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Examining the influences of site conditions and disturbance on rainforest structure through tree ring analyses in two Araucariaceae species

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ABSTRACT

Tree growth is central to the dynamics of forest ecosystems. Patterns in tree diameter growth from tree rings can yield an understanding of the growth trajectories of trees and how they vary with site conditions but detailed studies have been conducted on relatively few species in tropical forests. Furthermore, tree rings provide information on temporal patterns of tree establishment and thus the influences of disturbance and abiotic conditions on forest structure. Here, we confirm the annularity of growth rings in *Agathis robusta* and *Araucaria cunninghamii* from North Queensland, Australia. We then examine tree growth trajectories in two contrasting natural forests (Downfall Creek and Gillies Range) and a plantation. Growth in plantation over 70 years was high and growth trajectories were similar among trees within each species. In natural forests age and diameter were only weakly correlated for both species. Growth trajectories were similar and homogeneous for both *Agathis* and *Araucaria* in the plantation, whereas there was a great deal of variation in tree ages and growth trajectories observed for the two forest sites. These differences are likely related to dynamics driven by climate and soil that modulate boundaries between sclerophyll and rainforest over the long-term. Downfall Creek (a ridge with poor shallow soils) is likely recently invaded (past couple of hundred years) sclerophyll woodland. The alternative hypothesis—that structural and compositional characteristics result from local disturbance resulting from World War II training activities—was not strongly supported by *Agathis* establishment dates. The study of tree rings in tropical trees is underappreciated and can provide valuable information on the influences on tree growth and disturbance in tropical forests.

1. Introduction

There is a dearth of dendroecological studies in the tropics. Despite a long-history of study of tree rings dating back to the early 20th century (Worbes, 2002), the tropics are commonly thought of as everwet and thus supporting uninterrupted tree growth. However, a large proportion of tropical forests experience significant seasonal climatic rhythms. Seasonal annual rhythms in precipitation such as the occurrence of dry seasons in tropical forests with monsoonal climates, or the occurrence of annual flooding in the Amazon, have a marked impact on wood anatomy and drive the formation of annual growth rings in many tree species (Worbes, 2002; Rozendaal and Zuidema, 2011). Estimates of the number of ring-forming tropical tree species indicate substantial untapped capacity to study the dynamics of tropical forests through the use of tree rings (Worbes, 2002; Baker et al., 2005; Brienen and Zuidema, 2006b). While study of annual growth rings in trees—a pillar of forest mensuration—has provided a wealth of information on forest dynamics and patterns of influential disturbances in temperate and boreal ecosystems (Zackrisson, 1977; Oliver, 1981; Oliver and Larson, 1990; Archambault and Bergeron, 1992; Winter et al., 2002), the potential of tropical dendroecology remains relatively underdeveloped (Rozendaal and Zuidema, 2011; Zuidema et al., 2013).

Information from annual tree rings provides evidence of growth patterns in tropical trees, which is integral to understand many aspects of tropical forest dynamics. Information about the processes of tree recruitment (high or low light environments) can be gleaned from the record of juvenile growth (growth trajectories) present in tree rings of existing canopy trees (Baker and Bunyavejchewin, 2006; Brienen and Zuidema, 2006a). Growth trajectories can be linked to differences in species light demand (Baker and Bunyavejchewin, 2006), or to site conditions such as

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water availability in wetter versus drier forests (Brienen and Zuidema, 2006a,b).

Patterns of recruitment are related to canopy disturbance in light-demanding trees and yield insights into the timing and spatial extent of disturbance events (Baker and Bunyavejchewin, 2006; Middendorp et al., 2013). However, few researchers have applied this tool in tropical forests. This is despite long standing knowledge of tree rings in tropical forests (Worbes, 2002), and a demonstrated utility for looking into the past to understand contemporary patterns and processes in intensely studied tropical forest dynamics plots (Baker et al., 2005; Baker and Bunyavejchewin, 2006; Nock et al., 2009, 2011; Hietz et al., 2011; Middendorp et al., 2013).

The southern-hemisphere conifer family Araucariaceae is one of the tropical tree families in which a number of species have been documented to produce annual tree rings. Recent studies in have been successful in re-constructing the colonization of new sites by Araucariaceae (Silva et al., 2009) and in identifying climatic signals in tree rings of *Araucaria angustifolia* (Bertol.) O. Kuntze in Brazil (Oliveira et al., 2009; but see Boysen et al., 2014). Furthermore, *Agathis australis* has proved suitable for compiling a multi-millennial tree ring chronology in New Zealand (Boswijk et al., 2014).

The production of information on tree age and on long-term tree growth patterns is essential to disentangling the influences of site conditions and disturbance in forests and can help clarify the relative roles of these factors in seasonal tropical forests. Such information is an essential component of developing science-based conservation and management of tropical tree species. However, seldom has the potential to use tree rings been explored to understand forest composition or to evaluate growth trends in Australian rainforests (though see Heinrich et al., 2008), even though evidence suggests tree rings in *Agathis robusta* (C.Moore ex F.Muell.) Bailey and *Araucaria cunninghamii* Aiton ex D.Don var. *cunninghamii* could potentially be used to examine differences in growth rates and growth trajectories among sites, or as additional evidence for the temporal pattern of canopy disturbances (Ash, 1983).

Our objectives in the following study were threefold: first, we sought to validate the annularity of growth rings in *A. robusta* and *A. cunninghamii*. Second, we examine growth trajectories for *A. robusta* and *A. cunninghamii* and how they differ across the sites. Finally, we investigate possible differences in disturbance history by comparing patterns of *A. robusta* canopy tree establishment.

2. Methods

2.1. Species

Originating in the Triassic, the Araucariaceae developed a wide distribution in both hemispheres the Jurassic–Cretaceous period. In present times the Araucariaceae have a greatly restricted distribution represented by 20 *Agathis* and 19 Araucaria species in the southern hemisphere (Kershaw and Wagstaff, 2001; Ledru and Stevenson, 2012; Enright and Hill, 1995). *A. robusta* is endemic to north-east Queensland and grows from sea level to 1100 m altitude on soils that vary from deep sands to shallow or deep well-drained soils on basalt, metamorphic or granitic rocks (with the best growth on granitic soils) and on a variety of sites receiving 1100–1800 millimetres rainfall annually (Cooper and Cooper, 2004; Boland et al., 2006). *Agathis* grows as an emergent in some rainforest types but forms a dominant component of stands in dry marginal rainforest types. *Araucaria* is found in rainforests and marginal rainforests from sea level to 600 m altitude on a variety of soils receiving >800 mm rainfall annually along the east coast of Australia and also in New Guinea (Cooper and Cooper, 2004; Boland et al., 2006).

Historically, European settlement was associated with intensive exploitation of both *Agathis* and *Araucaria* for timber (Whitmore, 1977).

2.1.1. Dendrochronology in A. robusta and A. cunninghamii

Previous research has established the dendrochronological potential of *Araucaria*. Ogden (1978) wrote that rings in *A. cunninghamii* appeared to be aproximately annual in older trees. Early studies in northern Queensland by Ash (1983) on A. robusta suggested that growth rings were not strictly annual, and that the major factor limiting growth was dry periods. Recently, (Boysen et al., 2014) combined classical dendrochonological methods with analylsis of stable isotopes of oxygen in examining ring annularity and the drivers of cambial dormancy in *A. robusta*. Anatomical features of tree rings observed in our samples resembled those exhibited by Boysen et al. (2014; Fig. 3), with tree ring borders being demarcated by ‘‘latewood-like” darker coloured and thicker-walled tracheids.

2.2. Sites

2.2.1. Climate

The climate in the region is monsoonal and rainfall is strongly seasonal (based on data from the nearby town of Atherton), with a distinct summer wet period when most rain falls (wettest quarter 60% mean annual rainfall), and a winter dry season marked by very limited precipitation (driest quarter 5% mean annual rainfall). Total mean annual rainfall and temperature are ~1400 mm and 20.5 °C respectively, and average maximum and minimum temperature are 26 °C and 15 °C, respectively (data spanning 1940 – 2008; Australian Bureau of Meteorology, 2002).

2.2.2. Gadgarra plantation

Gadgarra State Forest is the site of a plantation of *Agathis* and *Araucaria* established in c.1933 and was used to verify growth ring annularity (Fig. 1). The site was formerly tall eucalypt woodland and open forest (Regional Ecosystem (henceforth RE) 7.11.31d *sensu* Queensland Government 2014) and occurs on well drained, strongly weathered soils of the Bicton Association (*sensu* Laffan and Rinder, 1988). Plantation establishment typically entailed commercial logging of rainforest, followed by clear felling and burning of the remaining original vegetation. Seedlings were grown under shade for about 12–14 months, transferred to metal tubes, and then kept in the full sun for up to several months before being planted out (Huth and Holzworth, 2005). Seedlings which died in initial years were typically replaced by younger stock (Kerry Hanrahan, pers. comm. 2008).

2.2.3. Downfall Creek forest

Downfall Creek is located on the eastern side of the Tinaroo Range (Danbulla National Park) and consists of simple notophyll vine forest (RE 7.12.16a) lightly logged in the 1970s. The site straddles a low, gently to moderately sloping ridge crest, along which there are sections of skeletal soils with abundant outcrops of coarse-grained biotite granite (Gillies-Gowrie complex *sensu* Laffan and Rinder, 1988). A permanently marked 0.5 ha forest mensuration plot was established at Downfall Creek in 1971 (EP2 of Bradford et al., 2014), at which time there was no evidence or record of recent disturbance of the forest by natural events. No direct evidence of recent logging operations was found within the 0.5 ha plot layout (i.e., no residual stumps or surface charcoal fragments are evident) although evidence of skidding tracks was present in the general area at the time of establishment and *Agathis* had been selectively logged in the area. No significant disturbances