previous observations, trends and hypotheses (Breshears *et al.* 1997; Martens *et al.* 2000; Breshears 2006; Zou *et al.* 2007). We found striking differences in hypothesized trends along the grassland–forest continuum for short trees with low canopies *versus* tall trees with high canopies, as depicted in Figure 7. The simulations of Martens *et al.* (2000) indicated a linear decrease in mean site near-ground solar radiation with increasing tree cover. Those simulations also indicated that the

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decrease became slightly curvilinear in a concave manner with increasing tree height. Our results led us to hypothesize that, in general for tall trees with high canopies and sparser foliar density, the relationship between mean site DSF and per cent canopy cover is highly curvilinear in a concave manner and drops off very rapidly with initial increases in tree cover, in contrast to the more linear decrease in DSF that occurs with increasing canopy cover for short trees. This pattern is consistent with expected effects of sun angle, and can, of course, be modified by foliar density. Due to sun angle effects, a unit of foliar-filled canopy that is taller can shade a larger area than the same unit that is located closer to the ground. Therefore, for taller trees a lower percentage of canopy cover is needed to near the potential maximum amount of site shading than is the case for low foliage trees. However, for sites with a greater percentage of canopy coverage, tall trees cannot provide as much shading – again, due to sun angle effects (see Terborgh 1985; Eagelson 2002 for related discussions). Our results indicated that these sun angle effects were not negated by the differences in foliar density (more than a factor of 2). Additional reductions in foliar density for tall trees would be expected to diminish the initial rate of reduction in DSF at low values of canopy cover and reduce the amount of shading at high values of canopy cover.

Similarly, we hypothesize that whereas for short trees with low foliage the site variance for near-ground solar radiation is very sensitive to changes in tree cover, this is generally less so for tall trees with tall foliage because of sun angle effects. Consequently, even though tall trees with higher and sparser foliage exhibited somewhat greater variance at intermediate levels of canopy cover, this variance was relatively low and, along with dampening by other factors, resulted in small, non-significant and perhaps ecologically unimportant differences between canopy and intercanopy patches.

Our findings are also relevant to a broader suite of conceptual models that focus on the dynamics of savannas and other ecosystems positioned intermediate along the grassland–forest continuum. In particular, some conceptual models and theories focus on heterogeneity between the canopies beneath woody plants and the intercanopies separating them (Breshears & Barnes 1999; House *et al.* 2003; Breshears 2006), while other models and theories largely ignore this heterogeneity (Walter 1971; Walker & Noy-Meir 1982; House *et al.* 2003). The ways in which trees modify patterns of incoming solar radiation are based on physical processes and, hence, offer promise for being among the most general of relationships among these systems (Martens *et al.* 2000; Breshears 2006).

In summary, our study highlights the importance of accounting for not only canopy cover and mean or maximum canopy height but also the minimum height of canopy foliage and its density. Because incoming energy inputs associated with solar radiation drive many ecosystem processes, differential effects of tree architecture strongly affect canopy–intercanopy heterogeneity and key ecosystem processes and dynamics. More generally, our results contribute to the ongoing development of an understanding of trends in ecosystem properties along the grassland–forest continuum that could be useful for understanding and managing ecological dynamics for a large portion of the terrestrial biosphere.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Transect name and location and topographic attributes for the Rocky Creek Study Site located near Tolga in Queensland, Australia.

Table S2. Individual tree canopy locations (including maximum height and both beginning and ending height of lower canopy foliage) along each of three 100-m transects at Rocky Creek, near Atherton, Queensland (there are no data for the 'Open' transect because it did not have trees).

Table S3. Individual location estimates of fraction of annual near-ground solar radiation using the metric of the Direct Site Factor (DSF) for locations at 3-m intervals at 1 m height along each of four 100-m transects at Rocky Creek, near Atherton, Queensland.

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