

Plant cover and composition in relation to density of *Callitris glaucophylla* (white cypress pine) along a rainfall gradient in eastern Australia

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Abstract. Despite the widespread distribution of *Callitris glaucophylla* J.Thompson & L.Johnson (white cypress pine) over large areas of eastern Australia, little is known about its impact on the diversity and cover of understorey plants. We examined *C. glaucophylla* woodlands to see whether stand density and land management influenced the cover and composition of the understorey vegetation. The cover and diversity of understorey plant communities were measured at 83 sites along a gradient in average annual rainfall (215–532 mm) in eastern Australia. The diversity and cover of understorey plants and the cover of trees increased, and the composition of the understorey community changed with increases in average annual rainfall. There were no clear relationships, however, between tree cover or density, and the cover or diversity of understorey plants. Sites that had not been logged contained significantly greater proportions of native and perennial vascular plants, and sites with extant eucalypts had a significantly higher proportion of shrubs than those sites without eucalypts. We attributed these differences to past forestry disturbance regimes which are correlated with the presence of mature eucalypts. Our results do not support the proposition that dense stands of *C. glaucophylla* suppress the understorey vegetation.

Introduction

White cypress pine (*Callitris glaucophylla*, formerly known as *C. glauca* and *C. columellaris*) is a distinctive, medium-sized tree native to Australia. It is found in all mainland states of Australia (Baker and Smith 1910; Thompson and Johnson 1986), frequently in single-age stands, with mature individuals often reaching heights of 20–30 m (Boland *et al.* 1984).

Within its original community structure, *C. glaucophylla* woodlands include a mosaic of other tree species such as *Eucalyptus* spp., *Allocasuarina leuhmannii* (R.Baker), *Acacia aneura* (F.Muell. ex Benth), *Casuarina* spp. and *Geijera parviflora* (Lindley) (Lindsay 1967; Lacey 1973; Boland *et al.* 1984) often supporting an extensive mid-storey and understorey component. *Acacia*, *Eremophila*, *Dodonea* and *Hakea* species typically form a large component of the shrub (mid-storey) layer (Boland *et al.* 1984). Open stands of *C. glaucophylla* often support a diversity of grasses, typically those belonging to the genera *Austrostipa*, *Austrodanthonia*, *Aristida*, *Chloris*, *Eragrostis*, *Panicum*, *Bromus* and *Vulpia* (Lacey 1973).

In eastern Australia *C. glaucophylla* once occupied extensive areas of the former box woodlands (Prober and Thiele 1995). Across much of its original distribution,

woodlands have been extensively cleared for agriculture (Sivertsen and Metcalfe 1995). Although it occurs on a wide variety of landforms and soils of varying fertility, its distribution is often limited by landform position, fire history and land management. *C. glaucophylla* tolerates a wide spectrum of average rainfall, occurring from ~200 to 750 mm average annual rainfall (Lacey 1973). Sandy and loamy soils provide ideal conditions for *C. glaucophylla* because they are freely draining (Lacey 1973).

Many of today's state forests have been substantially modified by early European occupants, whose scrub leases specified the removal of all mid-storey ('scrub') species, and most non-pine species such as eucalypts (Curby 1997; Allen 1998; Dargavel and Kowald 2001). Other early leasehold land fell under lease-improvement mandates requiring the compulsory thinning of immature pines (Lindsay 1967). Given its former widespread distribution over much of eastern Australia, the contemporary distribution of *C. glaucophylla* is now largely a reflection of previous land-use practices, particularly agriculture (Thompson and Eldridge 2005). Large areas of *Callitris*-dominant native woodlands have been extensively cleared during the past century, particularly in New South Wales (NSW) and Queensland (FCNSW 1989). The

majority of *Callitris* woodlands is under the management of state forests or leasehold or freehold landholders (Binnington 1997).

Callitris glaucophylla often dominates and out-competes other trees to form even-aged stands (Lacey 1973). These stands continue to increase in density as a result of insufficient self-thinning until they develop into a high-density stands where growth is limited and mortality is low (FCNSW 1988). In the semi-arid woodlands, intensive management of *C. glaucophylla* resulted in the 'opening up' of large areas for pastoralism (Noble and Tongway 1986), and encouraged the establishment of extensive tracts of 'wheatfield' pine regeneration (Lacey 1972; Nowland 1997). This regeneration has resulted in tree densities ranging from 120 000 to 2.5 million stems ha⁻¹ (Lacey 1972), with trees often stunted and exhibiting poor growth (FCNSW 1988; Hauenschield and Smith 1999). Thinning is known to improve the productivity of stands by reducing the competition by saplings (Lacey 1972; Johnston 1975; Horne and Robinson 1987; Horne 1990b), and is now an active part of the management practices of NSW cypress pine forests (FCNSW 1988).

There is abundant evidence in the scientific literature to suggest that increases in the cover and density of trees generally result in a reduction in the diversity of understorey species, primarily as a result of reduced availability of nutrients, water and sunlight (e.g. Walker *et al.* 1972; Scanlan and Burrows 1990; Gibbs *et al.* 1999; Hauenschield and Smith 1999). Anecdotal evidence suggests that dense stands of *C. glaucophylla* suppress the growth and cover of the understorey plant community (Boland *et al.* 1984; Clayton-Greene and Ashton 1990; Nowland 1997), although some thinning trials have cast doubt on this assertion (Andrews 2003). A recent study by Greening Australia (Andrews 2003) found a large variation in percentage groundcover beneath dense *C. glaucophylla* stands in north-western NSW. In addition, the study revealed that the impact of grazing on understorey cover exceeded that of tree cover (Andrews 2003). Despite this, little is known about how *C. glaucophylla* influences the diversity of understorey plants.

Until recently, most stands of *C. glaucophylla* have been managed for forestry or for grazing. The value of *Callitris* woodlands for maintaining and conserving biodiversity has only recently been explored (e.g. Shelly 1998a, 1998b; Eldridge 1999; Murphy 1999; Date *et al.* 2000) as the area of higher-productivity woodlands has continued to decline. There is an estimated 2.1 million hectares of *C. glaucophylla*-dominant and sub-dominant forests remaining in NSW, of which only 9% is held on conservation reserves (Binnington 1997), often as highly fragmented patches of woodlands.

In 2001, we commenced a study to examine canopy-understorey relationships in moderately dense

C. glaucophylla woodlands over a large area of its present range in eastern Australia. Woodland sites were examined along a gradient in rainfall within the south-eastern section of its range, allowing us to explore possible relationships between tree density and understorey vegetation in relation to average annual rainfall. The study enabled us to test the following four hypotheses about *C. glaucophylla* and its impact on vascular plants:

- (1) Given current observations and anecdotal information on the putative effect of *C. glaucophylla* on understorey vegetation (e.g. Lacey 1973; Clayton-Greene and Ashton 1990; Nowland 1997), we predict that increases in tree canopy cover would be associated with declines in the cover and diversity of the understorey vegetation, encompassing both mid- and groundstorey vegetation.
- (2) Rainfall has a major influence on the distribution, cover and dynamics of vegetation (Noy-Meir 1979; Westoby *et al.* 1989). We anticipate that the relationships between tree canopy cover and understorey plant cover and diversity would be moderated by differences in average annual rainfall, with cover and diversity of understorey vegetation declining with reduction in rainfall.
- (3) Some of the differences in the relationship between understorey species and tree cover could be due to previous management of *C. glaucophylla* woodlands, such as thinning or clearing, which are used to reduce tree densities and competition (Lacey 1972, 1973; Johnston 1975; FCNSW 1981; Horne and Robinson 1987; Horne 1990a, 1990b). Consequently, we hypothesise that there would be significant differences in plant cover, diversity, origin (native, exotic) and form (perennial, annual) among sites of different management histories (i.e. different histories of thinning or logging).
- (4) The past management of many *C. glaucophylla* woodlands and forests has typically involved the mandatory culling of all non-pine woody plants, particularly eucalypts (FCNSW 1981; Curby 1997; van Kempen 1997; Allen 1998). We expect that sites with extant mature eucalypts would have a greater diversity of plant species than non-eucalypt sites, as the presence of mature eucalypts indicates that these sites have not been markedly altered by clearing.

Materials and methods

Site selection

Site selection was based on a review of the geographic distribution of *Callitris glaucophylla* J.Thompson & L.Johnson and the need to sample along a rainfall gradient. Consequently, an east-to-west route was traversed along which sites were chosen opportunistically for assessment of vegetation and soils. The study area encompassed a large area of the distribution of *C. glaucophylla* within NSW and extended from Eugowra (33°24'S, 148°22'E) in the east to Pooncarie (33°22'S,

142°34'E) in the west. The study included sites in the Riverina region of southern Australia and the Cobar Penneplain, both of which contain significant areas of *C. glaucophylla* (FCNSW 1959; Lindsay 1967; Lacey 1972; Boland *et al.* 1984; Thompson and Eldridge, in press). Sites were chosen to encompass a range of tree densities, land uses (pastoralism, forestry, nature conservation) and land tenures (e.g. freehold and leasehold land, state forest, nature reserve, travelling stock reserves and roadside reserves). Certain requirements were met in relation to site selection. First, sites needed to be at least 2 ha in area in order to accommodate the sampling plots and to provide a buffer zone around the plots. The exceptions to this condition were roadside corridors, which did not always provide a buffer zone. Second, stand structure was selected to be relatively homogenous over the plot in order to simplify the classification of sites (i.e. regrowth or mature, spaced stands).

Climate, landform, soils and vegetation

Although rainfall is highly variable throughout the region (Lacey 1973; FCNSW 1988), there is slight winter dominance (~20% more rain falls in the six cooler months) in the southern part of the state (Iwazskiewicz and Semple 1988). *C. glaucophylla* occurs on a variety of landforms ranging from ridges with moderate slopes, to level and slightly undulating plains in the western part of the state. In general, the soils were well drained red earths (Gn2; Northcote 1979) and red brown earths (Dr2, Dr4), which are characterised by a neutral to slightly acidic pH at the surface (pH 5–7; Thompson and Eldridge 2005), low levels of nutrients (Johns 1983) and often a high erosion potential.

Callitris glaucophylla, an evergreen, is the dominant tree species in the community and, under natural conditions, rarely occurs in monospecific stands (Lindsay 1967). It is thought to be wind dispersed, and recruitment is highly episodic. Detailed life and natural history information is provided in Garden (1956) and Harden (1992–2002). Bimble box (*Eucalyptus populnea* F.Muell.)–white cypress pine is a common vegetation association in western NSW (Lacey 1973), occurring on a range of soil types. Other major tree species encountered included *Eucalyptus intertexta* (R.Baker), *E. microcarpa* (Maiden) Maiden and *C. glaucophylla*–*Allocasuarina luehmannii* (R.Baker) alliances. In particular, *C. glaucophylla*–*E. populnea* and *E. intertexta* alliances supported a substantial shrub layer, comprising *Dodonea* spp., *Eremophila* spp., *Acacia* spp. and *Senna* spp. (Iwazskiewicz and Semple 1988). Within the western plains, groundcover species within the *C. glaucophylla*–*E. populnea* alliance are sparse, although anecdotal evidence suggests that this depends on grazing management (Eldridge *et al.* 2003; Thompson and Eldridge 2005).

Site methods

Eighty-three sites were surveyed over a 6-week period between October and November 2001 and in January 2002. At each site, a 0.1-ha (20 × 50 m) plot was established, within which a 50-m transect was located along the central axis. A smaller 20 × 20 m plot, located centrally within the larger 20 × 50 m plot, formed the basis for tree measurements.

Within the 20 × 50 m plot, the cover of all vascular plants was measured, and data were separated into groundstorey, mid-storey and upperstorey components. The diameter at breast height (DBH, 1.30 m above ground level) of all trees was measured within the smaller plot. All trees greater than 2 m tall were measured by species and dead trees were noted. The cover of all vascular plants was recorded. All *C. glaucophylla* trees were categorised for stand structure (i.e. mature or regrowth) and silvicultural characteristics (i.e. degree of thinning and/or logging) and verified from records held at the Forbes and Narrandera Regional Offices of State Forests of NSW. As most *C. glaucophylla*

woodlands managed for forestry practices have been logged at some point in their history, classification of thinning and logging was based on forestry records for the 10 years prior to sampling. Sites were categorised as grazed or ungrazed, on the basis of evidence such as the presence of herbivores (cattle or sheep), dung or obvious signs of grazing.

Environmental variables

Each site was geo-referenced from the centre of the plot with a portable GPS. The longitudinal difference between each of the 83 sites and Sydney was calculated by using the Geoscience Australia coordinates for Sydney CBD (33°51'S, 151°12'E). Average annual rainfall was calculated from Bureau of Meteorology 30-year records (1930–1960) and SFNSW records. During the 6-month period (1 August 2001 to 31 January 2002), the region experienced rainfall anomalies of up to 200-mm deficit (Bureau of Meteorology 2002).

A sample of the top 5 cm of the surface was taken from each corner of the 20 × 20 m plot, bulked and air-dried, sieved through a 2-mm sieve to remove plant litter, and finely ground to pass through a 100- μ m sieve. Soil texture was determined by the bolus method (Northcote 1979). For statistical analyses, texture classes were converted to continuous variables from average clay contents given in Northcote (1979).

Data analysis

All vascular plants were identified to species level using local experts and published keys (e.g. Harden 1992–2002). Relationships between the various vegetation and environmental variables were examined by using one-way ANOVA after checking for normality and homogeneity of variance by Bartlett's test (Statistix Vers. 7), and after transformations where appropriate. Non-parametric (Kruskal–Wallis) tests were used where transformations failed to stabilise the variance.

A dataset was compiled consisting of a matrix of 83 sites by the cover of 325 groundstorey, mid-storey and overstorey vascular plant species. The dataset contained a large number (94%) of zero values. The number of species per site ranged from 3 to 38, and the number of sites at which a species was found ranged from 1 to 83. To increase the clarity and simplicity of this dataset, we excluded from the analyses species with <10% total cover over all sites. This reduced the influence of rare and infrequent species, and resulted in a reduced matrix of 83 sites by 53 species. A matrix comprising the cover of the reduced species matrix was converted to a similarity matrix by using the Bray–Curtis similarity coefficients contained within the PRIMER (Version 4) statistical package (Clarke and Warwick 1994). This similarity matrix was subjected to non-metric multi-dimensional scaling (MDS) by using one of the PRIMER (Version 4) routines in order to determine whether sites within a particular forestry-treatment class (e.g. logged, thinned) were characterised by a unique suite of plant species. Hypothesis tests of differences between groups, defined *a priori*, were performed with ANOSIM, which is comparable to a distribution-free two-way ANOVA (Clarke 1993). By using a number of random permutations on the similarity matrix, ANOSIM produces a test statistic (Global R) with a significance level, which we used to determine whether the floristics varied significantly among the various treatments.

Canonical correspondence analysis (CCA; ter Braak 1986) was used to examine the relationships between the measured environmental variables described above and the distribution of species. CCA expresses species relationships as a linear combination of environmental variables, and combines the features of correspondence analysis ordination with canonical correlation analysis (Gittins 1985). CCA ordines species data by using axes that are constrained to be linear combinations of the environmental variables. This provides a graphical representation of the relationships between species and environmental variables.

Results

Plant diversity

A total of 325 species from 58 families and 152 genera was recorded across the 83 study sites. About 10% of sites supported less than 10 species, 64% of sites had <20 species and only 7% of sites supported >30 species (Table 1). At the family level, there were six families with more than 10 species: Poaceae (50 spp.), Asteraceae (37 spp.), Chenopodiaceae (27 spp.), Fabaceae (12 spp.), Mimosaceae and Myoporaceae (11 spp. each). Only the *Acacia* genus (Mimosaceae) had more than 10 species recorded.

The groundstorey was dominated by forbs (166 taxa) with the most widespread species being *Einadia nutans* ssp. *nutans*, *Trifolium arvense* and *Chrysocephalum apiculatum*. There were 67 grass species, with *Austrostipa scabra*, *Vulpia myuros* and *Austrodanthonia caespitosa* being the most abundant. Of the 53 shrub species recorded, the dominant species were *Geijera parviflora* (which we treated as a shrub because of its small size), *Acacia deanei* and *Dodonaea viscosa* ssp. *cuneata*. The mid-storey also contained 26 sub-shrub species, with *Sclerolaena diacantha*, *Atriplex semibaccata* and *Rhagodia spinescens* being the most widespread. While the canopy was dominated by *C. glaucophylla*, 11 other tree species were recorded, the most numerous being *Eucalyptus* spp. (*E. microcarpa* and *E. populnea*). Only one vine species (*Parsonia eucalyptophylla*) was recorded during the survey.

Tree cover and density

Across all sites and pooled over all tree sizes, *C. glaucophylla* density ranged from 50 to 36 025 trees ha⁻¹. Mean (\pm s.e.m.) density was 8961 (\pm 999) trees ha⁻¹ (median = 6300 trees ha⁻¹). The cumulative rank order of tree densities indicated a steady increase in density over the sites (Fig. 1a). Tree cover ranged from 8 to 75% (median = 35%). Given that sites were chosen randomly along the east–west transect, there was no significant ($P=0.35$) trend for drier (more westerly) sites to have a greater or lesser density of trees (Fig. 1b).

Table 1. Distribution of sites in relation to the diversity of non-tree plant species

Total number of species	Number of sites	Percentage of sites
<10	8	9.6
11–15	27	32.5
16–20	18	21.7
21–25	18	21.7
26–30	6	7.2
31–35	3	3.6
36–40	3	3.6

Increases in the canopy cover of trees were associated with increased litter cover ($F_{1,82} = 13.42$, $P < 0.001$, $R^2 = 0.13$, Fig. 2a) and very weakly associated with increased diversity of all vascular plant species ($F_{1,82} = 4.50$, $P = 0.037$, $R^2 = 0.04$; Fig. 2b). However, changes in the canopy cover of either *C. glaucophylla* individually, or all tree species pooled together, were not related to the cover of vascular plants species ($P = 0.40$ and $P = 0.65$, respectively; Fig. 3).

Despite the common belief that dense stands of *C. glaucophylla* suppress both the cover and diversity of vascular plants (e.g. Boland *et al.* 1984; Clayton-Greene and Ashton 1990; Nowland 1997), we found no significant relationships between the stem density (expressed as either the total number of stems ha⁻¹) or the wood density (expressed as the sum of the total basal area of stems ha⁻¹) of *C. glaucophylla* and the diversity or cover of plant species (either including or excluding mid-storey species). The relationship was similar when either all trees were considered or when *C. glaucophylla* was examined separately ($P > 0.42$).

Environmental relationships

As the study was carried out along a substantial gradient in average annual rainfall (~ 530 – 215 mm year⁻¹), we

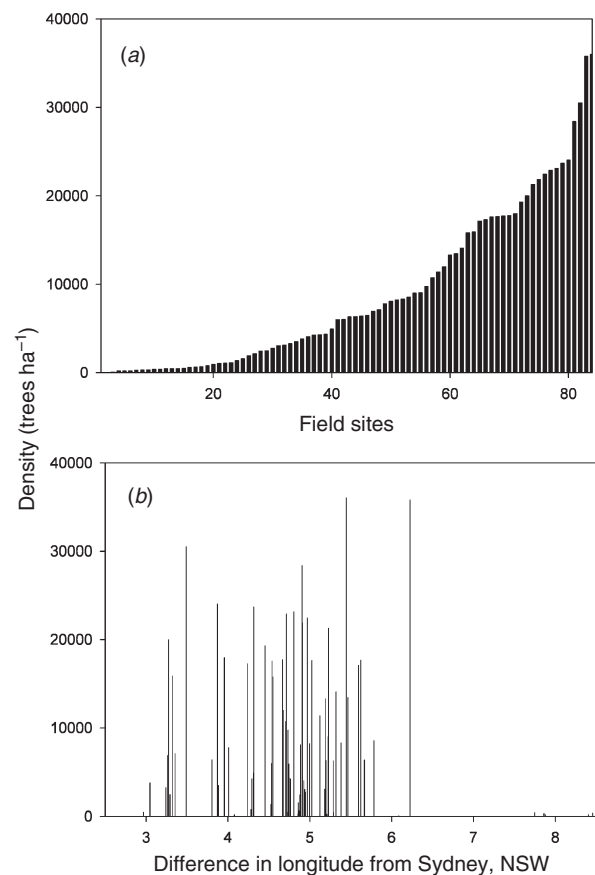


Fig. 1. *Callitris glaucophylla* density (trees ha⁻¹) by (a) rank order of sites and (b) distance in a westerly direction from Sydney.

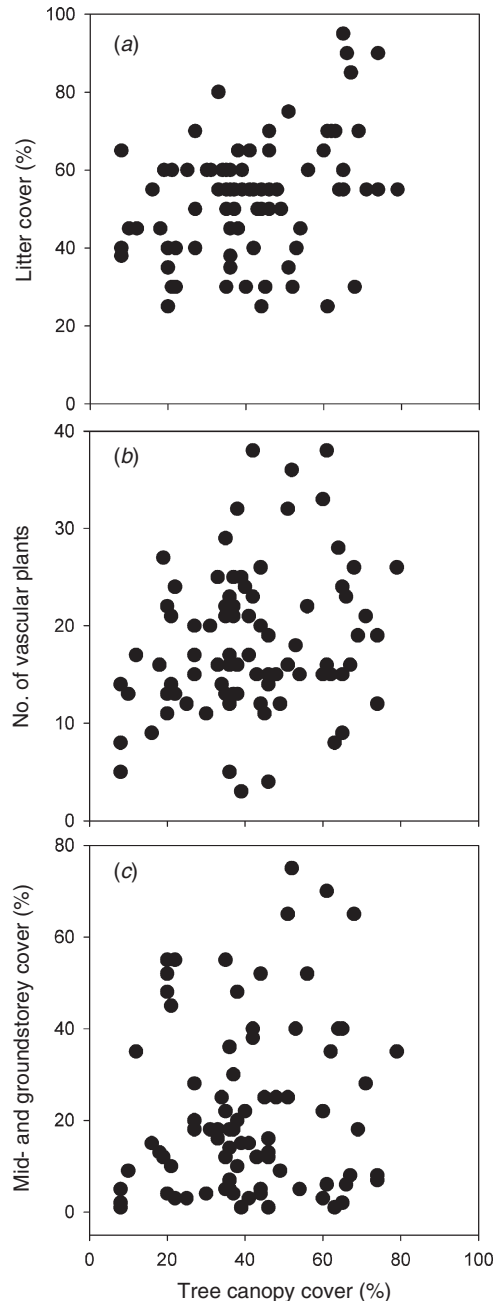


Fig. 2. Relationships between tree canopy cover (%) and (a) litter cover, (b) diversity of vascular plants and (c) cover of mid- and groundstorey plants (%).

expected variations in rainfall to influence the diversity of vascular plants. Sites were partitioned into three classes based on average annual rainfall (≤ 350 mm, 350–450 mm, >450 mm). Significantly ($F_{2,80} = 21.72$, $P < 0.001$) more species were recorded at the sites with higher rainfall than at the sites with lower rainfall. There was a significantly greater proportion of natives and a significantly greater proportion of perennial plants at the high-rainfall sites than at the

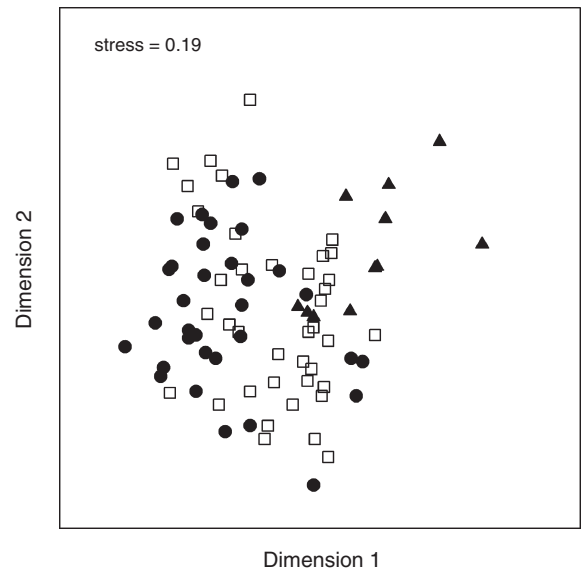


Fig. 3. The first two dimensions of the multi-dimensional scaling biplot coded for average annual rainfall. Triangles represent <350 mm rainfall, squares 350–450 mm rainfall, and circles >450 mm rainfall.

sites in the other rainfall areas (Kruskal–Wallis $H = 8.86$, $P = 0.01$ and $H = 9.72$, $P = 0.008$, for % native and % perennial, respectively). Analysis of similarities (ANOSIM) indicated a significant difference in the complement of species among the three rainfall zones (Global $R = 0.228$, $P = 0.001$).

Significant positive relationships were found between average annual rainfall and understorey plant diversity ($r = 0.57$, $P < 0.001$) and cover ($r = 0.50$, $P < 0.001$), tree cover ($r = 0.30$, $P = 0.005$), proportion of native plants ($r = 0.29$, $P = 0.008$) and proportion of perennial plants ($r = 0.27$, $P = 0.014$).

The CCA biplot indicated that three environmental variables (average annual rainfall, clay content of the soil and carbon content of the soil) explain $\sim 30\%$ of the variance in the species environment ($P < 0.005$). The first two axes of the CCA biplot explained 8.3% of the variance in species and 48.3% of the variance in species–environment relationships when both average annual rainfall and longitude were used as covariates to partition out the effects of the strong rainfall gradient. Although this suggests a correlation between rainfall and clay content, no significant ($r = 0.234$, $P > 0.05$) relationship existed. In general, the multivariate analyses reinforced the notion that rainfall is driving the species composition. The first dimension of the MDS biplot was highly negatively correlated with average annual rainfall ($F_{1,81} = 147.3$, $R^2 = 0.64$) and positively correlated with plant diversity ($F_{1,81} = 106.0$, $R^2 = 0.56$), plant cover ($F_{1,81} = 50.5$, $R^2 = 0.38$) and tree cover ($F_{1,81} = 17.4$, $R^2 = 0.167$). Predictably, the second dimension was highly correlated with plant perenniality (i.e. perennial v. annual,

$F_{1,81} = 55.5$, $R^2 = 0.40$) and plant origin (native v. exotic, $F_{1,81} = 47.3$, $R^2 = 0.36$).

Impact of clearing and logging on cover and diversity

The perennality and origin of the understorey vegetation were correlated, although poorly, with the logging history of the field plots. Unlogged sites had a significantly ($H = 7.51$, $P = 0.006$) greater proportion of perennial plants ($77.9 \pm 2.2\%$) than did logged sites ($63.5 \pm 3.7\%$), and a greater ($F_{1,82} = 10.7$, $P = 0.002$) proportion of native plants ($84.5 \pm 1.9\%$) than did logged sites ($71.0 \pm 4.3\%$). There were no significant ($P > 0.05$) differences in diversity or cover of understorey plants among sites that had been thinned or logged. We acknowledge that there were probably some differences in the recovery of sites after logging and thinning, on the basis of different time and intensity of treatments. As all state forests have been logged during some stage of their history, the thinning/logging classifications were generally based on the previous decade of management. However, we believe that any impact of different recovery intervals would have been minimal by the time our measurements were made.

As indicated above, the presence of mature eucalypt trees indicates that the site probably has not been substantially altered or managed for forestry, because the standard management strategy in *C. glaucophylla* state forests was to remove mature eucalypts to encourage growth of *C. glaucophylla* (Lacey 1972; Curby 1997; Allen 1998). In general, sites with a greater cover of *Eucalyptus* spp. tended to support more shrub species ($F_{1,82} = 13.43$, $P < 0.001$, $R^2 = 0.13$) and a greater shrub cover ($F_{1,82} = 11.68$, $P < 0.001$, $R^2 = 0.12$). However, there were no significant relationships between the cover of *C. glaucophylla* and the canopy cover or the diversity of shrubs ($P = 0.26$).

Discussion

We set out to examine possible relationships between *C. glaucophylla*-dominated woodlands and the cover and diversity of vascular plants. However, in a landscape where rainfall amount and variability change substantially from east to west, a significant influence of rainfall on plant cover and diversity was expected. Despite suggestions in the literature that the dense cover of trees limits the growth of understorey plants (Lacey 1973; Nowland 1997), we were unable to find a clear relationship between canopy cover or wood density and vascular plant cover or composition. As a result, we are unable to accept the initial hypothesis of differences in understorey vascular plant cover and wood density in relation to tree cover. This lack of a relationship was consistent even when we accounted for differences in rainfall.

We suggest that examination of understorey biomass might provide a better indication of landscape condition

beneath a dense canopy. In our study, stands of *C. glaucophylla* on leasehold or freehold grazing land supported 20% fewer species than did roadside reserves, travelling stock reserves or state forests, suggesting that differences in diversity may be linked, at least in part, to differences in grazing intensity. The lack of a clearly defined relationship between the understorey and overstorey components is probably related to differences in the intensity of grazing, which influences biomass, cover and diversity of the understorey plants at a range of spatial scales (Prober and Thiele 1995; Fensham *et al.* 1999; Yates *et al.* 2000).

The usual grazing strategy on pastoral lands is to have large paddocks and to fix the number of stock grazed ('set stocking'), with animals grazing different parts of the paddock to varying degrees. Roadside corridors used as travelling stock reserves are generally stocked intermittently. In terms of our study, this means that the sites may have been heavily grazed by stock, or, alternatively, they might have been lightly grazed, depending on the location of watering points and the types and number of grazing animals (Landsberg *et al.* 2003). As empirical data on grazing intensity could not be obtained for most sites, we had to rely on coarse-level information. Therefore, we characterised the degree of grazing as either grazed or ungrazed on the basis of our observations of grazing animals, the presence or absence of fresh dung and information obtained from individual land managers. The problems associated with assessing grazing were similar within *C. glaucophylla* state forests, where sheep and cattle grazing is used to prevent the build-up of fuel to reduce the risk of wildfire (FCNSW 1981; Wilson *et al.* 1997). Pastoralists with occupational permits to use state forests do not necessarily practice set stocking or use the total area of the lease (Wilson *et al.* 1997). Thus, the occurrence of a grazing lease on a state forest did not tell us anything about the extent or intensity of grazing. Similarly, the extent of grazing on travelling stock reserves could not be quantified other than to say that it was 'intermittent'. Had we been able to stratify our sites on the basis of more accurate empirical data on grazing intensity, then understorey trends in relation to tree density may have been apparent.

The lack of a clear relationship between tree cover and understorey floristics could also relate to differences in the climatic conditions during the period of data collection. Field data were collected during a period of below-average annual rainfall and, given the widely accepted view that recruitment in arid areas is largely driven by rainfall (Noy-Meir 1979), the lack of viable seeds in the soil may account for this. A high density of trees may have limited the dispersal of viable seed populations, particularly annuals, which have limited recruitment (Bertiller 1998).

Although the distribution of *C. glaucophylla* litter varied markedly among and within sites, increases in litter cover

were generally attributed to associated increases in tree cover. *C. glaucophylla* woodlands are typically underlain by an extensive layer of pine needles (Hawkins 1966; Lacey 1972; Harris *et al.* 2003), which often helps to stabilise the soil surface (Eldridge and Myers 1998). In some vegetation communities, litter is known to inhibit seedling germination (Barritt and Facelli 2001), whereas in others it has minimal or no effect (Facelli and Pickett 1991; Facelli *et al.* 1999; Hastwell and Facelli 2000). A recent study of the impact of *C. glaucophylla* litter on understorey plants suggests that it does not suppress the emergence and growth of understorey vegetation (Harris *et al.* 2003). Biological compounds in *C. glaucophylla* needles increase its natural ability to resist insect attack (Baker and Smith 1910; Lacey 1973) but may also have adverse effects on understorey cover (Harris *et al.* 2003). However, *C. glaucophylla* litter decomposes rapidly (Lacey 1973), possibly overriding the effects of the chemical compounds leaching into the soil. Suppression of plant germination by *C. glaucophylla* leachate may explain some of the variability observed across our sites, as well as the variability within sites with different cover and depth of litter.

Callitris litter is also known to have a major inhibitory effect on the infiltration of water (Eldridge and Freudenberger 2005). Some of this effect may be due to the presence of hydrophobic fungal hyphae and other biological agents in the litter (Bond and Harris 1964). The litter is likely to provide poor soil–seed contact and delay the imbibition of water at least until times of high water availability. However, where litter is mobilised by overland flow, which frequently occurs in pine forests on extensive sloping surfaces (Eddy *et al.* 1999), seeds readily germinate in the resultant litter dams where light and nutrient levels are enhanced (D. J. Eldridge, pers. obs.).

Overall, we suspect that the reasons for the poor relationships between tree cover and understorey are more obscure. Complex interactions between grazing, rainfall, plant physiology and previous management are involved, and are known to influence the cover and composition of *C. glaucophylla* understorey (Wilson *et al.* 1997; Andrews 2003). Indeed, in the Cobar area in the early 1960s, the failure of landholders to reduce stocking rates in dense *Callitris* woodlands in order to compensate for declining ground cover has been cited as a contributing factor to the resulting increase in regrowth and further declines in ground cover (Anon. 1969).

The multivariate analyses confirmed that, as expected, rainfall was largely driving the distribution of species across the east–west gradient, although soil texture and carbon were also implicated. Only 7% of sites contained more than 30 species, and these were all sites with more than 475 mm average annual rainfall. Despite the large differences in rainfall across our sites, we were unable to detect relationships between tree cover and understorey diversity under different rainfall classes.

Our study showed that the sites that had not been logged contained a greater proportion of perennials and natives, thus supporting our third hypothesis. Management of native cypress pine forests often involves thinning and logging for harvesting the commercially valuable timber. These practices (i.e. thinning and logging) require a certain level of disturbance; the machinery used in forestry operations creates disturbances that are likely to favour the establishment of annuals and/or exotics. Disturbances such as clearing and grazing in white box (*Eucalyptus albens*) woodlands are known to promote the establishment of weeds and reduce the richness of native species (Prober and Thiele 1995). Walker *et al.* (1995) showed that construction of an easement along the natural gas pipeline in western NSW resulted in long-lasting changes in plant floristics and a shift from perennials to annuals and Mediterranean weeds, which persisted for many years. Similarly, a study of *C. glaucophylla* woodlands on the Northern Tablelands of NSW indicated a high correlation between disturbance and the proportion of exotics in the groundstorey (Andrews 2003).

The third major result of our study was that sites where mature eucalypts were present had significantly greater cover and density of shrubs than did sites without eucalypts. The shrub component of these woodlands was confirmed by reference to early literature, which indicated that the *E. populnea*–*E. intertexta*–*C. glaucophylla* association originally supported a mixed shrub layer (see review by Iwazskiewicz and Semple 1988). Indeed, species such as *Acacia*, *Dodonaea*, *Eremophila* and *Chenopodium* were recorded in many of our sites. The link between shrubs and eucalypts suggests to us two things: either that eucalypts are augmenting the landscape to make them more conducive to the establishment and growth of shrubs, and/or that the presence of eucalypts is an indication that these sites have not been markedly affected by forestry practices.

Eucalypts have large canopies which typically reach diameters of greater than 20 m. They are known to produce large amounts of leaf litter (Eldridge and Rath 2002), which enhances soil nitrogen and carbon at distances beyond the edge of their canopies. Further, infiltration rates are known to be up to three times greater under the canopy than with open (non-canopy) sites (Eldridge and Rath 2002; Eldridge and Freudenberger 2005). It is conceivable, therefore, that shrubs may have benefited from being close to eucalypts, perhaps even benefiting from improved water relations and hydraulic lift close to large trees (Dawson 1993). Several bird-dispersed members of the family Chenopodiaceae (e.g. *Rhagodia spinescens*, *Enchylaena tomentosa*) were found below tree canopies, but in general, most shrubs did not grow directly under *C. glaucophylla* canopies.

The relationship between the presence of shrubs and eucalypts can be explored by examining the historic management of the *Callitris* woodlands. Until the 1960s and 1970s, the Forestry Commission of NSW

ringbarked, poisoned and removed eucalypts as part of a program designed to enhance the growth potential of *C. glaucophylla* (Lindsay 1967; FCNSW 1981; Curby 1997; Allen 1998). Non-pine timber was viewed as 'useless' in terms of timber production, as these trees were competing directly with commercially viable *C. glaucophylla*. In areas where forestry operations were less intensive, remnants of the original community mosaic still exist. Although it is not possible for us to verify the fourth hypothesis, we believe that the present distribution of shrubs is a reflection of the intensity of past forestry operations.

The implications of our work are that floristically rich understorey vegetation is not incompatible with a dense cover of *C. glaucophylla*. We acknowledge, however, that removal of some trees to stimulate a species response may be a management goal in some areas (Horne and Robinson 1987; FCNSW 1988). An ongoing study in the Northern Tablelands of NSW is currently monitoring tree growth and changes in groundstorey vegetation following thinning of *C. glaucophylla*. Preliminary results suggest that groundstorey vegetation can be suppressed under dense *Callitris* but the response depends on prior management (Andrews 2003). Little is known, however, about rates of tree removal required to generate an increase in understorey plants or the long-term impacts of removal of trees. In the mulga woodlands of NSW, Noble (1997) showed that the response to removal of woody species (in this case the shrub *Dodonaea viscosa*) of groundstorey plants, particularly perennial forbs and grasses, can be substantial, but only after 70–80% of the shrubs have been removed. If this is the case, then reinstating the floristically diverse understorey to some *C. glaucophylla* woodlands may be technically challenging. Our data suggest that tree cover and wood density alone account for very little of the variation in understorey cover and diversity and that other factors are more influential. Given the marked impact of grazing on groundstorey vegetation in other studies, and our general field observations (see Eldridge *et al.* 2003), we believe that grazing is strongly implicated.

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