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Variability in allometric relationships for temperate woodland *Eucalyptus* trees

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ABSTRACT

Essential to effective vegetation management and habitat conservation is an understanding of tree and stand structure. However, such data for Australian *Eucalyptus* woodlands come mostly from forestry research and tend to be restricted to production forest types, and merchantable stems and species. We aimed to improve understanding of allometric relationships and stand dynamics for temperate *Eucalyptus* from critically endangered temperate woodlands. We explored relationships among tree height, diameter at breast height (DBH), crown width, crown senescence, and vegetation density. We measured 3748 naturally-occurring trees on 105 one-hectare sites in remnant vegetation in an agricultural landscape in semi-arid eastern Australia. Four species accounted for 94% of trees measured: *Eucalyptus camaldulensis* Dehnh. (river red gum), *E. melliodora* A.Cunn. ex Schauer (yellow box), *E. microcarpa* Maiden (grey box) and *E. populnea* F.Muell. subsp. *bimbil* L.A.S.Johnson & K.D.Hill (poplar box). Six *Eucalyptus* species were present in relatively low numbers. At about 15 cm DBH, growth changed from being directed primarily at height gain to increasing relative crown width. Trees with DBH $\geqslant$ 15 cm showed large and increasing variation in shape with increasing DBH, and tree dimensions varied among species. For a given DBH, yellow box were taller with relatively narrow crowns than poplar box, and river red gum and grey box intermediate to these two species. Human manipulation of the agricultural landscapes has impacted on these allometric relationships. Past attempts by people to kill trees has resulted in frequent coppicing, with up to 13 trunks. Up to 50% of trees of each species (mean 29%) had multiple stems and multi-stemmed trees had relatively broader crowns than single-stemmed trees. Similarly, decreasing vegetation density by tree removal generally resulted in shorter trees with wider canopies for any DBH. Progression through crown development and senescence was similar among species except that it occurred at different trunk sizes for different species. The variability of allometric relationships within temperate *Eucalyptus* species, combined with their variable growth rates, makes it difficult to accurately predict outcomes of current land management decisions in terms of vegetation structure and biological habitat attributes.

1. Introduction

Allometric relationships in trees are used to estimate tree biomass and have become an important tool for calculating carbon stored in vegetated landscapes (Brack and Richards, 2002; Williams et al., 2005; Chave et al., 2005; Jonson and Freudenberger, 2011). They also play an important role in modelling of stand dynamics (Pretzsch et al., 2014), and predicting habitat value of individual trees (Vuidot et al., 2011; Rayner et al., 2014).

Trunk diameter and tree height are among the most important variables for predicting biomass (Chave et al., 2005; Paul et al., 2013), with reliable predictions of biomass across a broad range of tropical forest types made possible by compilation of large allometric datasets (Chave et al., 2005). The relationships among trunk diameter, height, biomass and tree density mean that diameter and height are frequently used to model stand dynamics (Ross et al., 2008; Pretzsch et al., 2014; Lung and Espira, 2015).

Trunk diameter and tree height, together with crown diameter, are also frequently positively correlated with abundance of fauna habitat features such as foraging substrates on foliage and bark, tree hollows, or crevices (Vesk et al., 2008; Rayner et al., 2011, 2014;

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Vuidot et al., 2011). As a result, there are clear links between tree and stand structure and the species guilds inhabiting vegetation (e.g., Holmes and Recher, 1986). There is also evidence that as trees age and senesce, crown structure becomes more complex (Ishii and McDowell, 2002; Bar-Ness et al., 2012) potentially providing a greater diversity of microhabitats (Vuidot et al., 2011). Therefore, understanding the process of development of crown dimensions and canopy senescence is likely to provide a better understanding of associated changes in availability of fauna habitat.

Extensive areas of Australia are covered by woodlands dominated by trees in the genus *Eucalyptus* (Gillison, 1994). Natural eucalypt woodlands are extremely variable in structure and different in stand structure to forest vegetation and plantations, but typically have trees that are relatively widely spaced with spreading canopies (Gillison, 1994). However, information on tree allometry in eucalypts is biased towards production forest types, often for merchantable stems and species, and stems within a certain size range (usually 20–100 cm diameter at breast height) (Keith et al., 2000). This means there are few data for small trees and very large trees, both of which have important habitat values in woodlands (Parkes et al., 2003; Bedward et al., 2009). Better understanding of crown development from very small trees through to very large trees will enable better temporal planning of woodland restoration.

Woodlands of the eastern and south-western Australian cropping belts are recognised as ecoregions in crisis on an international scale (Hoekstra et al., 2005), and as high priority for conservation due to extensive clearing and small amount of remaining natural vegetation (Pressey et al., 2000). Historical land use has altered the structure of these woodlands with changes in stem densities and species composition (Sivertsen, 1993; Lunt et al., 2006; Bedward et al., 2007). These human impacts may also have changed individual tree structure as many trees have resprouted after failed attempts to kill them by ringbarking during agricultural development (Bedward et al., 2007). Changes in structure at the stand and tree level are important due to their potential influence on growth rates and allometric relationships of individual tree trunks (Neilsen and Gerrand, 1999; Akhtar et al., 2008; Taylor et al., 2014), and the implications for rates at which trees develop fauna habitat features (e.g., hollows, Rayner et al., 2014).

Biases in existing data sources (Keith et al., 2000) mean that there are many vegetation types, tree species, tree sizes and tree densities in Australian woodlands for which there are few allometric data. It is difficult to extrapolate existing plantation-sourced data to woodlands or data from one species to another as allometric relationships vary within species among sites (Montagu et al., 2005; Williams et al., 2005) in relation to factors such as moisture (Barton and Montagu, 2006) or tree density (Akhtar et al., 2008; but see António et al., 2007).

Here, we have explored allometric relationships for ten species of *Eucalyptus*, all of which are widespread across inland eastern Australia. We aim to identify tree-level determinants of change in woodland stand structure, and variation in fauna habitat elements. Specifically we aimed to:

(i) describe the basic allometric relationship among diameter at breast height (DBH), crown dimensions, and tree shape (the ratio of crown width to tree height) and to compare this relationship among species of *Eucalyptus*,
(ii) examine allometric differences between single- and multi-stemmed trees,
(iii) examine the effect of site-level vegetation density on stand-level tree shape and individual tree shape,
(iv) quantify inter-specific differences in the relationship between tree size (DBH) and crown senescence (the loss of foliage and branches) to explore structural changes in woodland trees that occur over time.

2. Methods

2.1. Study area

We conducted our study within a 10,000 km^2 area of semi-arid woodland in central-western New South Wales, Australia. This area was originally dominated by *Eucalyptus*, *Callitris* and *Acacia* woodlands (Metcalfe et al., 2003), but since European settlement in the late 1800s, has been extensively cleared and structurally modified, primarily for agriculture (Sivertsen, 1993; Lunt et al., 2006). We located all sites in areas originally occupied by the Plains or Riparian vegetation types of Metcalfe et al. (2003), in the intergrade between the *E. microcarpa* woodlands of the south and the *E. populnea* woodlands of the north (Ellis et al., 2015). The mean annual rainfall of the area is about 500 mm (527 mm at Narromine to the east, >50-year mean, Bureau of Meteorology station 051037; 493 mm at Trangie to the west, >50-year mean, Bureau of Meteorology station 051049). The landforms, vegetation and climate are described in more detail in Metcalfe et al. (2003) and mapped in Ellis and Taylor (2013).

2.2. Sites and allometric measurements

To gain an understanding of how woodland *Eucalyptus* tree species would grow in the absence of competition, we measured 157 trees at 16 sites located in open environments (hereafter 'open sites') in August 2004. On these open sites all measured trees were at least one crown width from the nearest neighbour of similar or larger size (i.e., one crown width between outer edges of adjacent crowns). All of these trees were live, single-stemmed and showed no evidence of resprouting. These trees spanned the range of available stem diameters for each of the *Eucalyptus* species present, but this range was limited for some species. Forty-six of these trees were planted, with 41 of the planted trees having diameter at breast height (DBH at 1.35 m) < 15 cm. These 16 open sites were on roadsides, Travelling Stock Routes and Reserves (TSR), private property or in state forests.

We examined the development of crown structure in the 157 trees from open sites by measuring DBH, height, crown width and height above ground to the lowest green foliage (crown base height). For all trees that were taller than 1.35 m, we measured stem DBH over bark to the nearest centimetre using a diameter tape. We measured height, crown width and crown base height directly with a tape measure, or photogrammetrically, using a subset of the methods described in Dean (2003), using a digital photograph of each tree with a 1-m scale measure beside the tree.

To investigate the influence of site and stand characteristics on tree morphology, we collected allometric data from trees on an additional 105 one-hectare sites, 51 sites between January 2008 and February 2009 and the remainder between November 2010 and July 2011. On these sites, we measured all trees in the genus *Eucalyptus* with a DBH $\geqslant$ 15 cm. For trees with multiple stems branching from below breast height, if the combined cross-sectional area of all stems at breast height was greater than that of a 15-cm stem (i.e., area $\geqslant$ 176.7 cm^2), we recorded all stem diameters even if individual stems were <15 cm DBH. During the first sampling period (51 sites) we recorded any evidence of cutting or ringbarking of trunks that had been followed by resprouting resulting in multiple stems in one tree.

We individually tagged each tree and recorded its species, DBH, condition and form. As DBH is the strongest and most reliable predictor of a range of morphometric variables in woodland *Eucalyptus* species (Rayner et al., 2014), we measured DBH on all trees. Where a tree had multiple stems, we calculated the cross-sectional area, and derived an equivalent DBH for a single stem of the same cross-sectional area. We measured height to