



Sexual Reproduction and Early Plant Growth of the Wollemi Pine (*Wollemia nobilis*), a Rare and Threatened Australian Conifer

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The two known populations of the recently discovered rare and threatened Wollemi Pine (*Wollemia nobilis* Jones, Hill and Allen) consist of a small number of large multi-stemmed adult trees and small seedlings. Female and male cones are produced on adult trees with pollen release occurring in spring (October–November). Seed cones mature 16–19 months later in late summer and autumn and appear to be produced annually. Approximately 10% of seed produced in two consecutive years was viable, 25% of which was damaged by animals. Glasshouse studies showed that seed germination at 25 °C (day)/16 °C (night) proceeded slowly but steadily at approx. 4% per week until, after 6 months, 88% of apparently viable seed had germinated with the remainder of the seed rotting. Growth of potted seedlings in this temperature regime was continuous (after a lag period of 4–6 months) with the monopodial axis growing 0.05–0.25 m in the first year, 0.5–0.6 m in the second year and 0.25–0.35 m in the third year, attaining a total height of 0.8–1.2 m. Multiple orthotropic shoots developed on some plants at this stage, some of which outgrew the primary shoot in height. The diameter of the stem below the cotyledon (just above the soil) grew 3–7 mm in the first year, 10–14 mm in the second and 15–20 mm in the third at which time it was 25–34 mm. The average number of lateral branches produced was five–17 in the first year, 25–36 in the second year and 24–30 in the third year giving a total of 60–77. The establishment of Wollemi Pine in the wild does not appear limited by the inherent viability of seed and potential for early growth of seedlings.

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INTRODUCTION

The recently discovered rare and threatened Wollemi Pine (*Wollemia nobilis* W. G. Jones, K. D. Hill, J. M. Allen), possibly once a widespread genus according to fossil records (McPhail *et al.*, 1995; Chambers, Drinnan and McLoughlin, 1998), is restricted to two populations (Site 1: approx. 23 adult trees; Site 2: approx. 15 adult trees, sites approx. 2 km apart) in the Wollemi National Park in the Blue Mountains approx. 150 km north-west of Sydney, Australia. *Wollemia nobilis* was recently described as a new genus and species in the Araucariaceae and whilst sharing some features of the extant genera *Agathis* and *Araucaria*, it is distinguished by a number of characters including spongy, nodular bark that sheds in thin papery scales and the terminal placement of male and female strobili on first-order branches (Jones, Hill and Allen, 1995). Its current location, deep within a canyon, appears to have protected the species from major bushfire and weather extremes that can be experienced in the Blue Mountains. It survives, however, on thin layers of depauperate soil, the trees often perched on unstable rocky terraces, shaded and possibly out-competed by faster growing angiosperms such as *Doryphora sassafras* and *Ceratopetalum apetalum*. Although seed-bearing cones, similar in size and shape to those of some *Agathis* species, are produced on the upper branches of *Wollemia nobilis*,

survival of the species may depend on the plant's multi-stemmed and somewhat spreading habit, with emergent stems taking advantage of breaks in the canopy. Small seedlings are found in the immediate vicinity of the trunks, but there are few saplings, suggesting that there are very stringent establishment conditions. These seedlings grow very slowly and mortality appears high. The study of seed biology and early plant growth may shed light on the regeneration system and survival of this species.

MATERIALS AND METHODS

Cone and seed characteristics

The individual trunks of *W. nobilis* grow up to 35 m high with seed cones terminal on some of the upper branches (Fig. 1). These cones disintegrate once mature and most seeds fall to the ground after being dislodged by wind, branch movement or foraging birds. The female cones are almost inaccessible to humans because of their height above the ground, their terminal position on lateral branches, the lack of climbing purchase on the trunk and the general conditions in the canyon which make the situation dangerous.

In order to study structure and seed viability, cones were collected by helicopter in late February 1995 and mid-March 1998. The cones were removed from the tree at full maturity and about 50% shattered during picking and

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FIG. 1. Female cones of *Wollemia nobilis* terminate some of the branches near the apex of the trunk (photo C. Offord). This photo was taken in February 1996 and shows the mature cones in the middle and the next season's cones towards the top.

transport (Fig. 2). Intact cones were partitioned into putative viable seed, non-viable seed, scale and axis, and the relative position of parts within the cones noted. Putative viable seeds were initially determined by eye, based on their fullness and subsequently confirmed by dissection and germination (see below).

In 1996 and 1997 seeds were collected from Site 1 using 4.5×4.5 m nylon nets suspended horizontally underneath the trees (Fig. 3) in areas where greatest seed fall was observed in 1995. Nets were used instead of helicopter collection to monitor seed fall over the whole site. Because of the multi-stemmed habit of the trees (Fig. 4) and their relative closeness, the stem groups (putative trees) were assigned a number (1–23). The seed nets were emptied every 2 to 4 weeks and the number of seeds (viable and non-viable) and cone scales recorded.

Seed germination

Germination conditions. Putative viable seeds and non-viable seeds were sown separately 14 d after the 1995 cone harvest and subjected to the following glasshouse treatments for 30 d: seeds were sown in seed-raising mix and in cutting propagation mix; seeds were either exposed or covered; moisture was maintained by mist and by hand watering. An equal number of seeds were allocated to each treatment combination. The seed raising mix was sharp propagation sand and perlite (1:1 v/v), and the cutting propagation mix was coir, sand and perlite (2:1:4 v/v/v). Both mixes were steam sterilized at 60 °C for 30 min and poured into 100 mm (h) \times 50 mm (dia.) plastic tubes when cool. Seeds were laid flat on the mix and either covered with 3–5 mm of sand or left exposed. The tubes were placed onto capillary matting on adjacent benches, one of which was watered twice daily by hand, and the other frequently misted by a JEC mist controller. The root zone temperature was 23 ± 1.5 °C during the day and 16 ± 2 °C during the night. The aerial temperature was 25 ± 1.5 °C (day) and 16 ± 2.5 °C (night). Exposed seeds received 70% natural photosynthetically active radiation (PAR). Seeds were observed daily and considered germinated when the first 2 mm of the radical was visible.

Germination over time. To examine the germination pattern of *W. nobilis* seeds over time, 58 seeds were sown exposed on seed raising mix and misted as described above. The seeds were monitored until they either germinated or were observed to be non-viable due to microbial breakdown (6 months total).

Seedling development

The growth characteristics of seedlings of *W. nobilis* (resulting from the experiment to study germination conditions; see above) were measured on a weekly, monthly or tri-monthly basis, depending on the rate of growth, over a period of approx. 36 months. The seedlings were maintained in a temperature-controlled glasshouse [25 ± 1.5 °C (day)/ 16 ± 2.5 °C (night)] and received 50



FIG. 2. Partially shattered and intact cones of *Wollemia nobilis* (Tree 1). Arrow indicates cone axis. Cone approx. 7 cm long. The branches show rhythmic growth (photo C. Offord).



FIG. 3. Nylon nets (4.5 × 4.5 m) suspended horizontally beneath *Wollemia nobilis* to capture falling seed cone material (photo J. Plaza).



FIG. 4. Multi-stemmed habit of *Wollemia nobilis* (photo J. Plaza).

or 70% natural PAR (summer/winter). The following measurements were determined: height from soil to apex, diameter of hypocotyl below cotyledon, and number of lateral branches.

RESULTS AND DISCUSSION

Cone and seed characteristics

The phenological development of the Wollemi Pine appears similar to that of species of *Agathis* (Whitmore, 1977) and some provenances of *Araucaria cunninghamii* (Haines and Nickles, 1987). Pollination of Wollemi Pine occurs in October to November, 6 months to a year after female cones first appear, and seeds mature and fall in January–March,

16–19 months after pollination. The time of fertilization has yet to be determined. The female cones disintegrated in the same manner as those of *Agathis australis* (Licitis-Lindbergs, 1956) with the exception that the basal bract-scale complexes were partially persistent in some *W. nobilis* cones. Most seed cones shattered by the end of autumn (May) although seed persisted in the canopy for some months.

At maturity the axis appeared to dry out and contracted away from the scales and seeds. The scales turned brown on the inside and often the outer margin was tinged green. Basic seed and scale characteristics were described by Jones *et al.* (1995) and we observed that seeds were free from the scale at maturity but sometimes adhered because of a hardened resinous exudate. The characteristics of whole and partitioned cones are shown in Fig. 2 and Table 1. In most

cases the scales had one seed adjacent to or loosely adhering to the adaxial side, even at the poles of the cone where the scales and seeds became much reduced in size. The axes of the cones were approx. 27 mm in length, 9 mm at maximum width, and slightly incurved adaxially. Viable seeds had a plump appearance and a pale megagametophyte while the non-viable seeds often possessed an embryo, but it was shrivelled and brown. A large proportion of seeds were non-viable (Table 1). Mature viable seeds were on average 10.8 mm long (s.e. = 0.3 mm, $n = 10$), 8.6 mm at the widest point (s.e. = 0.13 mm), and 1.6 mm thick (s.e. = 0.05 mm). Viable seeds in the cone were mostly confined to an ovoid area on the outer and most exposed portion of the cone. This area may correspond with the area of greatest contact with wind dispersed pollen, and suggests that low seed viability may be the result of pollen limitation due, for example, to lack of thermal updraughts at crucial times in this remnant habitat in a deep narrow gorge. It may also be due to seasonal variations in pollen production. Further study may indicate other physical and biochemical restrictions. Embryo abortion due to genetic factors such as self-incompatibility and inbreeding depression or environmental conditions are other possibilities.

Viable seeds were observed in each of the 4 years of sampling (1995–1998). The proportion of viable to non-viable seed appeared to vary from year to year but was on average less than 11%. In the most thoroughly sampled period, 1996–1997, the trees across the population produced a similar proportion of viable to non-viable seed. Some trees produced more cones than others. Based on our observations of approx. 150 cones produced at Site 1 and 10% viability (25 seeds per cone), we estimate that there were 3–4000 viable seeds produced in 1996. The viability of seeds within cones was markedly different between 1995 and 1998 and this difference may reflect the time at which it was harvested (later in the season in 1998) when many of the fertile cones had already disintegrated. It may also point to variation between years such as that observed in *Agathis australis* which has a greater proportion of viable seeds every third year (Morrison and Lloyd, 1972). Some taxa in the Araucariaceae such as *Agathis* spp. show wide variations in the amount of viable seed produced within cones on different trees (Whitmore, 1977). This has not been observed in *W. nobilis* and although cones from individual trees have not been extensively sampled, the net collection data suggests

that seed production was uniformly low across Site 1 (Table 1).

Although similar in size to *W. nobilis*, *Agathis* seeds e.g. *A. australis* often have a substantial wing and this helps to bear the seed some distance away, especially in areas of high wind velocity (Mirams, 1957). Wind may play a part in the distribution of poorly winged but relatively light *W. nobilis* seeds and they may also be carried away by running water in the creek into which some seeds fall. Despite some potential for dispersal, establishment of seedlings more than 50 m away from the main group of trees has not been observed. At present the reason for this is not clear but may be due to poor conditions for germination coupled with heavy rates of predation.

The destruction of viable *W. nobilis* seeds appears to be rapid once they are released from the cones. A large percentage of presumably viable seeds falling into nets had been split open, chewed or bored into and the megagametophyte and embryo were damaged or missing completely (Table 1). Animals, particularly mice (Badan, 1986), rats and birds, and also fungi are major factors in the destruction of *Agathis australis* seeds (Ecroyd, 1982). Crimson Rosella (*Platycercus elegans*) were observed perching on the branches of Wollemi Pines, foraging the cones, and a species of rat is common on the forest floor (a skull of the introduced *Rattus rattus* has been found in the gorge). Insect damage was particularly prevalent in the cone axes collected late in the season in 1998 and may, in part, account for the apparent low viability as seeds may have been damaged before they had matured.

Seed germination

Germination conditions. Viable seeds were easily sorted by eye from non-viable seeds, the status of which was confirmed during the course of the experiment as no seeds deemed 'non-viable' germinated. Glasshouse seed germination of viable seeds was most affected by the type of watering received, irrespective of whether or not seeds were exposed (Table 2). Although treatment combinations were not analysed due to low replicate numbers, it appears that seed raising mix, mist and exposed seeds gave the best conditions for glasshouse germination. The higher germination in mist implies that the seed required a high level of moisture; this is consistent with the conditions found on the canyon

TABLE 1. Seed viability of *Wollemia nobilis* cones

	Time of collection	Viable seed (%)	Average number of viable seeds per cone	Viable seeds damaged by animals or insects (%)	Number of scales per cone
Intact cones	Feb 1995 ($n = 3$)	6.6 ± 1	18 ± 3.5	—	270 ± 10.5
	April 1998 ($n = 10$)	0.7 ± 0.2	2 ± 0.5	—	244 ± 7.6
Cone material collected in nets	Mar–Jul 1996 ($n = 9$)	9.2 ± 1.2	—	22.1 ± 5.4	—
	Feb–Jun 1997 ($n = 9$)	10.6 ± 1.4	—	24.1 ± 4.7	—

TABLE 2. Main effects of sowing treatments on germination of *W. nobilis* after 30 d

Treatment	Germination after 30 d (%)
Seed raising mix	16 (n = 30)
Cutting mix	10.5 (n = 28)
Hand watered (twice daily)	7 (n = 29)
Misted (4 sec per h)	19.5 (n = 29)
Seed exposed	19.5 (n = 32)
Seed covered	7 (n = 26)

floor where *W. nobilis* seeds germinate. Uncovered seeds germinated better than covered seeds either because they are stimulated by light or because they are not physically restrained. These results are similar to those observed for *Agathis australis* germination (Whitmore, 1977; Bielecki, pers. comm. reported by Ecroyd, 1982).

Germination over time. Seeds germinated steadily at a rate of approx. 4% per week over a period of 6 months under the conditions described (Fig. 5), until 88% had germinated, the remainder having rotted at various times. There are few reports documenting the time taken for germination of members of the Araucariaceae. However, most *Agathis* seeds germinate within 3–20 d under similar conditions (Whitmore, 1977; Ecroyd, 1982). Fresh excised embryos of *Araucaria angustifolia* show no dormancy but germinate more slowly at 10 °C than at the thermal optimum of 25–30 °C, with most germinating within 7 d and maximum germination occurring by 40 d (Salmen Espindola *et al.*, 1994). Similarly, *A. bidwillii* seeds germinate within 7 d with most germinating within the first 48 h (Burrows, Boag and Stockey, 1992). Results suggest that *W. nobilis* seeds may require a different temperature regime, or have a dormancy mechanism, or that they have a stratification requirement.

Whatever the mechanism, these results may imply a strategy by which seeds germinate at different times of the year, thus spreading the risk associated with climatic extremes. In the wild, once these seeds had fallen to the ground, many would not be retained long enough to germinate because of the rate of predation, which is probably even higher than that indicated in Table 1. There is also possible microbial deterioration on the forest floor.

Seedling development

Under glasshouse conditions with relatively constant temperatures and natural light, the *W. nobilis* seedlings formed a monopodial axis and tap root (Fig. 6A–F). They exhibited continuous growth in height, diameter and branch number after an initial lag phase of 4–6 months (Figs 8–10). Plant height, diameter and number of branches were strongly correlated ($R^2 = 0.95–0.97$) indicating that individuals grew consistently in the variables measured. Seedling roots were initially cream in colour turning gradually to red-brown. They lacked fibrous roots and the nodules found in older trees. Cotyledons (two per plant) were retained for more than 18 months.

The seedlings grew 0.05–0.25 m in the first year, 0.5–0.6 m in the second year and 0.25–0.35 m in the third year, attaining a total height of 0.8–1.2 m (Fig. 8). The diameter of the stem just below the cotyledons grew 3–7 mm in the first year, 10–14 mm in the second and 15–20 mm in the third, at which time it was 25–34 mm (Fig. 9). The size achieved is consistent with plantation data reported by Whitmore (1977) for various *Agathis* species, especially in tropical climates. In their natural state *A. australis* seedlings grow 0.1–0.25 m per year depending on the light intensity, whilst saplings grow 0.3–0.4 m with a diameter increment of 5 mm (Beveridge, 1977 as quoted by Whitmore, 1977). Although long-term monitoring of seedlings of *W.*

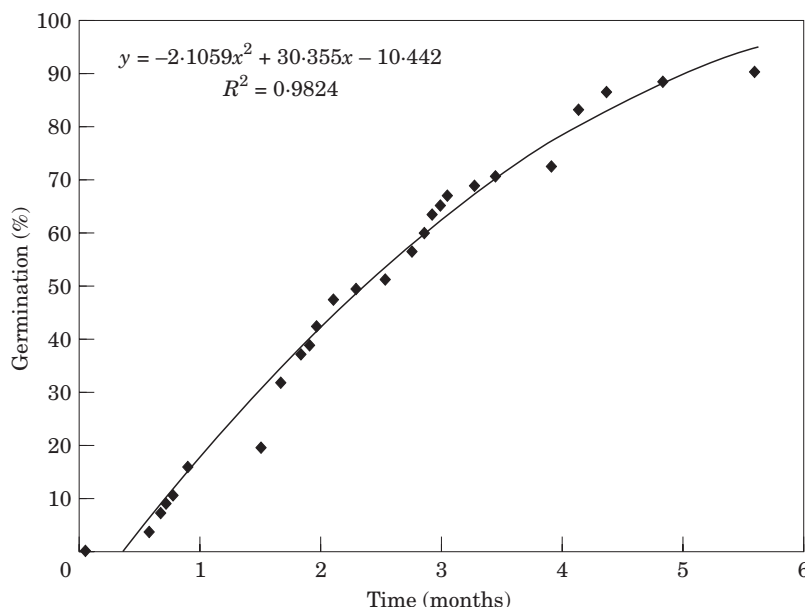


FIG. 5. Cumulative germination (%) of *Wollemia nobilis* seed at 23 ± 1.5 °C (day) and 16 ± 2 °C (night) in seed raising mix with 4 s of misting hourly under 70% natural light. Germination under these conditions is best described by a second order polynomial equation.



FIG. 6. *Wollemia nobilis* seedlings of different ages grown in a glasshouse: A, 1 week; B, 2 weeks, arrow indicates emerging cotyledons; C, 4 weeks; D, 7 weeks; E, 12 weeks; F, 13 weeks, oblique view of aerial parts to show orthotropic leading shoot and lateral branch. Bars = 5 mm (A–E); Bar = 3.75 mm (F). (Drawings N. Oram).



FIG. 7. *Wollemia nobilis* seedling, 32-months-old, grown in a glasshouse in a 265 mm diameter pot. Note the first order orthotropic shoot overtaking the original leader (photo J. Plaza).

nobilis in the wild is required, we have observed that they appear to die before they attain the proportions of the glasshouse-grown plants. The most likely constraints to seedling growth of *W. nobilis* in the wild are: inter- and intraspecific competition; burial by litter; temperature; low light intensity; nutrient deficiencies or imbalances; shallow soil; soil pH; lack of mycorrhizal associations and pathogens.

Many branches were developed by the seedlings (Figs 7 and 10) but most were lateral (first order plagiotropic), which rarely branched again unless damaged. The seedlings produced five–17 branches in the first year, 25–36 in the second year and 24–30 in the third year giving a total of 60–77. These branches grew during warmer months and the rhythmic phases are distinguished by the gradual increase in leaf length at the start of the season and decrease at the end (Fig. 2). In the *ex situ* seedling population, first order orthotropic shoots (up to four) arose spontaneously on more than 50% of the measured plants during spring when they were approx. 2.5 years old (0.6–0.9 m tall) (Figs 7 and 8). Some of these shoots quickly outgrew the original shoot towards the end of the third year (Fig. 7). In older wild plants orthotropic shoots also arose spontaneously giving rise to a highly branched tree (Hill, 1997).

It appears that trees of *W. nobilis* have at least one growth season per year in the wild, but overall growth of trees is slow and has not yet been fully characterized. It is reported that *A. australis* trees have at least one growth season, spring–early summer and, under favourable conditions, two seasons, namely spring and autumn (Ecroyd, 1982). A glasshouse study by Hawkins and Sweet (1989) on *A. australis* seedlings suggests that their optimum growth temperature is 27 °C with growth being suppressed at higher and lower temperatures and seedlings dying at 35 °C. These authors hypothesized that the growth behaviour of this

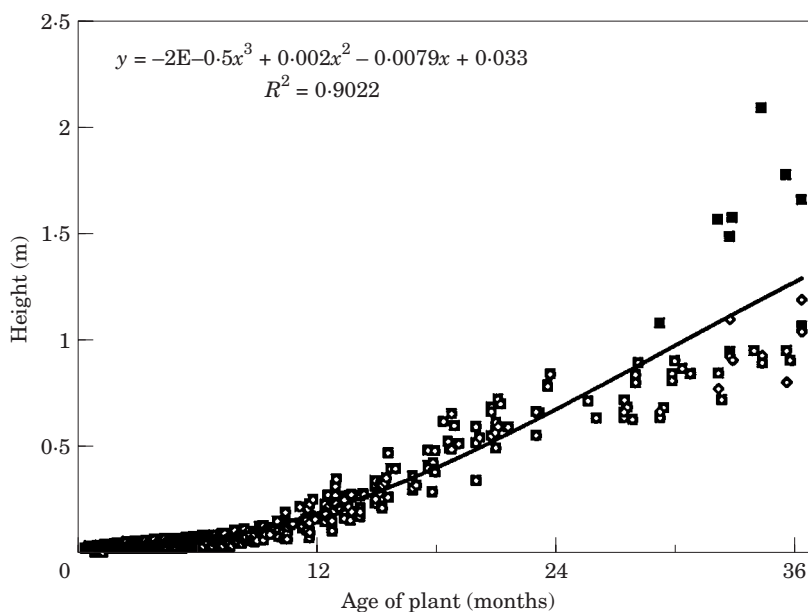


FIG. 8. Height of *Wollemia nobilis* seedlings measured over a 3 year period. Twenty plants were measured in the first 2 years, seven in the final year. ■, Represents overall height of plant including secondary leaders. Secondary leaders developed in four out of seven plants; ◇, represents height of primary leaders. Growth in overall height over this period is best described by a third order polynomial equation.

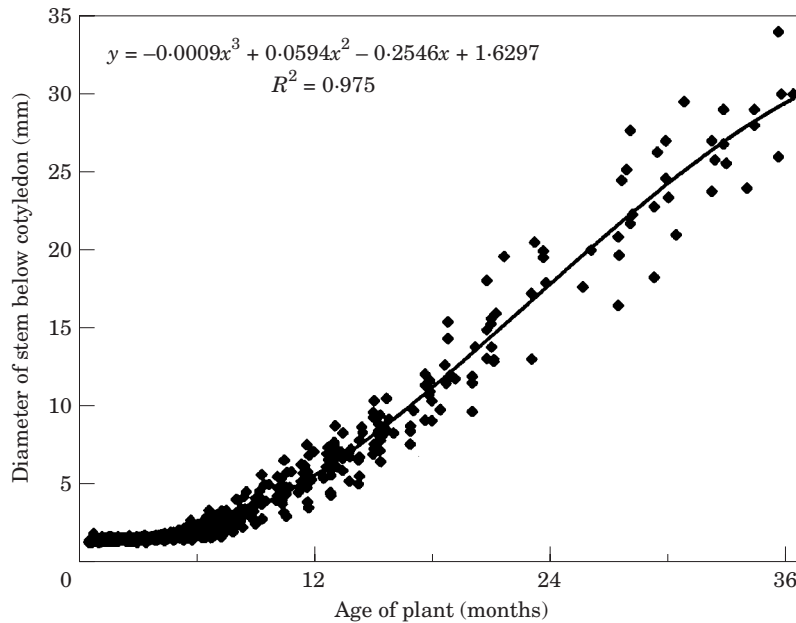


FIG. 9. Below cotyledon diameter of *Wollemia nobilis* seedlings measured over a 3 year period. Twenty plants were measured in the first 2 years, seven in the final year. Growth in diameter over this period is best described by a third order polynomial equation.

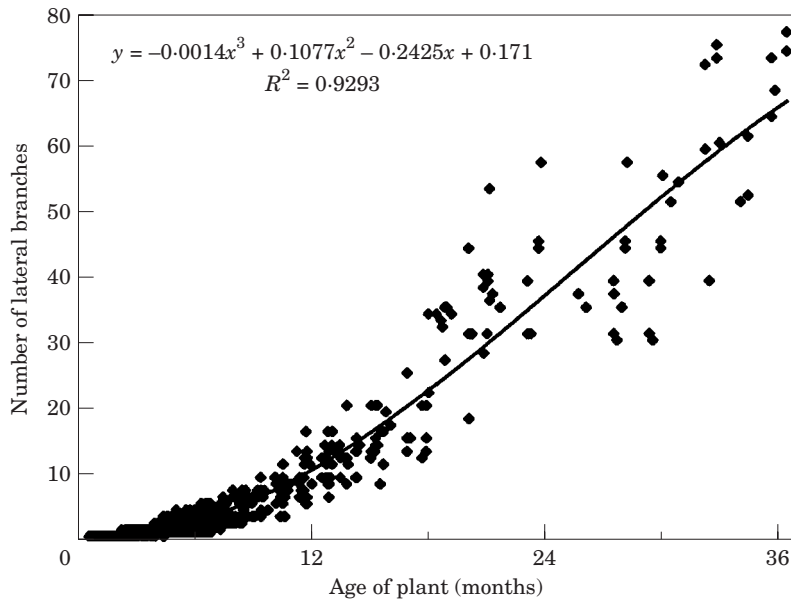


FIG. 10. Number of lateral (plagiotropic) juvenile branches produced by *Wollemia nobilis* seedlings measured over a 3 year period. Twenty plants were measured in the first 2 years, seven in the final year. Branch number increase over this period is best described by a third order polynomial equation.

species reflects its origin in the Jurassic period and that a general lowering of temperature may have contributed to the decline of such species. Further study correlating growth with temperature may provide insight into the evolutionary history of the Wollemi Pine.

CONCLUSIONS

There is strong evidence that the Wollemi Pine is able to reproduce sexually in the wild. We have shown that viable seeds are produced and that these seeds may germinate and

develop into healthy plants given suitable conditions. Growth of seedlings in the wild appears to be suppressed, however, as the current population structure consists only of small seedlings and large trees. Evidence of seedling recruitment within this area is provided by the existence of several young, essentially single-trunked trees in areas that are relatively open and free from interplant competition. Recruitment is probably happening at a measurable rate, albeit slowly and long-term monitoring of the population structure is required. It is interesting to note that no seedlings are found away from the very small area in which

the adult trees exist, although the adjacent areas appear ostensibly the same in terms of environment.

There is also some evidence of asexual regeneration of *W. nobilis* trees through self-coppicing and there is the possibility of re-establishment through root suckering. Although there is no definite evidence as yet that the latter occurs in Wollemi Pine populations, root suckering has been observed in *Agathis robusta* (Haley 1957, quoted by Whitmore, 1977), *Araucaria cunninghamii* (Burrows, 1990) and *A. araucana* (Burns, 1993).

It is most probable that the adult population structure of the Wollemi Pine consists of a small number of genets that have reproduced vegetatively with new genets slowly being added to the adult population from the relatively large population of young, seemingly suppressed seedlings, as breaks in the canopy occur due to fire or other events. Fire, evidence of which is found on some of the older trunks, may be a major determinant of *W. nobilis* population structure—a single fire of low intensity may increase the number of ramets able to produce seed and open up areas for seedling establishment, whilst a high intensity fire or series of low intensity fires may decimate or destroy a population. The response of this species to fire and other factors, such as soil and light, should be studied in order to determine why its distribution is so restricted.

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