

# Growth rates of *Eucalyptus* and other Australian native tree species derived from seven decades of growth monitoring

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**Abstract** There is widespread interest in estimating and forecasting individual tree and forest growth rates for restoration and carbon sequestration objectives. Outside intensively managed forests, past attempts have been limited by the lack of accurate long-term monitoring in multi-age mixed native forests to provide estimates of both expected mean diameter increments and the statistical variation in those estimates. A dataset from *Eucalyptus*-dominated native forests in subtropical Queensland, Australia offers an opportunity to provide accurate estimates of tree and forest growth rates. Over 86,400 trees from 155 native species were identified and remeasured between 1936 and 2011 in 641 permanent sample plots across a 500–2000 mm mean annual rainfall gradient. Individual tree diameter at breast height (DBH) increments observed for all species ranged mainly from 0.01 to 0.5 cm yr<sup>-1</sup> (94 % of values), with consistent

differences between rainfall zones (mean of 500–2000 mm yr<sup>-1</sup>), and varying differences between species (155) and stem diameter class (10–100 cm). For some species, diameter increment increased progressively with rainfall (e.g. *Eucalyptus siderophloia*, *Eucalyptus propinqua*, and *Lophostemon confertus*), but in others (e.g. *Corymbia citriodora* subsp. *variegata*, *Corymbia intermedia*, and *Eucalyptus biturbinata*) the greatest diameter increments were recorded between 1200 and 1600 mm yr<sup>-1</sup>. Where there were sufficient data, most species exhibited a quadratic relationship between DBH increment and DBH class, but two species (*Callitris glaucophylla* and *Eucalyptus crebra*) native to the 500–800 mm annual rainfall zone showed linear increases in DBH increment with increasing DBH. Continued monitoring of these plots would add to their already great value.

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## Introduction

Accurate data on growth rates of individual species are critical for: informing ecological restoration; estimating changes in tree biomass and timber production potential; facilitating species selection for seed source augmentation and ecosystem rehabilitation; and also for determining commercial cutting cycles, recovery time frames and silvicultural prescriptions (Korning and Balslev 1994; Silva et al. 2002; Bowman et al. 2013; Stephenson et al. 2014). Furthermore, in the last decade, tree planting for ecological restoration has been used as a greenhouse gas emissions offset (carbon farming) option by individuals, governments, and corporations in efforts to mitigate climate

change (Bekessy and Wintle 2008; United Nations 2008; Booth and Williams 2012). Additionally, acquisition, protection and management of native regrowth forests complemented with the enrichment planting of native species has also been used as an offset option intended to mitigate biodiversity losses associated with mining and infrastructure development (Commonwealth of Australia 2012).

There are at least 27 forestry-based carbon offset providers in the Australian market (Low Carbon Australia and the University of Queensland 2011) and similar initiatives can be found worldwide with over 200 forestry-based carbon offset providers in the marketplace (The Ecosystem Marketplace 2011). Most carbon offset plantings in Australia use propagules of locally occurring native plant species with the aim of delivering multiple benefits that include carbon storage and restoration of biodiversity values of degraded ecosystems (Atyeo and Thackway 2009; Booth and Williams 2012; Booth et al. 2012).

Currently, estimation of the benefits and risks of all these activities is hampered by a dearth of knowledge on rates of growth of native tree species. There is a vital place for models of forest dynamics (Botkin 1993; Ngugi et al. 2000; Ngugi and Botkin 2011; Ngugi et al. 2011) in the prediction of tree and forest growth in different environments and under different management regimes. Forest growth models depend on models of individual tree development, and these in turn depend on a reliable knowledge of the rates of stem diameter growth and the associated changes in height, stem volume and tree biomass (Stephenson et al. 2014). Therefore, stem diameter increment data are fundamental to sustainable forest management and carbon farming initiatives.

Although we present analyses for Australian forests of native tree species, these findings have broad application because Australian native tree species are cultivated and studied globally. For example, there are over 20 million hectares of *Eucalyptus* plantings in many countries including Brazil, India, China, Uruguay, Chile, South Africa, Portugal, Spain, Vietnam, Sudan and Thailand (GFI Forestry Consulting 2009; Ferraz Filho et al. 2014; Wu et al. 2014). The successes of these initiatives continue to be limited by a dearth of information on growth rates and growth patterns of numerous Australian native tree species that have potential but are of limited natural occurrence and cultivation (Ngugi et al. 2003, 2004; Dale and Dieters 2007).

In this study, we investigated mean annual diameter at breast height (DBH) increments of tree species in native forests receiving about 500–2000 mm mean annual rainfall in subtropical Queensland, Australia. We used diameter measurements made over periods up to 75 years (1936–2011) on more than 86,400 trees in 641 permanent forest plots. Our specific objective was to determine absolute estimates and the pattern of variation in annual

stem diameter increment of selected species across vegetation types, diameter classes and among rainfall zones.

## Materials and methods

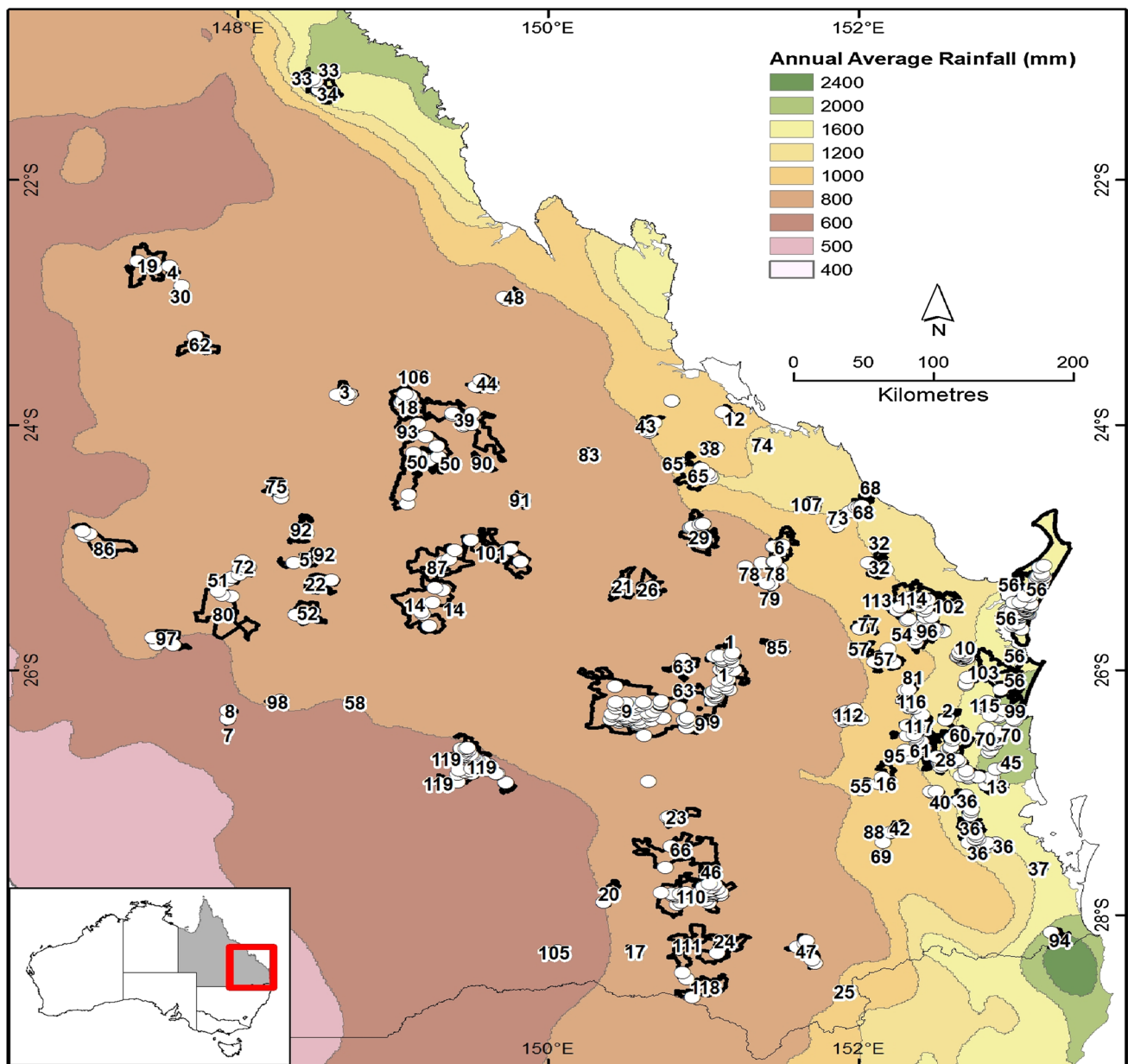
### Study area and location of plots

Our study area covered about 2.6 million hectares of State owned uneven-aged mixed species native forests in southern Queensland, between latitudes 21° and 29°S and longitudes 146° and 154°E. The forests ranged in elevation from 14 m.a.s.l on Fraser Island to 900 m.a.s.l at Blackdown Tableland National Park in central Queensland (Fig. 1). The regional climate is subtropical to semi-arid, characterised by hot humid summers (December–February) and cool, dry winters (June–August). Mean annual rainfall within the study area varies from 500 to 2000 mm. These subtropical forests in Queensland range from tall moist forests along the eastern coast (e.g. Mapleton and Ringtail State Forests, and Bauple National Park) to dry woodlands of central Queensland (Pluto and Umbercollie State Forests) (Tables 1, 4). Spatial data for rainfall zones 500–600, 600–800, 800–1000, 1000–1200, 1200–1600 and 1600–2000 mm were provided by Australian Bureau of Meteorology (BOM) based on data collected between 1961 and 1990 (BOM 2012). Rainfall zones are identified here by the upper value.

### History of management of native forest permanent plots

In the past 100 years these forests have been used for multiple purposes, including timber production and conservation of biological diversity (Queensland Government 1959). They are now held under various tenures, including Conservation Parks (3506 ha), Forest Reserves (120,711 ha), National Parks (536,387 ha) and State Forests (1,949,200 ha). The management goals for State forests in Queensland, as in all States and Territories in Australia, include perpetual protection of watersheds and biodiversity, and the supply of forest products (Queensland Government 1959).

Silvicultural treatments such as thinning of non-commercial trees and selective logging occurred during the history of these forests. Logging practices have included selective harvesting on 20–30-year cutting cycles for sawn timber, poles, girders, railway sleepers and fencing. Silvicultural guidelines determined the stem form, spacing and animal habitat quality of trees to be retained. In the lower rainfall zones (500–1200 mm), commercial harvesting usually used the single tree selection method, and in the wetter zones (1600 mm and above) group selection was



**Fig. 1** Average annual rainfall isohyets and distribution and location of permanent forest plots (white circles) in State forests and National parks (black outlines) in southern and central Queensland, Australia. A legend for forest estate names and plot counts is provided in Table 4

more commonly practiced (Florence 1996). Prescribed burning and cattle grazing have been part of the fire risk management strategy in the eucalypt forests, but fire has generally been purposely excluded from the fire-sensitive *Callitris* forest communities. Since 1995, these guidelines have been consistent with the principles of the Montreal Process (Montreal Process 2009).

#### Broad vegetation classification of native forests

The Queensland Herbarium is the agency now primarily responsible for mapping and classification of vegetation

in the study area (Neldner et al. 2012). Their classification system is hierarchical, ranging from broad classes (~1:5 million scale) down to regional ecosystems (RE) suitable for mapping at about 1:100,000 scale. These RE are combinations of vegetation types which are consistently associated with particular combinations of geology, landform, soil and climate (Neldner et al. 2012). We used a classification of broad vegetation groups (BVG) with nominal scale of 1:2 million, which divided the sub-tropical forests in this study into 16 broad vegetation groups (BVGs), ranging from tall moist forests along the eastern coast to dry woodlands of central

**Table 1** Brief broad vegetation group (BVG) description of forests represented by permanent plots in the study area, a count of number of plots located in each rainfall zone, and mean diameter increment and 95 % confidence interval (in italics) for the each BVG and within each rainfall zone

BVG	Description of broad vegetation group	Annual rainfall isohyets (mm)						Mean (cm yr <sup>-1</sup> )	CI (cm yr <sup>-1</sup> )
		600	800	1000	1200	1600	2000		
8a	Wet tall open-forest dominated by species such as <i>Eucalyptus grandis</i> or <i>E. saligna</i> , <i>E. resinifera</i> , <i>Syncarpia hilli</i> , <i>E. microcorys</i> on uplands and alluvia. <i>E. sphaerocarpa</i> <sup>a</sup>	–	–	–	13	56	6	0.24	<i>0.13</i>
8b	Moist open-forests to tall open-forests mostly dominated by <i>E. pilularis</i> on coastal sands, sub-coastal sandstones and basalt ranges	–	–	6	6	31	15	0.29	<i>0.18</i>
9a	Moist to dry eucalypt open-forests to woodlands, dominated by variety of species including <i>E. acmenoides</i> , <i>E. racemosa</i> , <i>E. cloeziana</i> , <i>E. siderophloia</i> , on coastal lowlands and ranges	–	5	15	58	23	15	0.20	<i>0.12</i>
9c	Open-forests of <i>Corymbia intermedia</i> or <i>Corymbia clarksoniana</i> , <i>E. tereticornis</i> predominantly on coastal ranges.	–	–	1	1	2	–	0.11	<i>0.08</i>
9f	Woodlands dominated by <i>Corymbia</i> spp. ( <i>C. intermedia</i> , <i>C. tessellaris</i> ) and/or <i>E. racemosa</i> , <i>E. tereticornis</i> frequently with <i>Banksia</i> spp on coastal dunes and beach ridges	–	–	–	–	6	–	0.20	<i>0.12</i>
9g	Moist woodlands dominated by <i>Eucalyptus tindaliae</i> or <i>E. racemosa</i> or <i>E. tereticornis</i> on coastal remnant Tertiary surfaces	–	–	–	–	2	4	0.21	<i>0.11</i>
9h	Dry woodlands dominated by species such as <i>Eucalyptus acmenoides</i> , <i>E. tereticornis</i> , <i>Corymbia trachyphloia</i> , <i>E. crebra</i> on undulating to hilly terrain	–	7	2	3	–	–	0.23	<i>0.11</i>
10a	Dry woodlands to open-woodlands dominated by <i>Corymbia citriodora</i> on undulating to hilly terrain	–	108	5	–	–	–	0.18	<i>0.10</i>
10b	Moist open-forests to woodlands dominated by <i>Corymbia citriodora</i> on undulating to hilly terrain	–	7	13	15	5	–	0.20	<i>0.11</i>
12a	Dry woodlands to open-woodlands dominated by ironbarks such as <i>Eucalyptus decorticans</i> , <i>E. fibrosa</i> , <i>Corymbia watsoniana</i> on sub-coastal/inland hills with shallow soils	–	24	3	1	–	–	0.24	<i>0.11</i>
13c	Woodlands of <i>Eucalyptus crebra</i> , <i>E. drepanophylla</i> , <i>E. fibrosa</i> on granite and metamorphic ranges	–	9	3	1	1	–	0.20	<i>0.11</i>
13d	Woodlands dominated by <i>Eucalyptus moluccana</i> on a range of substrates	–	8	6	4	–	–	0.17	<i>0.09</i>
15a	Woodlands and open-forests dominated by <i>Eucalyptus eugenioides</i> , <i>E. chloroclada</i> , <i>E. andrewsii</i>	–	–	1	–	–	–	0.11	<i>0.09</i>
17b	Woodlands to open-woodlands dominated by <i>Eucalyptus melanophloia</i> on sandplains and footslopes	2	1	–	–	–	–	0.16	<i>0.09</i>
18b	Woodlands dominated <i>Eucalyptus crebra</i> frequently with <i>Corymbia</i> spp. or <i>Callitris glaucophylla</i> on flat to undulating plains	3	29	–	–	–	–	0.24	<i>0.14</i>
20a	Woodlands to open-forests dominated by <i>Callitris glaucophylla</i> on flat to undulating plains	36	79	–	–	–	–	0.20	<i>0.09</i>
Mean diameter growth rates cm yr <sup>-1</sup>		0.23	0.20	0.18	0.24	0.27	0.27	0.23	
95 % confidence interval cm yr <sup>-1</sup>		<i>0.12</i>	<i>0.11</i>	<i>0.11</i>	<i>0.12</i>	<i>0.16</i>	<i>0.18</i>	0.13	
Total number of plots		41	277	55	102	126	40		

<sup>a</sup> Observed at Blackdown Tableland National park

Queensland (Table 1). Each plot was individually assigned to a BVG based on the dominant tree species, basal area stock of dominant species, height and foliage projected cover of the forests recorded at the site (DERM 2012). Consequently, this vegetation classification provided a detailed methodology of aggregating

plots on moisture availability, basal area, species combination and growth conditions. In other studies, stand basal area attribute, a component of this classification, has been used in growth modelling as a proxy for inter-tree competition (see Weiskittel et al. 2011; Prior and Bowman 2014).

## Native forests permanent sample plot data

The tree growth data used in this study were collected from 641 long-term permanent inventory plots located in 118 forest estates (Fig. 1; Table 4). The earliest plots were established in 1936 at Braemar State Forest and the last batch in the late 1990s. All permanent plots established prior to 1993 were subjectively selected from a systematic grid network of temporary forest inventory plots, to cover the range of stocking, species composition and site quality of major commercial stands within forest types (Beetson 1992). Plots established after 1993 were based on forest stratification data, to cover under-represented species mixtures and geographic distributions (Cant and Mannes 1995). There were 609 rectangular plots, varying in size from 0.2 to 0.5 ha, within which every tree with DBH > 10 cm that was suitable for commercial wood production was individually numbered, tagged and measured, complying with an established measurement manual (Cant and Mannes 1995). In a separate study on Fraser Island (Applegate 1982), 32 circular plots were established, within which trees with DBH > 10 cm were measured in an inner circle of radius of 17.8 m and trees with DBH > 30 cm measured in an outer circle with a radius of 39.9 m.

The measurement protocol was amended in 1993 to include sampling of all tree species irrespective of their potential for timber production. This amendment was aimed at promoting recovery of species diversity in forests used for timber production. In addition, trees <10 cm DBH but >3 m tall and or DBH > 2 cm were sampled using small circular plots ( $\leq 5$  m radius) located at the centre of each quarter of the rectangular plot. All plots irrespective of establishment year were re-measured every 2–10 years after their establishment, with additional measurements carried out after a logging, wildfire or silvicultural treatment. The total number of times a plot was monitored ranged from two to 18, with an average of five times per plot.

## Data analyses

Data analysis was undertaken using R programming language (R Development Core Team 2011). Annual diameter increment was calculated as the change in individual tree diameter between two consecutive measures as a function of time period in years (time period  $\geq 1$  year). Filtering was done to remove gross typing and recording errors, and errors associated with shifts in height at which diameter was measured due to recorded development of deformities at DBH. Trees with a defect at 1.3 m (DBH measure point) were excluded during diameter increment calculations. The growth rates were calculated for each 10 cm diameter class

and expressed as mean, and 95 % confidence interval (CI) about the mean. Relationships between tree diameter class (D) and diameter increment (Di) for individual species within a rainfall zone were explored graphically. Preliminary model fitting used different model forms (exponential, logarithmic, power function, polynomial and linear) and aggregations of data from several rainfall zones in an attempt to fit species-specific generalised models. Fitted models were compared using the coefficient of determination ( $r^2$ ). Models that best fitted the data and had  $r^2 > 0.5$  were retained.

## Results

### Growth rates of broad vegetation groups and species representation

The ranges of mean diameter increment for forest types among rainfall zones (0.18–0.27 cm yr<sup>-1</sup>) was less than that among BVGs (0.11–0.29 cm yr<sup>-1</sup>) (Table 1). The highest mean increment among BVGs (0.29  $\pm$  0.18 cm yr<sup>-1</sup>) was observed in BVG 8b, moist open-forests to tall open-forests dominated by *Eucalyptus pilularis* on coastal sands, sub-coastal sandstones and basalt ranges. For all BVGs, the 95 % confidence interval was about 57 % of the mean increment (data not shown).

Mean diameter growth rates and 95 % confidence intervals of 23 of the most abundant tree species are presented in Table 2. The most abundant data were available for *C. glaucophylla* (84,517 increment values), *C. citriodora* subsp. *variegata* (18,505 increment values), and *E. crebra* (16,409 increment values). Mean stem density for trees >10 cm DBH ranged from 287 to 399 stems ha<sup>-1</sup> but without any consistent relationship to rainfall. Mean stand basal areas for each rainfall zone, calculated across the entire sampling period, ranged from approximately 7.5 m<sup>2</sup> ha<sup>-1</sup> (600 mm rainfall zone) to 29 m<sup>2</sup> ha<sup>-1</sup> (1600 mm rainfall zone) (Fig. 2). The relatively low stand basal area (15 m<sup>2</sup> ha<sup>-1</sup>) in the 1200 mm rainfall zone reflects the extent of commercial utilisation in this forest zone.

### Species growth rates across diameter size classes within rainfall zones

Comparisons of growth rates across diameter classes for species with the highest number of annual increment determinations within each rainfall zone are presented in Fig. 3. Within the 600 mm zone, growth rates of *E. populnea*, *E. crebra* and *C. glaucophylla* remained relatively constant (between 0.15 and 0.3 cm yr<sup>-1</sup>) across the observed diameter range while *E. melanophloia* showed a

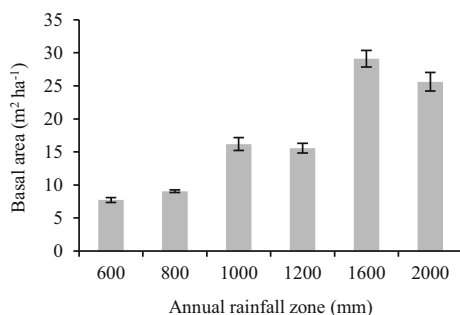
**Table 2** Mean diameter growth rates (cm yr<sup>-1</sup>) of selected tree species with >200 increment data values (n) across observed rainfall zones

Species	Rainfall zone (mm)											Mean	CI	n	
	600	800	1000	1200	1600	2000									
<i>Angophora floribunda</i>		0.54	0.28	0.21	0.23	0.14	0.15	0.76	0.30			0.39	0.24	347	
<i>Angophora leiocarpa</i>	0.49	0.19	0.21	0.12	0.18	0.15	0.23	0.10	0.10	0.13	0.02	0.05	0.24	0.13	1158
<i>Corymbia citriodora</i> <sup>a</sup>		0.19	0.11	0.14	0.08	0.23	0.16						0.19	0.11	323
<i>Corymbia citriodora</i> <sup>b</sup>		0.21	0.10	0.23	0.11	0.31	0.09	0.28	0.14				0.25	0.10	18,493
<i>Corymbia intermedia</i>		0.11	0.11	0.13	0.12	0.18	0.08	0.24	0.15	0.32	0.17		0.20	0.13	5887
<i>Corymbia trachyphloia</i> <sup>c</sup>	0.31	0.18	0.17	0.09	0.14	0.16	0.18	0.12	0.16	0.09	0.23	0.10	0.18	0.12	2681
<i>Eucalyptus acmenoides</i>		0.15	0.13	0.13	0.09	0.27	0.10	0.29	0.10	0.42	0.26		0.27	0.13	9868
<i>Eucalyptus biturbinata</i>		0.23	0.19	0.19	0.10	0.28	0.11	0.21	0.12	0.18	0.18		0.23	0.13	1620
<i>Eucalyptus cloeziana</i>			0.24	0.07		0.36	0.09	0.52	0.15				0.36	0.10	1079
<i>Eucalyptus crebra</i>	0.18	0.08	0.16	0.06	0.18	0.06	0.22	0.10	0.16	0.08			0.17	0.07	16,397
<i>Eucalyptus eugenioides</i>					0.21	0.14	0.11	0.12	0.40	0.13	0.28	0.15	0.25	0.14	235
<i>Eucalyptus exserta</i>	0.11	0.06	0.09	0.13	0.10	0.08	0.29	0.08					0.19	0.09	671
<i>Eucalyptus fibrosa</i> <sup>d</sup>	0.27	0.10	0.18	0.10	0.25	0.10	0.36	0.09	0.37	0.13			0.26	0.10	6231
<i>Eucalyptus grandis</i>									0.44	0.20	0.37	0.17	0.42	0.19	1030
<i>Eucalyptus melanophloia</i>	0.22	0.07	0.16	0.09	0.07	0.10	0.46	0.67					0.19	0.13	799
<i>Eucalyptus microcorys</i>					0.19	0.19	0.36	0.15	0.41	0.28	0.49	0.23	0.40	0.24	2239
<i>Eucalyptus moluccana</i>			0.25	0.15	0.26	0.09	0.36	0.17					0.28	0.14	2288
<i>Eucalyptus pilularis</i>					0.35	0.17	0.51	0.13	0.53	0.30	0.59	0.21	0.53	0.23	7265
<i>Eucalyptus propinqua</i>			0.20	0.10	0.21	0.12	0.27	0.12	0.24	0.15	0.34	0.31	0.26	0.15	2146
<i>Eucalyptus saligna</i> <sup>e</sup>					0.12	0.05	0.33	0.12	0.38	0.29			0.33	0.16	563
<i>Eucalyptus siderophloia</i>			0.15	0.16	0.15	0.07	0.27	0.09	0.27	0.13	0.35	0.19	0.25	0.11	5504
<i>Eucalyptus tereticornis</i>	0.67	0.48	0.22	0.19	0.19	0.11	0.28	0.15	0.24	0.15	0.32	0.15	0.24	0.16	1003
<i>Lophostemon confertus</i>			0.05	0.03	0.13	0.09	0.27	0.12	0.26	0.12	0.33	0.15	0.26	0.12	9729

95 % confidence interval (CI) in italics

A full list of species and increment measurements across rainfall zones is given in Table 5

<sup>a</sup> Subsp. *citriodora*; <sup>b</sup>subsp. *variegata*; <sup>c</sup>subsp. *trachyphloia*; <sup>d</sup>subsp. *fibrosa*; <sup>e</sup>subsp. *saligna*

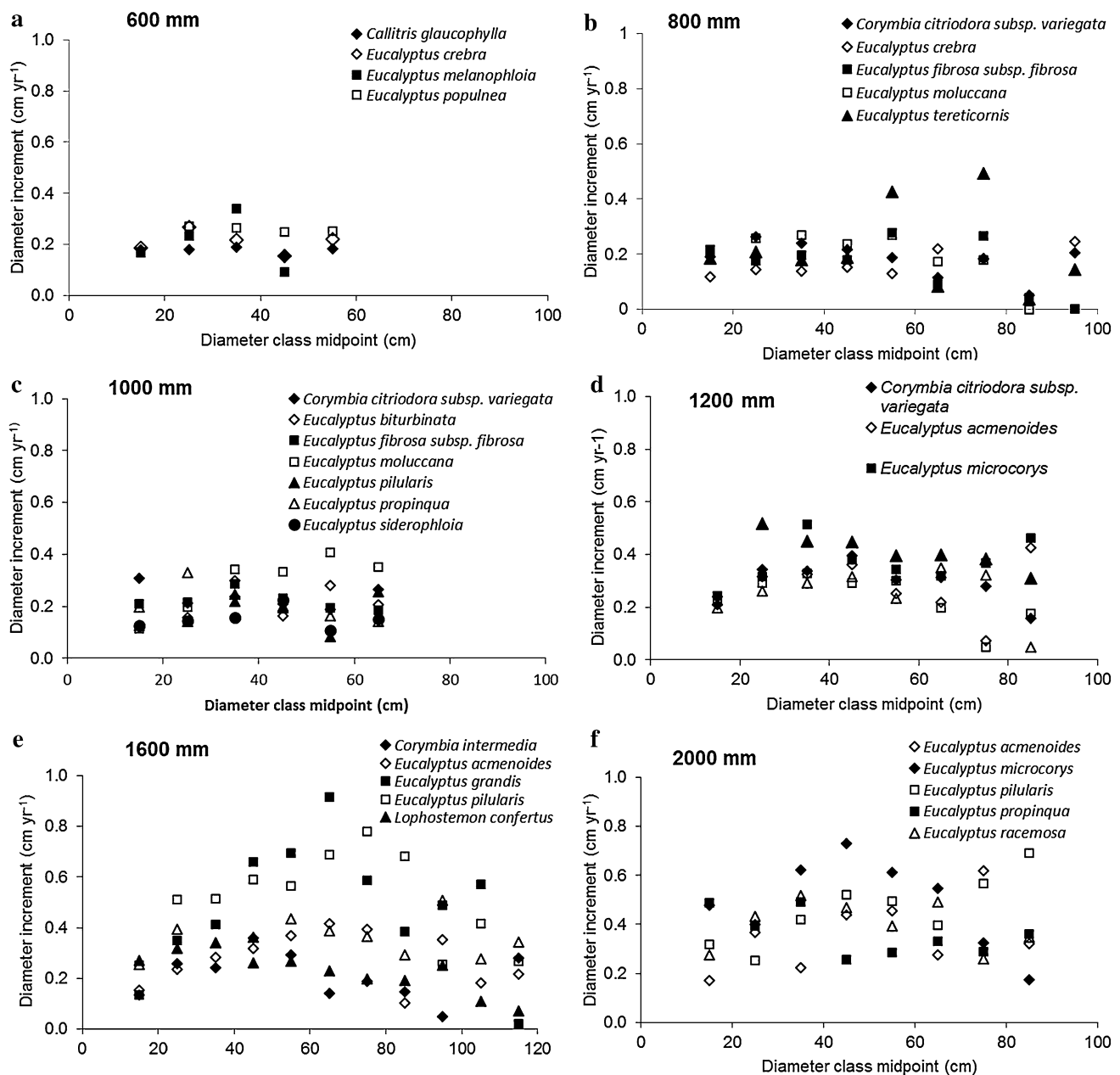


**Fig. 2** Mean stand basal area for rainfall zones calculated from all measurement occasions on all plots. Rainfall zones (range of mean annual total): 600 mm (500–600 mm); 800 mm (600–800 mm); 1000 mm, (800–1000 mm); 1200 mm, (1000–1200 mm); 1600 mm, (1200–1600 mm); 2000 mm, (1600–2000 mm)

maximum growth rate (0.34 cm yr<sup>-1</sup>) in the 30–40 cm diameter class (Fig. 3a). In the 800 mm rainfall zone, the growth rates of all frequent species were relatively

consistent in stems up to 50 cm DBH but were more variable (0.04–0.49 cm yr<sup>-1</sup> in larger stems (Fig. 3b). Growth rates for the frequent species within the 1000 mm zone ranged from 0.13 to 0.41 cm yr<sup>-1</sup> (Fig. 3c). Within species, there was no consistent pattern of variation in diameter increment with DBH but *E. moluccana* showed generally higher increments than *E. siderophloia* and *E. propinqua*.

Diameter growth rates for trees in the 1200 mm zone ranged between 0.2 and 0.52 cm yr<sup>-1</sup> for trees in the 10–70 cm DBH range, with generally consistent and higher rates in *E. microcorys* and in *E. sphaerocarpa*, a species confined to Blackdown Tableland National Park (Fig. 3d). Highest growth rates in other species were generally observed in the 30–50 cm diameter range. There was far greater variation in growth rate among species in the 1600 mm rainfall zone (Fig. 3e). *E. grandis* and *E. pilularis* showed maximum growth rates between about 0.8 and 0.9 cm yr<sup>-1</sup>) in contrast to about 0.4 cm yr<sup>-1</sup> in other



**Fig. 3** Comparative species diameter increments within each rainfall zone as defined in Fig. 2

frequent species in the zone. Highest growth rates were observed in the 30–70 cm DBH range. Great variability in diameter growth rates was also observed in the 2000 mm zone, where *E. microcorys*, *E. racemosa* and *E. pilularis* showed growth rates between 0.4 and 0.7 cm yr<sup>-1</sup> within the 30–70 cm DBH range (Fig. 3f).

#### Diameter growth rates across rainfall zones

Over 45 species in our dataset occurred across at least three rainfall zones (Tables 2, 5). The growth rates among species and rainfall zones ranged from 0.01 to 0.96 cm yr<sup>-1</sup>,

with an overall mean of  $0.25 \pm 0.13$  cm yr<sup>-1</sup>. A sample comparison of diameter growth rates of 10 species that occurred across 800 mm to 2000 mm rainfall zones is presented in Fig. 4. Relatively constant growth rates across rainfall zones were observed for *Corymbia trachyphloia* subs. *trachyphloia* (0.12–0.16 cm yr<sup>-1</sup>) but for the other nine species, two patterns were generally observed. *Eucalyptus siderophloia*, *E. propinqua*, *E. tereticornis*, *E. acmenoides* and *Lophostemon confertus* demonstrated increased diameter growth rates (up to 0.27–0.35 cm yr<sup>-1</sup>), with increasing rainfall (Fig. 4a). *Corymbia citriodora* subs. *variegata*, *E. biturbinata*, *Corymbia intermedia* and

**Table 3** Regressions of diameter increment (Di, cm yr<sup>-1</sup>) as a function of tree diameter (D, cm) for species and rainfall zones in which the regression coefficient of determination (r<sup>2</sup>) was >0.5

Species	Rainfall zone (mm)	Regression equation	Regression coefficient r <sup>2</sup>
<i>Callitris glaucophylla</i>	600	Di = 0.12 + 0.0018D	0.77
<i>Eucalyptus crebra</i>	800	Di = 0.0881 + 0.0018D	0.61
<i>Corymbia citriodora</i> subsp. <sup>a</sup>	1200	Di = 0.0463 + 0.0136D - 0.0001D <sup>2</sup>	0.87
<i>Corymbia citriodora</i> subsp. <sup>a</sup>	800	Di = 0.0792 + 0.0078D - 0.00009D <sup>2</sup>	0.80
<i>Lophostemon confertus</i>	2000	Di = 0.0795 + 0.0152D - 0.0002D <sup>2</sup>	0.56
<i>Eucalyptus acmenoides</i>	2000	Di = 0.0172 + 0.0126D - 0.0001D <sup>2</sup>	0.57
<i>Eucalyptus pilularis</i>	1600	Di = 0.0278 + 0.0188D - 0.0001D <sup>2</sup>	0.73
<i>Eucalyptus pilularis</i>	2000	Di = 0.2164 + 0.0057D - 0.00002D <sup>2</sup>	0.53
<i>Corymbia intermedia</i>	1200	Di = 0.0687 + 0.0079D - 0.0001D <sup>2</sup>	0.85
<i>Corymbia intermedia</i>	1600	Di = 0.0058 + 0.0125D - 0.0001D <sup>2</sup>	0.74
<i>Eucalyptus microcorys</i>	1600	Di = - 0.0455 + 0.0202D - 0.0002D <sup>2</sup>	0.66
<i>Eucalyptus fibrosa</i> subsp. <sup>b</sup>	1200	Di = 0.1152 + 0.014D - 0.0002D <sup>2</sup>	0.91
<i>Eucalyptus fibrosa</i> subsp. <sup>b</sup>	1600	Di = 0.2401 + 0.0085D - 0.0001D <sup>2</sup>	0.82

<sup>a</sup> *variegata*

<sup>b</sup> *fibrosa*

*Angophora leiocarpa*, demonstrated peak growth rates (0.21–0.31 cm yr<sup>-1</sup>) in the 1200 or 1600 rainfall zones (Fig. 4b).

#### Growth rate variation within diameter classes and across rainfall zones

Figure 5 illustrates the different patterns of variation in growth rate with diameter class for 10 common species that were distributed across several rainfall zones. There was little difference in diameter growth rates of *Allocasuarina luehmannii*, *Callitris glaucophylla*, *Corymbia intermedia* or *Eucalyptus crebra* within across rainfall zones and within diameter classes (Fig. 5). *Eucalyptus acmenoides*, *E. fibrosa* subsp. *fibrosa*, and *E. siderophloia* showed consistently lower growth rates in the lowest observed rainfall zones while *Corymbia citriodora* subsp. *variegata* and, *E. fibrosa* subsp. *fibrosa* showed higher growth rates in the highest rainfall zone of their occurrence. The variation in growth rates with diameter class and rainfall zone in *Lophostemon confertus* was inconsistent (Fig. 5).

Regression analyses of diameter increment as a function of tree diameter are presented in Table 3 for the species illustrated in Fig. 5. Although most species were observed across several rainfall zones, only in a few rainfall zones were the coefficients of determination values (r<sup>2</sup>) > 0.5. Species with the highest r<sup>2</sup> were *Eucalyptus fibrosa* subsp. *fibrosa* (r<sup>2</sup> = 0.91), *Corymbia citriodora* subsp. *variegata* (r<sup>2</sup> = 0.87) and *Corymbia intermedia* (r<sup>2</sup> = 0.85) growing in the 1200 mm rainfall zone.

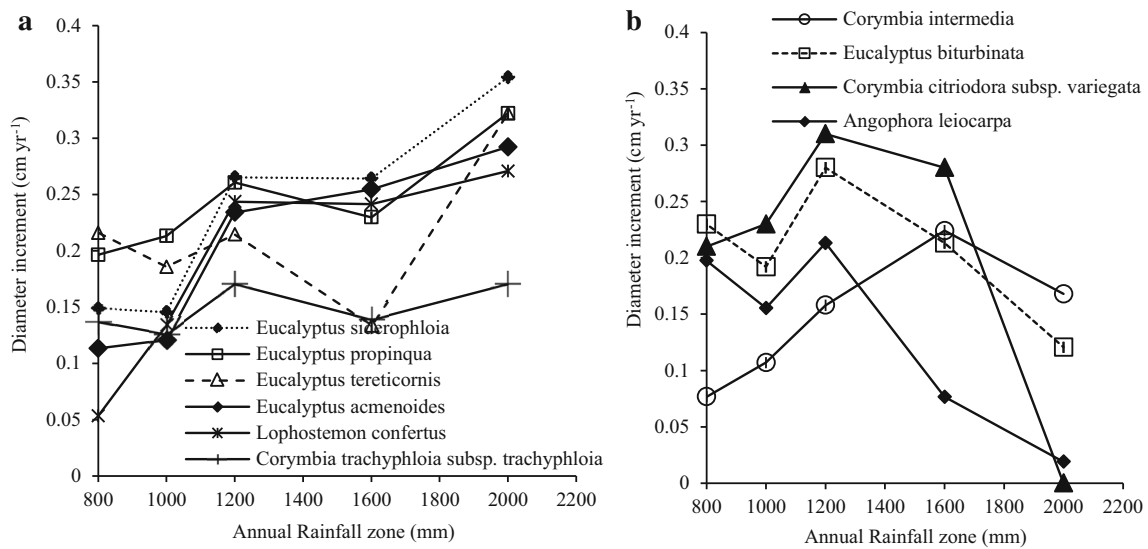
#### Discussion

Although the desirability of increasing forest carbon stocks in addressing climate change is well established (Bekessy and Wintle 2008; United Nations 2008; Booth and Williams 2012) and there are many estimates and methods for estimating carbon stocks (e.g. IPCC 2006), the rates at which these stocks accumulate in native forests are by comparison known imprecisely (Stephenson et al. 2014). Reliable empirical estimates of growth rates and patterns for 74 native tree species growing in natural forests in subtropical Australia were obtained from an extensive individual tree increment dataset (211,189 records). Growth rates and patterns varied markedly among broad vegetation groups and species in the observed rainfall zones and diameter size classes and the patterns were difficult to generalise. In the low rainfall zones (<800 mm) growth rates among species and across diameter classes were generally similar. Much greater fluctuations in growth rates were observed in the >1000 mm zones. Individual growth rates among all the species ranged from 0.01 to 0.96 cm yr<sup>-1</sup>.

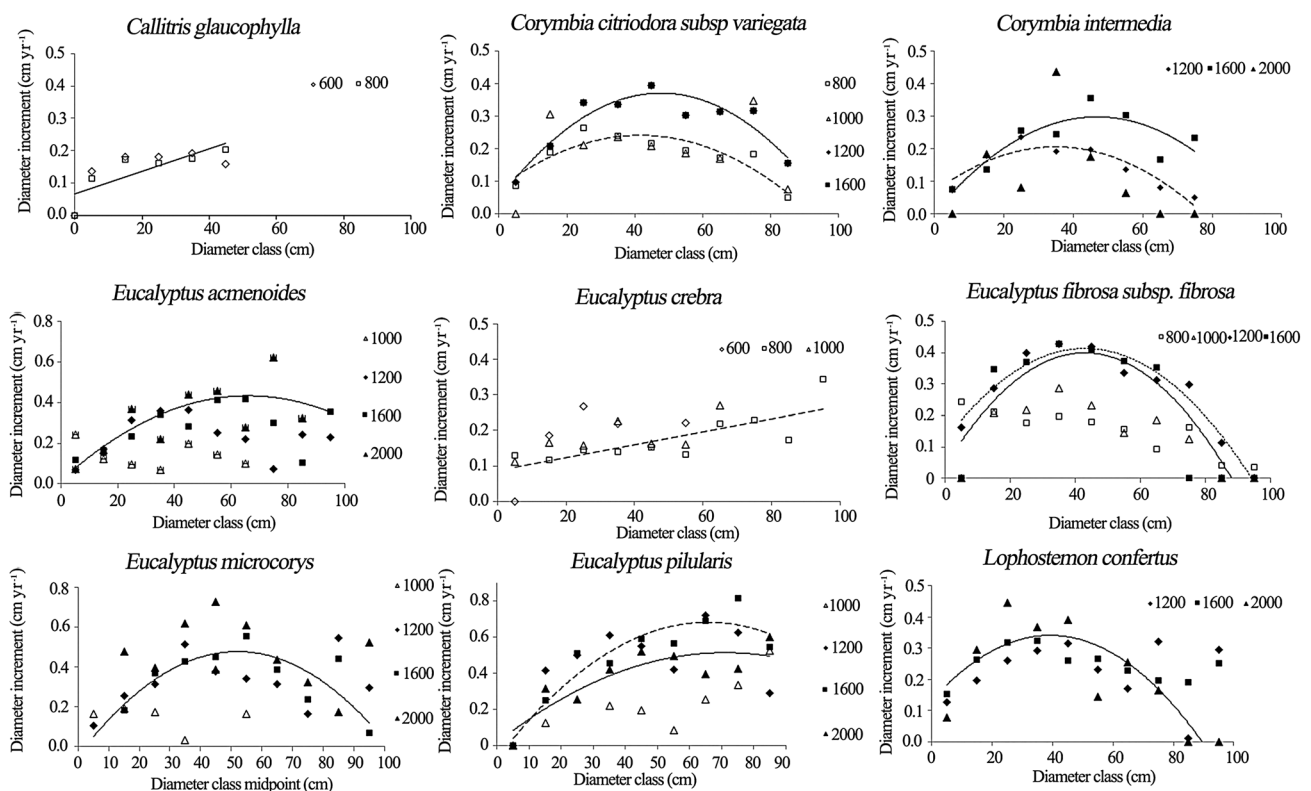
#### Mean annual diameter growth rates of species within each rainfall zone

The generally similar growth rates among frequently occurring species in the low rainfall areas in contrast to the pronounced differences observed in higher rainfall areas suggests that potential growth differences among species are small under low rainfall conditions as compared to





**Fig. 4** Variation in diameter growth rate of individual species with diameter class across 800–2000 mm rainfall zones with **a** showing species that demonstrated highest growth at highest rainfall and **b** species that demonstrated a peak and a decrease in diameter growth rates



**Fig. 5** Diameter increments across diameter size classes for ten species with distributions across several rainfall zones. Equations for the regression lines are presented in Table 3

higher rainfall conditions. The highest growth rates for most species in all rainfall zones were observed in trees with DBH between 20 and 60 cm. In these native forests, trees in the <20 cm DBH class are often in the understorey

and their growth is often suppressed by larger trees. Moreover, even though small trees may be numerous in a stand, their contribution to stand basal area and carbon stock is small compared with that of larger trees

(Stephenson et al. 2014). Compared to other studies, the growth rates observed in our study were considerably lower than those of 1–5 cm yr<sup>-1</sup> reported from 4 year-old plantation trial of eucalypts in the 1000 mm rainfall zone in southeast Queensland (Ngugi et al. 2004). However, unlike the natural growth conditions in our study, growth conditions under experimental trials or commercial plantations are modified through intensive ground preparation procedures involving deep ripping, fertilization and weed control (Ngugi et al. 2004) and the absence of competition for light, water and nutrients from established (old) trees.

The observed mean diameter increment for *Corymbia citriodora* subsp. *variegata* (0.25 ± 0.10 cm yr<sup>-1</sup>, n = 18,493) is consistent with results obtained for the species in southeast Queensland and northern New South Wales that ranged from 0.20 ± 0.03 in the lower rainfall areas, up to 0.29 ± 0.02 in the higher rainfall areas (Lewis et al. 2010). The mean individual tree growth rate range for all trees used in this study was 0.01–0.5 cm yr<sup>-1</sup> for 94 % of the data, with an overall mean of 0.25 cm yr<sup>-1</sup>. This range is consistent with that reported for *Eucalyptus* forests in temperate Australia (Bowman et al. 2014) but the mean value is higher than that for woodland (0.20 cm yr<sup>-1</sup>) and for open forests (0.16 cm yr<sup>-1</sup>) reported in north Australia savanna in a two-year study (Prior et al. 2004). Our mean is also within the range of 0.2–0.37 cm yr<sup>-1</sup> reported for subtropical forest trees in Puerto Rico (Brandeis 2009) and close to the 0.27 cm yr<sup>-1</sup> reported for tropical lowland tree species in the Amazonian Ecuador where the mean annual precipitation was 3244 mm (Korning and Balslev 1994).

Tree plantings for carbon capture often target species with the highest growth prospect within a rainfall area and geographic location. However, because some species have a wide geographical distribution, it is often difficult to assess relative environmental requirements and growth potential (Booth et al. 2012). For example, many species observed in our dataset occur across several rainfall zones (between 600 and 2000 mm). Because there is limited knowledge on where such species are likely to exhibit their highest growth rates, the selection of fast growing species for carbon accumulation for a particular local area is difficult. Using a sample of ten species that occurred between the 800 and 2000 mm rainfall zones, we attempted to identify the zone in which each of the species recorded the highest growth rates. For example, although *Corymbia intermedia* is widespread, the growth increment recorded in the 1200 mm zone was approximately four times higher than that recorded in the 800 mm zone and about 55 % higher than that recorded in the 1600 and 2000 mm rainfall zones. Contrary to the fluctuating growth increment patterns observed for the other eight species, there was a consistent three-fold increase in growth rates of *E.*

*siderophloia* and *E. acmenoides* with increase in rainfall from 800 to 2000 mm.

### Growth rates of individual species across diameter classes among rainfall zones

Growth rates of *C. glaucophylla* were relatively independent of tree diameter for trees greater than 10 cm DBH, with growth rates of trees <10 cm DBH being about half that of the larger trees. A similar pattern was observed for *Eucalyptus crebra* growing between the 800 and 1000 mm zones. However, in several species, including *C. citriodora* subsp. *variegata*, *Lophostemon confertus*, *E. acmenoides*, *E. siderophloia*, *Corymbia intermedia* and *E. fibrosa* subsp. *fibrosa*, there was an increase in growth rate with increase in diameter up to a DBH of 50 cm, generally followed by a decrease in larger trees. The large differences in growth rates across diameter classes suggest that the use of an average increment value for these species should be adopted cautiously and only when more detailed descriptions of increment are not available.

Natural multi-age forests in Australia are characterised by a large number of species and varying growing conditions. This study did not document all possible tree species and growing conditions but instead used a dataset that was initially aimed at collecting data for the purpose of estimating timber production in State Forests in Queensland. As a result, commercial timber species are well represented in the dataset relative to those perceived to have limited timber value. Increment estimates for some non-commercial species are now being obtained as a result of the changes in 1993 to the plot measurement protocol. Some of these non-commercial species indicate growth rates much higher than the over-storey eucalypt species (e.g. 0.96 cm yr<sup>-1</sup> for *Acacia melanoxylon* in the 2000 mm zone, n = 11; and 0.76 cm yr<sup>-1</sup> for *Angophora floribunda* in the 1600 mm zone, n = 6). The accuracy of estimates for understorey and short-lived species is currently limited by small sample sizes but will be enhanced as subsequent re-measurements occur. Estimates of growth rates for large trees (>80 cm) should be used very cautiously because of measurement errors resulting from bole deformities associated with aging of predominantly habitat trees and bias related to their limited representation in the dataset.

### Conclusions

Stem diameter increments for native species growing naturally in uneven-aged mixed species forests in subtropical Queensland typically range from 0.01 to 0.50 cm yr<sup>-1</sup> (94 % of observed values). While tree growth rate is influenced by a range of genetic, edaphic and climatic factors, this

study related increment to growth conditions (geology, landform, soil and rainfall), stem diameter (tree size) and rainfall, which are the most commonly recorded factors in a region where temperature variation is relatively small. In most species, increment is related to both rainfall and stem diameter class, but the relationships vary substantially between species and sometimes between rainfall zones. In some species, particularly from lower rainfall environments, increment does not vary consistently between either rainfall or stem diameter classes. For species that occurred across several rainfall zones, the highest growth rates were not necessarily observed in the highest rainfall zone. Within a rainfall zone, the highest growth rates within species were often observed in trees within the DBH range of 20–60 cm, following a unimodal curve within that range or with the increment either increasing linearly with stem diameter (often in lower rainfall zones and especially in *Callitris glaucophylla* and *Eucalyptus crebra*).

The dataset used for this study provided a consistent record of individual tree growth that avoids the errors and costs of repeated *de novo* assessments. However, many of the plots have not been remeasured in the last decade. With continued monitoring, the network of plots could provide a

robust scientific basis for directing sustainable forest management and assist in enhancing our understanding on carbon storage, impacts of rising atmospheric CO<sub>2</sub> concentration on tree growth, forest dynamics and improve accuracy of forest growth prediction tools.

**Acknowledgments** The data used for this study are stored in a database maintained by the Queensland Herbarium, Department of Science, Information Technology and Innovation (DSITI) and co-jointly held by the Forest Research, Department of Agriculture, Fisheries and Forestry (DAFF). The legacy and contribution of past Queensland Government Forestry Departments and staff in data collection, collation and maintenance for over seven decades is greatly acknowledged. Assistance provided by Jiaorong Li and Rosemary Niehus in GIS, Queensland Parks and Wildlife Service field staff, Jian Wang, David Moore, Rosemary Niehus and Sue Philips for 2011 field measurements is gratefully acknowledged. Peer review and suggestions provided by Dr Don Butler, Dr Arnon Accad and Dr John Neldner for earlier version of this manuscript are acknowledged with thanks.

## Appendix

See Tables 4 and 5.

**Table 4** Assigned forest identification numbers (FID), gazetted area and number of native forest permanent plots located in each forest, shown in Fig. 1

FID	Estate name	Area (ha)	No. of plots	FID	Estate name	Area (ha)	No. of plots
1	Allies Creek State Forest	70,900	36	60	Imbil State Forest 1	16,665	3
2	Amamoor State Forest	7011	1	61	Jimna State Forest	10,316	3
3	Amaroo State Forest	13,438	4	62	Kettle State Forest	20,825	1
4	Apsley State Forest	4981	1	63	Koko State Forest	19,140	1
5	Bandana State Forest	11,210	1	64	Kondalilla National Park	1591	2
6	Bania National Park	33,110	6	65	Kroombit Tops National Park	43,260	6
7	Barabanbel State Forest 1	1500	1	66	Kumbarilla State Forest	85,075	2
8	Barabanbel State Forest 3	1685	1	67	Littabella Conservation Park	2947	2
9	Barakula State Forest	283,500	74	68	Littabella National Park	8340	2
10	Bauple State Forest	9500	20	69	Lockyer Resources Reserve	612	1
11	Baywulla State Forest	1454	1	70	Mapleton National Park	6455	14
12	Beecher State Forest	1461	1	71	Mapleton National Park (Recovery)	3609	17
13	Beerburum West State Forest	9269	1	72	McLeay State Forest	12,800	5
14	Belington Hut State Forest	100,950	6	73	Monduran State Forest 1	7478	2
15	Bellthorpe National Park	7551	6	74	Mount Coulston State Forest	323	1
16	Benarkin State Forest	16,100	3	75	Mount Hope State Forest	15,831	3
17	Bendidee State Forest	4600	1	76	Mount Stowe State Forest	1231	1
18	Blackdown Tableland National Park	47,950	6	77	Mount Walsh National Park	10,727	1
19	Blair Athol State Forest	52,717	3	78	Mungy State Forest	5829	1
20	Booroondoo State Forest	9781	2	79	Nour Nour National Park	5054	3
21	Borania State Forest	18,300	1	80	Oakvale State Forest	84,200	3
22	Boxvale State Forest	22,400	2	81	Oakview National Park	3490	1

**Table 4** continued

FID	Estate name	Area (ha)	No. of plots	FID	Estate name	Area (ha)	No. of plots
23	Braemar State Forest	14,370	4	82	Oakview State Forest	1156	1
24	Bringalily State Forest	35,695	1	83	Overdeen State Forest	6449	2
25	Broadwater State Forest	918	1	84	Peachester State Forest	734	3
26	Calrossie State Forest	21,200	2	85	Pile Gully State Forest	8920	1
27	Cherbourg National Park	995	1	86	Pluto Timber Reserve	45,900	3
28	Conondale National Park	35,648	20	87	Presho Forest Reserve	64,002	2
29	Coominglah State Forest	41,043	11	88	Ravensbourne National Park	687	1
30	Copperfield State Forest	2379	1	89	Ravensbourne National Park	687	1
31	Cordalba National Park	2473	2	90	Redcliffe State Forest	4615	1
32	Cordalba State Forest	14,975	2	91	Roundstone State Forest	3994	2
33	Crediton Forest Reserve	12,813	2	92	Serocold State Forest	11,656	2
34	Crediton State Forest	19,562	1	93	Shotover State Forest	19,100	1
35	Crohamhurst Conservation Park	63	1	94	Springbrook National Park	6354	1
36	D'Aguilar National Park	36,422	20	95	Squirrel Creek State Forest	6689	4
37	Daisy Hill Conservation Park	571	3	96	St Mary State Forest 1	17,198	14
38	Dan Dan State Forest	4634	2	97	Sunnyside State Forest	24,080	3
39	Dawson Range State Forest	78,700	7	98	Taboonbay State Forest	4079	1
40	Deer Reserve National Park	3228	1	99	Tewantin National Park	2372	4
41	Deer Reserve State Forest	2894	3	100	Tewantin National Park (Recovery)	672	1
42	Deongwar State Forest	4740	3	101	Theodore State Forest	71,199	4
43	Don River State Forest	13,370	4	102	Thinoomba State Forest	2226	2
44	Duaranga State Forest	13,500	3	103	Toolara State Forest	41,590	1
45	Dularcha National Park	464	1	104	Tuchekoi National Park	371	1
46	Dunmore State Forest	19,700	2	105	Umbercollie State Forest	3950	2
47	Durikai State Forest	12,370	5	106	Walton State Forest	1443	1
48	Eugene State Forest	6530	2	107	Warro National Park	6032	1
49	Eumundi Conservation Park	496	1	108	Watalgan State Forest	2102	1
50	Expedition State Forest	108,330	8	109	West Cooroy State Forest	1150	2
51	Forfar State Forest	3391	2	110	Western Creek State Forest	79,428	34
52	Forrest State Forest	24,100	3	111	Whetstone State Forest	41,282	2
53	Gallangowan State Forest	4980	1	112	Wondai State Forest	12,015	17
54	Glenbar State Forest 1	7095	2	113	Wongi National Park	10,906	5
55	Googa State Forest	3610	1	114	Wongi State Forest	69,160	11
56	Great Sandy National Park	221,072	61	115	Woondum National Park	4001	10
57	Grongah National Park	22,900	4	116	Wrattens National Park	21,729	12
58	Gubberamunda State Forest 1	2310	1	117	Yabba State Forest	15,996	7
59	Gympie National Park	1768	3	118	Yelarbon State Forest	30,772	1

**Table 5** Mean diameter growth rates (cm yr<sup>-1</sup>) of species across rainfall zones

Species	Rainfall zone (mm)										Mean	95 % CI	
	600	800	1000	1200	1600	2000							
Section A: species with >30 increment values													
<i>Acacia aulacocarpa</i>		0.43	0.11		0.27	1.03						0.34	0.13
<i>Acacia doratoxylon</i>		0.23	0.07									0.23	0.07
<i>Acacia mearnsii</i>		0.39	0.21	0.31	0.09	0.59	0.23	0.45	0.27	0.22	0.10	0.42	0.19
<i>Acacia melanoxylon</i>						0.60	0.22	0.24	0.13	0.96	0.34	0.45	0.21
<i>Acacia sparsiflora</i>	0.39	0.13										0.39	0.13
<i>Agathis robusta</i>								0.31	0.22			0.31	0.22
<i>Alectryon oleifolius</i>		0.26	0.09									0.26	0.09
<i>Allocasuarina inophloia</i>		0.18	0.10	0.11	0.13							0.17	0.10
<i>Allocasuarina luehmannii</i>	0.21	0.11	0.11	0.06		0.04	0.03					0.13	0.07
<i>Allocasuarina littoralis</i>		0.04	0.03	0.08	0.05	0.02	0.06	0.25	0.07			0.17	0.06
<i>Allocasuarina torulosa</i>		0.08	0.03	0.20	0.09	0.14	0.07	0.16	0.11	0.17	0.10	0.15	0.09
<i>Alphitonia excelsa</i>		0.24	0.14			0.13	0.14	0.19	0.08	0.21	0.09	0.24	0.13
<i>Alphitonia petriei</i>				0.19	0.09			0.23	0.12	0.17	0.20	0.20	0.16
<i>Alstonia constricta</i>		0.10	0.09			0.13	0.08					0.11	0.09
<i>Anopterus macleayanus</i>						0.12	0.05	0.16	0.08			0.15	0.08
<i>Backhousia myrtifolia</i>								0.33	0.13			0.33	0.13
<i>Banksia integrifolia</i> <sup>a</sup>						0.22	0.25	0.19	0.18			0.20	0.19
<i>Brachychiton populneus</i> <sup>b</sup>		0.10	0.04	0.13	0.26	0.13	0.25					0.15	0.19
<i>Callitris columellaris</i>								0.17	0.02			0.17	0.02
<i>Callitris columellaris</i> <sup>c</sup>			0.33	0.14								0.33	0.14
<i>Callitris endlicheri</i>			0.25	0.06								0.25	0.06
<i>Callitris glaucophylla</i>	0.18	0.02	0.18	0.03								0.18	0.03
<i>Casuarina cristata</i>		0.50	0.13									0.50	0.13
<i>Corymbia bloxsomei</i>		0.19	0.12									0.19	0.12
<i>Corymbia gummifera</i>										0.13	0.10	0.13	0.10
<i>Corymbia watsoniana</i> <sup>d</sup>		0.13	0.06	0.09	0.06							0.12	0.06
<i>Cryptocarya glaucescens</i>								0.13	0.06	0.21	0.11	0.18	0.09
<i>Elaeocarpus eumundi</i>						0.47	0.15	0.14	0.05	0.38	0.15	0.34	0.11
<i>Eucalyptus andrewsii</i>				0.13	0.11	0.32	0.31					0.28	0.27
<i>Eucalyptus chloroclada</i>	0.33	0.12	0.21	0.15	0.22	0.15						0.22	0.14
<i>Eucalyptus dealbata</i>	0.20	0.07	0.28	0.16								0.26	0.13
<i>Eucalyptus decorticans</i>			0.19	0.06								0.19	0.06
<i>Eucalyptus fibrosa</i> <sup>e</sup>			0.19	0.18								0.19	0.18
<i>Eucalyptus longirostrata</i>						0.34	0.22					0.30	0.22
<i>Eucalyptus populnea</i>	0.23	0.23	0.13	0.06								0.18	0.13
<i>Eucalyptus racemosa</i>								0.32	0.16	0.38	0.17	0.35	0.17
<i>Eucalyptus resinifera</i>								0.21	0.14	0.29	0.12	0.23	0.14
<i>Eucalyptus sphaerocarpa</i>			0.33	0.11								0.33	0.11
<i>Harpullia pendula</i>								0.11	0.07			0.17	0.07
<i>Lophostemon suaveolens</i>		0.20	0.21	0.16	0.09	0.15	0.19	0.11	0.06			0.16	0.13
<i>Lysicarpus angustifolius</i>		0.11	0.11	0.04	0.02							0.10	0.11
<i>Melaleuca alternifolia</i>				0.10	0.14	0.16	0.10	0.26	0.01			0.16	0.10
<i>Melaleuca decora</i>			0.07	0.09								0.07	0.09
<i>Melaleuca linariifolia</i> <sup>f</sup>			0.11	0.07		0.21	0.16					0.18	0.13
<i>Schizomeria ovata</i>								0.41	0.16	0.15	0.07	0.31	0.12
<i>Syncarpia glomulifera</i> <sup>g</sup>						0.22	0.02	0.32	0.11	0.29	0.17	0.31	0.14

Table 5 continued

Species	Rainfall zone (mm)						Mean	95 % CI			
	600	800	1000	1200	1600	2000					
<i>Syncarpia hillii</i>					0.34	0.18	0.34	0.18			
<i>Synoum glandulosum</i> <sup>h</sup>				0.08	0.05	0.10	0.05	0.46	0.16	0.18	0.08
<i>Xylomelum pyriforme</i>		0.17	0.10							0.17	0.10
Section B: species with <30 increment values rainfall zone mm											
<i>Acacia concurrens</i>	0.48	0.15								0.48	0.16
<i>Acacia flavescens</i>				0.27	0.09					0.27	0.09
<i>Acacia leiocalyx</i>				0.26	0.01					0.26	
<i>Acacia rhodoxylon</i>		0.09	0.14							0.09	0.14
<i>Acacia sparsiflora</i>	0.39	0.13								0.39	0.12
<i>Acronychia wilcoxiana</i>					0.09	0.12				0.09	0.12
<i>Alstonia scholaris</i>				0.23	0.05	0.06				0.14	0.06
<i>Angophora woodsiana</i>							0.09	0.28		0.09	0.27
<i>Banksia serrata</i>					0.05	0.05				0.05	0.06
<i>Caldcluvia paniculosa</i>					0.16	0.05				0.16	0.04
<i>Callicoma serratifolia</i>							0.12	0.07		0.12	0.08
<i>Callistemon salignus</i>							0.10	0.04		0.10	0.04
<i>Canarium australianum</i>					0.28	0.02				0.28	0.02
<i>Canarium baileyianum</i>				0.42	0.16	0.14	0.28	0.18		0.23	0.16
<i>Cassine australis</i> var. <i>australis</i>							0.24	0.03		0.24	0.04
<i>Casuarina cunninghamiana</i>			0.70	0.32	0.11					0.41	0.31
<i>Ceratopetalum apetalum</i>					0.06	0.17				0.06	0.16
<i>Cinnamomum laubatii</i>					0.43					0.43	
<i>Cinnamomum oliveri</i>					0.07					0.07	
<i>Citronella moorei</i>					0.27					0.27	
<i>Corymbia clarksoniana</i>	0.36	0.14								0.36	0.14
<i>Corymbia polycarpa</i>		0.03	0.02							0.03	0.02
<i>Cryptocarya erythroxylon</i>							0.30	0.08		0.30	0.08
<i>Cryptocarya leucophylla</i>				0.32	0.44					0.32	0.43
<i>Cryptocarya macdonaldii</i>							0.10	0.07		0.10	0.06
<i>Cryptocarya microneura</i>						0.52				0.52	
<i>Cyanometra ramiflora</i>				0.09	0.05					0.09	0.06
<i>Daphnandra micrantha</i>						0.01	0.04			0.01	0.04
<i>Dendrocnide excelsa</i>				0.51	0.42					0.51	0.43
<i>Dendrocnide photinophylla</i>						0.39				0.39	
<i>Diospyros fasciculosa</i>						0.18	0.08	0.10		0.13	0.10
<i>Diploglottis australis</i>				0.10	0.04					0.10	0.04
<i>Doryphora sassafras</i>					0.14					0.14	
<i>Elaeocarpus grandis</i>				0.68	0.48	0.30	0.12	0.27		0.48	0.29
<i>Endiandra discolor</i>							0.21	0.17		0.21	0.16
<i>Endiandra sieberi</i>						0.32	0.53			0.32	0.53
<i>Eremophila mitchellii</i>	0.10	0.08	0.07	0.04						0.09	0.06
<i>Eucalyptus bancroftii</i>				0.24		0.06	0.08			0.15	0.08
<i>Eucalyptus crebra</i> x <i>E. woollsiana</i>		0.17								0.17	
<i>Eucalyptus drepanophylla</i>						0.04	0.06			0.04	0.06
<i>Eucalyptus melanoleuca</i>		0.05								0.05	
<i>Eucalyptus microcarpa</i>		0.20	0.08							0.20	0.08
<i>Eucalyptus pilligaensis</i>				0.18	0.08					0.18	0.08

**Table 5** continued

Species	Rainfall zone (mm)						Mean	95 % CI				
	600	800	1000	1200	1600	2000						
<i>Eucalyptus robusta</i>			0.21	<i>0.10</i>	0.14			0.19	<i>0.10</i>			
<i>Eucalyptus rubiginosa</i>		0.04	<i>0.04</i>					0.04	<i>0.04</i>			
<i>Eucalyptus sideroxylon</i>		0.14						0.14				
<i>Eucalyptus tenuipes</i>		0.09	<i>0.05</i>					0.09	<i>0.06</i>			
<i>Euodia bonwickii</i>						0.26	<i>0.21</i>	0.26	<i>0.22</i>			
<i>Euroschinus falcata</i> var. <i>falcata</i>						0.14	<i>0.27</i>	0.14	<i>0.27</i>			
<i>Flindersia bennettiana</i>							0.45	<i>0.52</i>	0.45	<i>0.53</i>		
<i>Flindersia schottiana</i>							0.19	<i>0.10</i>	0.19	<i>0.10</i>		
<i>Flindersia xanthoxyla</i>						0.26	<i>0.27</i>	0.26	<i>0.27</i>			
<i>Geijera parviflora</i>	0.26	<i>0.11</i>	0.09	<i>0.09</i>				0.17	<i>0.10</i>			
<i>Gmelina leichhardtii</i>				0.09		0.38		0.19				
<i>Guioa acutifolia</i>						0.42		0.42				
<i>Jacksonia scoparia</i>		0.12	<i>0.10</i>					0.12	<i>0.10</i>			
<i>Lepidozamia hopei</i>		0.23	<i>0.90</i>					0.23	<i>0.90</i>			
<i>Litsea leefeana</i>		0.21			0.11	<i>0.06</i>	0.10	<i>0.12</i>	0.14	<i>0.10</i>		
<i>Litsea reticulata</i>						0.45	<i>0.28</i>	0.45	<i>0.27</i>			
<i>Livistona</i> spp					0.09	<i>0.14</i>	0.03	<i>0.08</i>	0.06	<i>0.12</i>		
<i>Melaleuca quinquenervia</i>					0.13	<i>0.12</i>	0.13	<i>0.13</i>	0.13	<i>0.14</i>		
<i>Monotoca scoparia</i>						0.21	<i>0.19</i>	0.21	<i>0.18</i>			
<i>Myristica insipida</i>						0.21	<i>0.20</i>	0.21	<i>0.20</i>			
<i>Normanbya normanbyi</i>						0.07	<i>0.14</i>	0.07	<i>0.14</i>			
<i>Petalostigma pubescens</i>		0.08						0.08				
<i>Pittosporum phylliraeoides</i>		0.34						0.34				
<i>Pittosporum undulatum</i>							0.55	<i>0.20</i>	0.55	<i>0.20</i>		
<i>Podocarpus grayae</i>						0.10		0.20	<i>0.02</i>	0.18	<i>0.02</i>	
<i>Polyscias elegans</i>					0.27	<i>0.15</i>	0.10	<i>0.29</i>	0.39	<i>0.05</i>	0.26	<i>0.16</i>
<i>Polyscias murrayi</i>					0.24	<i>0.24</i>				0.24	<i>0.24</i>	
<i>Quintinia sieberi</i>						0.15	<i>0.17</i>			0.15	<i>0.18</i>	
<i>Randia fitzalanii</i>					0.19	<i>0.20</i>	0.14	<i>0.21</i>	0.29	<i>0.19</i>	0.19	<i>0.20</i>
<i>Rhodamnia rubescens</i>						0.06	<i>0.13</i>			0.06	<i>0.14</i>	
<i>Rhodosphaera rhodantha</i>					0.08		0.22	<i>0.17</i>	0.41	<i>0.12</i>	0.23	<i>0.14</i>
<i>Sloanea australis</i> subsp. <i>parviflora</i>						0.09	<i>0.06</i>			0.09	<i>0.06</i>	
<i>Sloanea woollsii</i>						0.33				0.33		
<i>Solanum torvum</i>		0.08	<i>0.08</i>							0.08	<i>0.08</i>	
<i>Syzygium crebrinerve</i>								0.41		0.41		
<i>Syzygium oleosum</i>						0.08	<i>0.06</i>	0.13	<i>0.09</i>	0.11	<i>0.08</i>	
<i>Toona ciliata</i>					0.76	<i>0.19</i>				0.76	<i>0.20</i>	
<i>Trochocarpa laurina</i>						0.04	<i>0.02</i>	0.31		0.18	<i>0.02</i>	

95 % confidence interval (CI) in italics

<sup>a</sup> Subsp. *integrifolia*; <sup>b</sup>subsp. *populneus*; <sup>c</sup>x *C. preissii* subsp. *verrucosa*; <sup>d</sup>subsp. *watsoniana*; <sup>e</sup>subsp. *nubila*; <sup>f</sup>var. *linariifolia*; <sup>g</sup>subsp. *glo-mulifera*; <sup>h</sup>var. *glandulosum*

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