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

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A B S T R A C T

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.

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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

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
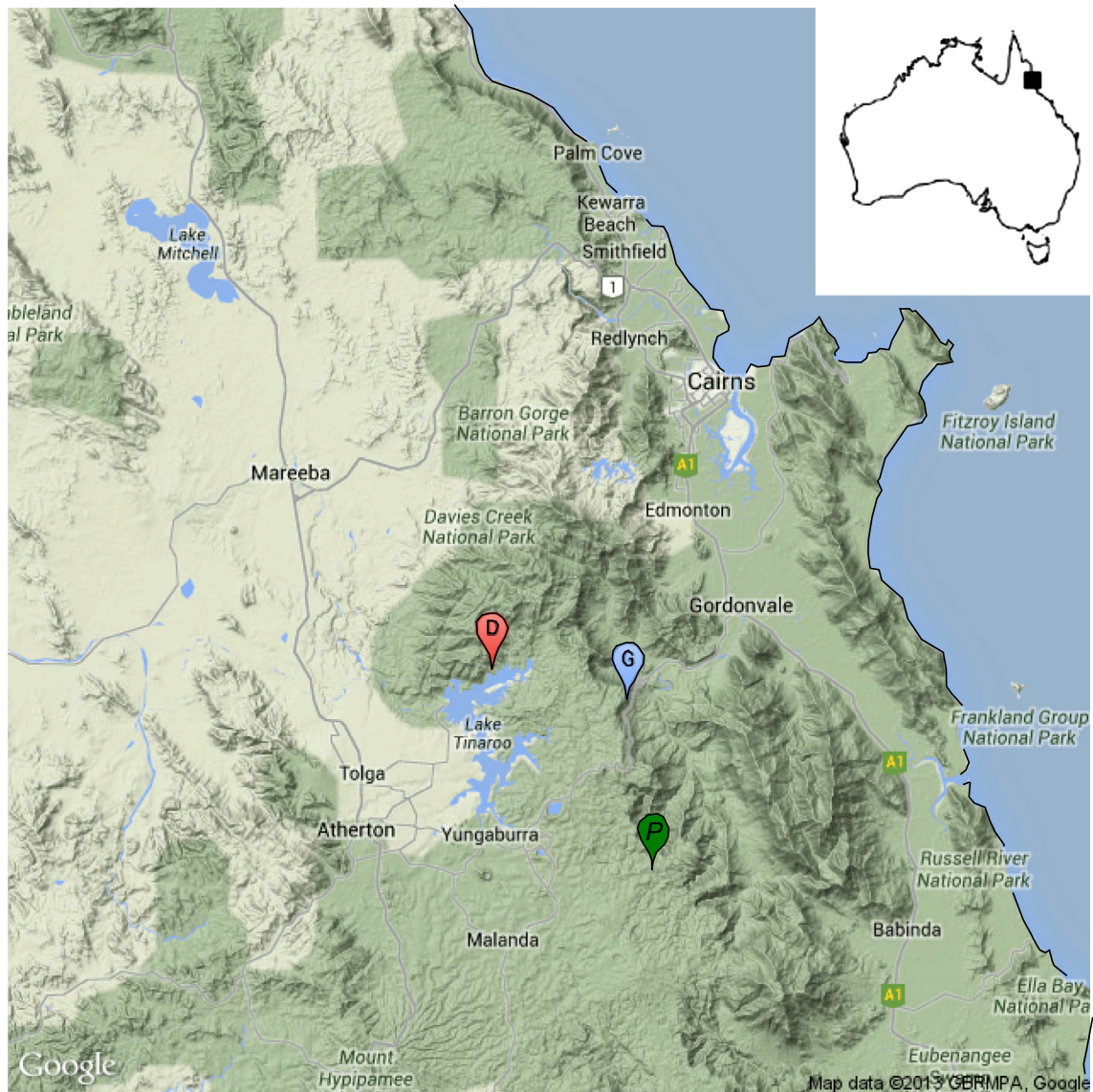
Fig. 1. Location of study sites Downfall Creek (D), Gillies Range (G) and Gadgarra Plantation (P) in North East Queensland, Australia. The two forest sites (D, G) are separated by a straightline distance of 12 km. The green boundary (darker grey in black and white) aproximates the boundary of tropical forest. Note: Map data ©2013 GBRMPA, Google.

have been recorded on the plot in the subsequent 44 years. The low basal area (34.1 m² ha⁻¹) and high stem density (1062 stems ⩾ 10 cm ha⁻¹) are typical of this forest type in infertile, seasonally dry habitats.

2.2.4. Gillies Range forest

The Gillies Range (Gadgarra National Park) is part of the coastal range system, and consists of steeply sloping granites and rhyolites with thin, often skeletal soils (Miscellaneous soils of the granitic hills and ranges *sensu* Laffan and Rinder, 1988). The upper slopes receive sufficient orogenic rainfall from the predominantly southeasterly winds to support rainforest. Lower slopes are covered in open eucalypt forest or woodland (RE 7.12.24b) with complex notophyll rainforest elements (RE 7.12.7a) with *Agathis* emergents along gullies where slightly deeper soils accumulate and dry season water is available. This forest type occasionally also supports natural populations of *Araucaria*—in this study, *Araucaria* and *Agathis* were found growing in close proximity. The canopy is much more open than at Downfall Creek and there is evidence of recent low intensity surface fire in form of fire scars on the upslope side of large *Agathis* trees. Over short distances the vegetation can

transition from rainforest into the drier vegetation type depending on the topography. Given the steep terrain the Gillies Range is unsuited to farming and we found no evidence of logging (tree stumps or skid trails).

2.3. Dendrochronology

Canopy trees were cored in June and September 2008. Two cores were extracted from smaller individuals (<20 cm dbh) and three cores from larger individuals at ~1.4 m. Cores were airdried in a lab, polished with a series of successively finer grained sandpaper (up to 600 grit) and then scanned at a high resolution (2400 dpi). We sampled six *Araucaria* and ten *Agathis* trees from the Gadgarra plantation, 23 *Agathis* and 16 *Araucaria* from the Gillies Range and 25 *Agathis* from Downfall Creek (seven of which are measured periodically as part of a permanent plot census).

Ring widths were measured in an image analysis program (Sigmascan Pro v.5.0.0, Systat Software Inc., San Jose, CA, USA) using a sub-routine developed to calculate ring widths (Hietz et al., 2011). To facilitate intra-tree cross-dating, we worked with multiple cores (images) simultaneously, progressively dating from

the bark towards the pith. For *Agathis*, counting both distinct as well as somewhat indistinct rings provided the closest match with radiocarbon ages in previous research (Ash, 1983), so both distinct and indistinct rings were measured and provided the closest match when dating cores.

2.3.1. Confirming the annual nature of growth rings

We validated the annularity of growth rings using two indicators: (1) consistency of tree ages with plantation age, and (2) a comparison of tree ring derived diameter growth to periodic plot based diameter measurements at Downfall Creek.

Ages of *Agathis* and *Araucaria* individuals from the plantation were estimated as the number of rings from the core which passed closest to the pith. Age estimates did not account for the time to reach coring height but this influence on dates was probably minimal due to rapid early growth, and in most samples the core did not exactly reach the pith, although curvature of inner rings generally indicated samples were close to the pith.

To compare measurements from the permanent plot made on supra-annual intervals to tree ring measurements, we plotted the diameter growth of *Agathis* individuals through time and compared it graphically to the estimate of diameter growth from the average of the cores taken from each *Agathis* in the plot. For one individual out of the seven sampled at EP2 (Fig. 2; AR6) there was a substantial offset between two estimates of tree diameter although the slopes of the lines for the change in diameter through time for the overlapping period were very similar. Re-inspection of the cores revealed one core to have much lower increments due to tree stem eccentricity and thus it was excluded from the comparison.

We also calculated the mean annual diameter growth for the years 1970 – 2006 for each tree in two ways using: (1) tree ring data, and, (2) the periodic plot measurements. We then compared these two estimates of the mean annual diameter growth for the period 1970 – 2006 by fitting a regression to a plot of the two growth rate estimates.

2.4. Species and site differences in tree growth trends and establishment dates

After intra-tree cross-dating, we compared tree growth rates and trajectories, as well as relationships between tree age and diameter for *Agathis* and *Araucaria* trees from the plantation (Gadgarra) and Downfall Creek and Gillies Range. To compare overall mean annual tree diameter growth among the sites (cm year^{-1}) we calculated the average annual growth for each tree and then calculated the mean for each species at each site. Growth trajectories were compared among sites and between the two species at a site by plotting diameter growth against tree age.

Finally, to gain insights into the possible influence of past disturbance at the Downfall Creek and Gillies Range sites dates of establishment were estimated from ring counts from the core with the greatest number of rings of the two to three cores that were obtained from each tree. Statistics and figures were generated in R, version 2.6.2 (R foundation for Statistical Computing, Vienna, Austria).

3. Results

3.1. Tree ring annularity

Estimated dates of establishment from ring counts for *Agathis* and *Araucaria* growing in the plantation were consistent with the known date of establishment for the plantation of ~1933. The mean year of the oldest tree ring in *Agathis* was 1937, and if the youngest tree was dropped the mean was 1936. For a few individuals estimated establishment dates were a number of years later than the plantation age, but in these trees fewer rings were counted near the center of the tree due to juvenile wood, in which rings are difficult to distinguish. Results for *Araucaria* were similar to those for *Agathis*; the mean year of the oldest ring for *Araucaria* was 1936.

Tree diameter growth through time estimated from tree ring measurements in *Agathis* was mostly in close agreement with diameter growth estimated from ~30 years of periodic plot measurements. For a few individuals we observed a slight offset between the two types of measurements (Fig. 2), although the slopes of the lines for the change in diameter through time for the overlapping period were very similar (e.g., AR6 in Fig. 2).

In general there was a close relationship between the mean annual growth rates obtained from tree rings and periodic measurements of tree diameter for the common interval 1970 to 2006. The value for the slope relating the measurement types was just slightly smaller than unity (slope = 0.88, r^2 = 0.97, $p < 0.001$; Fig. 3), but did not significantly differ from a slope of 1 (confidence interval = 0.75–1.00).
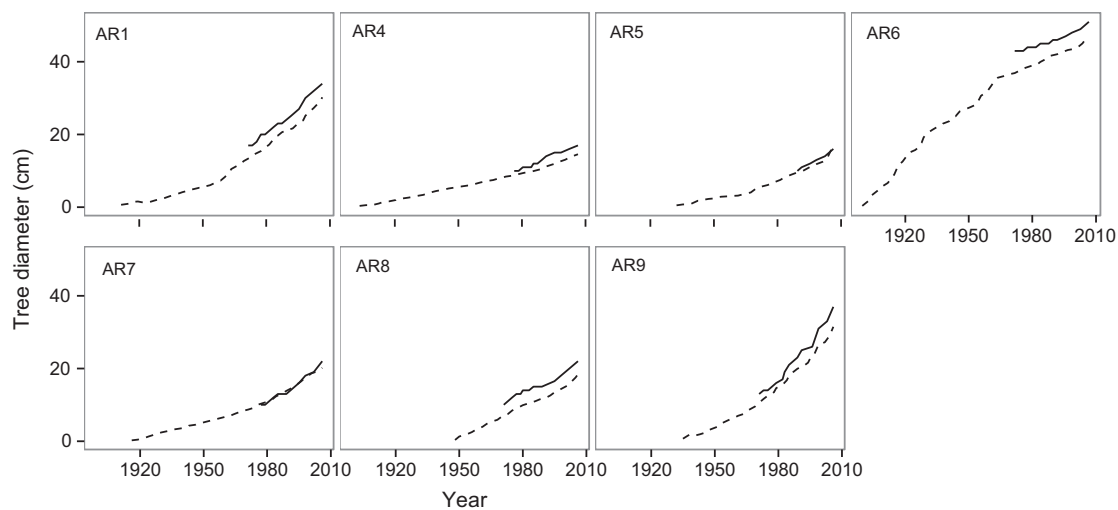

Fig. 2. Comparison of changes in tree diameter growth through time for seven individuals of *Agathis robusta* estimated from two methods: periodic measurements (solid line) and tree ring measurements (dashed line). Each panel is for one tree, with the sample code shown in the upper left corner. Diameter measurements on the plot commenced in the early 1970s. Data are from the Downfall Creek plot in north eastern Queensland.
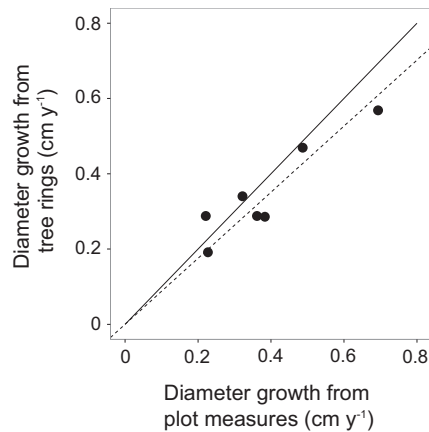
Fig. 3. Comparison of mean annual diameter growth (cm y^{-1}) obtained from tree ring measurements and mean annual diameter growth obtained from periodic measurements of tree diameter for 1970 to 2006. The solid line indicates the 1:1 relationship, the dotted line describes the fitted relationship (slope = 0.88, R^2 = 0.97, $p < 0.001$) which was not significantly different from 1 (confidence interval for the slope = 0.75–1.00). Average diameter growth from tree rings and from plot measurements were calculated using data for the period of overlap specific to each tree. Each point shows data for an individual tree.

Fig. 4. Relationship between tree age and diameter for *Agathis robusta* and *Araucaria cunninghamii* in two natural forests and a plantation in Northeast Queensland, Australia. Pearson correlations between tree diameter and age were the following: Downfall Creek *Agathis robusta* 0.42, Gillies Range *Agathis robusta* 0.69, Gillies Range *Araucaria cunninghamii* 0.56. Correlations not given for plantation as the trees are so close in age.

3.2. Site differences in growth rates

Mean annual diameter growth was much greater in the plantation than in the natural forests for both tree species (Table 1). The two species exhibited similar mean annual diameter increment in the plantation, and also at the Gilles Range (Table 1).

Trees in the plantation were of the same age and their diameter at 1.3 m height ranged between 36 cm and 58 cm in *Agathis* and between 51 cm and 65 cm in *Araucaria*. Within the natural forests there was substantial variation in tree diameter for a given age (Fig. 4). For example, tree diameter at 100 years of age at the Gillies Range ranged from a minimum of 10 cm to a maximum of 30 cm in *Agathis* (Fig. 5). At Downfall Creek, 175 year old *Araucaria* can range in diameter from 10 cm to 70 cm (Fig. 5). As expected, plantation grown trees were much larger given their age on average than in the natural forests, although a small number of *Agathis* individuals from the natural forests exhibited similar age:diameter ratios to the slowest growing plantation individuals (Fig. 4).

3.3. Growth trajectories

For both species growth trajectories were relatively uniform in the plantation, in contrast to the two natural forest sites where there was much more variation (Fig. 5). For example, for a plantation tree of either species that is 20 cm DBH, there was a very
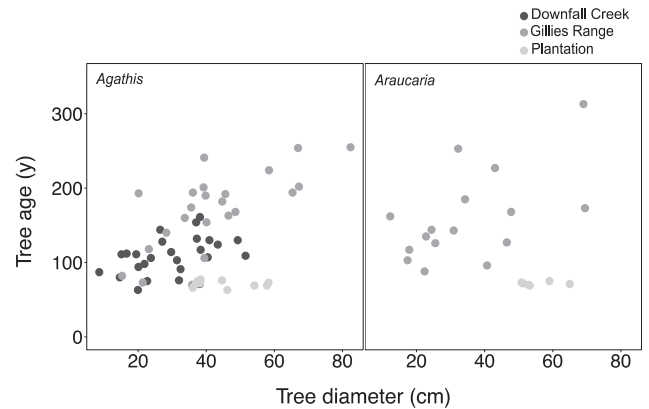
narrow range of ages (<10 years), whereas for the same diameter the range of ages was roughly an order of magnitude greater for the natural forest sites (Fig. 5). Comparing the two species in plantation, a number of *Agathis* exhibited evidence of a slowdown in growth, which was not very evident for *Araucaria* (Fig. 5). In contrast, in the natural forests *Araucaria* growth trajectories show a slowing of growth at large diameters and advanced ages (Fig. 5). Growth was characterized by generally high autocorrelation, with the fast growers remaining fast growing; this is evident in the lack of crossing lines for individual growth trajectories in Fig. 6. Early growth appeared to follow two general forms: either more or less linearly increasing diameter, or slower initial growth followed by increasing growth through time (i.e., curvilinear; Fig. 6).

3.4. Tree age, diameter and patterns of tree establishment

Agathis establishment patterns differed between the Downfall Creek and the Gillies Range (Fig. 7). Downfall Creek lacked individuals establishing before 1825, whereas we found a number of individuals of both *Agathis* and *Araucaria* that established before 1800 at the Gillies Range (Fig. 7).

4. Discussion

4.1. Annularity of growth rings in Agathis

Our first objective in the present study was to validate the results of Ash (1983). Based on ring counts and radiocarbon dating

Table 1
Summary of differences in mean annual diameter increment and mean increment age for *Agathis robusta* and *Araucaria cunninghamii* trees growing at two natural forests and a plantation in Queensland, Australia.

Species	Site	Mean annual diameter increment (cm y^{-1})	Standard error	Mean age of increments	Standard error
Agathis robusta					
	Plantation	0.62	0.04	36	0.70
	Gillies Range	0.25	0.02	85	5.54
	Downfall Creek	0.27	0.02	54	2.47
Araucaria cunninghamii					
	Plantation	0.76	0.03	36	0.44
	Gillies Range	0.22	0.02	80	7.58

Note: mean values were calculated first for each tree and subsequently mean values for each species at each site calculated. Values were calculated using all of the increments for each site.
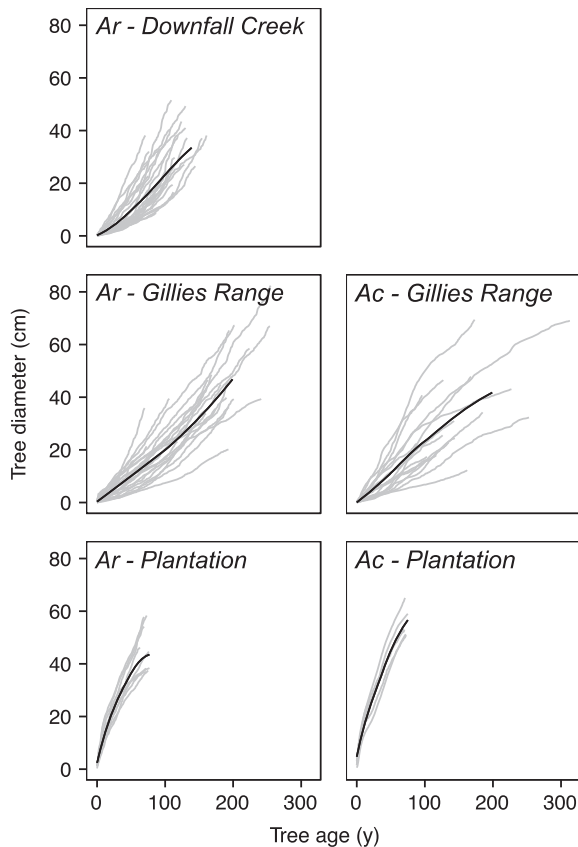
Fig. 5. Growth trajectories for *Agathis robusta* (Ar) and *Araucaria cunninghamii* (Ac) trees from two natural forests and a plantation. Each grey line shows the growth trajectory of an individual tree. The black line indicates the mean trend in the data series and is a loess curve.
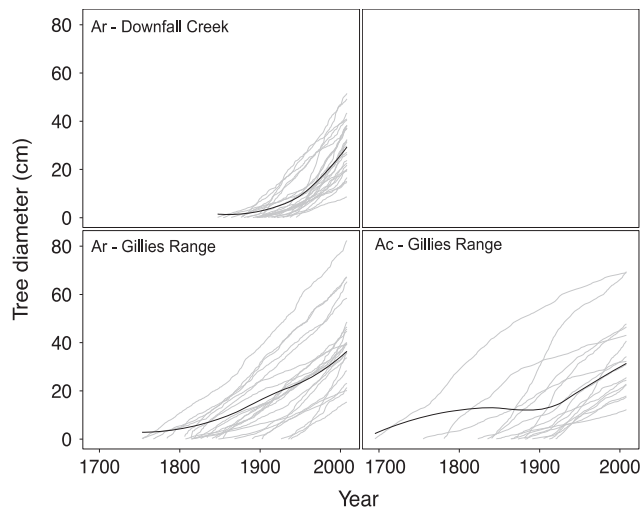

Fig. 6. Growth trajectories through time for *Agathis robusta* (Ar) and *Araucaria cunninghamii* (Ac) trees from two natural forests. Each grey line shows the growth trajectory of an individual tree. The black line indicates the mean trend in the data series and is a loess curve.
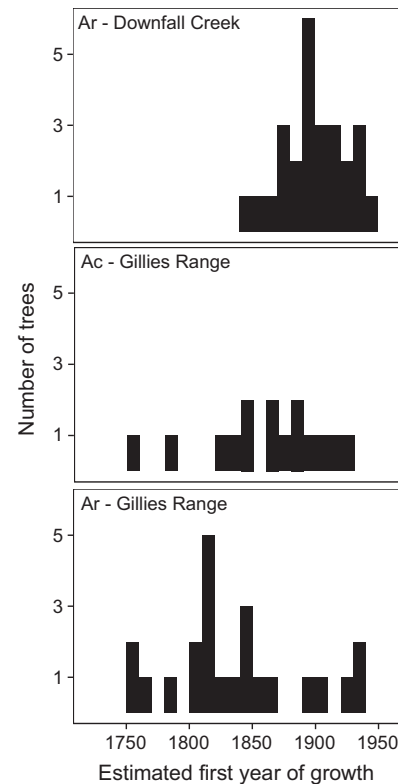

Fig. 7. Year of establishment of canopy trees of *Agathis robusta* (Ar) and *Araucaria cunninghamii* (Ac) estimated from the first year of growth measured from annual growth rings in two tropical forests: Downfall Creek and Gillies Range in Queensland, Australia.

Ash (1983) suggested that during the cooler and drier months of the year in Queensland, Australia, *A. robusta* and *A. cunninghamii* trees form growth rings with most trees forming one ring per year. Our comparison of ring counts for *Agathis* and *Araucaria* after approximately 70 years of growth with the known date of establishment for the plantation confirmed that growth ring formation in the two species is annual. Ring counts for *Agathis* and *Araucaria* growing in the plantation at Gadgarra suggested the oldest rings measured were produced in 1937 and 1936 respectively. The three to four year difference between the date of the oldest rings and the known date of establishment for the plantation (1933) is likely due to: (1) cores were collected at a height of 1.4 m, (2) plantation stock was generally germinated and grown in a nursery for ~2 years before being out-planted (Huth and Holzworth, 2005), and (3) sometimes the innermost rings were missing from the tree core sample.

We also show that for the ~30 years of overlapping periodic plot measurements and tree ring data there is good correspondence between tree diameter growth over time for *Agathis* trees (Fig. 2). We note that we did not account for bole eccentricity, the production and shedding of bark, and failure of the tree borer to pass exactly through the pith (tree center), although cores generally passed close to the pith as *Agathis* and *Araucaria* boles are rarely eccentric.

Growth rates estimated from the periodic plot measurements were not significantly different from growth rates estimated from tree ring measurements (Fig. 3). We found that in general different core samples from an individual could be synchronized, with clearly visible matching anatomical features and patterns in ring width variation. However, we also observed that false rings were formed in some individuals. Recently, Boysen et al. (2014) conducted a dendrochronological study of *A. robusta* also from the Atherton area and confirmed the occurrence of false rings using δ^{18}O. Given the correspondence between periodic diameter measurements and those derived from tree rings in the present study, it is likely that the occurrence of false rings and missing rings along the different axis (cores) were rare and generally equalizing. Indeed, Ash (1983) noted the occurrence of missing rings and other

anomalies in some individuals, although radiocarbon dates and ages from tree ring counts were still good matches.

More generally, our findings for *Agathis* and *Araucaria* are consistent with results from the literature, which suggest that for a number of Araucariaeceae dendroecological research is possible (Ogden, 1978, 1981; Buckley et al., 2000, Oliveira et al., 2009, Silva et al., 2009). Given that we show the ages are largely correct, the species examined here are likely suitable for ecological research investigating growth rates and age structures. However, it is also important to note that recent work on *Agathis* suggests that extreme care in dating and crossdating, and perhaps even data on intra-annual stable isotope variation may be required in some cases when the goal is to develop precise annual chronologies for climate-growth analyses (Boysen et al., 2014).

4.2. Growth trajectories

Growth rates found in *A. robusta* (Figs. 4 and 5) are similar to other *Agathis* species. For *Agathis australis* Ahmed and Ogden (1987) found mean annual diameter increments range from 0.15 to 0.46 cm y^{-1} on different sites with an overall average of 0.23 cm y^{-1}. In a more recent study, Enright and Goldblum (1998) found that for *Agathis ovata* diameter increment ranging from 0.14 to 0.22 cm y^{-1} in New Caledonia.

While growth trajectories were similar and homogeneous for both *Agathis* and *Araucaria* in the plantation, there was a great deal of variation observed for both the Downfall Creek site and for the Gillies Range forest. In comparing *Agathis* growth trajectories, we found that growth was initially slower at Downfall Creek but subsequently exceeded growth at the Gillies Range forest as trees matured (Fig. 5). The Gillies Range is a much more open forest, is drier, and is where we also observed evidence of low intensity surface fires in the form of fire scars on a number of large *Agathis* and *Araucaria*. It is thus possible that young *Agathis* experience more intense competitive pressure under lower light conditions (or higher densities) at Downfall Creek and thus exhibit slower initial growth, but growth rates increase with age and establishment because of more favourable overall site conditions. A minority of individuals at Downfall Creek exhibited juvenile growth trajectories similar to Gillies Range trees and are likely to have regenerated in gaps (Fig. 6). Langenheim et al. (1984), in a study of photosynthetic responses to light in seedlings, found that *Agathis* acclimated to high light (photon flux density) during growth and was adept at acclimating to sun and shade. Whitmore (1977) wrote extensively about the silviculture and ecology of *Agathis* species and also noted that while growth was most vigorous in high light, various *Agathis* species were observed to tolerate shade.

Although we did not specifically quantify the degree of growth autocorrelation it was clearly evident for both *Agathis* and *Araucaria* as persistent growth differences among trees that lasted for long time periods (referred to as *among tree autocorrelated growth*, Brienen et al., 2006; Fig. 5). Growth autocorrelation is important to both understanding and modeling the variation in tropical tree growth (Brienen et al., 2006); in this study differences between trees in site conditions or differences in competition for light are the most likely drivers of the observed persistent growth differences. For example, the more variable canopy structure and resultant light environments are likely the reason for the much greater variability in growth trajectories observed in the natural stands compared to the plantation (Fig. 5).

4.3. Influence of site conditions versus disturbance history on forest structure and composition

Indigenous Australians have occupied Australia for more than 40,000 years and are thought to have exerted a significant influence on rainforest vegetation (Kershaw, 1986). Nonetheless, the greatest changes in rainforest cover and composition have likely occurred since European settlement (Vanclay, 1996; Metcalfe and Ford, 2009).

When the plot network was established, researchers studying the rainforest vegetation in the Atherton area (Fig. 1) suspected the Downfall Creek forest had a unique developmental history based on: (1) individual tree characteristics, (2) stand structure, and (3) low floristic diversity (Graham, 2006). Tree characteristics such as basal branching were commonly observed and are known to occur when individuals develop in high-light, low-density conditions, which could indicate that the canopy of the site may have been relatively open to clear in the recent past. Relatively low tree height and low mean tree diameter was taken as evidence that the trees on the site were relatively young and perhaps only recently established following some type of disturbance. Given the evidence described above, it was hypothesized that the site was: (1) disturbed at some point in the recent past, perhaps around the period of World War II (~1940), (2) disturbed earlier by logging and settlement activities as the land was originally intended for farming, or, (3) a relatively recent rainforest colonization of a late Quaternary sclerophyll forest inlier, possibly retarded by the poor shallow soils on much of the ridgetop (Graham, 2006). In Queensland *Agathis* is present in various types of tropical and subtropical rain forests, and does not occur in the sclerophyll forests with which these are interdigitated (Webb, 1968, 1969; Whitmore, 1977).

Re-evaluating these different hypotheses with the additional knowledge of recruitment dates for the current canopy trees, (1) disturbance from nearby military training areas in the 1940s seems unlikely given that many of the current *Agathis* canopy trees were found to recruit circa 1885 – 1900. The second hypothesis, that the area was disturbed during early forestry and agricultural development, remains possible, as the village of Kulara (now flooded by Lake Tinaroo) was established in the 1880s. However, while smaller and shorter trees can be indicative of recent disturbance, it may also simply reflect slower growth resulting from site characteristics such as poor soils and seasonal drought (hypothesis 3), which the consistently slow growth rates of *Agathis* at Downfall Creek supports. This is also true for low plot basal area and high stem density. Indeed, we can see that compared to trees on the more fertile soils of the plantation, tree growth rates are much slower at Downfall Creek (although tree spacing is also wider and more uniform in the plantation). Growth rates were similar between Downfall Creek and the Gillies Range forest, so it is likely that timing of recruitment of the current canopy trees is an important factor in explaining the different stand structures. There are large eucalypts in the forest adjacent to the plot so one possibility is that the ridge where the Downfall Creek plot (rainforest) is situated is recently (<200 years) invaded sclerophyll woodland.

Recent studies in other forests have also been successful in reconstructing the colonization of new sites by Araucariacea (Silva et al., 2009) and in identifying climatic signals in tree rings of *A. angustifolia* in Brazil (Oliveira et al., 2009; but see Boysen et al., 2014). Thus, the Araucariaceae are one of the tropical tree families in which a large number of species have tree rings that can be studied and further discoveries and insights are likely on the horizon. The production of information on ages and long-term tree growth patterns is essential to understanding the influences of site conditions and disturbance in forests and can help clarify the relative roles of these factors in seasonal tropical forests. Finally, such information is an essential component of developing science-based conservation and management of tropical tree species.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.02.008.

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