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Foliage projective covers of overstorey and understorey strata of mature vegetation in Australia

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Abstract

At maturity, both overstorey and understorey foliage projective covers (FPC) tend to reach steady-state values which are correlated with the evaporative coefficient (k) *in the water balance equation of the soil–plant–atmosphere continuum.*

Overstorey FPCs of mature communities increase linearly from 20 to 85% along the moisture gradient from arid to humid regions. Understorey FPCs in mature communities are relatively constant along the same moisture gradient, increasing only slightly from 40 to 47%.

Plant communities which have overstorey FPCs different from the norm, appear to show a compensatory decrease or increase in understorey FPC so that the sum of the FPCs of overstorey and understorey is equal to that predicted for the region.

Introduction

In Australia, most native plant communities are dominated by evergreen, sclerophyllous overstoreys composed of species of *Eucalyptus, Acacia* or *Casuarina*. As many of these plant communities are found on soils low in plant nutrients, foliation and defoliation tend to be synchronous (Specht *et al.* 1983); thus, the foliage projective cover (FPC) of the overstorey remains relatively constant throughout the year. In a mature plant community, the overstorey canopy reaches a steady-state value of FPC, a value which has been shown to be correlated with the annual water balance of the ecosystem (Specht 1972, 1981a).

When the water store is limiting, field studies on the water balance of 10 evergreen plant communities have shown that:

$$E_a/E_0 = k\,(\text{Available Water}) = k\,(P - R - D + S_{ext}) \qquad (1)$$

where E_a = actual evapotranspiration per month, E_0 = pan evaporation (Class A pan) per month, P = precipitation for month, R = run-off per month, D = drainage, S_{ext} = extractable soil water at the beginning of the month and k is a constant termed the evaporative coefficient. The same values of k, derived from field observations, can be computed by iterative techniques so that S_{ext} remains at or above zero for every month of the year.

In the mature plant community, the FPC (%) of the overstorey appears to be related linearly to the evaporative coefficient k, increasing from 20 to 85% along a moisture gradient from arid to humid areas (Specht 1972).

Two points should be stressed here:

(a) The value of k (and hence overstorey FPC) remains constant for the region, in equilibrium with the evaporative power of the atmosphere, provided that Available Water is limiting for at least one month of the year; the amount of available water (below the optimum) has virtually no effect on the value of k (Specht 1972, pp. 285–7; 198lb, p. 313; 1981c, p.17).

(b) The second point concerns the plant communities characteristic of heavy clay soils which show an accumulation of Total Soluble Salts in the profile (e.g. in central Queensland to northern New South Wales). The overstorey vegetation (*Acacia harpophylla, Casuarina cristata, Eucalyptus populnea)* shows an FPC higher than that expected, compensating for the high leaf resistance to water vapour fluxes (Specht 1981c, p. 16).

Studies on pyric succession in heathland vegetation of southern Australia and South Africa (Specht *et al.* 1958; Specht & Morgan 1981; Specht *et al.* 1983) show that overstorey FPC (of the long-lived dominants) takes some 20–30 yr to reach a steady-state. (In heathlands, the overstorey stratum is difficult to distinguish unless the community is followed to maturity, i.e. 25–50 yr.) However, the total FPC (the sum of overstorey and understorey) reaches a steady-state value within about 5 yr, the balance between overstorey and understorey FPC gradually changing during the subsequent pyric succession until steady-state values are reached for both overstorey and understorey.

As far as the author is aware, no similar studies have been made on the changes in FPC of overstorey and understorey in other Australian plant communities following fire. Annual observations of overstorey and understorey FPCs of the grassy open-forest of the Taylor Range near Brisbane indicate that steady-state values are restored within 3–4 yr after fire: Steady-state values appear to be characteristic of overstorey and understorey strata in other mature communities throughout Australia (Specht & Morgan 1981).

This paper presents data for a range of mature plant communities which appear to have reached a steady-state relationship for the FPCs of both overstorey and understorey strata.

Selection of sampling sites

As plant communities throughout Australia have been subjected to many disturbances by European man over the last 200 yr, selection of representative samples of mature (steady-state) vegetation (relatively undisturbed for the last 20–30 yr) is difficult. Over 56 plant communities, from the humid to the arid zone, have been analysed. These extend from the Kimberleys in north-west Western Australia to Adelaide in South Australia.

Subsequent examination has shown that the overstorey trees/tall shrubs of some of the sample communities had been reduced by clearing or poisoning. As the FPCs of overstorey and understorey strata tend to be inversely related during the regeneration phase (Specht & Morgan 1981) so that Total FPC is a constant, the data collected for these communities are included below.

Estimation of Foliage Projective Cover (FPC)

At least two (sometimes up to 10) 50 m tapes were extended in random positions along the ground in representative plant communities. The Foliage Projective Cover (the percentage of land covered by photosynthetic organs, observed vertically) of overstorey trees and tall shrubs was recorded at 50 cm intervals along each 50 m tape by observing the presence or absence of evergreen foliage at the intersection of crosswires in a vertical sighting tube fitted, at eye level, with a 45° mirror. Overlapping foliage cover tended to be uncommon in the cross-wire observation made in open-communities and was ignored.

At the same 50 cm intervals, along the 50 m tape, the FPC of the ground stratum up to 2 m above the ground, but usually much shorter, was recorded by a downwards crosswire sighting tube (such as designed by Winkworth & Goodall 1962). As with the overstorey, only the presence and absence of foliage was recorded, overlapping FPC being ignored.

Both the overstorey and understorey strata of most of the communities included in the study were evergreen. In some communities, the foliage of a number of species in the ground stratum was seasonal, not evergreen. If dead and dying, as well as green, foliage were recorded during the drier part of the year, a reasonable estimate of the maximum and minimum values of the FPC of the seasonal foliage could be obtained. The mean monthly value of this seasonal FPC appears to be approximately equal to Minimum FPC + (Maximum FPC − Minimum FPC)/3, assuming that seasonal FPC follows monthly evapotranspiration.

In plant communities less than 2 m tall (for example, low shrublands, heathlands, hummock grasslands, tussock grasslands), overstorey species are the taller, long-lived dominants of the vegetation. Understorey species tend to be shorter in stature, often less than 25–100 cm; many fail to persist in the mature community. Communities with a very sparse scattering of low trees or shrubs, overtopping but not dominating the low communities, have not been included in this study.

In many sampling sites, close replication was observed in the two sets of 100 cross-wire records. Extra replication was necessary in the more variable, open-structured communities of drier environments.

Results

The structural attributes (height and foliage projective cover of overstorey and understorey strata) of 56 Australian plant communities (from the Kimberleys in north-west Australia to Adelaide in South Australia) are listed in Appendix 1. The plant communities are classified into plant formations (as outlined by Specht 1970) and the dominant species in the overstorey are listed.

Climatic data [Köppen climatic type, after Dick (1975); and the evaporative coefficient *k*, calculated

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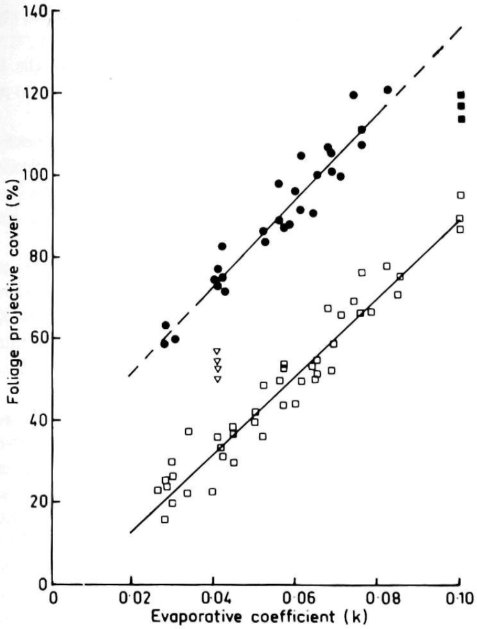

FIG. 1. Foliage projective covers (%) recorded for the overstorey (□) and overstorey + understorey (●) strata of 56 Australian plant communities plotted against the evaporative coefficient (k). Total FPCs for subtropical rainforest communities (■) include FPCs for only overstorey and ground strata; the foliage projective covers of epiphytes were not measured. Overstorey FPCs of plant communities on heavy clay soils, often gilgaied and high in Total Soluble Salts, in central Queensland are shown by a ▽.

by Specht (1972)] are shown for each sampling site tabulated in Appendix 1.

Values of overstorey FPC (%) were plotted (Fig. 1) against the evaporative coefficient (k) computed for the sampling site. Using 24 sampling sites, a linear regression with a coefficient of determination (r^2) = 0.81 had been demonstrated (Specht 1972, 1981a). In this paper, an extra 20 sampling sites (n = 44) enabled a closer fit of the linear regression to be computed with $r^2 = 0.94$:

$$\text{Overstorey FPC (\%)} = 960\,k - 6.0. \qquad (2)$$

Total FPC (%) was plotted (Fig. 1) against the evaporative coefficient (k) of the sampling site, giving the following linear regression:

$$\text{Total FPC (\%)} = 1070\,k + 30.5, \qquad (3)$$

$$(n = 29;\ r^2 = 0.93)$$

Discussion

Total Foliage Projective Cover (the sum of the FPCs of overstorey and understorey strata) in Australian plant communities appears to be closely related to the evaporative capacity of the environment (Fig. 1).

In general, mature plant communities reach steady-state values for the FPC of both overstorey and understorey strata (Specht *et al.* 1958; Specht & Morgan 1981; Specht *et al.* 1983). Regenerating communities, communities artificially or naturally thinned, or communities with dense overstoreys (compensating for high leaf resistances) may show overstorey FPCs below or above the optimal overstorey FPCs (Fig. 1), but the understorey FPC invariably responds to equilibrate Total FPC for the variation in overstorey. The steady-state values of most overstorey FPC are linearly related to the evaporative capacity of the environment (Fig. 1). Annual falls of leaf litter from these steady-state overstorey canopies are similarly related (see Specht 1981a).

The puzzling observation is the relatively constant amount of understorey FPC recorded in mature plant communities, from the humid to the arid zone. The linear regression lines of Fig. 1 are almost parallel, showing 40% understorey FPC in the arid zone, 47% in the humid zone. [Only 20–30% FPC was recorded in the ground stratum of subtropical rainforests (Fig. 1). It is probable that epiphytes may contribute a further 20% FPC to understorey FPC.] These values are observed in spite of the fact that 80% of the incident radiation penetrates the overstorey canopy in the arid zone, while less than 30% penetrates through the canopy of the tall open-forest to closed-forest communities.

In open-communities of low stature, such as Dark Island heathland (latitude 36°S), the overstorey shrubs, up to 2 m tall, shade 30–35% of the landscape directly below the shrubs (see Appendix 1). As well, the taller shrubs absorb the oblique direct-rays from the sun, shading the understorey vegetation between the shrubs. In winter, the area influenced by the shadow-path of the 2 m tall *Banksia* shrubs receives about 65% of the total daily radiation of 840 J cm^{-2} day^{-1}; in summer, the radiation is about 75% of 2500 J cm^{-2} day^{-1}. The influence of the 2 m tall *Banksia* extends over about 20 m^2, roughly the spacing of *Banksia ornata* shrubs of that size in a 20 yr old stand of heathland near Dark Island Soak. The understorey between the scattered *Banksia* shrubs (FPC 32%) has an FPC of 42%, or covers 60% of the gaps between the *Banksia* shrubs.

That many understorey species are able to absorb more radiant energy than overstorey species (Yates

1981; Specht & Yates in press) must be considered in analysing the energy balance of the ecosystem. In one year, these plants would have trapped enough *extra heat* to evaporate 150 mm of rainfall (if all the absorbed energy was used in evaporation). It should be possible to calculate the energy balance between incident radiation and its dispersal by reflection, radiation, convection and evaporation from the overstorey and understorey strata. Modelling the complex energetic systems within the plant community throughout the year should enable the relative constant understorey FPC values (*c*. 40% of mature communities) from arid to humid regions to be explained.

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Appendix 1. Climatic and structural data of 56 Australian plant communities

Locality	Köppen climatic type	Evaporative coefficient (*k*)	Plant formation	Dominant species	Height of dominants (m)	Foliage projective cover (%) Overstorey (evergreen)	Understorey (evergreen)	Understorey (seasonal)	Total
Queensland									
Lamington Nat. Pk. (28° 12′, 153° 05′)	Cfb	0.100	closed-forest (sub-tropical rainforest)	many spp.	35	**96***	18+	—	114+
Mt. Glorious (27° 20′, 152° 46′)	Cfb	0.100	closed-forest (sub-tropical rainforest)	many spp.	27–46	**88**	?	—	?
Boombana Nat. Pk. (27° 25′, 152° 50′)	Cfb	0.100	closed-forest (sub-tropical rainforest)	many spp.	34	**90**	30+	—	120+
Boombana Nat. Pk. (27° 25′, 152° 50′)	Cfb/Cfa	0.082	shrubby tall open-forest	*Eucalyptus microcorys* *E. propinqua* *Tristania suaveolens*	25–43	**79**	42	—	**121**
Mt. Coot-tha (27° 29′, 152° 57′)	Cfa	0.078	grassy open-forest (south slope)	*E. major* *E. microcorys* *Tristania suaveolens*	17	**67**	59	—	126

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Jolly's Lookout (27° 27′, 152° 53′)	Cfa	0.076	grassy open-forest	*E. drepanophylla* *E. intermedia* *E. major* *E. microcorys* *Tristania suaveolens*	21	**67**	57	—	**100–124**
North Stradbroke Is.[1] (27° 30′, 153° 30′)	Cfb/Cfa	0.076	shrubby open-forest	*E. intermedia* *E. pilularis*	16	**77**	34	—	**111**
Lamington Nat. Pk. (28° 12′, 153° 05′)	Cfb/Cfa	0.074	grassy open-forest	*E. intermedia* *E. microcorys* *E. propinqua*	25	**70**	46	14	**116–130**
North Stradbroke Is.[1] (27° 30′, 153° 30′)	Cfa	0.071	heathy low open-forest	*E. intermedia* *E. planchoniana*	9–10	**66**	34	—	**100**
Mt. Coot-tha (27° 29′, 152° 57′)	Cfa	0.069	grassy open-forest (north slope)	*E. acmenoides* *E. crebra* *E. maculata* *E. major*	14	**53**	38	29	**91–124**
Southport (27° 55′, 153° 24′)	Cfa	0.068	grassy open-forest	*E. acmenoides* *E. drepanophylla* *E. major* *Tristania suaveolens*	16	**68**	38	4	**106–110**
The Gap, Brisbane (27° 27′, 152° 58′)	Cfa	0.065	grassy open-forest	*E. acmenoides* *E. maculata* *E. major*	17–26	**52**	?	?	?
North Stradbroke Is.[1] (27° 30′, 153° 30′)	Cfa	0.065	heathy low open-forest	*E. signata*	7	**50**	50	—	**100**
Girraween Nat. Pk. (28° 50′, 151° 55′)	Cfb	0.064	heathy open-forest	*E. andrewsii*	15–20	**53**	38	—	**91**
Cairns[2] (16° 55′, 145° 46′)	Am	0.061	grassy open-forest	*E. intermedia* *E. tessellaris*	16	40	65	—	**105**
Jimna (26° 40′, 152° 28′)	Cfb	0.060	grassy open-forest	*E. moluccana*	16	**44**	52	—	**96**
Herries Range State Forest (28° 15′, 151° 40′)	Cfb	0.057	grassy/heathy open-forest	*E. fibrosa*	15–18	**54**	34	—	**88**
Herries Range State Forest (28° 15′, 151° 40′)	Cfb	0.057	grassy open-forest	*E. dealbata* *E. drepanophylla*	14–15	**53**	35	—	**88**
Mt. Gravatt (27° 33′, 153° 05′)	Cfb	0.056	heathy open-forest	*E. intermedia* *E. planchoniana* *E. umbra*	15–24	**50**	39	—	**89**
Redbank (27° 36′, 152° 52′)	Cfb	0.052	grassy open-forest	*Angophora costata* *E. intermedia* *E. major*	15–20	**49**	30	17	**79–96**
Whetstone State Forest (28° 30′, 150° 56′)	Cfb	0.043	grassy open-forest	*Callitris columellaris* *E. populnea*	14	56	15	3	**71–74**
Southwood Nat. Pk. (27° 50′, 150° 11′)	Cfa	0.041	open forest	*Callitris columellaris*	12	**36**	?	?	?
Southwood Nat. Pk. (27° 50′, 150° 11′)	Cfa	0.041	grassy-open forest	*E. populnea*	15	57	13	12	**70–82**
Southwood Nat. Pk. (27° 50′, 150° 11′)	Cfa	0.041	chenopod open-forest (on gilgai ridges)	*Acacia harpophylla*	10	54	10	26	**64–90**
Goondiwindi (north) (28° 25′, 150° 17′)	Cfa	0.041	chenopod open-forest (on gilgai ridges)	*Acacia harpophylla* *Casuarina cristata* *E. populnea*	10 10	52 55	17 14	15 24	**69–84** **69–93**
Charleville (26° 24′, 146° 15′)	BSh	0.034	open-scrub	*Acacia aneura*	9–10	**38**	?	?	?
Charleville (26° 24′, 146° 15′)	BSh	0.034	tussock grass-land	*Astrebla pectinata*	0.25	**22**	?	?	?
Windorah[3] (25° 25′, 142° 39′)	BWh	0.028	tall shrub-land	*Acacia aneura*	5	**16**	47	?	**63**
Thargomindah[4] (27° 59′, 143° 49′)	BWh	0.028	tall shrub-land (thinned)	*Acacia aneura*	4	6	53	?	**59**
Northern Territory									
Adelaide River[4] (12° 45′, 131° 30′)	Awi	0.050	grassy open-forest	*E. tetrodonta*	> 20	**40**	?	?	?
Humpty Doo[4] (12° 38′, 131° 15′)	Aw/Awi	0.045	grassy open-forest	*E. miniata* *E. tetrodonta*	15–20	**30**	?	?	?

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Wauchope (NW)[5] (20° 30′, 134° 00′)	BWhw	0.030	hummock grass-land	*Plectrachne schinzii*	0.3	**30**	2	?	?
Central Mt. Wedge (N)[5] (22° 30′, 131° 45′)	BWh	0.030	hummock grass-land	*Triodia basedowii*	0.3	**26**	1	1+	?
Alice Springs (99km N)[4] (22° 50′, 133° 30′)	BWh	0.029	hummock grass-land	*Triodia basedowii*	0.3	**26**	?	?	?
Alice Springs (87km N)[4] (22° 55′, 133° 30′)	BWh	0.029	tall shrub–land (intergrove)	*Acacia aneura*	5	12	24	?	?
Alice Springs (N)[5] (22° 55′, 131° 30′)	BWh	0.029	hummock grass-land	*Triodia basedowii*	0.3	**21**	2	1+	?
Finke (NW)[5] (25° 30′, 134° 15′)	BWh	0.029	hummock grass-land	*Triodia basedowii*	0.3	**24**	1	1+	?
Lake Nash (SSW)[5] (21° 50′, 137° 30′)	BWhw	0.027	hummock grass-land	*Triodia basedowii*	0.3	**23**	1	1+	?
Western Australia									
Kununurra[4] (15° 47′, 128° 44′)	BShw	0.030	woodland over hummock grasses	*E. miniata* *E. tetrodonta* *Plectrachne pungens*	16	**20**	28	10	48–6
Kununurra[4] (15° 47′, 128° 44′)	BShw	0.030	woodland over hummock grasses	*E. dichromophloia* *Plectrachne pungens*	12–15	**16**	36	10	52–6
New South Wales									
Hay (W) (34° 30′, 144° 51′)	BSk	0.040	low shrub-land	*Atriplex vesicaria*	0.3–0.6	**22**	?	?	?
Victoria									
Mt. Donna Buang[6] (37° 42′, 145° 41′)	Cfb	0.085	closed-forest	*Nothofagus cunninghamii*		**72**	?	—	?
Wallaby Creek[6] (38° 35′, 142° 55′)	Cfb	0.085	tall open-forest with tall shrubs	*E. regnans*	34–43	**64**	?	—	?
				Pomaderris aspera		**76**			
				Olearia argopylla	10–15	58			
Mt. Dandenong[7] (37° 50′, 145° 21′)	Cfb	0.065	grassy open-forest	*E. macrorhyncha* *E. radiata*	18–23	55	?	—	?
Frankston[8] (38° 09′, 145° 08′)	Cfb	0.061	open-heath	*Leptospermum myrsinoides*	1.0–1.3	**50**	42	—	92
Snowy River[9] (37° 00′, 148° 25′)	Cfa	0.057	grassy open-forest	*Callitris columellaris* *E. albens*	5–10	**44**	?	?	?
South Australia									
Mt. Lofty (34° 59′, 138° 43′)	Csb	0.069	heathy open-forest	*E. baxteri* *E. obliqua*	23–35	**59**	47	—	106
Belair Rec. Res. (35° 00′, 138° 38′)	Csb	0.052	heathy woodland to heathland	*E. leucoxylon*	5–14	15	71	—	86
Belair Rec. Res. (35° 00′, 138° 38′)	Csb	0.052	grassy open-forest	*E. leucoxylon*	14–17	**36**	?	?	?
Belair Rec. Res. (35° 00′, 138° 38′)	Csb	0.050	grassy open-forest	*E. odorata*	9–20	**42**	?	?	?
Monarto (35° 08′, 139° 08′)	BSk	0.048	open-tussock grassland	*Lomandra* spp.	0.3–0.5	26	?	?	?
Ferries-McDonald Nat. Pk. (35° 13′, 139° 09′)	BSk	0.045	open-scrub	*E. incrassata* *Melaleuca uncinata*	4–8	**37**	?	?	?
Murray Bridge (35° 07′, 139° 16′)	BSk	0.045	grassy open-scrub	*E. socialis*	5–8	**38**	?	?	?
Dark Island Soak, near Keith (36° 06′, 140° 31′)	Csb/BSk	0.042	open-scrub	*E. incrassata* *Melaleuca uncinata*	4–8	**34**	41	—	75
Dark Island Soak, near Keith (36° 06′, 140° 31′)	Csb/BSk	0.042	open-heath-land	*Banksia ornata* *Xanthorrhoea australis*	2	**32**	42	—	74

Additional observations, collected July–August 1983

Victoria									
Sparkes Lookout, Wilsons Promontory N.P. (39°00′, 146° 17′)	Cfb	0.075	heathy open-forest	*E. oblique*	20–30	70	38	—	108
Tidal River, Wilsons Promontory N.P. (39° 02′, 146° 20′)	Cfb	0.070	heathy open-forest	*E. baxteri*	6–8	60	37	—	97
Brisbane Ranges N.P. (37° 55′, 144° 20′)	Cfb	0.056	heathy open-forest	*E. obliqua* *E. macrorhyncha*	20–30	45	37	—	82

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Gellibrand Hill State Park (37° 40′, 144° 45′)	Cfb	0.056	grassy open-forest	*E. microcarpa*	15–20	65†	17	17	88
Melton (37° 41′, 144° 35′)	Cfb/BSk	0.055	open-scrub	*E. behriana* *Rhagodia parabolica*	10–12	51	37	4	88
South Australia									
Warrenben Cons. Park (35° 09′, 137° 05′)	Csb	0.050	heathy open-scrub	*E. diversifolia* *E. socialis*	4–8	42	43	—	85
Salter Springs (34° 11′, 138° 38′)	Csa	0.047	grassy open-forest	*E. odorata* *E. leucoxylon*	15–18	44	26	20	76
Para Wirra Rec. Park (34° 42′, 138° 50′)	Csb	0.045	heathy low open-forest	*E. goniocalyx* *E. fasciculosa*	10	39	39	—	78
Keith (36° 06′, 140° 21′)	Csb	0.042	grassy woodland	*E. leucoxylon*	15–18	30	?	?	?

[1]Specht and Morgan (1981);[2] J. McDonald and J. Neldner (pers. comm. Nov. 1981); [3] M. Bolton and G. Rimmington (pers. comm. July 1982); [4] J. A. Carnahan (pers. comm. Oct. 1982); [5] Winkworth (1967); [6] Ashton (1976); [7] D. H. Ashton and H. T. Clifford (pers. comm. Sept. 1982); [8] Winkworth (1955); [9] Clayton-Greene (1981); * Values of Overstorey and Total FPCs shown in bold type have been used in the calculation of the regression equations. † Many trees adjacent to the sampling site have been removed, apparently resulting in increased canopy growth of the remaining trees.

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