

Year-to-year variation in cone production in *Wollemia nobilis* (Wollemi Pine)

Heidi C. Zimmer¹, Patricia F. Meagher², Tony D. Auld³, Jaime Plaza⁴ and Catherine A. Offord²

¹Department of Forest and Ecosystem Science, University of Melbourne, Richmond, Victoria 3121 AUSTRALIA.

²The Australian PlantBank, The Royal Botanic Gardens and Domain Trust, The Australian Botanic Garden, Mount Annan, NSW 2567 AUSTRALIA.

³NSW Office of Environment and Heritage, P.O. Box 1967, Hurstville, NSW 2220 AUSTRALIA.

⁴The Royal Botanic Gardens and Domain Trust, Mrs Macquaries Rd, Sydney, NSW 2000 AUSTRALIA.

Abstract: Seed production varies from year-to-year in most species. Factors influencing this variation can include pollination and dispersal mechanisms, seed predation and resource availability. Here we examine a long-term (12– year) photographic record of seed cone production for the Australian endemic conifer *Wollemia nobilis* (Araucariaceae). Coefficient of variation (a commonly used measure of variation in seed production) was low for the two trees analysed, compared with published values for other polycarpic plants. Nevertheless, cone production decreased with increasing spring minimum temperatures (during pollination) and increased with summer total rainfall (during cone initiation). Hence, *Wollemia nobilis* cone production was correlated with weather, in line with the resource-matching hypothesis. Impacts of variation in cone production on the *Wollemia nobilis* population are likely to be buffered by the shade-tolerant, slow-growing juvenile life stage of *Wollemia nobilis*.

Keywords: Araucariaceae, climate, masting, weather, Wollemi National Park.

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Introduction

Most woody plants that produce seed many times in their lifetime (polycarpic plants) show variation in seed production from year-to-year (Herrera et al. 1998). Mast seeding is one extreme, and is defined as seed production that is highly variable, with synchronous production of large seed crops (Janzen 1971, Silvertown 1980, Norton and Kelly 1988, Kelly 1994). However, the existence of masting has been a source of debate, because of the difficulty in defining each year as either mast or non-mast, and determining how many individuals must show similar variation in seed production to achieve synchronicity (Kelly 1994, Herrera et al. 1998).

Factors that promote increased variation in seed production are wind pollination and seed predation, while decreased variation can be affected by animal dispersal and pollination (Kelly and Sork 2002). For example, seed production in wind-pollinated species is more variable than in animal-pollinated species (Herrera et al. 1998). This is because a synchronous increase in pollen production in wind-pollinated plants increases the probability of pollination (the wind pollination hypothesis, Kelly 1994; Nilsson and Wastjung 1987; Smith et al. 1990; Kelly et al. 2001). Alternatively, species responding to seed predation produce large numbers of seeds in some years, so that seed predators are satiated, and more seeds survive. Low numbers of seeds

are then produced in intervening years, so that seed predators are starved and hence predator populations decrease (Janzen 1971; Silvertown 1980). In contrast, species with animal-dispersed seeds typically show lower variability in seed production, as consistency in fruit production is maintained to support the population of the disperser animal (Janzen 1971, Herrera *et al.* 1998).

When these influences promoting high or low seed variation are absent, seed production will vary with environmental conditions (i.e., weather; Kelly 1994, Kelly and Sork 2002). The resource-matching hypothesis suggests that investment in reproduction (i.e., seed production in plants) is influenced by resource availability, which is influenced by the weather (Kelly 1994). Although resource matching is the simplest explanation for variation in seed production, it has been highlighted that the variation in weather is often not as great as the variation in seed production (Koenig *et al.* 2003, Kelly and Sork 2002), suggesting complexity in this relationship and, or the influence of other factors.

Significant synchronicity in seed production is known to occur in members of the Araucariaceae family (Enright and Hill 1995, Sanguinetti and Kitzberger 2008, Souza *et al.* 2010, Rigg *et al.* 2010). Year-to-year variation in seed-bearing female strobili (hereafter ‘cone’ for brevity and simplicity) production of *Wollemia nobilis* (Wollemi Pine) family Araucariaceae, is not known. Yet, seed production is likely to be important in maintaining the population of slow-growing, shade-tolerant juvenile *Wollemia nobilis* plants that exist in the understorey below the mature *Wollemia nobilis* trees (Zimmer *et al.* 2014). *Wollemia nobilis* is of high conservation value and is a State- and Federally-listed threatened species (NSW Department of Environment and Conservation 2006). It was discovered only in 1994 and within 200 km of Sydney, Australia. *Wollemia nobilis* is a long-lived tree, and is wind-pollinated, producing male and female cones on one plant (i.e. monoecious). Its seeds are generally dispersed by gravity, wind or water. Some dispersal by birds, which also feed on and destroy the seeds, may also occur. *Wollemia nobilis* seed viability is low, around 10%

Table 1. Timing of *Wollemia nobilis* cone development and growth.

Season	Lag (years)	Female cone	Male cone	Vegetative
Spring	-3			Growing
Summer	-2	Initiation	Initiation	
Autumn	-2			
Winter	-2			
Spring	-2	Pollination	Maturation	Growing
Summer	-1			
Autumn	-1			
Winter	-1			
Spring	-1	Fertilization		Growing
Summer	0			
Autumn	0	Seed fall		

(Offord *et al.* 1999; low viability has been recorded for other Araucariaceae e.g. Enright *et al.* 1999, Kettle *et al.* 2008). Seedling germination and initial survival is also low, and new seedling emergence is variable (Zimmer *et al.* 2014). Collection of year-to-year seed (cf. cone) production data in this species is difficult due to the inherent problems of inaccessibility and rarity. Regardless, it has been suggested that the rate of viable seed production varies (Offord *et al.* 1999; although the observed viability rate is also likely to be influenced by the date of sampling).

In this study seed cone production was estimated using a series of annual photos to explore annual seed production in *Wollemia* and to explore the following questions-

How much does *Wollemia nobilis* cone production vary from year-to-year?

Is cone production correlated among individual *Wollemia nobilis* trees?

Is variation in *Wollemia nobilis* cone production correlated with weather, in particular temperature and rainfall?

Methods

Photography and data collection

High-resolution photos of mature *Wollemia nobilis* tree canopies (e.g. Figure 1) were taken from permanent photo points at Site 1 (Benson and Allen 2007). Photos were taken every year, from 2002 to 2014 (except 2007). Photography, in late summer/early autumn (February–March), was timed to capture cone maturation. New female cones can first be seen in summer (with the naked eye), around two years before maturation, they are pollinated the following spring, fertilized in spring one year after that, and mature late in the following summer (Table 1). In several years (2002, 2003, 2005) photographs were also taken in October. This allowed us to check mature female cone counts, as unfertilized cones are markedly smaller than fertilized cones. Photos were taken with different cameras as technology improved (i.e., from film to digital). To begin with, photographs were taken with a Linhof 4” x 5” view camera and a 150 mm lens, while the later photos were taken with an Olympus EM-5 camera.

From these high-resolution photos we counted mature female cones (including newly shattered cones) on two individual trees, Trees 1 and 19. These trees were chosen because they were closest to the photography point, and the only trees where clear identification of cones (and differentiation among individual trees) was possible. In addition, identification of individual trees was clear, whereas photos of other parts of the site had trees with overlapping crowns. The mature female cone counts (hereafter cone counts) from Trees 1 and 19 constitute an index of cone production, as only the facing side of the tree can be seen. The same area of each tree was counted in every year (i.e. the area hidden by foliage from other trees that had grown up by 2014 was removed from counts for previous years).



Fig. 1. Photograph of the top of Tree 19 in summer, showing mature female cones (mid-section; brown colour) and the immature next year's cohort (top section; green colour). Photo: Jaime Plaza.

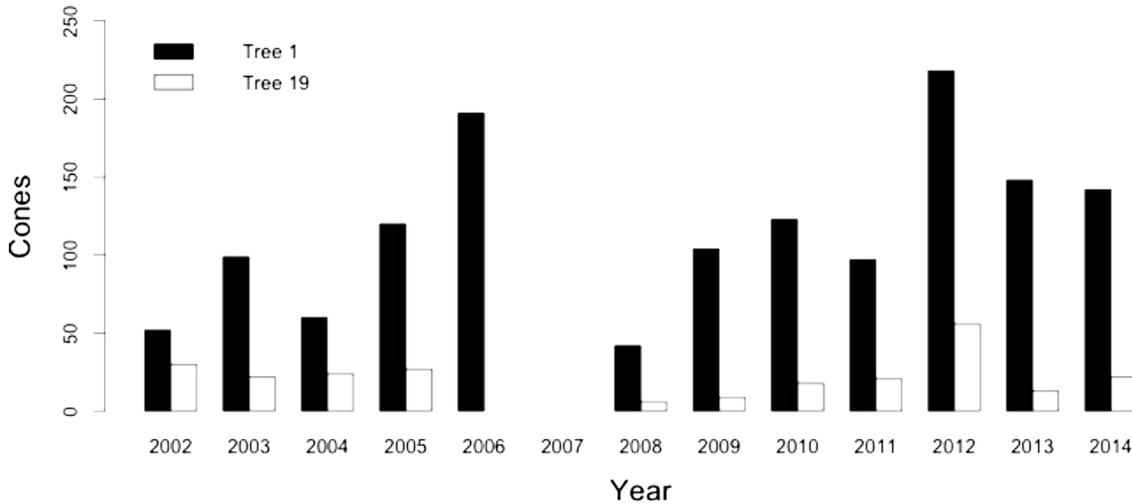


Fig. 2. Mature female cone production in Tree 1 and Tree 19 from 2002 to 2014. Photographs were taken in May 2002, March 2003, March 2004, March 2005, March 2006, January 2008, January 2009, January 2010, March 2011, March 2012, February 2013 and February 2014. There was no sampling in 2007 and no data for Tree 19 in 2006.

Statistical analyses

Correlation in cone counts between Tree 1 and Tree 19 was assessed using Spearman’s rank tests. Coefficient of variation (CV) in cone counts for each tree was calculated as the standard deviation divided by the mean. CV is a commonly used measure of year-to-year variation in seed production (Silvertown 1980; Kelly 1994; Herrera *et al.* 1998). CV is useful as a simple indicator of year-to-year variation. It is independent of the mean (McArdle and Gaston 1995), and therefore tree/population size. Most commonly CV is calculated to assess population-level year-to-year variation in seed crop (i.e., mean and standard deviation of total population seed output, Herrera 1998). In our study, single tree CVs are being used to indicate population-level variability, and comparison of cone counts between these two trees is being used as an indicator for synchronicity. We acknowledge that our sample size is small; this is why our conclusions are tentative.

Spearman’s rank tests were used to assess correlations between Tree 1 cone counts and weather. Tree 1 was selected for analysis because it had the longest data set, including two high cone count years. Cone count was correlated with weather factors for each season: (1) mean maximum temperature, (2) mean minimum temperature, (3) maximum temperature, (4) minimum temperature, (5) lowest maximum temperature (6) highest minimum temperature and (7) total rainfall. Seasons were summer (December – February), autumn (March – May), winter (June – August) and spring (September – November).

Cone development occurs over approximately two years (Table 1). Hence, the correlation between cone count and each weather factor was analysed for: the summer in which cone maturation occurred (summer₀; *n* = 7), the four seasons

before cone maturation (season₁; *n* = 28), the four seasons after initiation (season₂; *n* = 28) and the spring immediately before cone initiation (spring₃; *n* = 7). Because this was an exploratory study, multiple comparisons of the cone production data were made with the weather factors. For this reason, the probability of Type 1 errors (false positives) was increased, so *P*-values are not presented (all non-significant). Climate data were from Bureau of Meteorology (2014) from a weather station near the study site. Weather at the two sites is closely correlated (unpublished data). All analyses were completed using R (Version 3.03, R Core Team 2013).

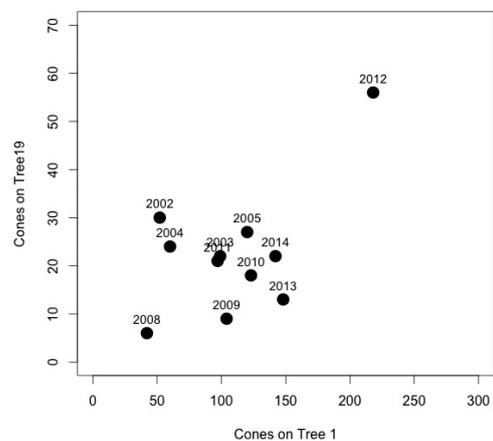


Fig. 3. Correlation between cone production in Tree 1 and Tree 19. Note axes scales differ.

Results

Cone counts varied from year-to-year and coefficients of variation were 0.45 and 0.58 for Tree 1 and Tree 19, respectively. Tree 1 cone count ranged from 42 to 218, while cone count for the smaller Tree 19 ranged from six to 56. The highest cone count for both trees was in 2012 (Figure 2), the second highest was in 2006 for Tree 1 (photos were not taken of Tree 19 in 2006). The correlation between year-to-year variation in cone count between the two trees was low ($\rho = 0.164$), although their lowest and highest cone count years were the same (Figure 3).

The strongest correlation between cone count and weather factors was with minimum temperature in spring₂ ($\rho = -0.76$), while the second strongest correlation with temperature was with spring₁ highest minimum temperature ($\rho = 0.62$). Hence, there were more cones when minimum temperatures were lower during pollination, and when minimum temperatures were higher during fertilization.

The highest correlation for rainfall was with summer₂ rainfall ($\rho = 0.67$). When rainfall increased during this period (which includes cone initiation), so did the number of cones.

Discussion

Year-to-year variation in *Wollemia nobilis* cone production was low (CV = 0.45 and 0.58 for mature female cones on two trees) compared to other polycarpic trees (Kelly 1994, Herrera et al. 1998). Reviews indicate that most plants have coefficients of variation for seed production between 0.8 and 1.2 (Kelly 1994, review of 42 datasets; Herrera et al. 1998, review of 296 datasets, mean CV = 1.2). Variation in CV does not differ significantly between gymnosperms and angiosperms (Herrera et al. 1998). Coefficients of variation higher than two have been recorded, such as 2.12 for *Nothofagus solandri* in New Zealand (Kelly et al. 2001). Alternatively, CVs lower than 0.4 are probably under-reported (Kelly 1994).

There was some evidence for synchronicity in cone counts between the two *Wollemia nobilis* in this study: the trees shared highest and lowest cone production years, but cone counts in other years were poorly correlated. Causes of between-year correlation for individual trees, apart from size, may include the number and size of neighbours (Haymes and Fox 2012). Cone production was consistently higher in Tree 1, the larger of the two trees and the dominant tree at the site. In addition, we know that the number of viable seeds per *Wollemia nobilis* cone varies (Offord et al. 1999), but we do not know whether the numbers of viable seeds increase when the number of cones increases; this is an important limitation of our study. In our discussion of influences on cone production, we assume that increased cone production results in increased seed production. This is an informed assumption. An 18-year seed collection dataset for *Araucaria araucana* describing regional-scale, year-to-year synchronicity in seed production, showed higher seed numbers and viabilities in high cone production years

(Sanguinetti and Kitzberger 2008). Notably, mean CV here was 1.16.

What causes variation in cone production in *Wollemia nobilis*? The most likely explanation is variation in resource availability, which is in turn influenced by weather (i.e. the resource-matching hypothesis). But the relationship between cone production and weather was not straightforward. As *Wollemia nobilis* growing season is in spring, a simple indicator of resource matching would have been strong correlations with temperature in spring before cone initiation (spring₃), as temperature controls photosynthesis and growth. While this was not the case, there was a strong correlation with rainfall during cone initiation (summer₂, $\rho = 0.67$). Where rainfall increased, so did the number of cones. On the other hand, temperature during pollination (when male cones are maturing and female cones are becoming receptive) showed the strongest correlation of any weather factor ($\rho = -0.76$).

Correlations with temperature during flower and cone initiation are usually attributed to temperature acting as a synchronizing cue, rather than directly influencing resource availability (Ashton et al. 1988, Norton and Kelly 1998, Schauber et al. 2002). The correlation between temperature during pollination and *Wollemia nobilis* cone production is difficult to explain as the cones were already initiated, and we do not have the data to quantify year-to-year variation in cone abortion. Increasing cone count with decreasing temperatures during pollination may indicate that a temperature-sensitive process is occurring at this time. Our conclusions about causes of variation in cone production are tentative because of our very small sample size.

Low variability in seed production fits with having a slow-growing, shade-tolerant bank of juveniles (as in *Wollemia nobilis*, Zimmer et al. 2014). Similar to species that maintain a soil seed bank (*sensu* Nathan and Muller-Landau 2000), the influence of variability in seed production on the population is reduced in species that maintain a juvenile bank. A further benefit of having a juvenile bank is that these juveniles are available to take advantage of increased resource availability when it occurs (e.g., via gap formation). This is different to species that do not maintain a juvenile bank (or soil seed bank), and rely on increased seed to produce more seedlings in favourable conditions. Interestingly, the limited records of seedling germination of *Wollemia nobilis* do not show increased seedling numbers after high cone counts, supporting the idea that seed availability is not always the main factor limiting the establishment of new *Wollemia nobilis* seedlings. Specifically, the highest *Wollemia nobilis* germination from 2001–2005 was in 2005, more than double the number of new seedlings of the next highest year (Zimmer et al. 2014), whereas cone production in 2005 was only slightly above the mean. *Wollemia nobilis* seedling recruitment is likely to be limited at multiple stages, not only seed availability (including seed viability), but also seed dispersal, seedling survival, growth and establishment (Clark et al. 1998). For example, research indicates that temperature and water availability influence *Wollemia nobilis* germination (Offord and Meagher 2001), growth and survival (Offord 2011). Limiting factors may vary from year-

to-year, with seed availability limiting in some years, and microsite availability in others (Eriksson and Ehrlen 1992). However, long-term changes to climate may be less able to be buffered by the juvenile bank.

Other factors that could influence variation in seed production are wind pollination and seed predation. We have observed an abundance of *Wollemia nobilis* pollen in the aerial environment during pollen release, and subsequently on cone scales under a light microscope (C. Offord and P. Meagher, pers. obs). No specific seed predators of *Wollemia nobilis* are known, but during the study by Offord *et al.* (1999) 25% of the seeds in seed traps were damaged by seed predators. Damage was attributed to animals, including insects (Offord *et al.* 1999). The high numbers of easily accessible seed in the nets may have attracted more predators than usual. Several seed-eating birds have been sighted near the *Wollemia nobilis* grove (S. Clarke, pers. obs). However, these birds are likely to forage widely, and their predation is unlikely to influence variability in seed production (Kelly *et al.* 2002).

Conclusion

Wollemia nobilis cone production shows low variability from year-to-year, and there was limited evidence for synchronicity between the two trees examined. Our results are tentative, because of this small sample size, but we found that cone production was most strongly correlated with summer₂ rainfall during cone initiation, and minimum temperatures in spring₂, during pollination. Availability of resources related to weather provides one explanation for variation in cone production. If cone production is influenced by weather, then future changes to climate, such as increased spring minimum temperatures, or decreased summer rainfall could negatively impact *Wollemia nobilis* cone production. The maintenance of a bank of juvenile *Wollemia nobilis* plants means that the impact of variation in seed input from year-to-year is reduced (compared with species reliant on annual germination to maintain a supply of recruits); however sustained changes to climate may have a greater effect.

Future research

This study has highlighted our knowledge gap around the relationship between *Wollemia nobilis* cone production and seed viability and we would like to raise the following questions for future research:

Is there a correlation between seed cone production and viable seed production? The work of Offord *et al.* (1999) needs to be extended.

Is variation in male cone production synchronous with variation in female cone production? A photographic record of cone production in October is required.

Is variation in male cone production accompanied by variation in pollen viability?

When does meristem initiation for *Wollemia nobilis* cones occur in the wild? If we knew exactly when cones were initiated we would be better able to target investigation of weather effects.

Could seed production in *Wollemia nobilis* be ovule limited? Ovule limitation occurs when all ovules are fertilised, but there are too few zygotes to completely use available resources (Harder and Routley 2006).

How common is self-fertilisation in *Wollemia nobilis*? Does selfing lead to fewer viable seeds? Or, is there differential development of self-fertilised to outcrossed embryos to maturity? If selfed seeds are less likely to be viable, this would promote among-species synchronicity in seed production.

Is *Wollemia nobilis* pollen limited in the wild? Anecdotal observation suggests that pollen is abundant, but experimental work, especially around levels of pollen viability, is lacking.

At what rate do *Wollemia nobilis* embryos and cones abort after initiation? Is this influenced by pollen availability and or successful pollination? And is pollination and fertilisation success affected by temperature?

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