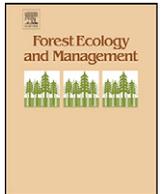




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Age and growth of a fire prone Tasmanian temperate old-growth forest stand dominated by *Eucalyptus regnans*, the world's tallest angiosperm

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ABSTRACT

Forests are key components of the global carbon cycle, with deforestation being an important driver of increased atmospheric carbon dioxide. Temperate old-growth forests have some of the highest above ground stores of carbon of any forest types on Earth. Unlike tropical forests, the ecology of many temperate forests is dominated by episodic disturbance, such as high intensity fire. An exemplar of a particularly carbon dense temperate forest system adapted to infrequent catastrophic fires is the *Eucalyptus regnans* forests of south eastern Australia. Knowledge of the growth and longevity of old-growth trees is crucial to understanding the carbon balance and fire regimes of these forest systems. In an old-growth *E. regnans* stand in the Styx Valley in southern Tasmania we used dendrochronological techniques and radiocarbon dating to determine the age and stem growth of *E. regnans* and *Phyllocladus aspleniifolius*, an understorey rainforest conifer. Our analysis revealed that an even-aged cohort of *E. regnans* and *P. aspleniifolius* established in 1490–1510AD, apparently after a stand-replacing fire. The stem growth rates of *E. regnans* in the first 100 years were very rapid compared to the co-occurring *P. aspleniifolius*. That the longevity of *E. regnans* is >500 years challenges the suggested 350–450 year timeframe proposed for the widely held model of succession from eucalypt to rainforest. These forests not only have the potential to store vast amounts of carbon, but can also maintain these high carbon densities for a long period of time. Estimates of the capacity of these forests to sequester and store carbon should explicitly consider past harvesting and fire regimes and the potential increases in the risk of fire associated with climate change.

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1. Introduction

Forests are of prime importance to the global carbon cycle, with deforestation since industrialisation contributing about 20% of the increased carbon dioxide (CO₂) in the atmosphere (IPCC, 2007; Bowman et al., 2009). There is an obvious need to reduce tropical deforestation in order to mitigate the effects of anthropogenic climate change (Skole and Tucker, 1993; IPCC, 2007), although attention is now also turning to the remaining old-growth forests outside the tropical zone. Recent reviews have found that old-growth temperate forests may constitute a substantial and largely neglected carbon sink (Luyssaert et al., 2008) and that estimates of biomass carbon densities in mature or primary forests are much higher for temperate moist forests than for tropical or boreal forests (Keith et al., 2009). Yet, unlike tropical rainfor-

est systems, the ecology of many temperate forests is dominated by episodic disturbance by fire (Agee, 1993; Attiwill, 1994). Thus the extra-ordinary carbon storage of old-growth temperate forest ecosystems is more apparent than real because the fires that maintain them result in a periodic efflux of carbon. A comprehensive understanding of the global carbon cycle must therefore include an understanding of the fire regimes that maintain temperate forests.

The advent of satellite imagery in the late 20th century has revolutionised our understanding of fire activity on Earth (Flannigan et al., 2009) and enabled detailed characterisation of fire regimes in frequently burnt areas such as tropical savannas (Russell-Smith et al., 2003). In forests where the return time of fires is considerably longer, the quantification of fire regimes requires historical reconstructions of fire events, usually through dendrochronological techniques (Fritts and Swetnam, 1989; Bowman, 2007). Dendrochronological studies of post-fire cohorts have enabled the characterisation of fire regimes for a range of high-biomass, old-growth temperate forests that experience high-severity, stand-replacing fire events at very long intervals (e.g. Hemstrom and Franklin, 1982; Silla et al., 2002; Winter et al., 2002). Old-growth

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Eucalyptus regnans forests appear to conform to the pattern of infrequent and intense stand replacing fires, yet the precise dates of pre-European fire events which are crucial for characterising the fire regimes of these forests remain largely unknown (McCarthy et al., 1999; Simkin and Baker, 2008), reflecting an Australia-wide paucity of dendrochronological studies (Pearson and Searson, 2002) and difficulties in applying classical dendrochronological techniques to eucalypts (Brookhouse, 2006). Understanding the return times of stand-replacing fires in *E. regnans* forests and their relationship with prevailing climatic conditions is critical for contextualising catastrophic fire events in south eastern Australia, such as the recent February 2009 'Black Saturday' fires that burnt vast areas of forest in Victoria, south eastern Australia, with the loss of 173 lives and more than 3000 homes.

High-severity ($>800 \text{ kW m}^{-1}$) fires are crucial for the regeneration of *E. regnans* forests that occur in high rainfall regions of Tasmania and Victoria (Ashton, 1981; Attiwill, 1994). An established ecological generalisation that is the basis of current silvicultural practice, is that *E. regnans* forests predominantly form single-age cohorts that arise following stand-replacing fires (Gilbert, 1959; Ashton, 1976; Attiwill, 1994), although multi-aged stands are not uncommon, developing after fires that kill only a fraction of the stand (McCarthy and Lindenmayer, 1998; Lindenmayer et al., 1999; Turner et al., 2009). *E. regnans* is not only the world's tallest flowering plant, but it is also unusual among the eucalypts in its sensitivity to fire. *E. regnans* is afforded limited protection from fire from its thin bark and the lack of a lignotuber makes for limited vegetative recovery following severe fire damage (Ashton, 1976, 1981). Regeneration is very limited in the absence of fire so *E. regnans* is aptly described as the world's largest obligate seeder. This peculiar biology has far reaching implications for the population ecology of this species. Single-aged cohorts of *E. regnans* are vulnerable to demographic collapse if fire intervals are shorter than the time to reach reproductive maturity. Likewise where fire intervals exceed the lifespan of the youngest cohort of *E. regnans*, the stand would be replaced by rainforest species that are able to regenerate without fire disturbance. In sum, the *E. regnans* system is held in a delicate balance by fire return intervals (Jackson, 1968). Despite being integral to their persistence in the landscape, there remains considerable uncertainty regarding the growth rates and longevity of *E. regnans* forests and thus the potential of this species to survive under varying fire frequencies. These questions are of considerable interest because they provide a temporal context for understanding the dynamics of carbon storage in *E. regnans* forests which have the highest known biomass carbon density of any forest in the world (Keith et al., 2009).

The purpose of this study is to characterise the age and pattern of stem growth of a stand of old-growth *E. regnans* in southern Tasmania. Our approach is to estimate the age and growth rates of co-occurring cohorts of *E. regnans* and *Phyllocladus aspleniifolius* (an understorey rainforest conifer) in an old-growth forest stand by applying a range of mutually reinforcing and independent dating techniques, namely; cross-dating of both *E. regnans* and *P. aspleniifolius* tree-ring series using dendrochronological techniques (Fritts, 1976; Fritts and Swetnam, 1989) and radiocarbon dating of sections of these cross-dated tree-ring series (Hua, 2009). *P. aspleniifolius* has been shown to be suitable for dendrochronological reconstructions using classical cross-dating techniques (Allen et al., 2001) but previous attempts to cross-date *E. regnans* have not been successful (Brookhouse, 2006; Simkin and Baker, 2008). We then use our findings to (a) evaluate previous estimates of the age of old-growth *E. regnans* trees (b) consider the implications for the model of forest succession proposed for *E. regnans*-rainforest systems and (c) consider the implications for the fire regimes and carbon storage of *E. regnans* forests.

2. Methods

2.1. Study area

The study was located in the Styx Valley in the southern Forests of Tasmania (Fig. 1a). The region experiences a mean annual rainfall of approximately 1175 mm, with a mean minimum and maximum annual temperature of 5.3 and 16.1 °C respectively (Australian Bureau of Meteorology, June 2009). The eucalypt forests of the Styx Valley are renowned for the presence of large numbers of giant trees that exceed 85 m in height. The forests of this region are comprised of a mosaic of (a) cool temperate rainforest dominated by *Nothofagus cunninghamii* and *Atherosperma moschatum*, (b) tall eucalypt forests with dense multi-layered understoreys dominated by rainforests species (mixed forests) or broadleaved shrubs and small trees (wet sclerophyll forests) and (c) managed production forests and plantations.

The study area was situated in a forest stand on a gently undulating plateau south of the Styx River that was harvested between December 2007 and February 2008 (Fig. 1b). The study site was chosen because it was an excellent example of an old-growth 'mixed' forest, having a low stocking of very tall *E. regnans* (height 55–75 m with 50–70% crown cover) emergent from a dense rainforest composed of *N. cunninghamii* and *A. moschatum* with *P. aspleniifolius*, *Eucryphia lucida* and *Anodopetalum biglandulosum* (see Fig. 2). The absence of cut stumps or fire scars intimated that the stand was undisturbed by past harvesting activities or recent fire.

2.2. Stand structure measurements and sampling of stem discs

Fieldwork occurred during the harvesting program, thus constraining baseline measurements, so the stand structure was determined by measuring tree diameters within two 1.3 ha⁻¹ plots immediately adjacent to the area where stems were sampled (Fig. 1c). Within each of these plots stem diameters were measured at breast height over bark at 1.3 m above ground level (DBH) for all live eucalypts $>10 \text{ cm}$ DBH. Where trees were heavily buttressed, diameters were measured as high as practical on the bole (i.e. Turner et al., 2009).

Collection of material for dendrochronological analysis was constrained by the practicalities of sampling very large trees (see Fig. 2) with pronounced buttressing, very hard dense wood and ubiquitous internal stem rot. Harvesting of this stand enabled collection of stem sections that weighed up to 300 kg from felled trees. This approach carried numerous practical and safety constraints associated with working closely with a harvesting operation and meant that ideal sampling strategies (i.e. sampling at consistent heights) and coring of large numbers of trees across multiple sites was impossible.

For each *E. regnans* tree selected for dendrochronological analysis, the DBH was determined prior to felling. Following felling, the interior of each stem was inspected for rot and stem discs were taken from eighteen trees at the point where the wood was sound with clearly visible centre rings (between 6.0 and 20.0 m above ground). Stem discs at 'stump height' (0.5–1.0 m) were acquired from twenty-four *P. aspleniifolius* trees from a small grove that was harvested in January 2008 (Fig. 1c). It was not possible to collect data on the size class distribution of *P. aspleniifolius* given the patchy occurrence of this species and safety issues associated with working in an area that was being harvested.

2.3. Chronology development

Depending on the size of the disc, each of the *E. regnans* discs were sectioned into two or four equally spaced radial segments of 200 mm width and polished with progressively finer grades of

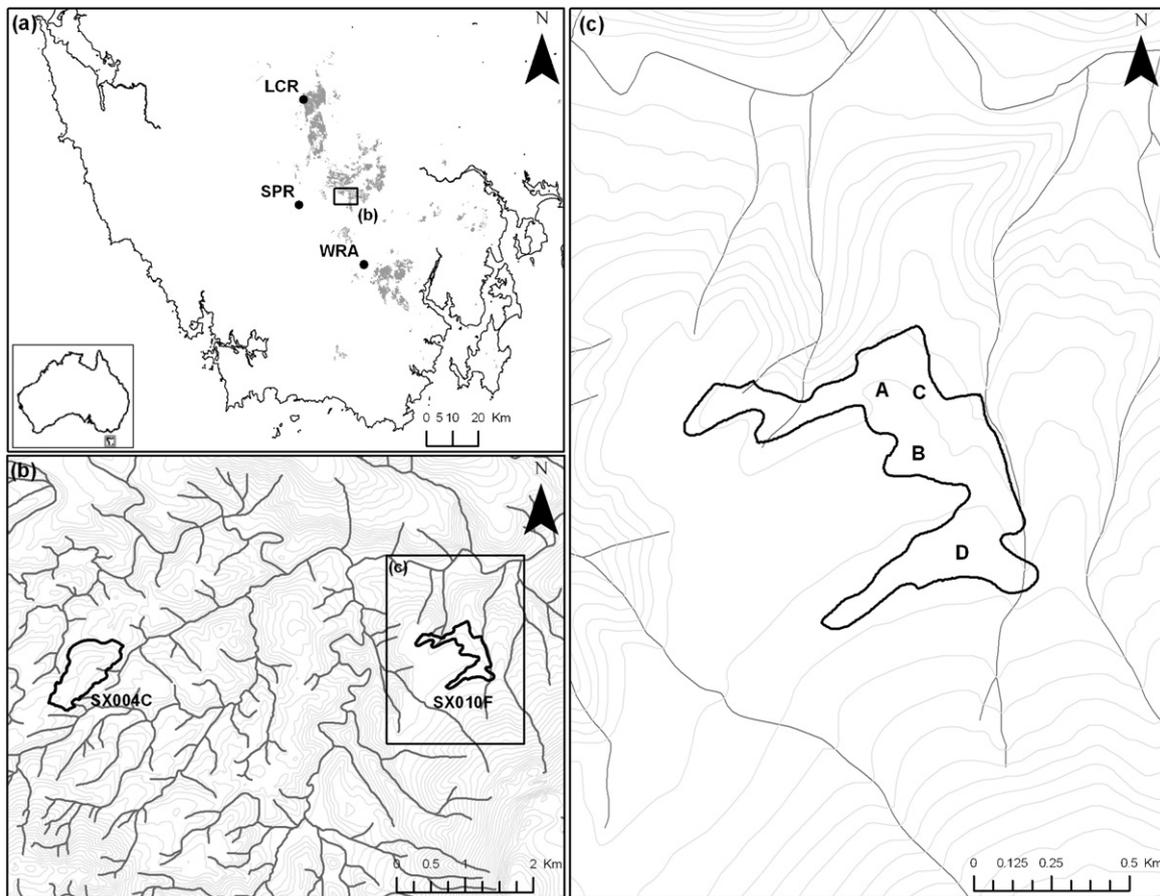


Fig. 1. Study locations for the Styx Valley dendrochronology study in the southern forests of Tasmania. (a) The distribution of *Eucalyptus regnans* forests in southern Tasmania (shaded), the location of the current study in the Styx Valley (box) and three *Phyllocladus aspleniifolius* stands for which previously published tree-ring chronologies are available (LCR: Lower Cole Road, SPR: Scotts Peak Road, WRA: Warra; Allen et al., 2001; Allen, 2002). (b) Locations of the study areas in the Styx Valley used by Dean and Roxburgh (2006) for biomass carbon estimation (SX004C) and for dendrochronological investigations in this study (SX010F). (c) Locations of sampling sites for *E. regnans* (A) and *P. aspleniifolius* (B), and the diameter survey plots (C and D) within the mapped photo-interpreted vegetation class (solid line).

sandpaper. Series of ring widths were measured to the nearest 0.01 mm along each radii using a measuring stage and microscope. The program COFECHA was used to develop a mean chronology from the measured tree-ring series and to facilitate the identification of measurement of cross-dating errors (Holmes, 1983; Grissino-Mayer, 2001). Most radii exhibited wide rings with relatively distinct (albeit diffuse) earlywood and latewood boundaries for the innermost ~125 rings (including the pith), beyond which measurement and cross-dating of tree rings on most radii became increasingly difficult due to a combination of exceedingly narrow rings, wedging or contortion and indistinct ring boundaries. Therefore, we focussed on the inner 125 rings that could be identified with confidence. When preparing the *E. regnans* chronology, the first ring of the chronology was initially assigned an arbitrary value of 'Year 1' and each series was progressively culled by 5 rings from year 125 backwards until COFECHA mean inter-series correlations exceeded 0.35 for all 30 year segments in the chronology. In effect, this resulted in a 'floating chronology'. The first ring of the *E. regnans* floating chronology was later 'anchored' to the absolute time scale using 'wiggly matching' of a sequence of radiocarbon dates (see following section) and all rings in the chronology were assigned a calendar year relative to this date.

Intact *P. aspleniifolius* discs were sanded and ring widths were measured to the nearest 0.01 mm along three radii for each disc. The program COFECHA was used to develop a mean chronology from the measured tree-ring series and to facilitate the identification of measurement of cross-dating errors (Holmes, 1983; Grissino-Mayer, 2001). Unlike *E. regnans*, the process of cross-dating of *P.*

aspleniifolius tree-ring series was inclusive of all rings from the pith to the cambium. Ring wedging is a common phenomenon in *P. aspleniifolius*, resulting in locally absent rings (Allen et al., 2001). Where this was the case the measured radius was temporarily rotated clockwise or anticlockwise until locally absent rings reappeared, then shifted back to the original radius. If rotations from the original radius exceeded 45° we followed Allen et al. (2001), where locally absent rings were substituted with the average ring width for other radii from the same tree.

Three previously published *P. aspleniifolius* chronologies from the Southern Forests region (Fig. 1a) were available to validate the annual resolution of the *P. aspleniifolius* chronology developed in this study. Details of these chronologies were presented in Allen et al. (2001) and Allen (2002). All chronologies, including the chronology produced in this study, were detrended using 128-year 50% cut-off cubic smoothing spline (Allen et al., 2001; Allen, 2002). Pearson correlations between all sites for the entire common length of each pair of chronologies were calculated for residual chronologies generated during the detrending process.

2.4. Dating of tree rings using radiocarbon dating

Radiocarbon dating of tree rings was used in this study for two objectives: (1) 'wiggly matching' of a sequence of radiocarbon dates was used to anchor the Styx Valley *E. regnans* floating chronology to the calendar time scale (Bronk-Ramsey et al., 2001; Hua, 2009) and (2) bomb ¹⁴C radiocarbon was used to independently validate the annual resolution of the Styx Valley *P. aspleniifolius* chronol-



Fig. 2. Old-growth *Eucalyptus regnans* stand with rainforest understorey in the Styx Valley in southern Tasmania sampled for dendrochronological analysis in this study. The *E. regnans* trees were 60–75 m tall with a measured diameter distribution of 160–350 cm DBH. Photo: Sam Wood.

ogy (Hua, 2009). For the first objective, nine sequential decadal samples were taken from a section of Tree 10 that coincided with years 11–20, 21–30 . . . 91–100 of the *E. regnans* floating chronology for accelerator mass spectrometry (AMS) ^{14}C analysis. For the second objective, wood samples were taken from two single tree rings that were assigned years 1963 and 1968AD in the *P. aspleniifolius* chronology for AMS ^{14}C analysis. The samples were pre-treated to

alpha-cellulose and converted to graphite following the methods described in Hua et al. (2004, 2001). The graphite was analysed for radiocarbon using the STAR AMS Facility at ANSTO (Fink et al., 2004). For each sample, ^{14}C concentration and/or radiocarbon age was determined after corrections for AMS machine background, procedural blank and isotopic fractionation using measured $\delta^{13}\text{C}$. Wiggle matching of ^{14}C radiocarbon dates from *E. regnans* to the SHcal04 calibration curve for the Southern Hemisphere (McCormac et al., 2004) to derive calendar dates was performed using the OxCal (Version 3.10) radiocarbon calibration program (Bronk-Ramsey, 2001). For the two single rings of *P. aspleniifolius*, ^{14}C concentrations were calibrated to calendar ages using the atmospheric bomb ^{14}C data for the Southern Hemisphere zone (Hua and Barbetti, 2004), and the CALIBomb program (Stuiver and Reimer, 1993).

2.5. Growth curves

Using the cross-dated chronologies and the results of the radiocarbon dating, all *E. regnans* and *P. aspleniifolius* trees that established contemporaneously were identified. For these trees, cumulative diameter growth at sampling height was reconstructed from cross-dated annual tree-ring width measurements. Average cumulative diameter growth for each species for the first 90 years was calculated from these reconstructions to compare the early growth rates of *E. regnans* and *P. aspleniifolius*. Models were fitted using non-linear least squares regression, to the formula $\text{Diameter} \sim a \times \text{Year}^b$, in which no intercept term was included. These models were used to illustrate growth curves for the entire lifespan of *E. regnans* and *P. aspleniifolius*. Given the non-conventional and inconsistent sampling heights of *E. regnans* trees (6.0–20.0 m), we avoided detailed modelling of growth rates and instead focussed on generalised comparisons of stem growth between the two species.

3. Results

3.1. *E. regnans* stand structure

The diameters of stems used in the dendrochronological analysis were comparable with the diameters of trees in the neighbouring unlogged plots (Fig. 3). These data indicate that this stand (Fig. 1c) consists of a single cohort of very large eucalypts. Of the 75 unlogged trees measured, 70 were >140 cm DBH with the

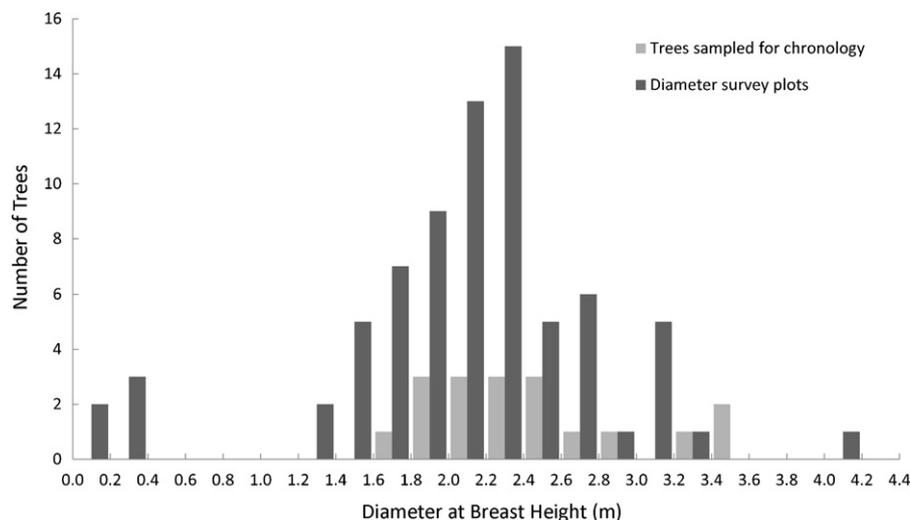


Fig. 3. Diameter distribution of *Eucalyptus regnans* trees (>10 cm DBH) measured in two 1.3 ha plots within the Styx Valley forest stand ($n = 75$) and the diameter distribution of *E. regnans* trees used to generate the cross-dated chronology ($n = 18$).

Table 1
Details of cross-dated tree-ring chronologies developed for *Eucalyptus regnans* and *Phyllocladus aspleniifolius* from the Styx Valley. Mean inter-series correlation was generated by the dendrochronology program COFECHA (Holmes, 1983; Grissino-Mayer, 2001).

Statistic	<i>E. regnans</i>	<i>P. aspleniifolius</i>
Period covered	Floating chronology	1511–2006AD
Length of chronology	100 years	495 years
Number of trees	18	24
Number of series/radii	57	63
Mean inter-series correlation	0.617	0.604
Average ring width (mm)	31.6	8.0
Average segment length and range (rings)	84 (60–97)	447 (197–492)

remaining five <40 cm DBH. These smaller trees were geographically constrained to a small area and appear to be associated with individual gap regeneration well after the establishment of the larger cohort.

3.2. *E. regnans* dendrochronology, radiocarbon dating and stand establishment dates

Iterative culling of the outermost rings of each tree-ring series included in the Styx Valley *E. regnans* ‘floating chronology’ resulted in an average segment length of 84 years and an overall chronology length of 100 years (Table 1). The high mean inter-series correlation of 0.62 calculated by COFECHA suggests a strong common signal between the tree-ring series. The ¹⁴C radiocarbon ages obtained for the sequence of cross-dated tree rings from the *E. regnans* chronology and the respective wiggle matched calendar dates are presented in Table 2 and illustrated in Fig. 4. Using data in Table 2, the first ring in the floating chronology was back-calculated to be 1512.5 ± 20.5AD (2σ) and all subsequent rings in the chronology were assigned a calendar year relative to this date. The calendar year of the pith for seventeen *E. regnans* trees (Fig. 5) fell within a 16 year time-span from 1512.5 ± 20.5AD (2σ) to 1528.5 ± 20.5AD (2σ). The statistically robust linear relationship between pith date and sampling height (R² = 0.76) allowed us to estimate height growth to be approximately 1.0 m per year (Fig. 5). This enabled us to calculate the number of years it took for each tree to reach its respective sample height, and therefore estimate an approximate establishment date for each tree at ground level. Using this methodology, we estimate that all seventeen *E. regnans* trees established between 1503 ± 20.5AD (2σ) and 1511 ± 20.5AD.

Table 2
¹⁴C radiocarbon ages and wiggle matched calendar age for a sequence of 10-year tree-ring samples from *Eucalyptus regnans* Tree 10. These samples are a portion of a cross-dated section from the Styx Valley *E. regnans* chronology. Wiggle matching of radiocarbon dates to the SHcal04 calibration curve for the Southern Hemisphere (McCormac et al., 2004) to derive calendar dates was performed using the OxCal radiocarbon calibration program Version 3.10 (Bronk-Ramsey, 2001) and is illustrated in Fig. 4. ¹⁴C radiocarbon ages are older for the younger wood samples because of the rising trend in the atmospheric ¹⁴C between 1500 and 1600AD (see Fig. 4).

Ring number	¹⁴ C age (BP)		Calendar age (AD)		Lab code
	Value	1σ	Cal AD	2σ	
11–20	335	26	1527.0	20.5	OZL735
21–30	368	28	1537.0	20.5	OZL736
31–40	308	28	1547.0	20.5	OZL737
41–50	348	24	1557.0	20.5	OZL738
51–60	390	31	1567.0	20.5	OZL739
61–70	405	30	1577.0	20.5	OZL740
71–80	357	31	1587.0	20.5	OZL741
81–90	426	31	1597.0	20.5	OZL742
91–100	406	26	1607.0	20.5	OZL743

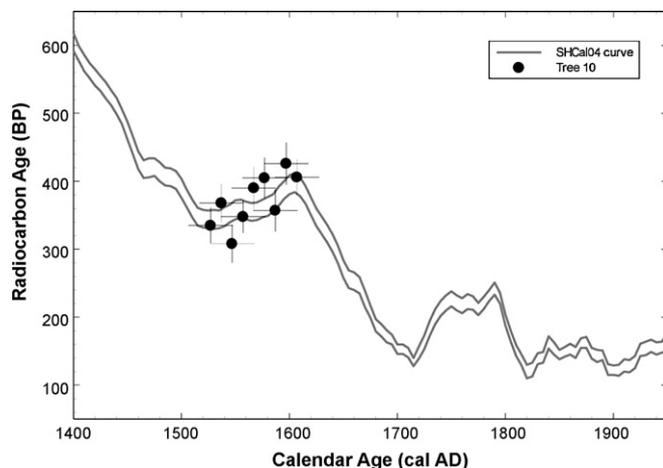


Fig. 4. Wiggle matching of ¹⁴C radiocarbon dates from a representative series of tree rings (Tree 10) from the *Eucalyptus regnans* chronology to the SHCal04 calibration curve for the Southern Hemisphere (McCormac et al., 2004). Analyses were performed using the OxCal (Version 3.10) radiocarbon calibration program (Bronk-Ramsey, 2001). SHCal04 curve is plotted in 1σ range. The error bars are 1σ for radiocarbon age and 2σ for calendar age.

3.3. *P. aspleniifolius* dendrochronology, radiocarbon dating and stand establishment dates

The Styx Valley *P. aspleniifolius* chronology spanned 495 years from 1511 AD to 2006 AD (Table 1). This chronology was supported by a high mean inter-series correlation of 0.60 calculated by COFECHA and consistently high inter-site correlations with three previously published *P. aspleniifolius* chronologies from the Tasmanian Southern Forests region (Fig. 1a and Table 3). The results of the ¹⁴C bomb pulse radiocarbon dating (Fig. 6) provide an independent validation of the annual resolution of the Styx Valley chronology. The pith dates of the *P. aspleniifolius* trees indicate a strong pulse of

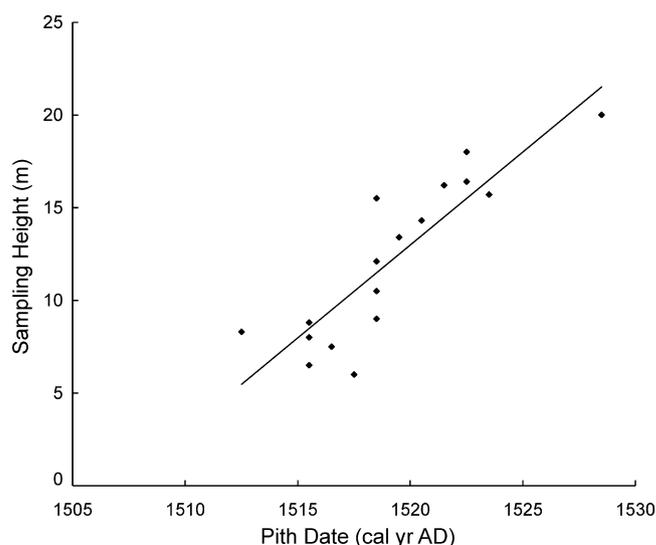


Fig. 5. The pith date of seventeen *Eucalyptus regnans* trees from the Styx Valley stand and the relationship with sampling height. The pith dates were estimated from the *E. regnans* floating chronology, which was anchored to the absolute timescale (calendar year AD) using wiggle matching of a sequence of radiocarbon dates (see text). The pith dates plotted in this diagram are mean calendar year AD without uncertainties. The relationship between sampling height and pith date (solid line) is given by $y = 1.003x - 1511.6$ ($R^2 = 0.76$, $n = 17$) indicating a height growth of approximately 1.0 m per year. Tree 1 was missing the pith and was not included in calculating this figure. The date of the innermost ring for Tree 1 was estimated to be 1528.5 ± 20.5AD (2σ).

Table 3
Correlation matrix for four *Phyllocladus aspleniifolius* chronologies from the Tasmanian Southern Forests (Fig. 1a): the Styx Valley (STYX: this study), Scotts Peak Road (SPR: Allen et al., 2001), Lower Cole Road (LCR: Allen et al., 2001) and Warra (WRA: Allen, 2002). Pearson correlations between all sites for the entire common length of each pair of chronologies were calculated for residual chronologies generated following detrending.

	STYX	SPR	WRA	LCR
STYX	1.00	0.68	0.68	0.77
SPR		1.00	0.68	0.64
WRA			1.00	0.62
LCR				1.00

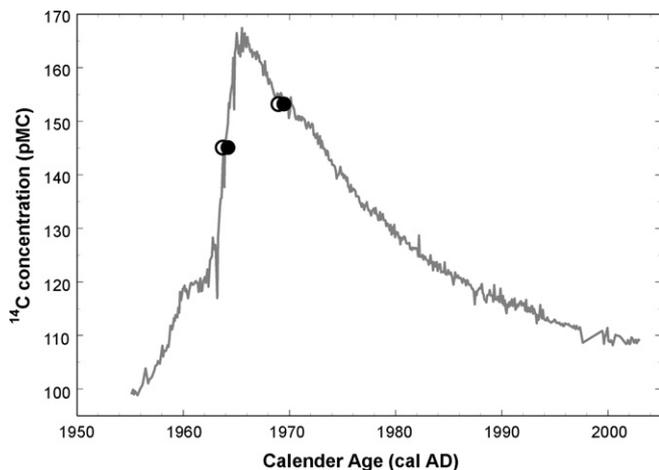


Fig. 6. Temporal positions of two single tree rings (1963 and 1968AD) from the *Phyllocladus aspleniifolius* chronology based on dendrochronology (open symbols) vs those derived from bomb pulse ¹⁴C dating (solid symbols). These symbols should be plotted in the same positions. However, they are displayed in the diagrams with small temporal offsets for reason of clarity. The grey line is the atmospheric bomb ¹⁴C curve for the Southern Hemisphere from Hua and Barbetti (2004).

tree establishment in the early 1500s and a weaker pulse of tree establishment in the mid to late 1600s (Fig. 7). The chronology revealed that fifteen of the sampled stems reached sampling height between the years 1511 AD and 1531 AD, and four reached sampling height between the years 1662 AD and 1672 AD. The declining number of establishment dates after 1725 AD is an artefact of sampling the largest *P. aspleniifolius* in the stand.



Fig. 7. Establishment history for *Phyllocladus aspleniifolius* trees from the Styx Valley stand based on pith dates derived from the cross-dated tree-ring chronology. The decreasing number of establishment dates after 1750 is an artefact of the targeting of large trees >50 cm DBH for this study.

3.4. Comparison of *E. regnans* and *P. aspleniifolius* growth curves

We identified seventeen *E. regnans* trees (Fig. 5) and fifteen *P. aspleniifolius* trees (Fig. 7) that had pith dates indicating regeneration in the early 1500s. Modelled growth curves in Fig. 8 illustrate much more rapid early diameter growth for *E. regnans* compared to *P. aspleniifolius*. At age 25, *E. regnans* attained a diameter approximately 5 times greater than *P. aspleniifolius* and at age 90, diameter was approximately 3 times greater. Almost 45% of the total diameter of the ~500 year old *E. regnans* trees is achieved in the first 90 years of growth.

4. Discussion

Given the stand structural data (single cohort), and the congruence between the establishment dates of the earliest *P. aspleniifolius* cohort (1511–1531AD) and the estimated establishment date of the *E. regnans* cohort (1503–1511 ± 20.5AD (2σ)), we conclude that the Styx Valley study site comprises an even-aged cohort of *E. regnans* established following a stand-replacing disturbance event before 1511AD and probably within the period 1490–1510AD. Given the importance of fire in the regeneration ecology of *E. regnans* (Gilbert, 1959; Ashton, 1976, 1981; Attiwill, 1994), there is little doubt that the cause of this regeneration event was a stand-replacing fire. This conclusion is consistent with that of a number of past studies which have suggested that some areas of old-growth forests in southern Tasmania may have regenerated after fire “in the early 1500’s” (Gilbert, 1959; Hickey et al., 1999; Alcorn et al., 2001; Allen, 2002). These previous studies were based on ring counts of eucalypt stumps in the field and the age of a limited number of individual *P. aspleniifolius* trees from cross-dated chronologies that were developed for dendroclimatology research rather than for identifying post-fire cohorts. The methods employed by these studies are of far less reliability than the approach we used here, and therefore, we provide the first robust identification of a pre-European fire event in the southern forests of Tasmania. We conclude that *E. regnans* has a longevity that may exceed 500 years given that observations of the sampled trees indicated that they were not completely senescent (Fig. 2). Consequently, our findings challenge the commonly held view that the longevity of *E. regnans* is around 350–450 years (Gilbert, 1959; Jackson, 1968; Wells and Hickey, 1999).

Gilbert (1959) and Jackson (1968) proposed that if the period between two fires exceeds the lifespan of *E. regnans*, the eucalypts will be eliminated and replaced by ‘climax’ rainforest,

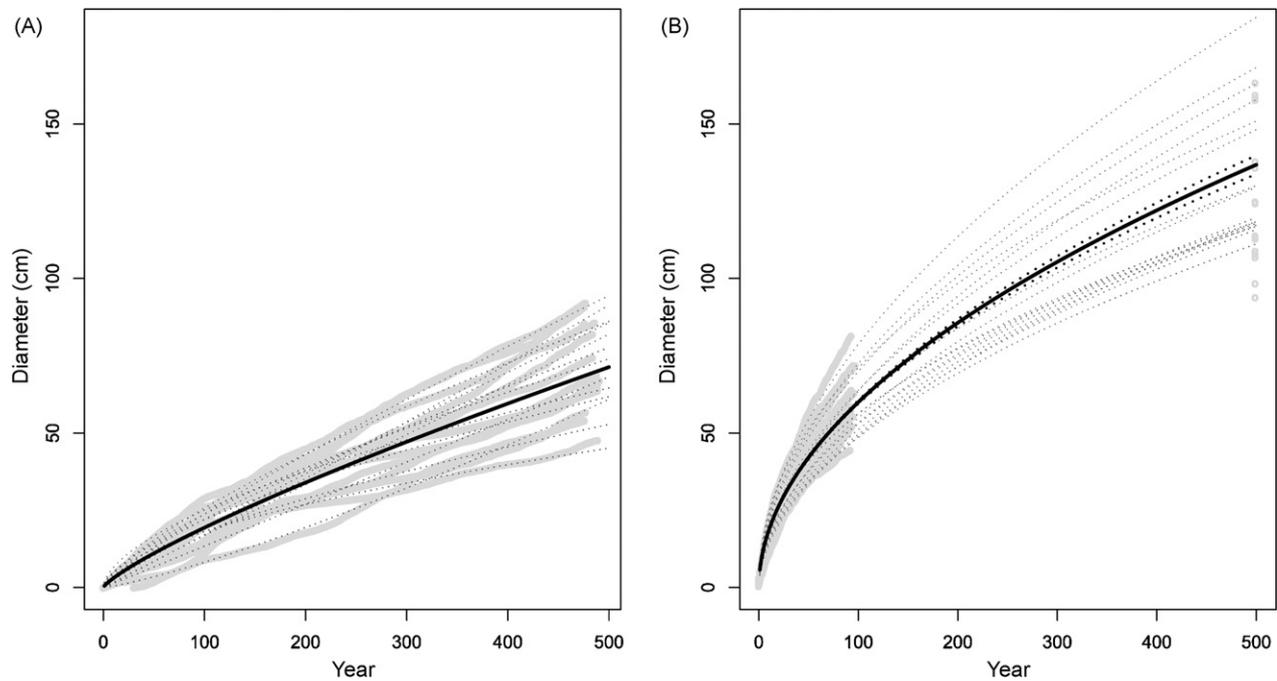


Fig. 8. Diameter growth curves for co-occurring (a) understorey *Phyllocladus aspleniifolius* and (b) overstorey *Eucalyptus regnans* trees established after a stand-replacing fire in the Styx Valley in 1490–1510AD. Growth curves for each tree (solid grey lines) are for cumulative diameter growth at sampling height (PA: 0.5–1.0 m, ER: 6.0–20.0 m) and were reconstructed from cross-dated, annual tree-ring width measurements. The upper limit of growth of *E. regnans* was constrained by disc diameter measurements on trees assumed to be 500 years old. Models were fitted using non-linear least squares regression, to the formula $Diameter \sim a \times Year^b$, in which no intercept term was included. Models were fitted for each tree (dashed black lines) and for all trees of each species together (solid black lines). Standard errors for the combined curves are indicated with dotted lines.

because shade intolerant *E. regnans* seedlings cannot survive in the low light intensity under the rainforest canopy. Our data contributes to current understanding of the temporal dynamics of the Gilbert–Jackson model in two ways. Firstly, the revised longevity for *E. regnans* suggests that the proposed transition to rainforest would take more than 500 years for a single cohort stand. Secondly, by contrasting the comparatively rapid post-disturbance growth rates of *E. regnans* with the concurrently growing *P. aspleniifolius* we illustrate the mechanism whereby the light demanding *E. regnans* can form an upper stratum to compete against the slow-growing and continuously regenerating rainforest understorey. These contrasting ‘tortoise and the hare’ growth rates support the view of Bond (1989) that tree growth rates in the regeneration niche are crucial to understanding the stand dynamics of many mixed angiosperm and gymnosperm forests and are consistent with the model of single cohort, mixed species stands proposed by Oliver and Larson (1996) and Franklin et al. (2002). The rapid initial growth of *E. regnans*, where almost half the total stem diameter growth occurs in the first 90 years, forms the basis for the proposed silvicultural rotation times for these forests (i.e. 90 years, Whiteley, 1999). Beyond 90 years we have no data on annual stem diameter growth for *E. regnans*. Sillett et al. (2010) report that the growth rate of the lower stems of *E. regnans* trees decreases (or does not change) with increasing age (from 80 years up to 299 years old), yet the upper stems and crown continue to increase growth regardless of age. Given these growth rates, *E. regnans* trees achieve a size and longevity rivalled by only the evergreen coniferous forests of the Pacific Northwest of the USA (Waring and Franklin, 1979).

An assumption of the Gilbert–Jackson model of forest succession is that the forests are made up of a single cohort of overstorey eucalypts. While the stand we studied conforms to this assumption, it appears that single cohort forest stands are the exception rather than the rule in old-growth *E. regnans* forests (Lindenmayer et al., 2000; Lindenmayer, 2009; Turner et al., 2009). Turner et al.

(2009) used diameter distributions to infer stand ages and variation in cohort structures in unlogged contemporary southern Tasmanian wet eucalypt forests. They found that for pure *E. regnans* stands with trees assumed to be >110 years old, only 15% were comprised of a single cohort, and inferred that the average time since stand-replacing fire for these stands was approximately 230 years. The rarity of >110 year old, single-cohort *E. regnans* stands in the landscape, combined with the longevity of the dominant trees (>500 years), implies that there is currently a limited capacity for widespread succession of *E. regnans* forest to rainforest in southern Tasmania under current fire regimes. Whether fire regimes and the age structure of these forests, and thus the likelihood of succession, were different under Aboriginal management remains uncertain.

Our data confirm that at least some parts of the Tasmanian forest landscape can be characterised by a fire regime of high-severity, stand-replacing fires with a return time of >500 years. A range of temperate forest stands throughout the world have been shown to have developed from stand-replacing fires over 450 years ago in the Pacific Northwest (Hemstrom and Franklin, 1982; Agee, 1993; Winter et al., 2002; Weisberg and Swanson, 2003) and Rocky Mountains (Romme and Knight, 1981; Kipfmüller and Baker, 2000; Buechling and Baker, 2004) regions of North America and in Northern Patagonia in South America (Lara et al., 1999; Veblen et al., 1999). By analysing long-term regional patterns of fire events in relation to long-term reconstructed climate variation, several of these studies have been able to identify climatic conditions conducive to regional stand replacing fire events (e.g. Hemstrom and Franklin, 1982; Veblen et al., 1999; Weisberg and Swanson, 2003; Buechling and Baker, 2004). In Tasmania, analyses of short term (1952–2002) relationships between fire and climate revealed that summer rainfall and indices of the El Niño–Southern Oscillation are important climatic factors influencing the area burnt each summer (Nicholls and Lucas, 2007). Simkin and Baker (2008) demonstrated the use of dendrochronology for precisely deter-

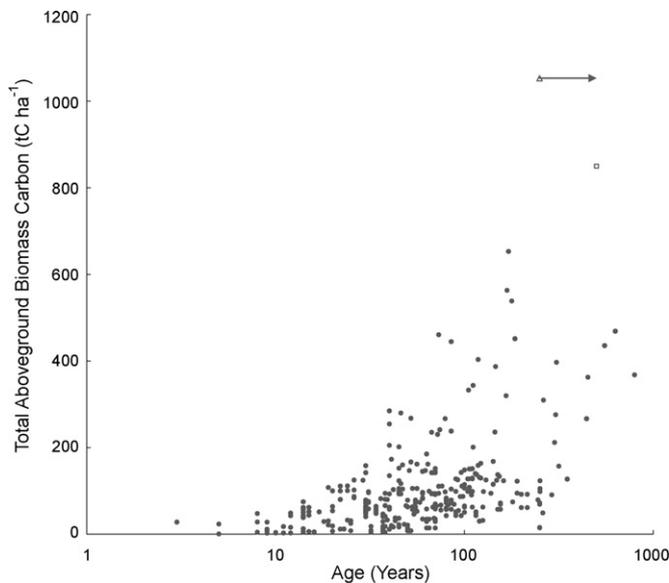


Fig. 9. Carbon storage as a function of stand age for temperate forest ecosystems, shown as the relationship between above ground biomass carbon (tonnes carbon per hectare: $tC\ ha^{-1}$) and the logarithm of stand age. Each data point represents a forest stand, many of which have different growing conditions and species composition. Closed circles represent temperate forests and are from the publically available database compiled by Luyssaert et al. (2007). The open square represents an *E. regnans* stand in the Styx Valley in Tasmania, with biomass carbon based on an old-growth *E. regnans* stand studied by Dean and Roxburgh (2006) and stand age based on dendrochronological data from this study. These two Styx Valley stands were only 6 km apart (Fig. 1b) and had a similar stand structure of low density, large diameter *E. regnans* trees over a rainforest understorey. The open triangle is for the average biomass carbon for 13 *E. regnans* stands in the Central Highlands of Victoria, south eastern Australia, with the oldest cohorts assumed to be >250 years old (Keith et al., 2009). Our data indicate that the oldest cohorts in the Victorian study may be – or may become – over 500 years old (see arrow).

mining recent fire events in wet sclerophyll *E. regnans* forests of Victoria (i.e. the 1939 ‘Black Friday’ fires). Our study comprises an important first step in identifying pre-European fire events in *E. regnans* forests to extend fire–climate analyses over century time-scales. However, significant advances on the current long-term dendro-climatological record – which is currently limited to long-term temperature reconstructions generated from *Lagarostrobos franklinii* tree rings (Cook et al., 2006) – are required to elucidate fire activity with century-scale climate variation. Developing this area of research within *E. regnans* forests is of fundamental importance for contextualizing catastrophic fire events such as the February 2009 ‘Black Saturday’ fire in Victoria that burnt over 450,000 ha – including vast areas of *E. regnans* forest – and for predicting the occurrence of stand-replacing fires under future climate scenarios (Lucas et al., 2007).

A review by Keith et al. (2009) revealed that the amount of carbon storage in *E. regnans* forests is unparalleled throughout the world, with 13 old-growth stands (estimated to be >250 years old) in the Central Highlands of Victoria containing an average of 1053 tonnes of carbon per hectare ($tC\ ha^{-1}$) in living above ground biomass (Keith et al., 2009). Indeed, a single cohort, old-growth *E. regnans*-rainforest stand in the Styx Valley some 6 km from our study site (Fig. 1b) was estimated to contain $850\ tC\ ha^{-1}$ in living above ground biomass (Dean et al., 2003; Dean and Roxburgh, 2006). Our data show that these forests not only store vast amounts of carbon, but also accumulate biomass quickly and maintain these high carbon densities for a long period of time (Fig. 9). This is particularly important given the recent recognition that many old-growth forests up to 800 years of age continue to function as carbon sinks (Luyssaert et al., 2008) and that wood production increases with tree size through old age in unsuppressed *E. regnans* trees

(Sillett et al., 2010). We suspect that *E. regnans* stands made up of old-growth eucalypts with a well developed rainforest understorey constitute a particularly carbon rich successional stage. However, there are few biomass data available for southern Tasmania to predict the carbon storage implications for these forests if the transition to rainforest occurs in the prolonged absence of disturbance or through conversion to regenerating forest by wildfire or harvesting.

Keith et al. (2009) argued that conserving forests with large stocks of biomass from deforestation and degradation, and restoration of a forests carbon sequestration potential should be among allowable mitigation activities under the United Nations Framework Convention on Climate Change. Estimates of both the magnitude and duration of maximum carbon storage discussed here provide useful upper bounds to which carbon storage of forests in various stages of successional in the landscape can be compared, and the carbon sequestration potential estimated (Smithwick et al., 2002; Roxburgh et al., 2006; Mackey et al., 2008). This is best accomplished using landscape-level approaches such as the modelling studies of Dean et al. (2003, 2004) and Dean and Roxburgh (2006), who explicitly incorporate topographic and climatic variability and a range of fire and harvesting scenarios to forecast carbon sequestration in *E. regnans* systems. Ideally, such modelling would be underpinned by precise data on past fire events identified using dendrochronological techniques such as those developed here, but also account for potential changes in fire regimes under future climate scenarios. The occurrence of extreme fire weather is predicted to increase in south eastern Australia (Lucas et al., 2007) and subsequent increases in fire frequencies are likely to have a profound influence on fluxes and storage of carbon in forest systems prone to stand-replacing fire (i.e. Kasischke et al., 1995; Kashian et al., 2006). Consequently, management of these forests to maximise their carbon storage potential must not only focus on the effects of harvesting on carbon storage (e.g. Mackey et al., 2008), but also consider the management of fire in the landscape (e.g. Hurteau et al., 2008; Bradstock and Williams, 2009).

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