Journal of Tropical Ecology (2006) **22**:621–629. Copyright © 2006 Cambridge University Press
doi:10.1017/S0266467406003464 Printed in the United Kingdom

Does tree size influence timing of flowering in *Cerberiopsis candelabra* (Apocynaceae), a long-lived monocarpic rain-forest tree?

Jennifer Read*[1], Gordon D. Sanson*, Tanguy Jaffré† and Martin Burd*

* School of Biological Sciences, Monash University, Victoria 3800, Australia
† IRD – Laboratoire de Botanique et d'Écologie Végétale Appliquée, Institut de recherche pour le développement, Centre de Nouméa, B.P. A5 Nouméa – 98848, New Caledonia

(*Accepted 14 May 2006*)

Abstract: *Cerberiopsis candelabra* is a long-lived monocarpic rain-forest tree endemic to New Caledonia that shows mass flowering across a substantial proportion of a population, and across a substantial number of populations. We investigated the relationship between tree size and flowering (and subsequent dying) across 18 populations from the flowering event of 2003 in order to understand the role of possible size thresholds for flowering in the life history and regeneration ecology of this monocarpic species. There was a strong positive correlation between trunk diameter and the incidence of flowering when population data were combined. However, the relationship between size and flowering was complex in that flowering occurred across a wide range of tree sizes, with almost complete overlap in size between flowering (5–79 cm dbh) and non-flowering trees (5–64 cm dbh), and with large trees in both the flowering and non-flowering state in the same population. In about half the populations studied there was no significant difference in mean trunk diameter of flowering and non-flowering trees. Nonetheless, we suggest that tree size may play a fundamental role in the life history and regeneration ecology of this species. The seedlings appear to be relatively shade-intolerant and dependent on large canopy gaps for recruitment. A significant effect of mass flowering and subsequent death of multiple large trees is the potential to form large canopy gaps and enhance seedling survival, as the gap is temporally linked with seed germination. However, it is unclear why there is such a large size range of flowering trees, i.e. whether this is just a consequence of the proximate cue, or whether the optimal size for flowering does indeed vary among individuals.

Key Words: delayed reproduction, mass flowering, masting, monocarpy, New Caledonia, plant life history, reproductive strategy, semelparity

INTRODUCTION

Cerberiopsis candelabra Vieillard ex Pancher & Sébert (Apocynaceae) is a long-lived monocarpic (=semelparous) tree, i.e. it flowers once then dies. It also shows mass flowering, with flowering synchronous across a substantial proportion of a population, and across many populations. This is an unusual life history for a long-lived tree, with monocarpy known in only four genera of such trees and an uncertain number of species (*c.* 30) (Poorter *et al.* 2005, Whitmore 1998). This 'suicidal' strategy (Foster 1977) does not seem adaptive for a long-lived tree since it takes a risk in putting its whole reproductive effort into a single period that may prove to be unfavourable for seedling recruitment. However, there are several factors that may reduce this risk. For example, *C. candelabra* is endemic to a region that experiences a relatively equable tropical climate. It grows in the central mountain ranges and the south of the main island of New Caledonia which experience a high rainfall, other than a 2–3-mo dry season of variable severity. It is unlikely to experience severe climatic stress through most of its range unless there is a particularly harsh dry season during the first years of seedling growth. Opportunities for recruitment may instead be limited largely by competition with other species. However, synchronous death of many parent trees following reproduction may provide large, long-lasting canopy gaps suited to establishment and rapid growth of their seedlings, thereby increasing their chance of recruitment to the canopy.

This species is not rare, and hence its monocarpic and mass flowering strategy is successful. However, it has

---

[1] Corresponding author. Email: Jenny.Read@sci.monash.edu.au

almost died out on one of our rain forest permanent plots where it was a major species until 1996 (unpubl. data), raising questions regarding its regeneration ecology and the advantage of its life history in this environment. The adaptive significance of both monocarpy and mass flowering in a long-lived tree is uncertain. Basic life history theory suggests that the greater the ratio of juvenile to adult survival rates, the more favourable monocarpy becomes (Charnov & Schaffer 1973). Consistent with this theory, Kitajima & Augspurger (1989) found that the monocarpic rain-forest tree *Tachigali versicolor* (native to central America) has, relative to co-occurring polycarpic (=iteroparous) species, high seed mass, dispersal capability, photosynthetic flexibility and probability of seedling survival in its first few years. In contrast, Poorter *et al.* (2005) found that while seedlings of the monocarpic *T. vasquezii* from the Bolivian Amazon have a higher survival rate than co-occurring polycarpic species, rates of sapling mortality are high.

Foster (1977) suggested that delayed reproduction associated with monocarpy allows *T. versicolor* to achieve rapid growth rates. But Poorter *et al.* (2005) found that the success of *T. vasquezii* may be related to earlier reproduction compared with the polycarpic strategy, rather than deriving from delayed reproduction; investment in large leafy crowns and low-cost wood of low density allows rapid pre-reproductive growth, an earlier onset of reproduction and thus an increased probability of reaching reproductive maturity. Hence the potentially negative effects of a once-only flowering strategy may be offset by advanced reproduction (Poorter *et al.* 2005).

Foster (1977) also suggested that death of an adult *T. versicolor* tree may facilitate recruitment of its own offspring into the canopy gaps created. Such a process is unlikely on its own to favour the evolution of monocarpy, much as 'suicide' through self-flammability is unlikely to be favoured by individual selection (Zedler 1995), but it may be a contributing factor to the selective advantage of a monocarpic life history in a canopy tree species.

In contrast to *T. vasquezii*, *C. candelabra* shows mass flowering. This trait, together with apparently poor recruitment of *C. candelabra* seedlings within the rain forest, suggests differences in the mechanisms by which these monocarpic species remain competitive in forests of polycarpic species. Little is known of the ecology of *C. candelabra*, other than studies by Veillon (1971) that focus on its architecture and the flowering events of 1967 and 1969. It is not clear what triggers flowering, since *C. candelabra* is commonly gregarious with only some trees of a population flowering during any mass flowering event, and it is not known how it responds in terms of recruitment. Because the reproductive ecology of *C. candelabra* is so poorly known, we took advantage of a mass flowering of this species observed in November–December 2003 across the south of the main island of New Caledonia to characterize the difference between reproductive and non-reproductive trees, and returned in 2004 to record mortality and establish permanent plots. Here we report on diameter distributions of flowering (and subsequently dying) and non-flowering trees across 18 populations, in order to investigate the extent to which tree size influences the occurrence of flowering within a population. We then discuss the potential role of tree size in the life history of this monocarpic tree.

METHODS

Characteristics of *Cerberiopsis candelabra*

Cerberiopsis candelabra var. *candelabra*, referred to henceforth as *C. candelabra*, is a tall tree (up to *c.* 30 m tall) found in the upper canopy of rain forests. The other variety, *C. candelabra* var. *vexillaria* is a small tree to *c.* 4 m high, apparently confined to one small island (Boiteau & Allorge 1981). We have not seen this variety, and will not consider it further. The two other *Cerberiopsis* species (*C. obtusifolia* and *C. neriifolia*) are polycarpic. *Cerberiopsis candelabra* occurs only on ultramafic soils (typically with high levels of metals such as Fe and Ni, and low levels of P, K and Ca: Jaffré 1992, Read *et al.* 2006) which cover one-third of the main island (Figure 1). However, it occurs across a range of these soils, from hypermagnesian to ferritic ferralitic soils, and from eroded soils on slopes and ridges to colluvial and alluvial soils. It grows in lowland coastal rain forest near sea level and up to *c.* 400–500 m asl on the massifs. It is most common in the south of

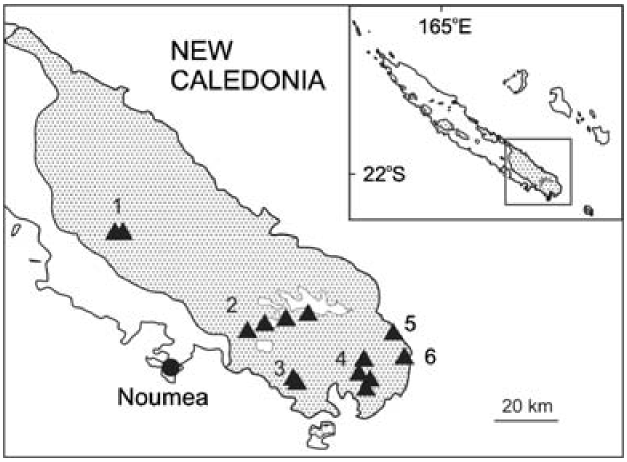

Figure 1. A map of New Caledonia showing the location of study sites (triangles). The stippled area indicates the distribution of peridotite. 1, Tontouta (sites 1–4); 2, (east to west) Mouirange, Col de Mouirange, Col de Deux Tétons, Forêt Caché; 3, Col de N'Go; 4, (north to south) Aerodrome (2 sites), Pic du Grand Kaori, Forêt Stephane, Forêt Nord (2 sites); 5, St Raphael; 6, Kuebini.

the main island where ultramafic soils predominate, with isolated occurrences in the north-east.

We witnessed mass flowering events in 1996 and 2003. Herbarium records show flowering events from 1868 to 1984, with an average of 6 y between flowering events from 1903 to 2003 (but specimens have not necessarily been lodged from each flowering event). The only exceptions we have seen to fatal flowering were several trees in which flowering was restricted to a single branch, a phenomenon also reported by Veillon (1971). In those cases the flowering branch died, but the tree remained alive (also recorded in *Tachigali versicolor*: Foster 1977). We have seen only two trees flowering in non-mast years, following damage to the main trunk (by fire and by impact from another falling tree). Since isolated flowering can occur, not all herbarium specimens may represent mass flowering events, and so the average frequency of these events remains tentative. Flowering tends to occur in the drier season (August to December), with all apical meristems differentiating to produce terminal paniculate inflorescences (Veillon 1971). The flowers are white and perfumed, and green immature winged fruits develop after *c.* 1 mo, with the large dry brown fruits containing a single seed dispersing about 1 mo later (Veillon 1971). The fruits are heavy and although winged most fall below the parent (Veillon 1971).

Study sites and data collection

We established 18 plots in forests containing *C. candelabra* in November–December 2004, across a range of environments in terms of location (Figure 1), topography and vegetation composition, from the coast (*c.* 20 m asl) to lower mountain slopes (320 m asl). All study plots were in separate patches of forest except those at Forêt Nord and Aerodrome, where two populations were sampled, separated from each other by *c.* 500 m of rain forest in which *C. candelabra* was rare or absent. Some stands at Tontouta were closer to each other (*c.* 100–400 m separation), but separated by contrasting vegetation (shrub-dominated) or by a river. We treat all plots as separate stands. In these plots, ranging from 300 m^2 to 1 ha, we measured trunk diameters at breast height (dbh, at 1.3 m above ground) of all individuals of *C. candelabra* $\geq$ 5 cm dbh, noting whether trees were alive, or had flowered and died. Some trees were still standing that had died from an earlier flowering event (probably 1996), but these were easily distinguished from recently flowering trees since the latter still supported fine inflorescence branches, whereas all fine branches had fallen from trees that had died earlier. A total of 757 stems $\geq$ 5 cm were measured. The three largest trunk diameters on each plot were averaged and used as a measure of site differences (different stand ages or growth rates of the largest trees). Trunk increment cores were also collected on two plots (Col de Mouirange and Col de N'Go) to estimate tree age from rings. Overlap of tree (trunk) size between flowering and non-flowering trees was measured by Horn's index of overlap (Horn 1966, Randall & Myers 2001).

Randomized block ANOVA (plot = block) was used to determine whether flowering and non-flowering trees differed in trunk diameter. However, an interaction with site was apparent, so ANOVA (using log$_e$-transformation where necessary) is reported separately for each site. Tests were only conducted where there were at least five trees in both categories. The association between tree size and flowering was then investigated across the combined dataset using logistic regression. The fit of the model was tested using the likelihood ratio χ^2 statistic, G^2 (Quinn & Keough 2002), with McFadden's rho^2 as the logistic analogue of R^2. SYSTAT v. 11 was used for all analyses, with a critical level of $\alpha = 0.05$ for hypothesis tests.

RESULTS

The percentage of *Cerberiopsis candelabra* trees that flowered and subsequently died on these study sites in the 2003 event ranged from nil (one site) to 93%. Flowering trees ranged in size 5–79 cm dbh, and live trees (not having flowered) 5–64 cm (no smaller flowering trees were recorded in a concurrent demographic study). There was a significant effect of tree size on flowering at only 6 of the 12 stands for which analyses could be undertaken, with dead trees being 1.2–2.3-fold larger in diameter on average than live trees (Figure 2). A difference in mean size between flowering and non-flowering trees was most common in stands with the largest trees (Figure 2). Similarly, the degree of overlap in size between flowering and non-flowering trees, as measured by Horn's index (R_o), correlated negatively with site mean maximum trunk diameter, when the outlying point at Col de N'Go Alluvium was excluded (Figure 3).

However, even where there was a significant difference in size, the relationship between size and flowering is complex. There can be similar size distributions of non-flowering trees and flowering trees at the same site (Figure 4). The largest trees on a site were non-flowering rather than flowering on four plots (e.g. Mouirange in Figure 4), and on four plots the smallest flowering tree was smaller than, or equal in size to, the smallest non-flowering tree. Furthermore, there were many cases of flowering trees occurring adjacent (within 10 m) to non-flowering trees of virtually identical size. In the populations with large trees (> 40 cm dbh) that flowered in 2003, there was always evidence of an earlier flowering event, probably in 1996 (the last event known to us). These 'early' flowerers often included trees with

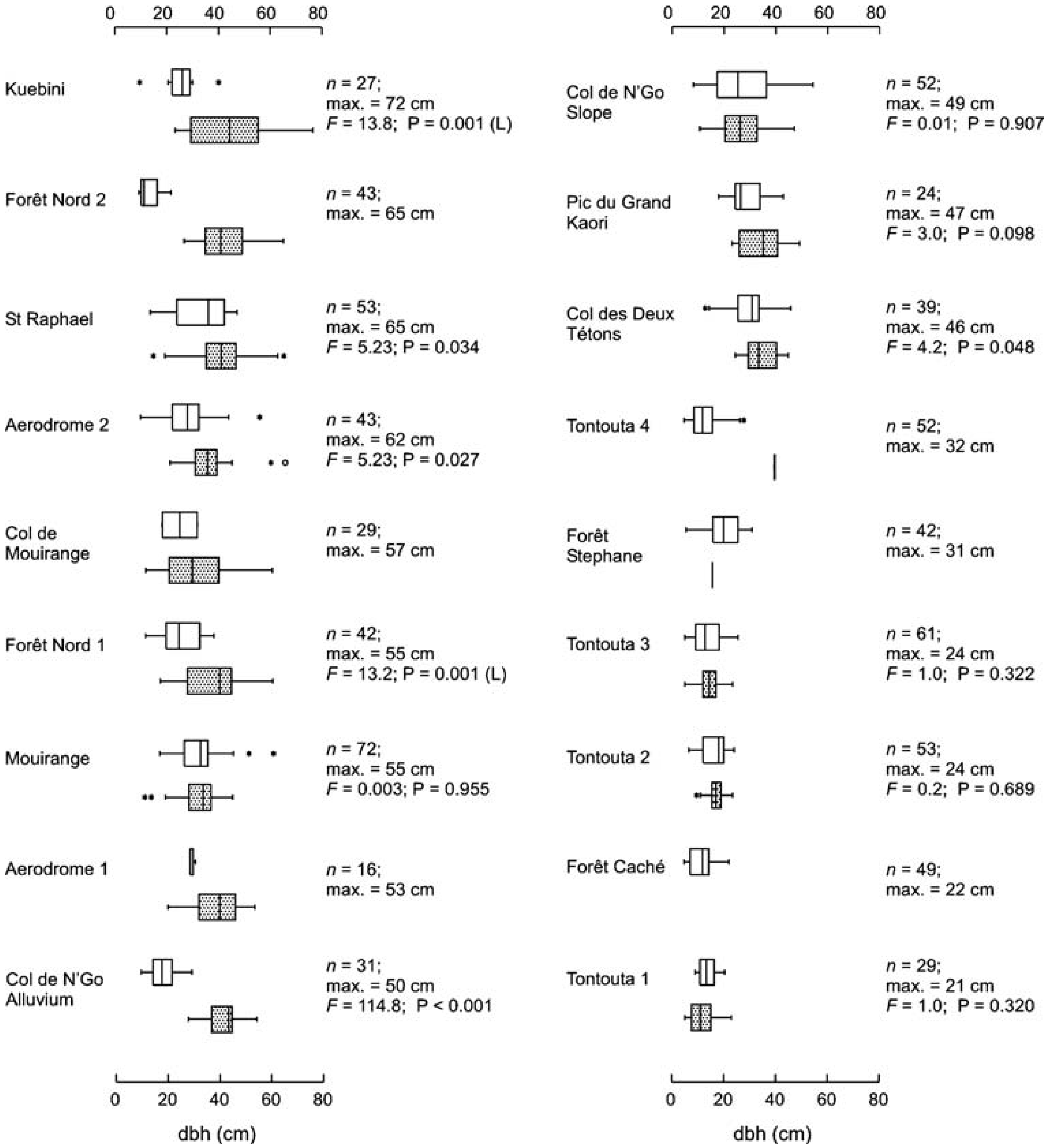

Figure 2. Comparisons of *Cerberiopsis candelabra* trunk diameters of flowering (in 2003) (stippled boxes) versus non-flowering (open boxes) trees in 18 stands in New Caledonia. Sites are shown in descending order of maximum tree size within each column of box plots. The results of ANOVA are given where there are at least five trees in each category. *n*, total number of trees; max. = average of the three largest trunk dbh values; L, data $\log_e$-transformed for analysis.

substantially smaller diameters than some that did not flower until 2003 (or at all). Hence, even allowing for growth since 1996, the pattern we have described of non-flowering trees overlapping the size profile of flowering trees appears to be also true for the 1996 flowering event. However, when the data from all 18 sites were combined, there was a very strong association between tree diameter and the probability of flowering ($G^2 = 235$, df = 1, $P < 0.001$) (Figure 5). Nevertheless, tree size as measured by trunk diameter explained only 23% of the likelihood of flowering (McFadden's $\text{rho}^2 = 0.228$).

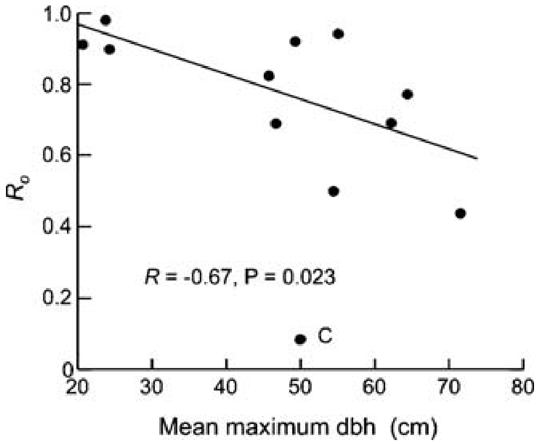

Figure 3. The relationship between size overlap of flowering and non-flowering trees of *Cerberiopsis candelabra*, measured by Horn's index of overlap (R_0), and mean maximum tree size (average of the three largest trunk dbh values) across study sites. Higher values of R_0 indicate greater overlap. Sites are included only where there are at least five trees in each category. C, Col de N'Go Alluvium.

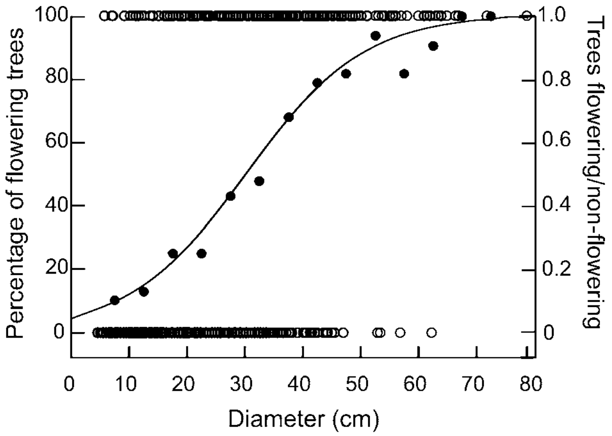

Figure 5. The association between tree size and flowering status in *Cerberiopsis candelabra* across all study sites. The flowering status is shown for all individual trees (open circles) with respect to trunk diameter, with the curve indicating the predicted probability of flowering derived by logistic regression. Also shown is the percentage of trees flowering in 5 cm diameter classes (solid circles). In total 757 trees were included in the analysis.

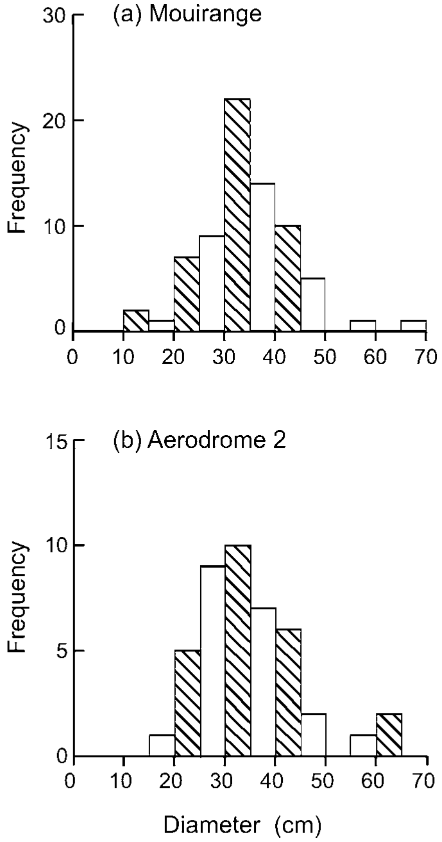

Figure 4. Size distributions of flowering (filled bars) and non-flowering (open bars) trees of *Cerberiopsis candelabra* at Mouirange (a), where there was no size difference between flowering and non-flowering trees, and Aerodrome 2 (b), where flowering trees were significantly larger than non-flowering trees.

On two plots there was a single flowering tree (Forêt Stephane and Tontouta 4), and at Forêt Caché there were no flowering trees, even though trees of similar size to the non-flowering trees were flowering in other populations. However, these trees may have differed in age. Unfortunately, tree rings were intermittent in the collected increment cores, with no cores having rings for more than 30% of the length of the core. A cohort of *Nothofagus aequilateralis* (Nothofagaceae) co-occurring with *C. candelabra* at Col de Mouirange may have established at the same time, given the even-aged size structure and apparent high light requirements of both species for recruitment (unpubl. data), and has been tentatively aged at *c.* 85 y from tree rings. This may represent an intermediate age for flowering and life span, given that much smaller and much larger trees of *C. candelabra* flowered on other study sites.

DISCUSSION

The relationship between tree size and flowering

There was a strong relationship between tree size and the incidence of flowering in *Cerberiopsis candelabra*, but the relationship appears complex. First, the size range of flowering trees was large (5–79 cm dbh). Similarly, Veillon (1971) noted flowering in 2–3-m-high plants, although more often in trees of 20–30-m height. Second, there was almost complete overlap in size between flowering and non-flowering trees (albeit with less overlap on sites with the largest trees), and in about half the populations there was no difference in mean trunk diameter of flowering and non-flowering trees. Hence, size per se is unlikely to be the sole trigger for flowering in *C. candelabra. Tachigali versicolor* also shows overlap in size between flowering and non-flowering trees (Foster 1977), but the extent of overlap has not been reported.

Generally, size appears more important than age in triggering flowering in herbaceous monocarpic species (Metcalf *et al.* 2003). Studies of both short- and long-lived species have shown that the probability of flowering may increase with plant size (Gross 1981, Tissue & Nobel 1990, Werner 1975), with a critical threshold size for flowering (Augspurger 1985, de Jong *et al.* 1989, Gross 1981, Tissue & Nobel 1990, Werner 1975), although the time to reach that size may vary according to site conditions (Augspurger 1985). However, large size variation has been noted among flowering individuals of several species (Augspurger 1985, Metcalf *et al.* 2003, Simons & Johnston 2003, Tissue & Nobel 1990), as in our study. This variation is generally attributed to either age-dependent reproduction (with high variation in growth rates), or genotypic differences in inherent growth rates and programmed reproductive sizes (Augspurger 1985). Elsewhere, we show that simple models of optimal monocarpic life histories predict a broad range of flowering sizes when growth trajectories, which link age with size, vary due to micro-environmental heterogeneity (Burd *et al.* in press). Thus, the flowering triggers in *C. candelabra* are likely to involve plasticity for both age and size at reproduction. However, we cannot yet determine tree age, and therefore do not know the relationship between size and age at flowering in *C. candelabra*.

Although trunk diameter is a useful measure of size, and commonly correlates with height, height may be a better indicator of access to light in these rain forests, and consequently of carbohydrate reserves that may be necessary to trigger or support flowering. The larger trees of *C. candelabra* (both flowering and non-flowering) are typically taller (often *c.* 5–15 m) than most co-occurring species, so emerge above the main canopy.

Tree size and life history in *Cerberiopsis candelabra*

There are several notable components of this monocarpic life history in *C. candelabra*. These potentially have adaptive significance independently of each other, but may also act synergistically. Here we discuss the relationship between tree size and these life-history traits.

Length of the pre-reproductive period. Most monocarpic species are annuals, but there are numerous examples of perennials, with some showing lengthy pre-reproductive growth, even of more than 100 y (Bell 1980, Janzen 1976). Delayed maturation (in either polycarpic or monocarpic species) may be predicted if fecundity increases with age (Bell 1980), as it almost always does (Metcalf *et al.* 2003). Delayed maturation in a monocarpic tree may allow diversion of resources from reproduction to growth (Foster 1977). However, since neither monocarpic nor polycarpic canopy trees invest in reproduction at the sapling stage, a growth advantage due to any delay in reproduction that might occur in monocarps must be restricted to later growth phases. Rapid growth and resource pre-emption to facilitate success in reaching the upper rain forest canopy should be particularly important in the early growth phase of shade-intolerant trees, increasing fitness by increasing the likelihood of survival and later fecundity (Bell 1980, Harper 1977, Obeso 2002, Schaffer 1974, Stearns 1976) for both polycarpic and monocarpic species. What differs for monocarps is that less investment may be needed in some structural components such as a mechanically robust trunk and branch system, since the trees need survive through only one reproductive event (Poorter *et al.* 2005). If monocarpic trees grow faster because of such trends in biomass allocation, reproduction may actually occur earlier than for the equivalent polycarp, as suggested in *Tachigali vasquezii* (Poorter *et al.* 2005), with the risk of dying before reproductive maturity reduced so long as any reduction in mechanical structure does not offset this advantage. Therefore, as in *T. vasquezii*, we predict architecture and biomass allocation patterns in *C. candelabra* that enhance growth rate.

However, our data suggest there is either a large temporal delay in reproduction in many *C. candelabra* trees (relative to both conspecifics and co-occurring polycarps), or at least a delay in flowering in relation to the size and physical position of the tree within the forest. The size range of flowering trees is more substantial than indicated in *T. vasquezii* (on average 50–70 cm dbh; Poorter *et al.* 2005) and many trees do not flower even when reaching 5–15 m above the main forest canopy – this must be considered a substantial delay in ecological terms.

Post-reproductive death. Observations suggest that seedlings of *C. candelabra* may need a substantial gap to survive. Hence recruitment may rely substantially on synchronicity between reproduction and creation of a sufficient canopy gap. If death of the parent has created a substantial gap, it may enhance recruitment of its offspring (most seeds fall below the parent tree; Veillon 1971), particularly in these forests where reproduction in co-occurring polycarps does not necessarily occur every year, so fast-growing competitors are less likely to arrive concurrently in gaps created by *C. candelabra*. In this scenario, the death of a single parent may only facilitate recruitment if the tree is large and occurs in the upper canopy, and so effective suicidal reproduction may be strongly linked to 'ecologically' delayed reproduction past the minimum size at which flowering can occur (5 cm dbh), for those plants on rapid growth trajectories that can reach the canopy. This scenario is consistent with models predicting that monocarpy may be favoured when there is substantially delayed reproduction (Roff 1992), when fecundity increases more than proportionally with reproductive effort (Schaffer 1974), and when juvenile survivorship is high relative to adult survivorship (Charnov & Schaffer 1973, Stearns 1976, Young 1981). While the long pre-reproductive period may contribute in part to competitive success in pre-reproductive *C. candelabra*, resulting in later increased fecundity, the key feature may be that postponing reproduction (in size, if not in age) means that the tree is physically larger when it flowers and dies, allowing creation of larger gaps for establishment of offspring, i.e. potentially increasing recruitment. Smaller trees may be forced into flowering if their likelihood of survival to canopy stature is poor. This can be an optimal strategy of flowering plasticity (Burd *et al.* in press).

The proximate cause of tree death in *C. candelabra* is potentially linked to one or more of the following: nutrient starvation due to reallocation of resources (Noodén *et al.* 1997, Wilson 1997), a lack of vegetative meristems (Veillon 1971) potentially leading to critical carbon deficit, or programmed senescence (Noodén *et al.* 1997, Wilson 1997). Increment cores collected in November–December 2003 at the time of flowering/early fruiting had a dark stain suggesting rot, and were watery, even when only one branch was reproductive, in contrast to the clean pale wood of non-reproductive trees. At this time the plants were healthy in outward appearance. The trunk rot may be triggered by reproduction or its consequences (nutrient starvation or hormonal signal; Wilson 1997), or alternatively may directly or indirectly trigger the flowering event. However, since reproduction and progress towards death appear very closely linked in time, without outward signs of stress, a direct genetically programmed link between these two events seems more likely in *C. candelabra* than death being just a physiological consequence of flowering.

What type of trigger is likely to cause synchronous flowering across many populations of *C. candelabra* in such a way that trees of any size (beyond *c.* 5 cm dbh) can flower, and that trees of the same size are differentially affected, even when standing side by side? It seems likely that external conditions must be involved (either directly, or by initiating senescence), together with age or size (or some consequence of these). The influence of size may be masked to some extent by interactions with other factors, such as growth rate. Growth rate itself might trigger flowering, or signal an underlying condition (either stress or resource-abundance) that triggers flowering. There may also be an age × stage interaction which results in different fates of individuals with different growth rates (Burd *et al.* in press, Young 1985). Within any size class older plants will have grown more slowly than younger plants, so if stress or growth rate is a trigger for flowering, some but not all plants of a particular size class might flower (Young 1985), as found in our study. An example is shown in *Lobelia telekii* (life span of 40–70 y) in which slower-growing plants were more likely to flower than faster-growing plants among small rosettes, but with the opposite pattern in larger rosettes (Young 1985).

An external trigger might not be stress-related, but instead may be similar to conditions suggested to induce, or be a necessary condition for, mass flowering in polycarpic species, such as climate conditions allowing accumulation of nutritional reserves for flowering (Iwasa 2000, Stearns 1976, Tissue & Nobel 1990). Certain climate conditions may trigger flowering (Norton & Kelly 1988), but only when sufficient reserves have accumulated (Rees *et al.* 2002). Environmental factors may alternatively act as cues that indicate favourable conditions ahead (Stearns 1976). For example, linking flowering to cyclones could favour recruitment for a shade-intolerant species, with flowering possibly triggered by mechanical stress or defoliation. Kelly (1994) suggests that 'environmental prediction' is likely only in specific habitats (fire-prone) and plant groups (herbaceous perennial) given the time taken from flower initiation to seed germination. However, growth rates are low on these ultramafic soils and not all trees produce seed annually, so canopy gaps created by a cyclone may persist through the time it takes to initiate flower buds and produce seeds.

Mass flowering and masting. Not all monocarpic species with a long pre-reproductive period show mass flowering. For example, while other species of *Tachigali* show masting behaviour, *T. vasquezii* does not (Poorter *et al.* 2005). *Cerberiopsis candelabra* shows mass flowering across a substantial proportion of a population, and among populations. This has three components, synchronicity, timing (already discussed) and periodicity, the latter referring to the duration between flowering events in a population rather than within a species as can occur in a polycarp. Whether the periodicity of flowering has any separate adaptive advantage, or is just a consequence of optimization of timing of flowering in relation to proximate environmental and internal ('readiness') cues, is unclear and probably difficult to disentangle. There may be several advantages to synchronicity, including satiation of predators of seeds and seedlings (particularly when there are long and/or unpredictable intervals between masts) (Ims 1990, Janzen 1976, Kelly 1994, Klinkhamer *et al.* 1997), both enhancing seedling survival. For example, recruitment of *T. versicolor* seedlings was enhanced when grown in high densities (Augspurger & Kitajima 1992), although direct observation of seed fates did not strongly support the predator satiation hypothesis (Forget *et al.* 1999).

Mass flowering might also enhance attraction of animal pollinators (Kelly 1994, Kelly & Sork 2002). However, for *C. candelabra* mass death may be as important as mass flowering and seeding, since our observations suggest that seedlings recruit only on sites with substantial opening of the canopy, i.e. any advantage of the economy of scale (Norton & Kelly 1988) in this monocarp may be largely due to the link between mass death (canopy opening via death of parents, but potentially by death of other trees damaged by falling parents) and mass reproduction. Hence the success of monocarpy in this species may be tightly linked with its masting behaviour plus gregariousness, as suggested by Keeley & Bond (1999) for bamboos. Incomplete synchronicity within a population (the failure of all trees to flower in the same flowering event) may increase the likelihood of successful recruitment if it increases opportunities to link reproduction with favourable environments, or enhances success of recruitment of earlier seedling cohorts by supplementary canopy gaps.

To date we have explored only the flowering behaviour of *C. candelabra*, without quantitative evidence for effects of parental tree size and conspecific flowering and mortality on seedling recruitment. It is unclear whether stands of *C. candelabra* are generally persistent through repeated flowering and regeneration events or instead form a more variable spatial and temporal (shifting) mosaic through a landscape influenced by catastrophic disturbance. At Col de Mouirange only two trees ≥ 20 cm dbh remain out of 52 recorded in 1991, and juveniles are infrequent. At two other rain forest permanent plots, the last remaining trees (2–3 per plot) have died without seedlings having established. Future studies will focus on the regeneration dynamics of *C. candelabra*, including the influence of parent size and conspecific density on recruitment.

ACKNOWLEDGEMENTS

We thank Stephane McCoy, Jerome Munzinger and Gilles Dagostini for suggesting some study sites, the Province Sud for permission to work in these forests, and Dave Kelly for helpful comments on the manuscript. This study was funded by the National Geographic Society and a Monash Small Grant.

LITERATURE CITED

AUGSPURGER, C. K. 1985. Demography and life history variation of *Puya dasylirioides*, a long-lived rosette in tropical subalpine bogs. *Oikos* 45:341–352.

AUGSPURGER, C. K. & KITAJIMA, K. 1992. Experimental studies of seedling recruitment from contrasting seed distributions. *Ecology* 73:1270–1284.

BELL, G. 1980. The costs of reproduction and their consequences. *American Naturalist* 116:45–76.

BOITEAU, P. & ALLORGE, L. 1981. *Flora de la Nouvelle Calédonie et Dépendances 10. Apocynaceae*. Muséum National D'Histoire Naturelle, Paris.

BURD, M., READ, J., SANSON, G. D. & JAFFRÉ, T. (accepted manuscript). Age-size plasticity for reproduction in monocarpic plants. *Ecology*.

CHARNOV, E. L. & SCHAFFER, W. M. 1973. Life history consequences of natural selection: Cole's result revisited. *American Naturalist* 107:791–793.

DE JONG, T. J., KLINKHAMER, P. G. L., GERITZ, S. A. H. & VAN DER MEIJDEN, E. 1989. Why biennials delay flowering: an optimization model and field data on *Cirsium vulgare* and *Cynoglossum officinale*. *Acta Botanica Neerlandica* 38:41–55.

FORGET, P.-M., KITAJIMA, K. & FOSTER, R. B. 1999. Pre- and post-dispersal seed predation in *Tachigali versicolor* (Caesalpiniaceae): effects of timing of fruiting and variation among trees. *Journal of Tropical Ecology* 15:61–81.

FOSTER, R. B. 1977. *Tachigalia versicolor* is a suicidal neotropical tree. *Nature* 268:624–626.

GROSS, K. L. 1981. Predictions of fate from rosette size in four "biennial" plant species: *Verbascum thapsus*, *Oenothera biennis*, *Daucus carota* and *Tragopogon dubius*. *Oecologia* 48:209–213.

HARPER, J. L. 1977. *Population biology of plants*. Academic Press, New York. 892 pp.

HORN, H. S. 1966. Measurement of "overlap" in comparative ecological studies. *American Naturalist* 100:419–424.

IMS, R. A. 1990. The ecology and evolution of reproductive synchrony. *Trends in Ecology and Evolution* 5:135–140.

IWASA, Y. 2000. Dynamic optimization of plant growth. *Evolutionary Ecology Research* 2:437–455.

JAFFRÉ, T. 1992. Floristic and ecological diversity of the vegetation on ultramafic rocks in New Caledonia. Pp. 101–107 in Baker, A. J. M., Proctor, J. & Reeves, R. D. (eds). *The vegetation of ultramafic (serpentine) soils*. Intercept Ltd, Andover.

JANZEN, D. H. 1976. Why bamboos wait so long to flower. *Annual Review of Ecology and Systematics* 7:347–391.

KEELEY, J. E. & BOND, W. J. 1999. Mast flowering and semelparity in bamboos: the bamboo fire cycle hypothesis. *American Naturalist* 154:383–391.

KELLY, D. 1994. The evolutionary ecology of mast seeding. *Trends in Ecology and Evolution* 9:465–470.

KELLY, D. & SORK, V. L. 2002. Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics* 33:427–447.

KITAJIMA, K. & AUGSPURGER, C. K. 1989. Seed and seedling ecology of a monocarpic tropical tree, *Tachigalia versicolor*. *Ecology* 70:1102–1114.

KLINKHAMER, P. G. L., KUBO, T. & IWASA, Y. 1997. Herbivores and the evolution of the semelparous perennial life-history of plants. *Journal of Evolutionary Biology* 10:529–550.

METCALF, J. C., ROSE, K. E. & REES, M. 2003. Evolutionary demography of monocarpic perennials. *Trends in Ecology and Evolution* 18:471–480.

NOODÉN, L. D., GUIAMÉT, J. J. & JOHN, I. 1997. Senescence mechanisms. *Physiologia Plantarum* 101:746–753.

NORTON, D. A. & KELLY, D. 1988. Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. *Functional Ecology* 2:399–408.

OBESO, J. R. 2002. The costs of reproduction in plants. *New Phytologist* 155:321–348.

POORTER, L., ZUIDEMA, P. A., PEÑA-CLAROS, M. & BOOT, R. G. A. 2005. A monocarpic tree species in a polycarpic world: how can *Tachigali vasquezii* maintain itself so successfully in a tropical rain forest community? *Journal of Ecology* 93:268–278.

QUINN, G. P. & KEOUGH, M. J. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge. 537 pp.

RANDALL, P. J. & MYERS, A. A. 2001. Effects of resource matrix, gut region analysed and sample size on diet statistics in co-existing species of flatfish. *Journal of the Marine Biological Association of the United Kingdom* 81:1041–1048.

READ, J., JAFFRÉ, T., FERRIS, J. M., MCCOY, S. &. HOPE, G. S. 2006. Does soil determine the boundaries of monodominant rainforest with adjacent mixed rainforest and maquis on ultramafic soils in New Caledonia? *Journal of Biogeography* 33:1055–1065.

REES, M., KELLY, D. & BJØRNSTAD, O. N. 2002. Snow tussocks, chaos, and the evolution of mast seeding. *American Naturalist* 160:44–59.

ROFF, D. A. 1992. *The evolution of life histories: theory and analysis*. Chapman & Hall, New York. 535 pp.

SCHAFFER, W. M. 1974. Selection for optimal life histories: the effects of age structure. *Ecology* 55:291–303.

SIMONS, A. M. & JOHNSTON, M. O. 2003. Suboptimal timing of reproduction in *Lobelia inflata* may be a conservative bet-hedging strategy. *Journal of Evolutionary Biology* 16:233–243.

STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. *The Quarterly Review of Biology* 51:3–47.

TISSUE, D. T. & NOBEL, P. S. 1990. Carbon relations of flowering in a semelparous clonal desert perennial. *Ecology* 71:273–281.

VEILLON, J. M. 1971. Une Apocynacée monocarpique de Nouvelle-Calédonie *Cerberiopsis candelabrum* Vieill. *Adansonia*, ser 2, 11:625–639.

WERNER, P. A. 1975. Predictions of fate from rosette size in teasel (*Dipsacus fullonum* L.) *Oecologia* 20:197–201.

WHITMORE, T. C. 1998. *An introduction to tropical rain forests*. (Second edition). Oxford University Press, Oxford. 282 pp.

WILSON, J. B. 1997. An evolutionary perspective on the 'death hormone' hypothesis in plants. *Physiologia Plantarum* 99:511–516.

YOUNG, T. P. 1981. A general model of comparative fecundity for semelparous and iteroparous life histories. *American Naturalist* 118:27–36.

YOUNG, T. P. 1985. *Lobelia telekii* herbivory, mortality, and size at reproduction: variation with growth rate. *Ecology* 66:1879–1883.

ZEDLER, P. M. 1995. Are some plants born to burn? *Trends in Ecology and Evolution* 10:393–395.