The contribution of horticulture to the conservation of critically endangered *Wollemia nobilis*

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Abstract

After the critically endangered conifer *Wollemia nobilis* (Wollemi pine) was discovered in late 1994, an urgent task was to determine its cultivation requirements so that an *ex situ* population could be established. Propagation from extremely limited material was the first challenge, followed by development of a genetically representative *ex situ* conservation population. While the *ex situ* population was developed for insurance against loss of diversity in the wild population, it has also been used for research, and as the source of material for translocations, dispersed garden plantings and a botanic garden metacollection. Here, we report how these challenges were approached, based on nascent understanding of *W. nobilis* – as an Araucarian and as a rainforest emergent. As studies into the morphology and biology of the species progressed, these findings were used to refine propagation techniques. The establishment of this species in gardens around the world has expanded our knowledge of its biology and ecology. Insights concerning its behaviour in cultivation include its intolerance of extreme heat, extreme cold, high light and drought, and a preference for free-draining and acid soils – conditions approximating to its temperate rainforest origin. Now that these garden plants have begun to produce seeds, there is the opportunity for deeper research into factors influencing seed viability and plant establishment from seeds. This paper reviews many of the published studies aimed at understanding various aspects of *W. nobilis* biology, particularly those relevant to informing its requirements in cultivation. We also present data and conclusions drawn from unpublished studies which cumulatively aid efforts to conserve the species *ex situ*.

Introduction

Wollemia nobilis W.G. Jones, K.D. Hill & J.M. Allen (family Araucariaceae) was discovered in late 1994 in a remote canyon in Wollemi National Park (New South Wales (NSW), Australia). It was described as 'the botanical discovery of the century', akin to 'finding a small dinosaur still alive on earth' (Professor Carrick Chambers, in Woodford, 2005).

Wollemia nobilis currently exists in the wild as several stands comprising fewer than 100 trees and juveniles (Mackenzie *et al.*, 2022). They grow from the sides or floors of deep canyons to become canopy emergent trees, with a maximum height of around 42 m, and are typically multi-stemmed. Individual stems can live for at least 400 years (Banks, 2002), with rootstocks persisting for possibly thousands of years.

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With origins in the Cretaceous, *Wollemia nobilis* has been through many changes of climate, including several ice ages (MacPhail *et al.*, 1995; Chambers *et al.*, 1998; Kershaw & Wagstaff, 2001). It evolved in a high carbon dioxide (CO_2) environment (Haworth *et al.*, 2011), and while CO_2 is stimulatory for growth, increasing temperatures, predicted to occur with climate change, are expected to limit its ability to persist in its current location (Lewis *et al.*, 2015; Offord, 2011). Furthermore, the limited genetic variability in the wild (Peakall *et al.*, 2003; Greenfield *et al.*, 2016; Stevenson *et al.*, 2023), means it is likely that *W. nobilis* has limited capacity to adapt to change. The current location of the wild population provides a climate micro-refuge, the cooler and moister canyon environment buffering this species from climatic extremes (Ashcroft *et al.*, 2012; Selwood & Zimmer, 2020).

Discovery and 'recovery' planning

The recognition of *Wollemia nobilis* as a species new to science broke as front-page news in the *Sydney Morning Herald* on 14 December 1994. While this species constitutes the monotypic genus *Wollemia* of the southern hemisphere gymnosperm family Araucariaceae, the common name 'Wollemi pine' was quickly adopted and has persisted despite the species not being from the Pinaceae.

From the time of its discovery, it was recognised that there were multiple threats to the survival of *Wollemia nobilis*, including its extremely small population size and geographic distribution, unauthorised site visitation and collection, introduced disease and adverse fire regimes (Jones *et al.*, 1995; NPWS, 1998). To understand and manage these threats, a 'recovery team' of experts was assembled from the NSW National Parks and Wildlife Service, Botanic Gardens of Sydney (BGS) and elsewhere. When legal protection for threatened species was enhanced in NSW (NSW Threatened Species Conservation Act, 1995), *W. nobilis* was the first species in the state to have a comprehensive 'recovery plan' developed (NPWS, 1998). Currently, *W. nobilis* has the highest level of Australian state and federal legal protection (NSW Biodiversity Conservation Act, 2016, Australian Environment Protection and Biodiversity Conservation Act, 1999) and is listed as Critically Endangered in the IUCN Red List of Threatened Species (Auld & Mackenzie, 2024; IUCN, 2024).

Cultivation for conservation

Such was the scientific and public interest generated by the discovery of *Wollemia nobilis*, and the ensuing demand for plants, that the BGS, primarily at its Australian Botanic Garden Mount Annan (ABG), developed a programme of propagation for conservation. Araucariaceae species, such as *Araucaria heterophylla* (Norfolk Island pine) and *A. araucana* (monkey puzzle), are extremely popular in cultivation around the world, and the thousands of requests for *W. nobilis* plant material alerted the recovery team to the threat of illegal collection of plant material for horticulture (Benson, 1996). While *W. nobilis* now has strong legal protection, there was an awareness of previous examples of inappropriate and highly damaging exploitation of desirable threatened species, such as *Wodyetia bifurcata* (foxtail palm) in North Queensland, Australia (Dransfield, 1997). Hence, the programme of research and propagation for conservation of *W. nobilis* sought to ensure minimal disturbance to wild plants, enabling firstly the establishment of a representative *ex situ* population, and secondly the release of this population for widespread cultivation, backed by strong conservation messaging (Offord, 1996; Offord & Zimmer, 2024).

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Realising the horticultural potential of Wollemia nobilis*: first, how to propagate?*

Early propagation attempts for this species were necessarily painstakingly slow and frustrated by lack of knowledge of suitable material and techniques specific to this species. *Wollemia nobilis* is a large tree, with its main canopy elevated on one or more substantial stems (trunks). The first *W. nobilis* to be established in cultivation were several small wild seedlings (plants with cotyledons) transplanted from rocks or logs. They were collected by NSW National Parks and Wildlife staff and sent to a BGS nursery in November 1994. While these plants were easily established, they had limited value for propagation and establishment of a genetically representative *ex situ* population.

Araucariaceae, such as Norfolk Island pine, are predominantly propagated from seed for wide-scale horticulture (see, for example, Fullaway, 1972; Whitmore, 1977). However, this was not an option for Wollemi pine initially. Within a year of the tree's discovery, it was recognised that although the wild *Wollemia nobilis* trees produce an annual crop of seed cones, few viable seeds are produced, and these are extremely difficult to collect (Offord *et al.*, 1999). The few seed cones available for research in the early years were primarily gained through hazardous helicopter collection (Fig. 1). For this reason, most seeds were reserved for conservation seed banking or seed biology research (see, for example, Offord *et al.*, 1999; Offord & Meagher, 2001).

The breakthrough in establishing a genetically representative *ex situ* population of this species occurred when the wild trees were assessed by horticulturists skilled in propagating threatened species. The use of material collected from Site 1, Tree 19 by Graeme Errington in February 2006 enabled staff at ABG to establish the basic parameters for propagation from vegetative cuttings which has formed the basis for all subsequent programmes.



Fig. 1 Collection of *Wollemia nobilis* seeds by helicopter for early seed biology studies. Photo: J. Plaza, Royal Botanic Gardens and Domain Trust.

Vegetative propagation of Wollemia nobilis*: which branch and why?*

With very little published information available on vegetative propagation of members of Araucariaceae, the work of Whitmore (1977) and Bowen & Whitmore (1980) on *Agathis* species indicated that while vegetative propagation might be possible, the choice of material is important.

The architecture of the *Wollemia nobilis* tree is unique in the Araucariaceae in that it most closely follows the Massart model

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but has other features, such that Hill (1997) assigns it a modified Cook model where an individual plant develops from a single orthotropic leader, with a crown of whorled plagiotropic branches (Fig. 2). These branches mostly do not branch further, do not extend indeterminately and are blastotelic (having no terminating reproductive structures) when juvenile, often dropping off completely. Mature branches are terminated by a male or female strobilus after four to ten years (Hill, 1997). Clean abscission of all branches is extremely unusual in trees, as is absence of permanent structural branches (Burrows *et al.*, 2007).

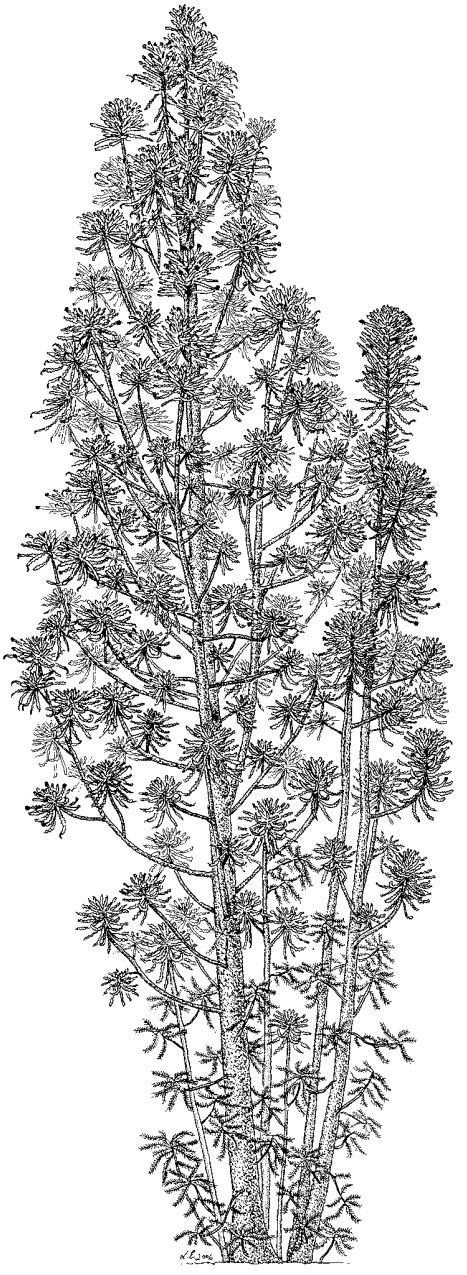


Fig. 2 Tree architecture of *Wollemia nobilis*. Illustration: Lesley Elkan © Royal Botanic Gardens and Domain Trust.

Wollemia nobilis has a constant coppicing habit (Hill, 1997), producing multiple stems, some of which develop into trunks. Some trees have >20 trunks, and the closeness of the trees means that it can be difficult to define individuals. Over time, one or more trunks become dominant, giving the tree its distinctive multi-crowned appearance. We suspect that individual trees may have many dominant leaders over their lifetime, as individual trunks are killed and damaged – for example by fire or rockfall – and are replaced (Mackenzie *et al.*, 2022). They also produce multiple epicormic shoots from the lower regions of larger trunks (Hill, 1997; Burrows, 2021; Fig. 3). This resprouting trait is uncommon in gymnosperms (Burrows, 2021) and is an advantage for propagation as it provides a source of vegetative cuttings capable of producing adventitious roots (Bonga, 2016) and was successfully used to propagate *W. nobilis* (Fensom & Offord, 1997).

Branches of *Wollemia nobilis* display distichous (two-ranked) grading to tetrastichous (four-ranked) leaf arrangements (Jones *et al.*, 1995) as they mature. Each branch exhibits rhythmic annual or seasonal growth extension (Hill, 1997; Fig. 4), with leaflets increasing in size over the warmer months and then decreasing in size over the cooler months in a pattern similar to that found in myristicaceous trees such

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Fig. 3 Self-coppicing stems and epicormic shoots on the lower section of a *Wollemia nobilis* plant in the wild. Photo: J. Plaza, Royal Botanic Gardens and Domain Trust.

as *Myristica fragrans* (nutmeg) (Halle *et al.*, 1978). This growth pattern easily dates the age of the branch, which may persist for five to approximately fifteen years (Hill, 1997; Burrows *et al.*, 2007). The branch leaf axils have buds or meristems – a rare trait in conifers, but typical of Araucariaceae (Burrows, 1999) – and may continue to branch, usually if damaged (Offord *et al.*, 1999), once a strobilis has fallen (Burrows *et al.*, 2007) and sometimes without obvious stimulus (Hnatiuk, 2023), a characteristic that enables propagation of functional plants using plagiotropic branches (Meagher & Offord, 2009). When these branches are used for propagation, the resulting plant has a decumbent habit. Often, five to seven years after propagation, as the branch diameter increases, one or more of the plagiotropic branches on these plants may revert to orthotropy (Meagher & Offord, 2009).

Refining vegetative propagation of Wollemia nobilis

An understanding of the shoot and branching arrangements of *Wollemia nobilis*, and testing the propagation potential of various plant parts (Fensom & Offord, 1997), enabled the usefulness of these parts to be ranked (from least to most useful): mature orthotropic < mature plagiotropic shoot < juvenile branch < juvenile orthotropic shoot (Fig. 5). The majority of vegetatively propagated plants in cultivation have been produced from orthotropic shoots (Fig. 6). Plants propagated from orthotropic shoots generally maintain upright growth, similar in shape to seedlings, but produce one or more orthotropic stems, sometimes spontaneously and commonly after removal of the apical meristem, for example by pruning.

The initial research into propagation of *Wollemia nobilis* at ABG included trialling the

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Fig. 4 Juvenile *Wollemia nobilis* showing seasonal rhythmic growth of leaves. Photo: M. Phelan, Royal Botanic Gardens and Domain Trust.

effects of a range of commonly used plant growth regulators (PGR) and concentrations/formulations, including indolebutyric acid (IBA), length of cuttings, as well as different humidity and temperature regimes. We found no discernible effects on cutting strike rates using PGR of any type or concentration, a result that was later confirmed by the work of Trueman & Peters (2006). We did find that root establishment (striking of roots on cuttings percentage and root growth) was favoured by a lower root-zone temperature (18 °C vs 24 °C) and a drier fog environment rather than in mist, and that longer cuttings (8 cm) were more successful than shorter cuttings (4 cm). Strike rate also varied by source tree, and these differences were also noted by Trueman *et al.* (2007), indicating a genetic component to propagation success.

Material from the wild *Wollemia nobilis* trees is very slow to strike roots, often taking six to twelve months, or often not striking at all. In spite of this, an effective propagation protocol was developed at the ABG nursery, resulting in the majority of known, mature (putative) individuals from the wild stands eventually being represented in the *ex situ* population. Each of these individuals has been replicated over the years, and we maintain at least three replicates of each individual of each wild tree in the *ex situ* population at ABG. Since the *ex situ* programme's inception, record-keeping for individual trees and their clones has been meticulous, and this approach has paid off in terms of conservation and research into *W. nobilis*. Examples include production of plants for the horticultural release programme (Trueman *et al.*, 2007), maximum diversity of plants in translocations to new wild locations (Zimmer *et al.*, 2016b; Mackenzie *et al.*, 2022), reliable provenance for genetic studies (for example, Peakall *et al.*, 2003; Greenfield *et al.*, 2016; Yap *et al.*, 2015; Stevenson *et al.*, 2023) and plant growth and survival studies (for example, Offord, 2011; Zimmer *et al.*, 2015; Zimmer *et al.*, 2016a, 2016b).

Other vegetative propagation techniques

Other vegetative propagation methods have been assessed for *Wollemia nobilis*, including tissue culture (somatic embryogenesis, shoot culture). These methods, while having some success for Araucariaceae species of forestry significance (Burrows *et al.*, 1988; Aitken-Christie & Platt, 1992), have limited potential in large-scale production of *W. nobilis* (Grace *et al.*, 2005; Trueman *et al.*, 2007), but may be of use in *ex situ* conservation of this species (Niu *et al.*, 2013).

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Fig. 5 Struck cuttings from three branch/shoot types of *Wollemia nobilis*. Left to right: adult plagiotropic branch, juvenile orthotropic shoot, juvenile plagiotropic branch. Photo: J. Plaza, Royal Botanic Gardens and Domain Trust.



Fig. 6 Growth form of *Wollemia nobilis* plant grown from an orthotropic shoot. Photo: J. Plaza, Royal Botanic Gardens and Domain Trust.

Air layering has successfully produced *Wollemia nobilis* potted plants (Offord *et al.*, 2021). The bark is wounded to expose the cambium and then a plant growth regulator applied (for example, IBA at 500 ppm). The plant is then wrapped in sphagnum moss and encased in an air-layering pot. Once adventitious roots form (three months if set in spring, six months in autumn and twelve months in winter) the shoot can be removed and treated as a rooted cutting (M. Phelan, pers. comm.).

In preliminary trials at ABG, *Wollemia nobilis* seedlings and mature scions have been successfully grafted by the cotyledon micrograft technique (Hartmann *et al.*, 1990) onto *Agathis atropurpurea* and *A. robusta* seedlings. Similar attempts using *Araucaria bidwillii* and *A. cunninghamia* seedlings failed after six months (E. Mills, pers. comm.), suggesting tissue, cambium bark and wood compatibility of *Wollemia* with *Agathis*, but

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possibly not *Araucaria*. These results align with the closer phylogenetic relationship between *Wollemia* and *Agathis* (Escapa & Catalano, 2013). The long-term compatibility of grafted plants is unknown (the current oldest plant in the *Wollemia–Agathis* grafting trial is seven years old) and should be carefully considered for any amenity plantings, as graft failure is common and can happen without warning (Offord, 2021).

Commercial propagation

While the development of preliminary propagation techniques enabled the establishment of the *ex situ* conservation population at ABG, further refinements were required for domestication and commercial release. From 1999 these refinements were made by the Queensland Department of Primary Industries and Fisheries (QDPIF), which was part of a consortium (Wollemi Australia Pty Ltd) contracted to deliver the horticultural propagation and release programme (Lake, 2000; Trueman *et al.*, 2007). The refinements were based on techniques used for production of elite clones of *Araucaria cunninghamia* (hoop pine), described by Trueman *et al.* (2007) as follows. The system developed used orthotropic cuttings taken from 'hedged' potted plants (pruned to produce the growth of multiple orthotropic shoots/cuttings). Cuttings were placed into a propagation mix in tubes and maintained under mist for six months, at which time their strike rate was assessed. Higher strike rates were found on plants propagated from seedling ortets (the original plant from which a clone is derived) when compared to mature plant ortets, probably due to the higher propensity for juvenile plant material (plants < 3 m, as defined by Zimmer *et al.*, 2014) to produce adventitious roots (Bonga, 2016). Further incremental refinements raised the level of rooted cuttings to 80 per cent, enabling an exponential increase in stockplant numbers. Most plants distributed from 2006 were from seedling ortets. The slower-rooting plants from mature wild ortets (which can be traced back to their original source tree in the wild) were used for the elite plants that went to an auction conducted by Sotheby's in 2005 (Trueman *et al.*, 2007). These plants were assigned names associated with significant botanists, such as the late Dr John Banks from the Australian National University, who conducted some of the original wood-anatomy research into *Wollemia nobilis*.

While the majority of *Wollemia nobilis* trees growing in cultivation today were produced from cuttings, there are many now being grown from seeds produced by established garden plants (Offord & Zimmer, 2024).

Seed biology and germination of Wollemia nobilis

Wollemia nobilis is monoecious, with male and female strobili (cones) on each plant, although not necessarily at the same time. A third type of cone has been described as a teratological bisexual unit (Dörken & Rudall, 2019). In cultivation, the male cones often appear first, sometimes as early as five years after propagation, and female cones thereafter, from around eight years. In general, however, productive seed cones may not be present until 12–15 years post propagation. As with many plants, it is likely that cone production is associated with plant size rather than with plant age. Moreover, anecdotal observations suggest that *W. nobilis* trees planted in deep shade may be less likely to produce cones than similar-sized trees planted in situations with more light availability. For example, *W. nobilis* trees planted at the Blue Mountains Botanic Garden Mount Tomah (BMBG) first

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produced female cones after 24 years despite the relative health and growth of the plants (Table 1; Fig. 7 A). While the reproductive biology of *W. nobilis*, from cone initiation to seed production, is not well understood, it appears to be similar to that of other Araucariaceae (Goeten *et al.*, 2020), taking 20–24 months from the appearance of female cones on the branches to seed maturation, which is characterised by browning of the scales and disintegration of the cone from the axis. Variation in cone production in the wild has been linked to variation in temperature and rainfall, although the relationship with seed viability remains uncertain (Zimmer *et al.*, 2015). In the global survey of cultivated *W. nobilis* (Zimmer & Offord, 2019) it was reported that seed cones generally mature in mid-to-late summer (January to March in the southern hemisphere, June to September in the northern hemisphere).

Wollemia nobilis appears to produce seeds through sexual reproduction (Offord *et al.*, 1999), but this is yet to be confirmed. Pollen is produced in spring on wild and cultivated trees and observed to be borne by wind to female cones. Reports of viable seeds being produced on isolated cultivated *W. nobilis* (C. Offord, pers. obs.) indicate that this species may have some level of self-compatibility or apomixis. While this phenomenon is not known to occur naturally in the Araucariaceae family (Mogie, 1992), it is a possibility in other gymnosperms, for example, *Pinus* spp. (Tretyakova & Mineev, 2021). Monoecious trees of *Araucaria angustifolia* produce seeds after self-fertilisation, albeit at low rates (7 per cent) and with decreased heterozygosity (Danner *et al.*, 2013). If self-fertilisation is occurring in cultivated *W. nobilis*, this may explain findings indicating inbreeding (Peakall *et al.*, 2003; Stevenson *et al.*, 2023).

Female cones contain around 250 potential seeds which are held freely on the scales. In the wild we have observed low seed viability, often less than 10 per cent (Offord *et al.*, 1999), but viability has been observed to be as high as 15–20 per cent in seeds from cultivated trees. Other Araucariaceae, such as *Agathis* spp., have similarly low viability rates in the wild (Whitmore, 1977). Research has not yet uncovered the reason for low/variable viability in *Wollemia nobilis* seed, and potential explanations range from pollen limitation to climatic factors. Rather than relying on regular seedling establishment from seed, this species instead may have maintained a bank of juvenile plants growing very slowly in the dark understorey, a common strategy for rainforest trees (Zimmer *et al.*, 2015).

Despite early low seed availability after the discovery of the species, the seed germination parameters for *Wollemia nobilis* were established with carefully designed experiments using just 58 seeds (Offord *et al.*, 1999). Further exploration of seed biology (Offord & Meagher, 2001) was enabled by development of a low-impact collection technique using purpose-made nets suspended between trees to catch seeds falling from nearby trees. With the maturation of cultivated *W. nobilis* in gardens in many parts of the world, widespread propagation by seeds is now occurring.

Viable *Wollemia nobilis* seeds are characterised by weight (7–44 mg) (Ng *et al.*, 2024) and possess a 'filled' appearance, like a flattened pea. They bear small wings (Fig. 8), and make a distinct 'plinking' sound when dropped onto a hard surface from 30 cm. They are often darker in colour than unfilled seeds, due to the high oil content (c. 40 per cent) (Ng *et al.*, 2024). A viable seed of *W. nobilis* consists of an embryo within a

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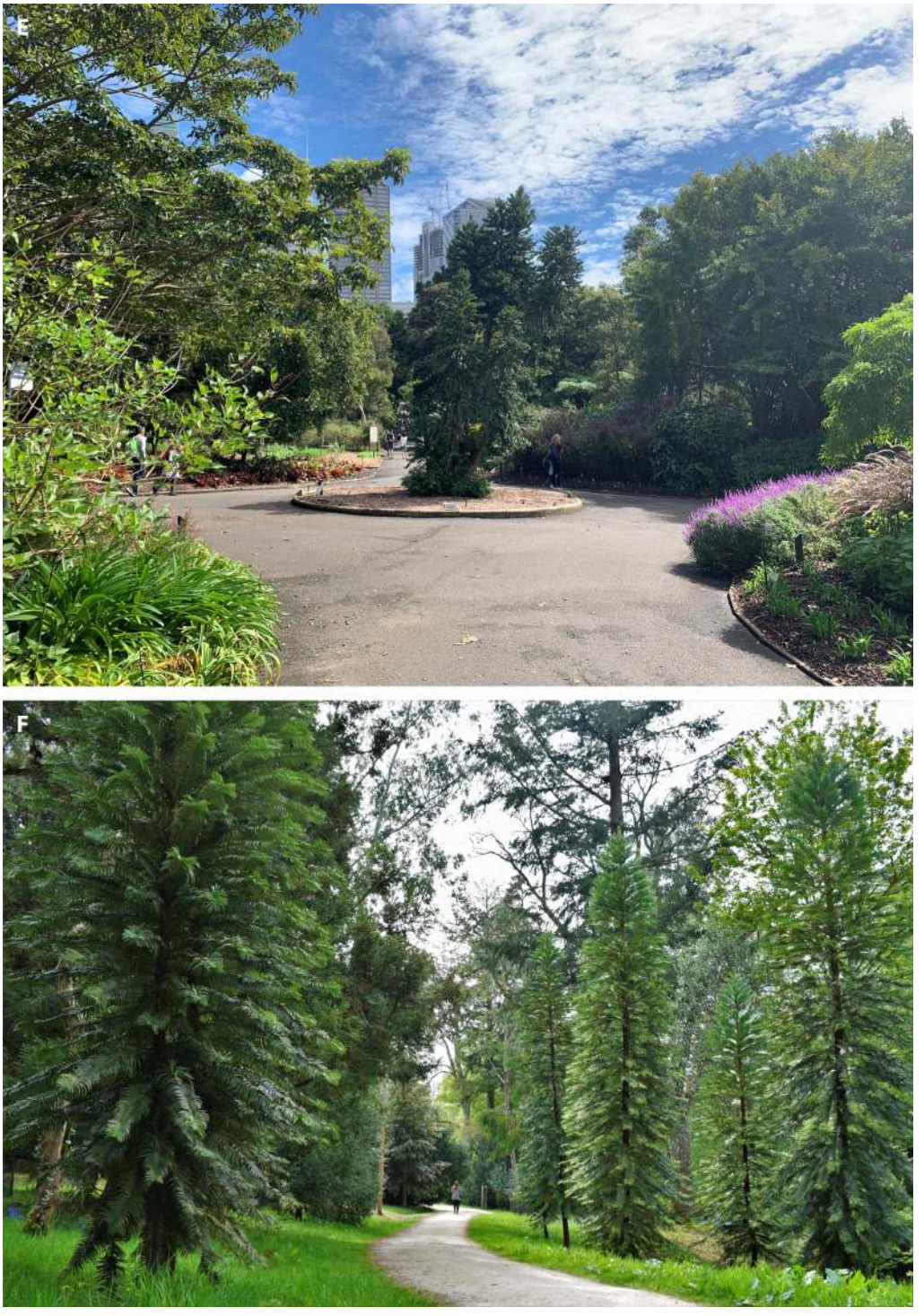


Fig. 7 *Wollemia nobilis* growing in various botanic and private gardens. A. Blue Mountains Botanic Garden, Mount Tomah, Australia (Photo: Stuart Allen); B. Royal Botanic Garden Edinburgh, UK (Photo: David Knott); C. Huntington Botanical Gardens, San Marino, USA (Photo: Sean Lahmeyer); D. Private garden, Millthorpe, Australia (Photo: Ian Rogan); E. Royal Botanic Garden, Sydney, Australia (Photo: Maureen Phelan); F. Wakehurst Place, West Sussex, UK (Photo: Ellen McHale ©RBG Kew).

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Fig. 8 Viable seeds of *Wollemia nobilis*. Length of seed ~10 mm. Photo: Royal Botanic Gardens and Domain Trust.

megagametophyte, surrounded by a papery testa (Fig. 9).

Viable *Wollemia nobilis* seeds display non-deep physiological dormancy (Offord & Meagher, 2001; Baskin & Baskin, 2014). They can germinate over a range of temperatures, but germination may be prolonged (months). Seeds that are aged for six months or more, or which are stratified for several weeks in cold moist conditions (5–10 °C), germinate more rapidly and uniformly at 26 °C than fresh seeds (Offord & Meagher, 2001).

Seed size in Araucariaceae species is predictive of seed storage potential (Tompsett, 1984) and, given the small size of *Wollemia nobilis* seed (Ng *et al.*, 2024) compared with other Araucariaceae (Whitmore, 1977; Tompsett, 1984), it might be predicted that *Wollemia* exhibits intermediate, if not orthodox, seed storage behaviour at low temperatures. Seeds of *W. nobilis* appeared to demonstrate orthodox

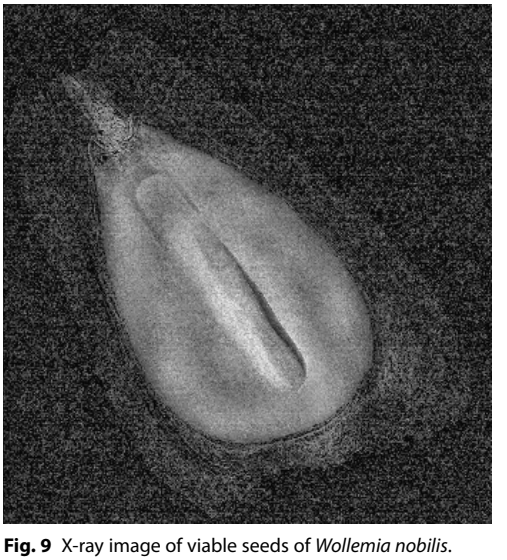


Fig. 9 X-ray image of viable seeds of *Wollemia nobilis*. Length of seed ~10 mm. Photo: Royal Botanic Gardens and Domain Trust.

or intermediate seed storage behaviour in a study by Ng *et al.* (2024) with seeds stored for five years at –18 °C showing no loss of viability. Seed stored at 5 °C for the same

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period lost around 50 per cent of viability, possibly associated with lipid peroxidation (Ng *et al.*, 2024). The long-term seed viability of this species at –18 °C (the standard temperature for storing orthodox seeds) (Martyn Yenson *et al.*, 2021) is unknown and is under examination.

Cultivation of *Wollemia nobilis*

How and where are they growing?

The first *Wollemia nobilis* to be planted were seedlings, some of which can be seen at the Royal Botanic Garden Sydney (planted in February 1998), the BMBG (August 1998) and the ABG (September 1998) (Table 1; Fig. 7 E, A). Since then, many thousands of cutting-grown plants have been planted around the world (Offord & Zimmer, 2024; see profiles of selected plants in Table 1 and Fig. 7), and there have been several translocations where cultivated material has been planted in wild locations (Zimmer *et al.*, 2016b; Mackenzie *et al.*, 2022). Cultivated trees have so far conformed to the growth of juvenile plants in the wild, initially developing a single leader and, after 5–15 years, secondary shoots from the base or lower-to-mid stems of the leader (Figs 3 and 7 F). The tallest trees in cultivation at the time of writing are 12–15 m in height and are growing in a range of soil types (Offord & Zimmer, 2024).

The now-matured first-planted Wollemi pine seedling in the Royal Botanic Garden Sydney has developed a pronounced 'lean' to the north (Fig. 7 E), reminiscent of the directional lean (angle of vertical growth) of *Araucaria columnaris* (Cook pine) towards the equator, regardless of hemisphere, which is increasingly pronounced with latitude (Johns *et al.*, 2017).

Factors influencing cultivation of Wollemia nobilis

Soil environment

Wollemia nobilis grows naturally in a temperate rainforest in soils derived primarily from sandstone with shale and basalt components (Jones *et al.*, 1995), low in nutrients, with low pH (c. 3.5) (Offord *et al.*, 2014; Rigg *et al.*, 2016a), and with soil air-filled porosity and total water-holding capacity of 25 per cent (Rigg *et al.*, 2016b).

Wollemia nobilis, as with other species that grow in nutrient-poor natural soils, often relies on the presence of, and relationships with, a range of microorganisms, such as mycorrhizae, to establish in disturbed landscapes (Bellgard, 1991). *W. nobilis* plants form mycorrhizal associations (where the root forms a symbiosis with a fungus) (McGee *et al.*, 1999), as well as relationships with free-living soil microorganisms. These microorganisms are associated with *W. nobili*s in its wild location (Rigg *et al.*, 2016b), in a translocation (Rigg *et al.*, 2017) and in cultivation (McGee *et al.*, 1999; Rigg *et al.*, 2016a), and appear to contribute to the plant's growth. There is evidence that *W. nobilis* may influence the soil microbial assemblages, as well as abiotic factors such as pH, possibly lowering soil pH via root exudates (Rigg *et al.*, 2016b). In one study, inoculation of *W. nobilis* with a range of mycorrhizal species did not find evidence of root colonisation, but endophytic fungal structures were detected (Biggs, 2009). Further investigation is required of the role of microbial partners in the establishment and growth of *W. nobilis*, including interactions with other biota such as pathogens, and abiotic factors such as soil pH, moisture and nutrient availability (Rigg *et al.*, 2017).

Little is known about the fertiliser requirements for cultivated *Wollemia nobilis*. Pohio *et al.* (2005) found that incorporation

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Table 1 Profiles of selected older, cultivated *Wollemia nobilis*. Climate averages for each profile: Gardens 1–4, Bureau of Meteorology (BoM) (2022) 1. Station 068192, 2. Stations 63013 (rainfall) and 63292 (temperature), 3. Station 0660062, 4. Station 63303; Gardens 5–8, average rainfall and temperatures from Bioclim, BoM or Met Office, or supplied by garden. Cultural information supplied by gardens. Profiles 1 and 2 extracted from Offord & Zimmer (2024).

Profile number	1	2	3	4	5	6	7	8
Garden	**Australian Botanic Garden Mount Annan**	**Blue Mountains Botanic Garden Mount Tomah**	**Royal Botanic Garden Sydney**	**Millthorpe**	**Logan Botanic Garden**	**Royal Botanic Garden Edinburgh**	**Wakehurst Place**	**Huntington, California**
Country	Australia	Australia	Australia	Australia	Scotland	Scotland	England	USA
Latitude **Longitude**	34.1° S 150.7° E	33.5° S 150.4° E	33.8° S 151.2° E	33.4° S 149.2° E	54.7° N 4.9° W	55.9° N 3.2° W	51.1° N 0.09° W	34.1° N 118.1° W
Age (years in ground + years in pot before planting)	26 (2 in pot)	27 (4 in pot)	25 (2 in pot)	18 (5 in pot)	18 (3 in pot)	20 (7 in pot)	22 (5 in pot)	18 (2 in pot)
Height of plant (m)	7	12.9	8.2	12	10	4.3	10.5	5.8
Diameter of main trunk at breast height (cm)	16	15	16	17	19	10	21	17.5
Number of trunks or large stems	1 leader, 1 secondary	1	3 leaders, 6 secondaries	2 leaders, 5 secondaries	1	1 large, 4 basal	3	2
Has the plant produced male and/or female cones?	Female noted from 2011	Male (few only) and female noted from 2022	Male (2 only) and female noted from 2018	Many male and female	No	Male and female noted from 2010	Male and female	Male 2014; female 2018
Is the plant in full sun or shade?	Originally full sun, part shade from 2014	Partial to full shade (S aspect)	Originally part shade, full sun from 2005	Partial shade	Partial shade	Part shaded in winter	Partial shade	Full sun
Soil type	Clay loam on shale	Clay loam on basalt	Sandy loam	Loamy – basalt derived	Silty loam	Light sandy loam	Sandy clay	Sandy loam to sandy gravelly loam
Soil pH	6.3	5.0	6.03	7.0–7.5	6.1	6.5	Slightly acid	7.3
Does the plant receive fertiliser?	No	No	Indirectly, planted in a fertilised bed	No	No	Only when planted	No	Yes, every 4 months when lawn fertilised
Other than natural rainfall, is the plant watered?	In summer	No	Yes	In summer	No	Only in extreme drought	First 2 years after planting	In summer, 1–2 times
Average annual rainfall (mm)	797	1439	1213	924	1012	749	763	428
Average temp coldest month (°C)	3.0	2.6	0.5	0	−0.3	−0.5	0.5	6.2
Average temp hottest month (°C)	29.7	24.3	27.4	26	17.8	18.7	21.7	31.3
Coldest recorded temperature since planting (°C)	−6.0	−3.6	2.1	−8.3	−10	−14	−10	–
Highest recorded temperature since planting (°C)	46.4	33.1	38.9	38.9	–	27	39.1 (Charlwood July 2022)	49

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of slow-release fertiliser into propagation mix increased root growth of cuttings. Potted stock plants in the ABG nursery have been maintained for 5–20 years using a slow-release fertiliser (such as N:P:K:18-3.9-8.3, 1.2 Mg, plus trace elements), and no problems with phosphorus toxicity (commonly found in some Australian species) have been observed (M. Phelan, pers. comm.). It was commonly noted in the 'I Spy a Wollemi Pine' survey (Zimmer & Offord, 2019; Offord & Zimmer, 2024) that many *W. nobilis* plants growing in the ground (for example, plants growing on basalt-based soil at the BMBG) do not require fertiliser (I. Allen, pers. comm.), and that growth is favoured by well-drained, acidic soils.

Light, temperature and rainfall

Young wild *Wollemia nobilis* seedlings and juveniles experience extremely low levels of light (as low as 3 per cent full sunlight in midsummer) (Offord *et al.*, 2014). In early horticultural growth studies at ABG, cutting-grown plants which were approximately 12 months old were grown under 25 per cent, 50 per cent and 100 per cent full sunlight for six months (Aug–Jan). We observed that the plants growing in the 100 per cent full sunlight conditions were shorter and exhibited leaf damage (yellowing and poor growth), probably as a result of photoinhibition (impaired photosynthesis which can result in poor growth), which is experienced by seedlings of some rainforest species such as *Agathis robusta* when transferred from lower light to full sunlight (Langenheim *et al.*, 1984). In a glasshouse experiment, seedling plants grown at 5 per cent, 15 per cent and 50 per cent full sunlight had greater growth in height as light increased, but invested in greater stem production at low light (Offord *et al.*, 2014). We conclude that young *W. nobilis* plants grow faster in higher light situations, to a point (which will be determined by the ambient conditions) beyond which poorer growth can be expected. In areas where high levels of light are experienced, younger plants in cultivation should be protected from strong sunlight, as in Australia during summer. Paradoxically, when planted as part of a translocation, *W. nobilis* survival was poorer in low light conditions, with mortality attributed to *Botryosphaeria* infection (Zimmer *et al.*, 2015).

Temperature is a critical factor in *Wollemia nobilis* growth and establishment. *W. nobilis* is the most southerly occurring, cold-tolerant and heat-sensitive of the Australian Araucariaceae species. They are predicted to grow optimally in temperatures between –11 °C and 37 °C (Offord, 2011), and while they can suffer leaf and stem damage during periods at lower or higher temperatures, plants may survive and reshoot (Offord & Zimmer, 2024). The temperature tolerance range of *W. nobilis* places it in Plant Hardiness Zone 2 for Australia (the tablelands of south-east Queensland, New South Wales and Victoria) (Dawson, 1991), which equates to USA Plant Zone 8a (–9.4 °C to –12 °C). Factors other than temperature, such as soil moisture, however, may affect plant hardiness, influencing the suitability of a species for a location (McKenney *et al.*, 2007).

The effect of drought on *Wollemia nobilis* is not well understood; observing water stress is complicated by its relationship with other edaphic and biotic factors such as temperature – drought is often accompanied by increased temperature (Adams *et al.*, 2017) and interactions with pathogens (for example, pathogenic impacts can be more visible when a plant is moisture-stressed) (Cahill *et al.*, 2008). Cultivated *W. nobilis*

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grows in a wide range of environments and care regimes, from well-watered ones to those reliant only on natural rainfall (Offord & Zimmer, 2024). In a nursery trial, we found that plants grown over summer at ABG required watering at least twice a week, and that plants watered less frequently (once a week, fortnight or month) had less branch growth extension and a higher number of shed branches. Results of a pot-based experiment suggest that *W. nobilis* is more drought-sensitive than *Araucaria bidwillii, A. heterophylla* and *A. cunninghamia*, more naturally widespread and commonly cultivated species (Zimmer *et al.*, 2015). *W. nobilis* plants under extreme water stress in this experiment exhibited crown mortality, which may be related to the unusual xylem structure and branch shedding habit (Burrows *et al.*, 2007). *W. nobilis* plants often shed their lower branches, and sometimes upper branches, possibly in response to drought. The shedding is facilitated by the highly constricted cross-sectional area of the xylem at the base of the branch (Burrows *et al.*, 2007) in addition to the weak wood due to a high proportion of ray parenchyma found in the constricted zone (Heady & Burrows, 2008). The Huber value (measure of the water supply capacity) is in the low-to-normal conifer range for the *W. nobilis* branch xylem, but in the constriction zone includes values amongst the lowest ever recorded (Burrows *et al.*, 2007). This shedding habit appears to give *W. nobilis* the ability to drop its branches during times of water stress, and this may have contributed to the species' survival of continental drying. Paradoxically, the low vascular water supply may limit photosynthesis and hence reduce the plant's competitiveness – contributing to the overall decline of this species in the wild (Burrows *et al.*, 2007).

Pests and diseases

A wide range of pests and disease-bearing organisms have been found in association with *Wollemia nobilis*, the majority of which cause few problems. Some fungi – for example, *Pestalotiopsis* (Trueman *et al.*, 2007) – may act largely as secondary colonisers on dead plant material. The diseases of most concern in *W. nobilis* are phytophthora root rot (*Phytophthora cinnamomi* and *P. multivora*) (Bullock *et al.*, 2000; Puno *et al.*, 2015) and fusicoccum dieback (*Fusicoccum* spp. or *Botryosphaera* spp.) (Slippers *et al.*, 2005). These dieback diseases are often found in association with stressed plants in warmer and wetter conditions. Phytophthora is particularly pernicious and can result in significant loss of plants. Plant hygiene is an essential line of defence against these diseases (Summerell & Liew, 2020). Insect pests of *W. nobilis* have been studied less than microbial disease. Trueman *et al.* (2007) describe a range of Lepidoptera (butterflies or moths) and Hemiptera (bugs), and one species of Thysantoptera (thrips) associated with this species which mainly cause defoliation, stem damage and occasional death.

Securing the future of *Wollemia nobilis* in the wild and in cultivation: developing translocated and metacollection populations

What emerges from 30 years of study and cultivation of *Wollemia nobilis* is that it is a fragile survivor with a number of unique traits which influence its survival *in situ* and *ex situ*. It is an extremely long-lived species, but establishment of plants is tenuous and requires particular conditions, many of which are yet to be fully understood. Early horticultural ventures with this species met with mixed success, but key factors have

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emerged over time, in particular the limiting effects of temperature, drought and soil-borne disease. The sum of horticultural knowledge, teamed with recent advances in genetic techniques, has enabled us to identify diversity in *W. nobilis* (J. Bragg, pers. comm.; Stevenson *et al.*, 2023), and this combined knowledge is being used to establish translocated populations in suitable wild habitats (Mackenzie *et al.*, 2022). These populations are being monitored to gauge establishment and growth and will no doubt contribute to our understanding of this species.

The need for a dispersed, documented and well-managed *ex situ* collection of *Wollemia nobilis* germplasm was highlighted by the scale of the Black Summer fires in eastern Australia in 2019–2020 that burnt through over 10 million ha in an event that was unprecedented in extent and severity (Nolan *et al.*, 2020; Collins *et al.*, 2021). The wild population as well as a number of botanic gardens were affected by these fires (see case study in Biggs *et al.*, 2023). While fire-fighting efforts largely contained the fire in the wild population of *W. nobilis*, damage occurred to adult and in particular to juvenile trees; only the short-term effects of this event are yet known (Mackenzie *et al.*, 2022; Price *et al.*, 2023). Climate change also means that the frequency of such fires is predicted to increase in Australia (Canadell *et al.*, 2021). It is clear from this event that *ex situ* repositories in botanic gardens or arboreta of genetically distinct individuals of *W. nobilis* need to be geographically dispersed and held on several different continents as a metacollection. Work towards this goal is under way. In late 2023 we embarked on a programme of metacollection of *W. nobilis*, partnering with Botanic Gardens Conservation International (BGCI) and Forestry England to distribute genetically identified plants to international gardens and arboreta. The initial sets of six vegetatively propagated plants were sent from ABG to locations in Europe, the United Kingdom, USA and Australia. Each set has a different mix of individuals so that, across the global collection, species diversity will be maintained. We are monitoring the progress of these plantings and will report on the growth of plants in various location and cultivation regimes as these plantings establish.

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References

ADAMS, H.D., BARRON-GAFFORD, G.A., MINOR, R.L., GARDEA, A.A., BENTLEY, L.P., LAW, D.J., BRESHEREAS, D.D., MCDOWELL, N.G. & HUXMAN, T.E. (2017). Temperature response surfaces for

mortality risk of tree species with future drought. *Environmental Research Letters*, 12: 115014. doi: https://doi.org/10.1088/1748-9326/aa93be

AITKEN-CHRISTIE, J. & PLATT, G.C. (1992). *Agathis australis*: a new era for kauri propagation. *Combined Proceedings – International Plant Propagators' Society*, 42: 321–326.

ASHCROFT, M.B., GOLLAN, J.R., WARTON, D.I. & RAMP, D. (2012). A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. *Global Change Biology*, 18(6): 1866–1879. doi: https://doi.org/10.1111/j.1365-2486.2012.02661.x

AULD, T.D. & MACKENZIE, B.D.E. (2024). *Wollemia nobilis*. The IUCN Red List of Threatened Species 2024: e.T34926A150329250 Available online: www.iucnredlist.org/species/34926/276111449 (accessed 31 October 2024).

BANKS, J. (2002). Wollemi pine: tree find of the 20th century. In: *Australia's ever-changing forests V. Proceedings of the Fifth National Conference on Australian Forest History*. Centre for Resource and Environmental Studies, ANU, Canberra, pp. 85–101.

BASKIN, C.C. & BASKIN, J.M. (2014). *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*, 2nd edn. Academic/Elsevier, San Diego, CA.

BELLGARD, S.E. (1991). Mycorrhizal associations of plant-species in Hawkesbury sandstone vegetation. *Australian Journal of Botany*, 39(4): 357–364. doi: https://doi.org/10.1071/BT9910357

BENSON, J. (1996). Threatened by discovery: research and management of the Wollemi Pine, *Wollemia nobilis* Jones, Hill & Allen. In: STEPHENS, S. & MAXWELL, S. (EDS), *Back from the Brink: Refining the Threatened Species Recovery Process*. Surrey Beatty & Sons, Sydney, pp. 105–109.

BIGGS, J.R., GRAY, J., WEST, J., WRIGLEY, D., OFFORD, C.A., ZIMMER, H.C., MACKENZIE, B.D., DUVAL, D., GUERIN, J., TE, T. & PARROTT, M.L. (2023). Ex situ responses to the 2019–20 wildfires. In: RUMPFF, L., LEGGE, S.M., VAN LEEUWEN, S., WINTLE, B.A. & WOINARSKI, J.C.Z. (EDS), *Biodiversity Impacts and Lessons from 2019–2020*, CSIRO Publishing, Clayton, pp. 357–373.

BIGGS, L.E. (2009). Mycorrhizal inoculation, endophytic colonization, and allelopathic potential of Wollemi Pine *(Wollemia nobilis)* roots. Unpublished PhD dissertation, University of British Columbia. doi: https://dx.doi.org/10.14288/1.0067721

BONGA, J.M. (2016). Conifer clonal propagation in tree improvement programs. Vegetative propagation of forest trees. In: PARK, Y-S., BONGA, J.M. & MOON, H-K. (EDS), *Vegetative Propagation of Forest Trees*, National Institute of Forest Science (NIFoS), Seoul, pp. 3–31.

BOWEN, M. & WHITMORE, T. (1980). A second look at Agathis. C.F.I. Occasional Papers No 13. Available online: https://ora.ox.ac.uk/objects/uuid:5bde6054-f8da-49ab-bf04-0a5293f21c55/files/md48fd65a2d9fa6935e5e109e2fc34808 (accessed 31 October 2024).

BULLOCK, S., SUMMERELL, B.A. & GUNN, L.V. (2000). Pathogens of the Wollemi pine, *Wollemia nobilis*. *Australasian Plant Pathology*, 29(3): 211–214.

BURROWS, G.E. (1999). Wollemi pine (*Wollemia nobilis*, Araucariaceae) possesses the same unusual leaf axil anatomy as the other investigated members of the family. *Australian Journal of Botany*, 47(1): 61–68. doi: https://doi.org/10.1071/BT97029

BURROWS, G.E. (2021). Gymnosperm resprouting – a review. *Plants*, 10(12): 2551. doi: https://doi.org/10.3390/plants10122551

BURROWS, G.E., DOLEY, D.D., HAINES, R.J. & NIKLES, D.G. (1988). In vitro propagation of *Araucaria cunninghamii* and other species of the Araucariaceae via axillary meristems. *Australian Journal of Botany*, 36(6): 665–676. doi: https://doi.org/10.1071/BT9880665

BURROWS, G.E., MEAGHER, P.F. & HEADY, R.D. (2007). An anatomical assessment of branch abscission and branch-base hydraulic architecture in the endangered *Wollemia nobilis*. *Annals of Botany,* 99(4): 609–623. doi: https://doi.org/10.1093/aob/mcm003

CAHILL, D.M., ROOKES, J.E., WILSON, B.A., GIBSON, L. & MCDOUGALL, K.L. (2008). *Phytophthora cinnamomi* and Australia's biodiversity: impacts, predictions and progress towards control. *Australian Journal of Botany*, 56(4): 279–310. doi: https://doi.org/10.1071/BT07159

CANADELL, J.G., MEYER, C.P., COOK, G.D., DOWDY, A., BRIGGS, P.R., KNAUER, J., PEPLER, A. & HAVERD, V. (2021). Multi-decadal increase of forest burned area in Australia is linked to climate

change. *Nature Communications*, 12(1): 6921. doi: https://doi.org/10.1038/s41467-021-27225-4

CHAMBERS, T.C., DRINNAN, A.N. & MCLOUGHLIN, S. (1998). Some morphological features of Wollemi pine (*Wollemia nobilis*: Araucariaceae) and their comparison to Cretaceous plant fossils. *International Journal of Plant Sciences*, 159(1): 160–171. doi: https://doi.org/10.1086/297534

COLLINS, L., BRADSTOCK, R.A., CLARKE, H., CLARKE, M.F., NOLAN, R.H. & PENMAN, T.D. (2021). The 2019/2020 mega-fires exposed Australian ecosystems to an unprecedented extent of high-severity fire. *Environmental Research Letters*, 16(4): 044029. doi: https://doi.org/10.1088/1748-9326/abeb9e

DANNER, M.A., RIBEIRO, J.Z., ZANETTE, F., BITTENCOURT, J.V.M. & SEBBENN, A.M. (2013). Impact of monoecy in the genetic structure of a predominately dioecious conifer species, *Araucaria angustifolia* (Bert.) O. Kuntze. *Plant Systematics and Evolution*, 299(5): 949–958. doi: https://doi.org/10.1007/s00606-013-0775-0

DAWSON, I. (1991). Plant Hardiness Zones for Australia. *Australian Horticulture,* 89(8): 37–39.

DÖRKEN, V.M. & RUDALL, P.J. (2019). Structure and abnormalities in cones of the Wollemi pine (*Wollemia nobilis*). *Kew Bulletin*, 74: 1–10. doi: https://doi.org/10.1007/s12225-018-9789-7

DRANSFIELD, J. (1997). Madagascar as a source of new palm introductions. In: *II International Symposium on Ornamental Palms & other Monocots from the Tropics* 486, pp. 21–32.

ESCAPA, I.H. & CATALANO, S.A. (2013). Phylogenetic analysis of Araucariaceae: integrating molecules, morphology, and fossils. *International Journal of Plant Sciences*, 174(8): 1153–1170. doi: https://doi.org/10.1086/672369

FENSOM, G. & OFFORD, C. (1997). Propagation of the Wollemi pine. *Combined Proceedings – International Plant Propagators' Society*, 47: 66–67.

FULLAWAY, D.T. (1972). Norfolk Island pine culture: collecting and storing seed, propagating, growing, harvesting, marketing. Available online: https://scholarspace.manoa.hawaii.edu/bitstream/10125/40983/1/norfolkculture.pdf (accessed 31 October 2024).

GOETEN, D., ROGGE-RENNER, G.D., SCHMIDT, É.C., BOUZON, Z.L., FARIAS-SOARES, F.L., GUERRA, M.P. & STEINER, N. (2020). Updating embryonic ontogenesis in *Araucaria angustifolia*: from Burlingame (1915) to the present. *Protoplasma*, 257: 931–948. doi: https://doi.org/10.1007/s00709-020-01481-5

GRACE, L., COOK, J., HARGREAVES, C., MEAGHER, P., MENZIES, M., OFFORD, C. & TRUEMAN, S. (2005). Somatic embryogenesis in Wollemi pine (*Wollemia nobilis*). In: *Proceedings of the 16th Biennial Meeting of the New Zealand Branch of the International Association for Plant Tissue Culture and Biotechnology*, Christchurch, p. 45.

GREENFIELD, A., MCPHERSON, H., AULD, T., DELANEY, S., OFFORD, C.A., VAN DER MERWE, M., YAP, J.Y.S. & ROSSETTO, M. (2016). Whole-chloroplast analysis as an approach for fine-tuning the preservation of a highly charismatic but critically endangered species, *Wollemia nobilis* (Araucariaceae). *Australian Journal of Botany*, 64(8): 654–658. doi: https://doi.org/10.1071/BT16105

HALLE, F., OLDEMAN, R.A.A. & TOMLINSON, P.B. (1978). *Tropical Trees and Forests, an Architectural Analysis*. Springer, Berlin–Heidelberg**.**

HARTMANN, H.T., KESTER, D.E & DAVIES, F.T. (1990). *Plant Propagation: Principles and Practices*. Prentice Hall, Englewood Cliffs, NJ.

HAWORTH, M., ELLIOTT-KINGSTON, C. & MCELWAIN, J.C. (2011). The stomatal CO_2 proxy does not saturate at high atmospheric CO_2 concentrations: evidence from stomatal index responses of Araucariaceae conifers. *Oecologia*, 167: 11–19. doi: https://doi.org/10.1007/s00442-011-1969-1

HEADY, R.D. & BURROWS, G.E. (2008). Features of the secondary xylem that facilitate branch abscission in juvenile *Wollemia nobilis*. *IAWA Journal*, 29(3): 225–236. doi: https://doi.org/10.1163/22941932-90000182

HILL, K.D. (1997). Architecture of the Wollemi pine (*Wollemia nobilis*, Araucariaceae), a unique combination of model and reiteration. *Australian Journal of Botany*, 45(5): 817–826. doi: https://doi.org/10.1071/BT96053

HNATIUK, R. (2023). Secondary branching in *Wollemia nobilis* (Araucariaceae), an unexpected occurrence. *Australian Journal of Botany*, 71(4): 216–222. doi: https://doi.org/10.1071/BT22049

IUCN (2024). *The IUCN Red List of Threatened Species*. Version 2024–2. Available online: https://www.iucnredlist.org (accessed 31 October 2024).

JOHNS, J.W., YOST, J.M., NICOLLE, D., IGIC, B. & RITTER, M.K. (2017). Worldwide hemisphere-dependent lean in Cook pines. *Ecology*, 98(9): 2482–2484. doi: https://doi.org/10.1002/ecy.1850

JONES, W.G., HILL, K.D. & ALLEN, J.M. (1995). *Wollemia nobilis*, a new living Australian genus in the Araucariaceae. *Telopea*, 6: 173–176. doi: https://doi.org/10.7751/telopea19953014

KERSHAW, P. & WAGSTAFF, B. (2001). The southern conifer family Araucariaceae: history, status, and value for paleoenvironmental reconstruction. *Annual Review of Ecology and Systematics*, 32(1): 397–414. doi: https://doi.org/10.1146/annurev.ecolsys.32.081501.114059

LAKE, J. (2000). 'Living fossil' set to become next trend. *Australian Horticulture*, 95(6): 41–44.

LANGENHEIM, J.H., OSMOND, C.B., BROOKS, A. & FERRAR, P.J. (1984). Photosynthetic responses to light in seedlings of selected Amazonian and Australian rainforest tree species. *Oecologia*, 63: 215–224.

LEWIS, J.D., PHILLIPS, N.G., LOGAN, B.A., SMITH, R.A., ARANJUELO, I., CLARKE, S., OFFORD, C.A., FRITH, A., BARBOUR, M., HUXMAN, T. & TISSUE, D.T. (2015). Rising temperature may negate the stimulatory effect of rising CO_2 on growth and physiology of Wollemi pine (*Wollemia nobilis*). *Functional Plant Biology*, 42(9): 836–850. doi: https://doi.org/10.1071/FP14256

MACKENZIE, B.D.E., CLARKE, S.W., ZIMMER, H.C., LIEW, E.C., PHELAN, M.T., OFFORD, C.A., MENKE, L.K., CRUST, D.W., BRAGG, J., MCPHERSON, H. & ROSSETTO, M. (2022). Ecology and conservation of a living fossil: Australia's Wollemi Pine (*Wollemia nobilis*). In: DELLASALA, D.A. & GOLDSTEIN. M.I. (EDS), *Imperiled: The Encyclopedia of Conservation*. Elsevier Science, Amsterdam, pp. 884-894. doi: https://doi.org/10.1016/B978-0-12-821139-7.00188-4

MACPHAIL, M., PARTRIDGE, A.D. & TRUSWELL, E. (1995). 'Wollemi Pine' – old pollen records for a newly discovered genus of gymnosperms. *Geology Today*, 11: 48–50.

MARTYN YENSON, A.J., COMMANDER, L.E., OFFORD, C.A. & MAKINSON, R.O. (2021). Introduction. In: MARTYN YENSON, A.J., OFFORD, C.A., MEAGHER, P.M., AULD, T., BUSH, D., COATES, D.J., COMMANDER, L.E., GUJA, L.K., NORTON, S.L., MAKINSON, R.O., STANLEY, R., WALSH, N. ET AL. (EDS), *Plant Germplasm Conservation in Australia: Strategies and Guidelines for Developing, Managing and Utilising ex situ Collections*, 3rd edn. Australian Network for Plant Conservation, Canberra, pp. 1–21.

MCGEE, P.A., BULLOCK, S. & SUMMERELL, B.A. (1999). Structure of mycorrhizae of the Wollemi pine (*Wollemia noblis*) and related Araucariaceae. *Australian Journal of Botany*, 47(1): 85–95. doi: https://doi.org/10.1071/BT97064

MCKENNEY, D.W., PEDLAR, J.H., LAWRENCE, K., CAMPBELL, K. & HUTCHINSON, M.F. (2007). Beyond traditional hardiness zones: using climate envelopes to map plant range limits. *BioScience*, 57(11): 929–937. doi: https://doi.org/10.1641/B571105

MEAGHER, P.F. & OFFORD, C.A. (2009). Understanding the Wollemi pine: strategies for conservation. In: BIELESKI, R.L. & WILCOX, M.D. (EDS), *Araucariaceae: Proceedings of the 2002 Araucariaceae Symposium, Araucaria-Agathis-Wollemia, IDS, Auckland, NZ 14–17 March 2002*. The International Dendrology Society, Dunedin, pp. 335–343.

MOGIE, M. (1992). *The Evolution of Asexual Reproduction in Plants*. Chapman & Hall, London.

NG, M.C., TRAN, V.H., DUKE, R.K., OFFORD, C.A., MEAGHER, P.F., CUI, P.H. & DUKE, C.C. (2024). Lipid profile of fresh and aged *Wollemia nobilis* seeds: Omega-3 Epoxylipid in older stored seeds. *Lipidology*, 1(2): 92–104. doi: https://doi.org/10.3390/lipidology1020007

NIU, Y., DU, J., ZHANG, Q., PEI, X. & ZHAN, X. (2013). An efficient axillary shoots induction system for the living fossil plant – Wollemi pine (*Wollemia nobilis*). *Forest Systems*, 22(3): 564–567. doi: https://doi.org/10.5424/fs/2013223-03997

NOLAN, R.H., BOER, M.M., COLLINS, L., RESCO DE DIOS, V., CLARKE, H., JENKINS, M., KENNY, B. & BRADSTOCK, R.A. (2020). Causes and consequences of eastern Australia's 2019–20 season of mega-fires. *Global Change Biology*, 26(3): 1039–1041. doi: https://doi.org/10.1111/gcb.14987

NSW NATIONAL PARKS AND WILDLIFE SERVICE (1998). *Wollemi Pine Recovery Plan*. NPWS, Sydney.

Available online: www.wollemipine.com/watch/Recovery_Plan.pdf (accessed 31 October 2024).

OFFORD, C.A. (1996). Conserving the Wollemi pine: an integrated approach. *Danthonia*, 5(2): 12–14. doi: https://doi.org/10.5962/p.374035

OFFORD, C.A. (2011). Pushed to the limit: consequences of climate change for the Araucariaceae: a relictual rainforest family. *Annals of Botany*, 108(2): 347–357. doi: https://doi.org/10.1093/aob/mcr135

OFFORD, C.A. & MEAGHER, P.F. (2001). Effects of temperature, light and stratification on seed germination of Wollemi pine (*Wollemia nobilis*, Araucariaceae). *Australian Journal of Botany*, 49(6): 699–704. doi: https://doi.org/10.1071/BT00061

OFFORD, C.A., MEAGHER, P.F. & ZIMMER, H.C. (2014). Growing up or growing out? How soil pH and light affect seedling growth of a relictual rainforest tree. *AoB Plants*, 6: plu011. doi: https://doi.org/10.1093/aobpla/plu011

OFFORD, C.A., MILLS, E., PERCIVAL, J., SHADE, A., TURNER, S.R., VILER, M. & WORBOYS, W. (2021). The role of the nursery in ex situ conservation. In: MARTYN YENSON, A.J., OFFORD, C.A., MEAGHER, P.M., AULD, T., BUSH, D., COATES, D.J., COMMANDER, L.E., GUJA, L.K., NORTON, S.L., MAKINSON, R.O., STANLEY, R., WALSH, N. ET AL. (EDS), *Plant Germplasm Conservation in Australia: Strategies and Guidelines for Developing, Managing and Utilising ex situ Collections*, 3rd edn. Australian Network for Plant Conservation, Canberra, pp. 241–278.

OFFORD, C.A., PORTER, C.L., MEAGHER, P.F. & ERRINGTON, G. (1999). Sexual reproduction and early plant growth of the Wollemi pine (*Wollemia nobilis*), a rare and threatened Australian conifer. *Annals of Botany*, 84(1): 1–9. doi: https://doi.org/10.1006/anbo.1999.0882

OFFORD, C.A. & ZIMMER, H.C. (2024). Home gardens contribute to conservation of the critically endangered Wollemi Pine: Evaluation of a botanic garden-led horticultural release programme. *Plants, People, Planet*, 6(1): 116–127. doi: https://doi.org/10.1002/ppp3.10410

PEAKALL, R., EBERT, D., SCOTT, L.J., MEAGHER, P.F. & OFFORD, C.A. (2003). Comparative genetic study confirms exceptionally low genetic variation in the ancient and endangered relictual conifer, *Wollemia nobilis* (Araucariaceae). *Molecular Ecology*, 12(9): 2331–2343. doi: https://doi.org/10.1046/j.1365-294X.2003.01926.x

POHIO, K.E., WALLACE, H.M., PETERS, R.F., SMITH, T.E. & TRUEMAN, S.J. (2005). Cuttings of Wollemi pine tolerate moderate photoinhibition and remain highly capable of root formation. *Trees*, 19: 587–595. doi: https://doi.org/10.1007/s00468-005-0418-3

PRICE, O.F., MIKAC, K., WILSON, N., ROBERTS, B., CRITESCU, R.H., GALLAGHER, R., MALLEE, J., DONATIOU, P., WEBB, J., KEITH, D.A. & LETNIC, M. (2023). Short-term impacts of the 2019–20 fire season on biodiversity in eastern Australia. *Austral Ecology*, 48(1): 3–11. doi: https://doi.org/10.1111/aec.13247

PUNO, V.I., LAURENCE, M.H., GUEST, D.I. & LIEW, E.C.Y. (2015). Detection of *Phytophthora multivora* in the Wollemi Pine site and pathogenicity to *Wollemia nobilis*. *Australasian Plant Pathology*, 44: 205–215. doi: https://doi.org/10.1007/s13313-014-0344-1

RIGG, J.L., OFFORD, C.A., SINGH, B.K., ANDERSON, I.C., CLARKE, S. & POWELL, J.R. (2016a). Soil microbial communities influence seedling growth of a rare conifer independent of plant–soil feedback. *Ecology*, 97(12): 3346–3358. doi: https://doi.org/10.1002/ecy.1594

RIGG, J.L., OFFORD, C.A., SINGH, B.K., ANDERSON, I.C., CLARKE, S. & POWELL, J.R. (2016b). Variation in soil microbial communities associated with critically endangered Wollemi pine affects fungal, but not bacterial, assembly within seedling roots. *Pedobiologia*, 59(1–2): 61–71. doi: https://doi.org/10.1016/j.pedobi.2016.01.001

RIGG, J.L., OFFORD, C.A., ZIMMER, H., ANDERSON, I.C., SINGH, B.K. & POWELL, J.R. (2017). Conservation by translocation: establishment of Wollemi pine and associated microbial communities in novel environments. *Plant and Soil*, 411: 209–225. doi: https://doi.org/10.1007/sl1104-016-3010-2

SELWOOD, K.E. & ZIMMER, H.C. (2020). Refuges for biodiversity conservation: A review of the evidence. *Biological Conservation*, 245: 108502. doi: https://doi.org/10.1016/j.biocon.2020.108502

SLIPPERS, B., SUMMERELL, B.A., CROUS, P.W., COUTINHO, T.A., WINGFIELD, B.D. & WINGFIELD,

M.J. (2005). Preliminary studies on *Botryosphaeria* species from Southern Hemisphere conifers in Australasia and South Africa. *Australasian Plant Pathology*, 34: 213–220. doi: https://doi.org/10.1071/AP05020

STEVENSON, D.W., RAMAKRISHNAN, S., DE SANTIS ALVES, C., COELHO, L.A., KRAMER, M., GOODWIN, S., RAMOS, O.M., ESHEL, G., SONDERVAN, V.M., FRANGOS, S. & ZUMAJO-CARDONA, C. (2023). The genome of the Wollemi pine, a critically endangered 'living fossil' unchanged since the Cretaceous, reveals extensive ancient transposon activity. *bioRxiv*. doi: https://doi.org/10.1101/2023.08.24.554647

SUMMERELL, B.A. & LIEW, E.C. (2020). Phytophthora root rot: its impact in botanic gardens and on threatened species conservation. *Sibbaldia*, 18: 89–104. doi: https://doi.org/10.24823/Sibbaldia.2020.290

TOMPSETT, P.B. (1984). Desiccation studies in relation to the storage of Araucaria seed. *Annals of Applied Biology*, 105(3): 581–586. doi: https://doi.org/10.1111/j.1744-7348.1984.tb03085.x

TRETYAKOVA, I.N. & MINEEV, V.V. (2021). Reproductive potential of conifers, somatic embryogenesis and apomixis. *Russian Journal of Developmental Biology*, 52: 75–86. doi: https://doi.org/10.1134/S1062360421020089

TRUEMAN, S.J., PEGG, G.S. & KING, J. (2007). Domestication for conservation of an endangered species: the case of the Wollemi pine. *Tree and Forestry Science and Biotechnology*, 1: 1–10.

TRUEMAN, S.J. & PETERS, R.F. (2006). Propagation of Wollemi pine from tip cuttings and lower segment cuttings does not require rooting hormones. *Scientia Horticulturae*, 109(4): 394–397. doi: https://doi.org/10.1016/j.scienta.2006.05.011

WHITMORE, T.C. (1977). A first look at Agathis. Tropical Forestry Papers No 11. Unit of Tropical Silviculture, Commonwealth Forestry Institute, University of Oxford.

WOODFORD, J. (2005). *The Wollemi Pine: the Incredible Discovery of a Living Fossil from the Age of the Dinosaurs*. Text Publishing, Melbourne.

YAP, J.Y.S., ROHNER, T., GREENFIELD, A., VAN DER MERWE, M., MCPHERSON, H., GLENN, W., KORNFELD, G., MARENDY, E., PAN, A.Y., WILTON, A. & WILKINS, M.R. (2015). Complete chloroplast genome of the Wollemi pine (*Wollemia nobilis*): structure and evolution. *PloS One*, 10(6): p.e0128126. doi: https://doi.org/10.1371/journal.pone.0128126

ZIMMER, H.C., AULD, T.D., BENSON, J. & BAKER, P.J. (2014). Recruitment bottlenecks in the rare Australian conifer *Wollemia nobilis*. *Biodiversity and Conservation*, 23: 203–221. doi: https://doi.org/10.1007/s10531-013-0593-2

ZIMMER, H.C., BRODRIBB, T.J., DELZON, S. & BAKER, P.J. (2016a). Drought avoidance and vulnerability in the Australian Araucariaceae. *Tree Physiology*, 36(2): 218–228. doi: https://doi.org/10.1093/treephys/tpv111

ZIMMER, H.C., MEAGHER, P.F., AULD, T.D., PLAZA, J. & OFFORD, C.A. (2015). Year-to-year variation in cone production in *Wollemia nobilis* (Wollemi pine). *Cunninghamia*, 15: 79–85. doi: https://doi.org/10.7751/cunninghamia.2015.15.004

ZIMMER, H. & OFFORD C. (2019). Backyard gardeners around the world are helping to save Australia's deeply ancient Wollemi pine. *The Conversation*. Available online: https://theconversation.com/backyard-gardeners-around-the-world-are-helping-to-save-australias-deeply-ancient-wollemi-pine-138797 (accessed 31 October 2024).

ZIMMER, H.C., OFFORD, C.A., AULD, T.D. & BAKER, P.J. (2016b). Establishing a wild, ex situ population of a critically endangered shade-tolerant rainforest conifer: A translocation experiment. *PLoS One*, 11(7): e0157559. doi: https://doi.org/10.1371/journal.pone.0157559