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Recruitment bottlenecks in the rare Australian conifer *Wollemia nobilis*

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Abstract

Seedling survival plays a critical role in maintaining a supply of potential recruits. We examined seedling recruitment, survival and growth in *Wollemia nobilis*, a rare, long-lived Australian conifer. *Wollemia nobilis* seedlings and juveniles were monitored for 16 years (1996–2011). While *W. nobilis* can recruit from seed and, unlike most conifers, persist through resprouting, seed-based recruitment was the primary focus of this study. Sixty-five per cent of new seedlings died within their first year and only 7% persisted for the 16-year monitoring period. However, 44% of established juvenile plants (of unknown age at the beginning of the study) persisted throughout the 16-year monitoring period. Growth of seedlings and juveniles was very slow; growth estimates for most individuals had 95% confidence intervals that included zero. The recruitment strategy of *W. nobilis* may be to maintain a slow-growing juvenile bank–a strategy typical of other shade-tolerant rainforest trees, including other Araucariaceae. Seedling recruitment in *W. nobilis* may act together with resprouting to maintain the population.

Introduction

The seedling stage represents a significant bottleneck in the life cycle of trees because seedlings are the most sensitive to environmental conditions and perturbations. As a result seedlings typically experience much higher mortality rates than saplings and adult trees (Harper 1977). Understanding the factors that limit species-specific seedling survival and growth is central to understanding how populations of trees persist in forest communities. This is of particular concern in rare tree species, where stochastic mortality of adults and low survival of seedlings may place populations at risk of local extirpation, and in the case of the smallest populations, possibly extinction (Boyce 1992; Caughley 1994). For trees in closed-canopy forests, recruitment strategies are associated with a trade-off between seed dispersal and growth rate versus shade tolerance (Tilman 1994, Rees *et al.* 2001). At one extreme, shade-intolerant pioneers rely on long-distance seed dispersal and fast-growing juveniles to take advantage of gap creation. At the other extreme, some species maintain a juvenile bank of shade-tolerant and very slow-growing plants (i.e., Oskars *sensu* Silvertown 1982; Whitmore 1989). Across the full range of recruitment strategies, though, seedlings tend to benefit from the formation of gaps in the forest canopy, either through germination and rapid growth or through increased survival and moderately increased growth rates (Spies and Gray 1996; Delcamp *et al.* 2009; Rüger *et al.* 2009). An understanding of mechanisms of tree species regeneration is critical to managing forests for diversity, and is particularly important the management of rare species.

In this study we examine the recruitment of a rare, long-lived conifer, *Wollemia nobilis* W. G. Jones, K. D. Hill, J. M. Allen (Araucariaceae) within a warm temperate rainforest community. The wild *W. nobilis* population consists of 83 mature individuals (Benson and Allen 2007) and its current distribution is restricted to a single catchment in Wollemi National Park, New South Wales, Australia. *Wollemia nobilis* recruit from seed and can also persist via resprouting, a trait that is relatively rare in mature conifers (Del Tredici 2001; Bond and Midgley 2003). Small juveniles constitute the most numerous *W. nobilis* life stage (New South Wales Department of Conservation 2006). Since its discovery in 1994 considerable conservation effort has been made to maintain the wild population of *W. nobilis* due to its taxonomic significance: it is the most restricted of the

three genera in Araucariaceae and is the sole monotypic genus (New South Wales Department of Conservation 2006). Moreover, *W. nobilis* has an important context in conservation science because it is a new and charismatic species, discovered <200 km from Australia's most populous city, in an age where discovery of new tree species is rare. Key threats to *W. nobilis* are climate change, fire and infection with *Phytophthora cinnamomi* (New South Wales Department of Conservation 2006), as well *W. nobilis* has been shown to lack genetic diversity (Peakall *et al.* 2003).

Climatic change, increased fire and competition with angiosperms provide three inter-related explanations for the decline of *Wollemia* over the past 50 Ma. *Wollemia* appears first in the fossil record of the late Cretaceous, reaching its maximum in the Eocene (Hill and Brodribb 1999, Kershaw and Wagstaff 2001, McLoughlin and Vajda 2005); the last known fossils are from the Pliocene (late Tertiary; Macphail *et al.* 1994). The decline of *Wollemia* from the Eocene corresponds with global cooling, and the northward movement and drying of Australia in the Tertiary period (McLoughlin and Vadja 2005). Correspondingly, fire increased in Australia from the mid-Tertiary, and is likely to have continued to be important in Australian ecology into the Quaternary (Kershaw *et al.* 2002). Seedlings are the life stage most vulnerable to mortality via stochastic changes in the environment. Drying climate is a potential recruitment stressor because the small root systems of seedlings make them more susceptible to drought (McDowell *et al.* 2008). Tree seedlings are also vulnerable to fire because thick bark and lignotuber development (if it occurs) typically occurs at later developmental stages (Gill and Ashton 1968; Pinard and Huffman 1997; Lawes *et al.* 2011). Moreover, increasing aridity, and increasing frequency and intensity of fire, are hypothesised to have promoted the global spread of angiosperms in the Cretaceous (Bond and Scott 2010; and in Australia in the late Cretaceous, Nagalignum *et al.* 2002). Angiosperms, in productive environments, usually have higher maximum growth rates than gymnosperms (Bond 1989), and therefore produce more biomass (i.e., potential fuel, Bond and Scott 2010). On productive sites, gymnosperms can be outcompeted, and potentially excluded, because of their slower growth, time to maturity and associated juvenile risk, and lesser ability to take advantage of disturbance-mediated increases in resources compared with angiosperm pioneers (e.g., gap formation; Bond 1989). Gymnosperms are commonly restricted to poorer sites, where they can better compete with angiosperms. However, gymnosperms survive in angiosperm-dominated forests where, despite slow growth,

their longevity allows them to compete with angiosperms (Bond 1989), and they can even become canopy emergents (Araucariaceae; Enright and Hill 1995; Enright *et al.* 1999); this may be the case for *Wollemia nobilis*.

The restricted distribution of *W. nobilis*, in addition to the evidence of long-term decline, raises important concerns about the viability of the remnant *W. nobilis* population. The long-term maintenance of plant populations is dependent upon the recruitment of new individuals to replace those that die (Harper 1977). In this study we ask if *W. nobilis* is recruitment limited, and if so, why? To do this we addressed three specific questions:

1. Is *W. nobilis* recruiting in the wild?
2. What factors (i.e, plant size, age) influence growth and mortality of *W. nobilis* recruits?
3. What are the implications for the persistence and conservation of *W. nobilis* in the wild?

Methods

Study site and species

Wollemia nobilis is a multi-stemmed conifer that grows to ~40 m tall. It can recruit from seed and multi-stemmed adults indicate the potential for vegetative recruitment. Tree-rings suggest stem ages of up to 450 years (Banks 2002), although individual plants may be much older. It is restricted to one population scattered across four sites within within a single catchment in a remote sandstone gorge system in Wollemi National Park, north-west of Sydney, Australia (Jones *et al.* 1995; Benson and Allen 2007). Elevation within the park ranges from 300 to 1100 m (New South Wales Parks and Wildlife Service 2001). Maximum temperatures up to 30°C occur from November to February, while from June to August maximum temperatures are ≤15°C, with minimum temperatures near freezing (New South Wales Department of Conservation 2006). Mean annual rainfall is 952 mm (Bureau of Meteorology 2013). The wettest months are November to February (41% of annual rainfall). *Wollemia nobilis* occurs in association with warm temperate rainforest species; upper edges of the *W. nobilis* population grade into sclerophyllous *Eucalyptus* forest on steep slopes (Benson and Allen 2007).

Study design

We used a combination of static and repeated surveys to characterise the structure and dynamics of the *W. nobilis* regeneration. These included: a one-time survey of *W. nobilis* regeneration across all four sites, long-term repeated measurements of individuals at one site, and annual surveys of regeneration at one site. In each survey, we defined seedlings as plants with cotyledons and juveniles as small plants (<3 m) without cotyledons. Cotyledons may remain on a plant for 1 to 2 years before falling (Auld TD, personal observation). We measured the length of each stem and counted the number of leafy branches of every seedling or juvenile we found. Stem length was measured rather than plant height because many plants did not grow vertically. The following sections provide detailed descriptions of each of the surveys.

Distribution of seedling and juvenile cohorts among the four sites

We conducted a systematic survey of *W. nobilis* regeneration at each of the four sites during a six-month period in 2002–2003 to characterise the scale and variability in regeneration among the four sites. We sampled all accessible habitat (safety considerations precluded accessing some habitat on areas at several sites). Total area of habitat surveyed for *W. nobilis* regeneration was measured within each site. We then estimated the total area of available habitat (area of occupancy *sensu* IUCN 2001) at each site using air photos, 1:25,000 map sheets and ground truthing. The proportion of the total habitat surveyed for regeneration was calculated as the ratio of surveyed habitat to total habitat.

Seedling emergence

From 2001–2005 we conducted intense searches of accessible habitat at one site, ‘Site 1’, to estimate the rate of recruitment of new seedlings into the population. During each census any new seedlings were tagged and their stem length measured.

Long-term monitoring of seedlings and juveniles

Seedlings and juveniles were tagged at the site with the most *W. nobilis*, Site 1, between July 1995 and March 1996 and further seedlings were tagged during surveys from 2000 to 2011 (i.e., 1995, 2001, 2002, 2003, 2004, 2005, 2008, 2011). Repeated visits to this site enabled us to follow individual plant survival and growth for up to 16 years (1995–2011) for 241 seedlings and juveniles. Stem length of each plant was measured and number of leafy branches counted.

Data analyses

To assess among-site differences in seedlings and juveniles, we compared stem length and the number of branches among sites using one-factor ANOVA. We did this for seedlings and all juveniles, as well as separately for juveniles with >30 cm and <30 cm stem length. We used a Fligner test to assess homogeneity of variances. If Fligner tests were significant (P <0.01), we log-transformed the data to achieve homogeneous variances (Underwood 1997).

Survival for seedlings and juveniles at Site 1 was estimated separately for seedlings and juveniles using failure-time analysis (Fox 2001) using the survival package for R (Therneu 2011; R Development Core Team 2012). Because of multi-year intervals between some surveys, data were treated as interval censored. Live and dead stem length was compared using a Welch two-sample t-test in R.

We analysed growth of seedlings and juveniles at Site 1 using linear mixed–effects models in the lme4 package for R (Bates *et al.* 2012). Linear mixed-effects models were used because of their capacity to accommodate variation in growth patterns among individuals. Only plants that were recorded in four or more surveys (i.e., three or more census intervals) were included in the analysis. In addition, we removed any plants for which growth increments were >500 or < –20 mm as these were likely to be the result of measurement or recording errors or damage to plants. We modelled variation in seedling and juvenile stem length (i.e., growth) with time, evaluating population-average and individual based-estimates of intercept and slope. Resulting parameter estimates were compared with initial height using linear regression.

Results

Distribution of seedling and juvenile cohorts among the four sites

Seedlings and juveniles were found at all four of the sites at which adult *W. nobilis* occur. Seedling and juvenile abundance were greatest where the largest fraction of available habitat was occupied by *W. nobilis* and *W. nobilis* adult plant numbers were highest (Table 1). Seedling and juvenile abundance were two to six times greater than adult abundance across the four sites (Table 1). Small juveniles (i.e., <30 cm in length) were the most abundant life–history stage (Fig. 1). Site 3, which has the fewest adult *W. nobilis*, had only one juvenile >30 cm tall (45 cm), while at the three other sites the largest juveniles were 1.5, 2.5, and 2.7 m tall.

Differences in seedling and juvenile stem length among sites were not significant (ANOVA; $F_{3,21} = 0.87$, $P = 0.47$ and $F_{3,256} = 1.28$, $P = 0.68$, respectively; Table 2). Juvenile data were also analysed separately for plants >30 cm and <30 cm. Large juveniles (>30 cm) did not differ significantly among sites in stem length ($F_{3,47} = 0.78$, $P = 0.51$) or number of leafy branches ($F_{3,45} = 0.70$, $P = 0.56$). Small juvenile branching also did not (<30 cm) differ significantly among sites ($F_{3,202} = 2.56$, $P = 0.06$). There was, however, a significant difference in the stem length of small juveniles among sites ($F_{3,202} = 2.81$, $P = 0.04$). This was primarily due to plants from Site 1 being taller than those from Site 4 (Tukeys HSD; $P = 0.04$).

Seedling emergence

Emergence of new seedlings at Site 1 varied across the five intensely sampled years (2001–2005). The number of seedlings that emerged represents a minimum value because we could not access all areas of Site 1 due to the steep terrain. No seedlings emerged in 2003, while the most seedlings (61) emerged in 2005. Total number of seedlings emerged in other years were 10 in 2001, 9 in 2002 and 29 in 2004.

Long-term monitoring of seedlings and juveniles

Survivorship of seedlings and juveniles at Site 1 varied with plant age (Fig. 2). For seedlings, survival was lowest in young seedlings, only 27% survived for more than one year. For juveniles (where age was unknown, as the plant was first surveyed after it had lost its cotyledons) survival was much higher, with 72% of plants surviving >1 year and 44% of plants surviving the entire 16-year monitoring period. In all survey periods, mortality was largely confined to plants <30 cm high. Mean stem length at death was 6.6 cm, while mean stem length of live plants was 41 cm (t = 6.65, df = 87.71, P < 0.0001).

Inter-annual variation in growth of seedlings and juveniles

Seedling and juvenile growth rates (at Site 1) were slow. The mean stem growth rates of seedlings and juveniles included in the model were 10.4 mm/yr and 18.5 mm/yr.

Seedling and juvenile data were pooled for the model of stem growth, as seedlings that survived for four censuses became juveniles. The model with individual-based slopes and intercepts provided the best fit to the data (AIC = 5222), compared with individual-based intercepts (AIC = 5399), and individual-based intercepts and population-average slope (AIC = 5289). Figures detailing individual data and model fits are included in Supplementary Material 1.

The fixed effect parameter estimate for slope, an indication of stem growth rate, was 5.2 mm/yr (95% CI = 3.5 – 6.9 mm/yr). However, when random effects were incorporated, the slope parameter estimates for most individuals had confidence intervals that included zero (i.e., no growth, Fig. 3). The taller individuals typically produced the highest estimates for slope. Random effect parameter estimates for the intercept were significantly positively correlated with initial stem length (R^2 = 0.97, P < 0.0001). This is due to the strong influence of initial stem length in defining intercepts for this model of stem length and time. Parameter estimates for slope were also positively associated to initial stem length (R^2 = 0.24, P < 0.0001), growth increasing with increasing stem length.

Discussion

Recruitment dynamics are critical to long-term population viability. We describe seedling emergence, and seedling and juvenile survival and growth, for the critically endangered Australian conifer *Wollemia nobilis* (IUCN 2011). Our study focussed on limitations to seedling and juvenile establishment, with the key finding that although seedling survival is low, survival of established juveniles is high.

The first question we asked was whether there was any evidence for the emergence of new seedlings. We found that emergence of new seedlings occurred during every surveyed year (with one exception), but was highly variable with a low of zero new seedlings in 2003 and a high of 61 new seedlings in 2005. Annual seedling emergence provides a regular supply of potential recruits, and counters the high rates of seedling mortality that we observed. The high level of seedling emergence in 2005 may be due to climatic conditions, reduced seed predation, herbivory and/or fungal attack, or absence of other drivers of mortality (e.g. fire). One possible explanation is a species–specific tendency for supra-annual mass fruiting events, which have been recorded for other Araucariaceae, such as *Araucaria laubensfeldii* in New Caledonia (Rigg *et al.* 2010) and *Araucaria araucana* in Argentina and Chile (Sanguinetti and Kitzberger 2008). There is some evidence for masting in *W. nobilis* (inter-annual variation in cone production, Zimmer *et al.* unpublished data). Masting is selected for in wind-pollinated species, such as *W. nobilis*, though increased pollination efficiency and therefore pollination success (Kelly and Sork 2002). Indeed, *W. nobilis* seed viability has been recorded at ~10 %, with pollen limitation noted as a potential cause (Offord *et al.* 1999). Variable pollination success and seed viability would account for the variation in seedling emergence we have observed.

Once *W. nobilis* seedlings emerged, did they survive? Most *W. nobilis* seedling mortality occurred during the first year post–germination. As expected, the mortality rate was lower for established seedlings and small juveniles, and yet again lower for large juveniles (i.e., recruitment bottleneck). Correspondingly, mortality was correlated with plant size, with smaller plants more likely to die. The recruitment bank of *W. nobilis* included accumulated cohorts of juvenile plants that were highly shade tolerant, with

303 little annual mortality and very slow growth rates. There are several examples of forest
304 tree species exhibiting high levels of juvenile mortality that, once established, persist
305 and become canopy species, including *Chrysophyllum* in northern Australia (Connell
306 and Green 2000), dipterocarps in Malaysia (Turner 1990; Itoh *et al.* 1995; De Lissio *et*
307 *al.* 2002), several species in the rainforests of Barro Colorado Island (De Steven 1994).
308 *Wollemia nobilis*' recruitment patterns, characterised by high rates of mortality at the
309 seedling stage followed by low rates of mortality once established, are not unique nor
310 limited to rare species.
311
312 Although established juvenile survival rates were high, growth rates were low. Growth
313 rates for both seedlings and juveniles were slow; mean annual growth rates were 10 and
314 19 mm for seedlings and juveniles, respectively. Growth was positively, although
315 weakly, correlated with stem length. Slow growth and high survival in the understory is
316 typical of Araucariaceae. For example, *Araucaria laubensfeldii* in New Caledonia is
317 long-lived, grows very slowly, can tolerate low light levels (i.e., 8% of full sunlight),
318 and has residency times of up to 90 years in the seedling stage (Rigg *et al.* 2010).
319 *Agathis ovata,* also in New Caledonia, can grow very slowly in the forest understory,
320 remaining as juveniles <30 cm tall for up to 55 years (Enright *et al.* 2003). Similarly,
321 the shaded seedlings of *Agathis australis* in New Zealand have been reported to
322 "stagnate" or grow very slowly for 50 years or more (Steward and Beveridge 2010).
323 Juvenile persistence in the understory is not without risk. Smaller plants are more prone
324 to mortality via stochastic events such as drought, fire and herbivory (Bond 1989);
325 persisting in smaller size classes results in longer exposure to these risks. Juvenile risk is
326 particularly important in species such as *W. nobilis,* where successful recruitment from
327 seedling to juvenile is infrequent. Indeed, juvenile susceptibility to drought, fire and
328 herbivory, may have contributed to the long-term decline of the species. Nevertheless,
329 longevity, ≥450 years in *W. nobilis* (Banks 2002), may mitigate against such juvenile
330 mortality resulting in extinction. Long-lived species, via the presence of a persistent
331 adult stage, are more robust to loss of individuals in regenerative phases (seedlings and
332 juveniles; Alvarez-Bullya *et al.* 1996).
333
334 Infrequent recruitment of *W. nobilis* seedlings to canopy trees may indicate that their
335 regeneration strategy depends on the maintenance of a slow-growing juvenile bank (i.e.,
336 Oskars *sensu* Silvertown 1987). Growth of *W. nobilis* juveniles in cultivation under high

light can be 600 mm per year (Offord *et al.* 1999). This high potential growth rate, compared with slow height growth recorded in the low light conditions of the wild, suggests that *W. nobilis* seedlings and juveniles are resource-limited in the wild. Gap formation (e.g., by tree mortality, branch fall) can provide resource release, particularly light, in closed forests. It can also alter rooting environment, litter depth and/or surface soil (Brokaw 1985, Whitmore 1989). Windstorms, recorded in the tree-ring record of *W. nobilis* (Banks 2002), are a likely source of disturbance precipitating tree and branch fall, and may therefore be important in producing an increase in resource availability in *W. nobilis'* environment. However, there is currently no data describing the transition of *W. nobilis* from juvenile to canopy tree.

Infrequent recruitment of *W. nobilis* seedlings to the canopy may also derive from the ability of *W. nobilis* to resprout. *Wollemia nobilis* coppices consistently (Burrows and Bullock 1999; Burrows *et al.* 2003) and this investment in sprouting may result in lower seed output and reduced seedling growth rates (i.e., trade-offs in persistence versus recruitment; Bond and Midgley 2003). An individual *W. nobilis* may have as many as 100 stems (Burrows and Bullock 1999) which, because of their position in higher strata and access to the extensive root system of the parent tree, may be able to respond more quickly to gap formation. Seedlings may be in competition for light with sprouts from their parents (Dietze and Clark 2008). Despite these potential negative interactions among recruitment strategies, it may be that the capacity of *W. nobilis* to recruit by seed and persist by sprout has allowed it to survive through environmental and climatic change in Australia for millions of years. Reproduction via seed has advantages including maintenance of gene flow and the potential for dispersal and colonisation (Eckert 2002). Alternately, resprouting allows individuals to persist after disturbance, rapidly re-occupy growing space, and potentially resume seed production (Bellingham and Sparrow 2000; Bond and Midgley 2003). The capacity to resprout may have been particularly important to its persistence in Australia during the dry and fire-prone climate of the Quaternary.

While our focus has been on the recruitment dynamics of *W. nobilis*, it is important to recognise that these dynamics occur within a warm temperate rainforest community that is typically dominated by *Doryphora sassafras*, *Syzigium smithii* and *Ceratopetalum apetalum*. Maintenance of a juvenile bank within an angiosperm-dominated rainforest is

consistent with Bond's (1989) model of gymnosperm-angiosperm competition, where gymnosperm seedlings grow slowly, but eventually compete with their angiosperm neighbours, in the absence of disturbance. Given the potential height (40 m, Jones *et al.* 1995) and stem age (≥450 years, Banks 2002) of *W. nobilis*, compared with potential heights and ages of competitors, *W. nobilis* certainly has the potential to be competitive with the angiosperm canopy species in the long-term (*D. sassafras*, <20 m, Benson and McDougall 1997; *S. smithii*, <20 m and 100-200 years, Benson and McDougall 1998; *C. apetalum* <30 m and <200 years, Benson and McDougall 1995). Moreover, *W. nobilis* capacity to resprout may enhance competitiveness in the post-disturbance environment, although its competitors share this ability to resprout (Johnstone and Lacey 1983). While these results provide a detailed picture of the early dynamics of the *W. nobilis* life cycle, they highlight the role of the transition from juveniles to adults in population persistence, and our poor understanding of how this transition occurs.

Conclusion

Wollemia nobilis has a highly restricted distribution, limited to four sites, but all four sites had a juvenile bank. While seedling survival rates were low, forty-four per cent of juveniles (that had established before the first survey) survived the 16-year monitoring period. This indicates the potential for long-term survival in the shade in which, environments where disturbance is infrequent, is potentially more important than growth (Montgomery and Chazdon 2002). Moreover, maintenance of a juvenile bank is also a recruitment strategy characteristic of other shade-tolerant rainforest trees. For *W. nobilis*, the key question is whether the existing juvenile plants will ever reach maturity. Although we have not recorded growth release in this study, the ability of *W. nobilis* to respond to increased light and nutrients is known (Offord *et al.* 1999) indicating that the formation of a large canopy gap would provide an opportunity for recruitment from juvenile to adult. In the absence of disturbance, however, it is likely that *W. nobilis* will persist via resprouting and its juvenile bank will survive in the shade. Future demographic research should focus on the transition from juvenile to adult. Dendrochronology may be able to be used to determine whether successful canopy trees have experienced periods of suppression and release, or if they grew rapidly from the outset, indicating recruitment from the understory (i.e., the juvenile bank) or in a high light environment (i.e., post-disturbance).

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565 **Table 1**. Estimated abundance and densities of *Wollemia nobilis* seedlings and juveniles
566 in the wild, in relation to area of habitat and adult plant abundance.
567

Site	Approx. Habitat sampled (%)	Seedling number	Seeding density (/ha)	Juvenile number	Juvenile density (/ha)	Adult[1] number	Adult[1] density	Area of Occupancy[2]
1	80%	10	5.9	127	74.7	33	19.4	1.7
2	40%	1	1.1	36	40	19	21.1	0.9
3	50%	3	30	16	160	6	60	0.1
4	70%	4	5	112	140	18	22.5	0.8
Total		18		291		76		

568
569 [1] Data from Benson and Auld (unpubl).
570 [2] Area of occupancy (AOO) in hectares, *sensu* IUCN (2001).
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575 **Table 2.** Mean seeding and juvenile stem length and number of branches according to
576 site (±1 s.e.) and results from ANOVAs. Asterisk indicates significant differences ($P < 0.05$).
577 Within each variable, means sharing the same letter are not significantly different.

	Site 1	Site 2	Site 3	Site 4
Seedling stem length	51.7 (±7.3)	30 (±0)	80 (±20)	62.5 (±10.3)
Juvenile stem length	237.0 (±34.9)	300.6 (±70.5)	134.7 (±22.0)	305.0 (±41.6)
Tall juv. stem length	726.9 (±154.6)	950 (±162.8)	450 (±0)	954.2 (±108.7)
Small juv. stem length*	134.4 (7.4) **ab**	108.1 (8.9) **a**	115 (10.3) **ab**	108.9 (±6.7) **b**
Tall juv. branches	20.3 (±17)	26.4 (±6.4)	17 (±0)	31.1 (±6.5)
Small juv. branches*	4.5 (0.2) **ab**	3.4 (0.2) **a**	4.4 (0.4) ab	4.7 (0.3) **b**

578 Juvenile stem length was log-transformed for analysis

Figure 1. Frequency of juveniles by height classes at four *Wollemia nobilis* sites in 2002 and 2003. Note y-axis varies.

Figure 2. (a) Seedling and (b) juvenile *Wollemia nobilis* survival curves with 95% CIs. Crosses indicate where data is censored (i.e., plants in this cohort were still alive at end of monitoring period).

Figure 3. Individual-based parameter estimates for slope (with 95% CIs) from the linear mixed effects model of variation of *Wollemia nobilis* seedling and juvenile height with time. Slope is an indication of growth rate.

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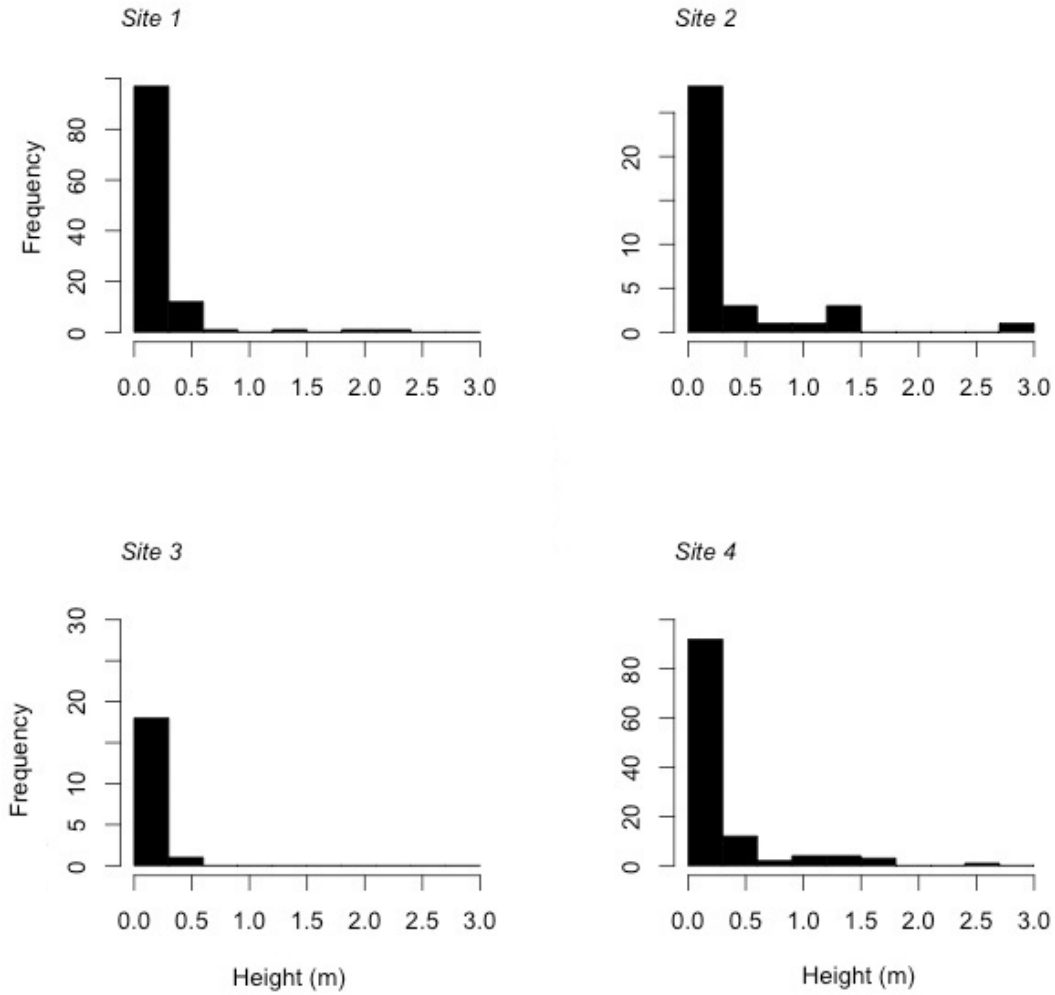
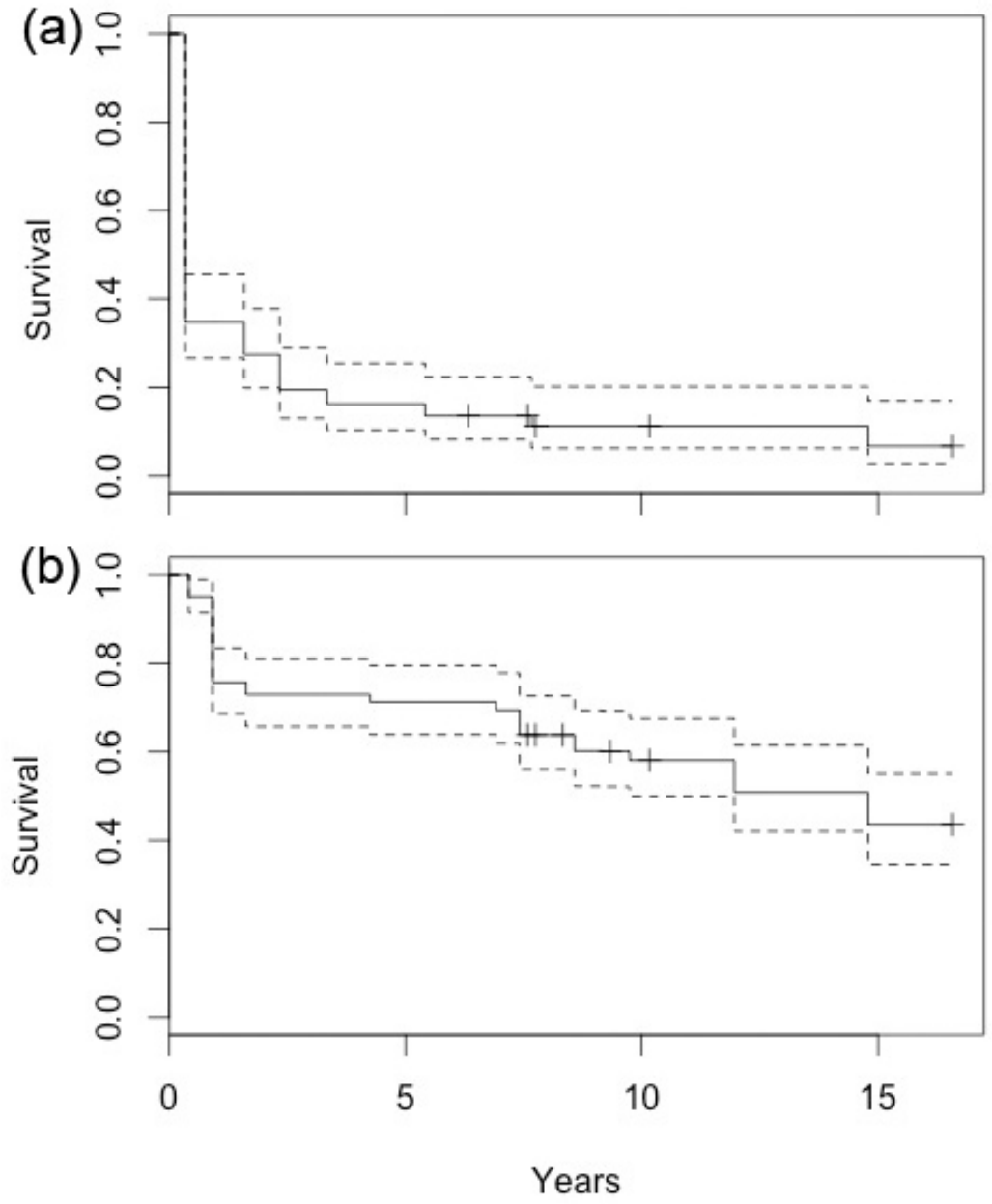
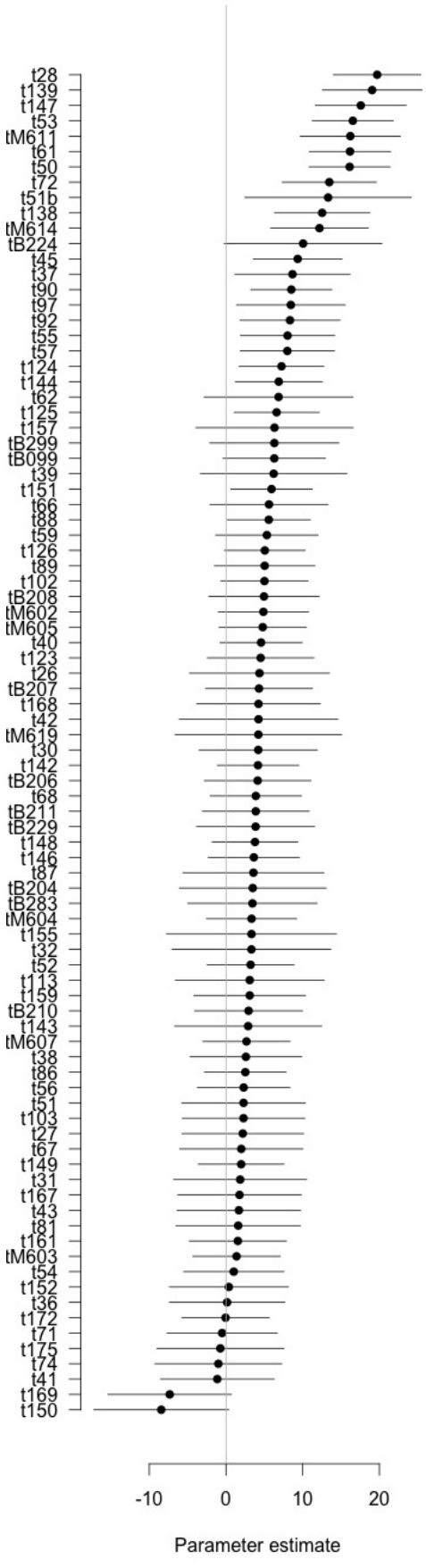

Site 1
Frequency
0
20
40
60
80
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Site 2
0
5
10
20
Site 3
0
5
10
20
30
Height (m)
Site 4
0
20
40
60
80
Height (m)

595

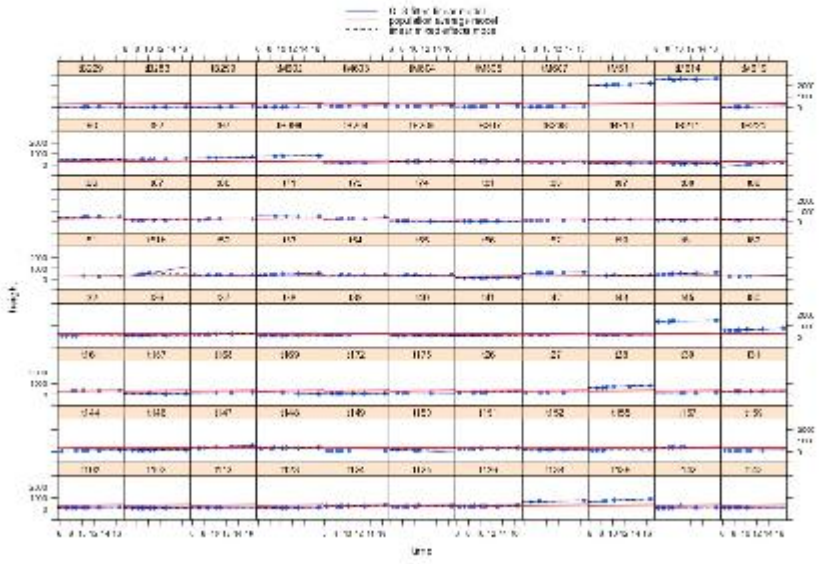

(a)
Survival
0.0
0.2
0.4
0.6
0.8
1.0
(b)
Survival
0.0
0.2
0.4
0.6
0.8
1.0
0
5
10
15
Years

596


t28
t139
t147
t53
tM611
t61
t50
t72
t51b
t138
tM614
tB224
t45
t37
t90
t97
t92
t55
t57
t124
t144
t62
t125
t157
tB299
tB099
t39
t151
t66
t88
t59
t126
t89
t102
tB208
tM602
tM605
t40
t123
t26
tB207
t168
t42
tM619
t30
t142
tB206
t68
tB211
tB229
t148
t146
t87
tB204
tB283
tM604
t155
t32
t52
t113
t159
tB210
t143
tM607
t38
t86
t56
t51
t103
t27
t67
t149
t31
t167
t43
t81
t161
tM603
t54
t152
t36
t172
t71
t175
t74
t41
t169
t150
-10
0
10
20
Parameter estimate

597

Supplementary Material 1



Supplementary material. Figure 1. Variation in stem length with time model fits for individual seedlings and juveniles. Three models are overlain on the data: a simple linear model fitted for each individual (blue), population-average model (red, with population-average intercept and slope) and the individual-based mixed effects model (black, with random intercept and slope).

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