

A mast flowering event in a eucalypt of tropical upland dry sclerophyll forest

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^CDeceased 22 Aug. 2015

Abstract

Synchronised flowering of individuals of long-lived plant species at intervals of greater than one year, and which is bimodal between “much” and “few”, is known as masting. Masting appears to be common among eucalypts but has not been formally described as such. We provide quantitative data on a mass-flowering event in the Inland White Mahogany (*Eucalyptus mediocris*) in upland dry sclerophyll forest in north Queensland, along with anecdotal evidence that mass-flowering events in this species occur as infrequently as once per decade. Based on a survey of 549 trees spread across 37 sites, we estimate that 97% of healthy, mature Inland White Mahogany flowered between late November 2013 and February 2014, and 75% of these flowered heavily. Within the study area, flowering was staggered over about 12 weeks, with local synchrony being greater than regional synchrony. Fourteen percent of trees had capsules from a previous flowering event, and these trees displayed lower flowering effort than those without capsules. We argue that the event is appropriately described as masting. The factors driving masting in eucalypts are unknown, but this event may have been synchronised by a short but sharp drought 12 months prior.

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Handling editor: Stephen Murphy

Citation: Franklin DC, Barnes TA, Winlaw A. 2016. A mast flowering event in a eucalypt of tropical upland dry sclerophyll forest. *North Queensland Naturalist* 46: 1-10.

Introduction

Many shrubs and trees flower and fruit annually and at a more-or-less set time of year, and if flowering varies in intensity from year to year, it is a direct response to limiting conditions in that year. A few species, however, flower only at intervals of two or more years (supra-annually), and if this is synchronised among individuals to produce major flowering events, it is known as *masting*. Masting is rarely a categorical state, however, a more typical form being in which a few individuals flower in most years but most individuals flower together supra-annually (Kelly 1994). Masting is well-known among dipterocarp

trees in south-east Asia (Sakai 2002), a variety of trees in New Zealand (Schauber *et al.* 2002), and a variety of plants elsewhere (Kelly and Sork 2002). It has recently been described for a species of Mulga (*Acacia aptaneura*) and a species of *Triodia* in central Australia (Wright and Zuur 2014; Wright *et al.* 2014).

Many eucalypts do not flower annually and stands may exhibit a periodicity of two to four years between major flowering events (Ashton 1975; Law *et al.* 2000; Birtchnell and Gibson 2006). In northern Australia, large variation between years in flowering intensity has been reported for Darwin

Woollybutt *Eucalyptus miniata*, Darwin Stringybark *E. tetradonta* and Long-fruited Bloodwood *Corymbia polycarpa* (Setterfield and Williams 1996; Williams 1997; Brady 2009). Burrows and Burrows (1992) documented a “pattern of light and heavy seed production ... over different years” in a number of eucalypt species in the seasonally-dry sub-tropical area of Rockhampton, Queensland. For the most part, the reported year-to-year variations appear to grossly exceed environmental (e.g. rainfall) variation. Notwithstanding, the term “masting” has never, to our knowledge, been applied to eucalypts, though it is implicit in the predator satiation study of *Eucalyptus delegatensis* by O’Dowd and Gill (1984). In seeming confirmation of the latter point, a Web of Science search (<http://thomsonreuters.com/thomson-reuters-web-of-science/>, 19 May 2014) on the terms “eucalypt*” and “mast*” yielded not one listing of relevance. It hardly needs stating that the dominance of eucalypts in the Australian landscape means that masting has major implications for the variety of fauna that depend on them for nectar and seed.

In this paper we report on the timing and intensity of a mass-flowering event in Inland White Mahogany (*Eucalyptus mediocris* L.A.S.Johnson & K.D.Hill; but see below for issues with the naming of this taxon) in the Herberton area of north Queensland in 2013/14. We also provide anecdotal evidence that this was a “once-in-a-decade” event that strongly suggests masting.

Methods

Study species and area

Inland White Mahogany (Fig. 1) is a member of the *E. acmenoides* (white mahogany) complex of species for which the taxonomy and nomenclature remains ill-resolved. Members of the complex in the Herberton area were known as *E. acmenoides* until Hill (1999) split the species and named local populations as *E. irritans*. The Centre for Plant Biodiversity Research (CPBR 2006) merged *E. irritans* into another species described by Hill, *E. mediocris*, arguing that “the type specimens are virtually identical and there are no consistent morphological differences between numerous herbarium specimens of the two.” CPBR’s resolution of this and other members of the complex has been adopted by the Australian Plant Census (<https://www.anbg.gov.au/chah/apc/>,

updated 2011, downloaded June 2013), and is adopted here. However, in the Queensland Herbarium’s most recent checklist (Queensland Herbarium 2014) and the official description of Queensland’s regional ecosystems (REDD v8.0, http://www.ehp.qld.gov.au/ecosystems/biodiversity/regionalecosystems/how_to_download_redd.html, downloaded 1 Jan. 2014), white mahoganies in the Herberton area are known as *E. portuensis*. *E. portuensis* was described by Hill (1999) as restricted to the vicinity of the Whitsunday Passage on the central Queensland coast, and we know of no published morphological basis for interpreting white mahoganies in the Herberton area as belonging to that taxon.

In the Herberton area, Inland White Mahogany is widespread in dry sclerophyll forest on well-drained granite- and metamorphic-derived soils, and may be the most abundant eucalypt on these parent materials. As mapped in Fig. 2, there is an estimated 87.5 km² of forest in which Inland White Mahogany is a primary species and a further 121.25 km² of forest in which it is secondary, the former mostly east of a line just west of Herberton and the latter mostly further west. (Areas

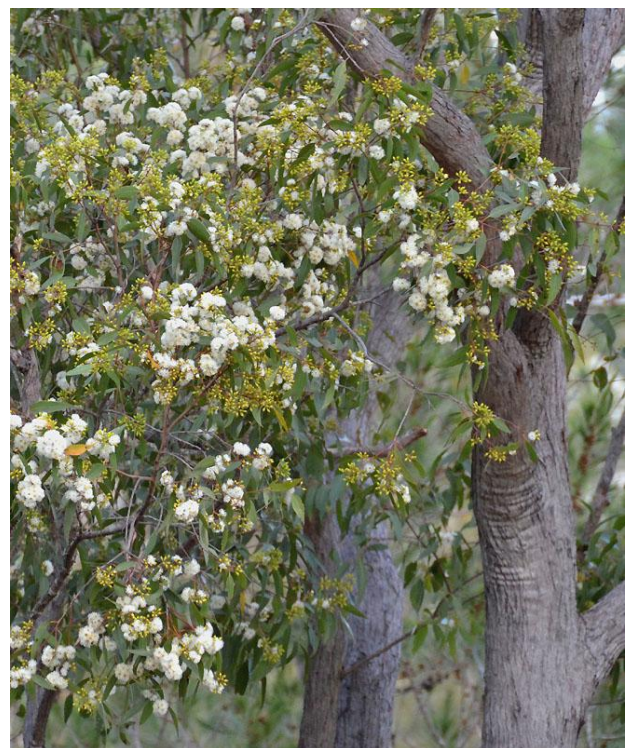


Figure 1. Inland White Mahogany (*Eucalyptus mediocris*): bark, foliage and flowers.

Photo: Don Franklin, Herberton, 12 Dec. 2013

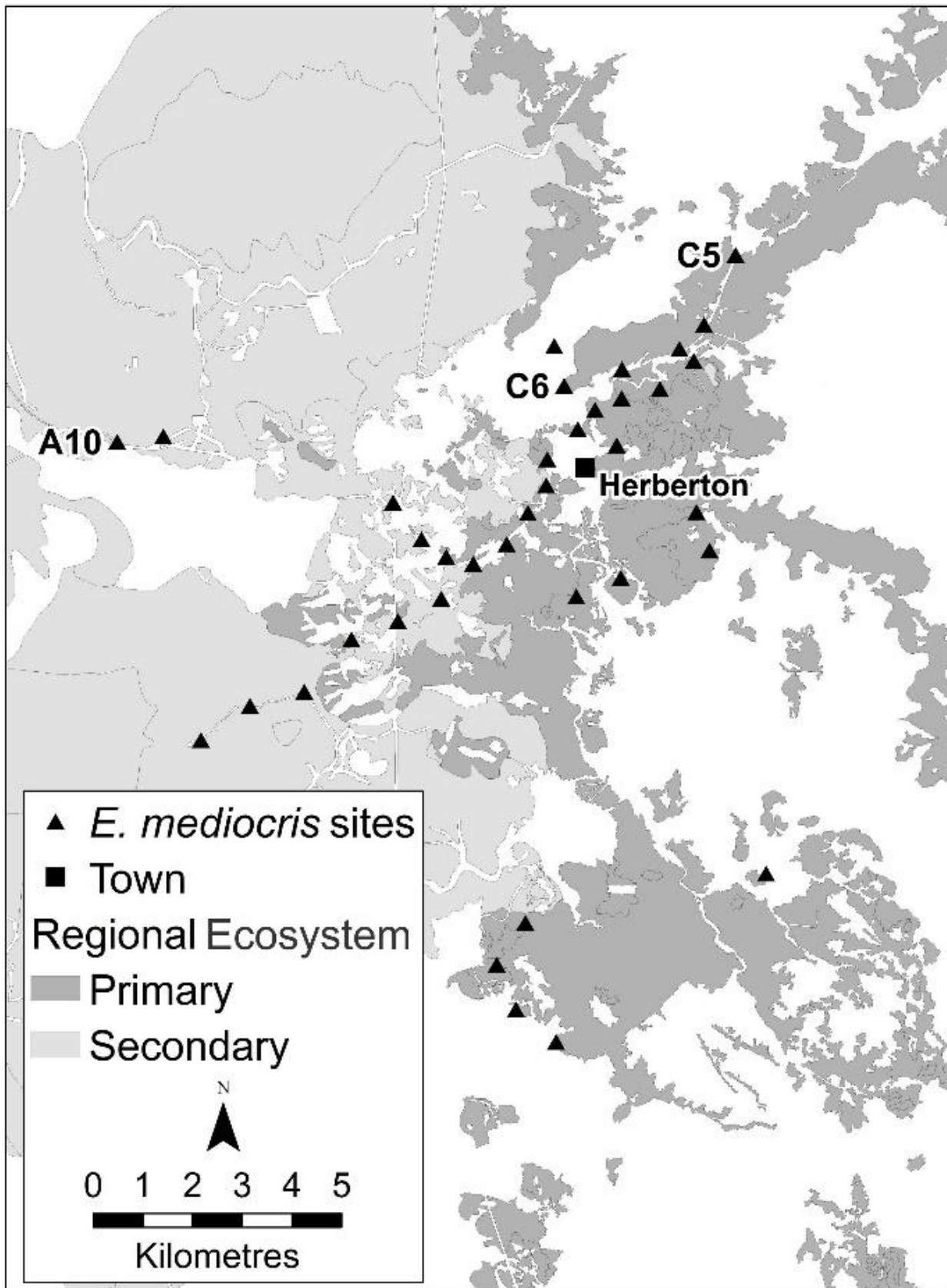


Figure 2. Distribution of survey sites and regional ecosystems featuring Inland White Mahogany (*Eucalyptus mediocris*) in the vicinity of Herberton, north Queensland. "Primary" and "Secondary" reflect the prominence of Inland White Mahogany in descriptions of regional ecosystems (DEHP 2014).

estimated by imposition of a 0.5 km grid on the map [legend area excluded] and counting the intercepts, each intercept thus representing 0.25 km² of vegetation.) Our sites (below) ranged in elevation from 850 to 1,050 m ASL, a range that is probably representative of its local occurrence. Inland White Mahogany is often co-dominant with Lemon-scented Gum (*Corymbia citriodora*) with a number of other eucalypt species interspersed, but at wetter, higher elevation sites it occurs with Tindal's Stringybark (*Eucalyptus tindaliae*, also known as *E. reducta*).

Field surveys

On six days between 21 Dec. 2013 and 4 Jan. 2014, we surveyed flowering of *E. mediocris* at 3 to 10 sites per day, 37 sites in total, in open forests within 12 km of Herberton (Fig. 2). On each day we took a different route radiating out from Herberton, following roads and forest trails where habitat was suitable. Sites were selected for their abundance of *E. mediocris* and were separated by at least 0.5 km and mostly by at least 1.0 km. The location and elevation of each site was determined using a GPS. At each site, we evaluated 15 trees (at one site only 9 met our criteria), a total of 549 trees. For inclusion in the survey, *E. mediocris* had to meet the following criteria:

1. be not adjacent to a major disturbance such as a road or cleared land;
2. be greater than 10 cm diameter at breast height over bark (the approx. size of maturity); and
3. to have a crown not comprised principally of epicormic sprouts that were judged likely to have arisen in the previous 12 months (generally less than c. 50 cm long).

At each site, we selected the first available tree that was more than a canopy's width from a road, then repeated the process with the nearest qualifying neighbour not previously assessed until the quota of 15 trees was met.

The diameter of each tree was measured to the nearest 1 cm with a diameter tape. The reproductive state of the tree was visually estimated during a c. 1 min. scan of the canopy as follows:

- the proportion of current-season reproductive organs that was each of buds/flowers/spent flowers (the latter includes fruit) in categories

of zero, less than 25% and greater than 25% of the available reproductive organs. "flowers" were defined as any reproductive organ with stamens present and "spent flowers" as any reproductive organ from which all stamens had dropped (i.e. various stages of developing fruit).

- the extent of current-season reproductive effort was scored relative to potential in classes of 0 = 0%; 1 = 1–25%; 2 = 26–50%; 3 = 51–75%; 4 = 76–100%. Because buds are produced sub-terminally on leafy shoots, and leaves are confined to the outer portion of shoots, this is effectively a measure of the percentage of leafy shoots with reproductive organs present, a measure that was readily attributed to these abundance classes.
- the presence of fruit (capsules) from a previous flowering season, in classes of "none", "few" and "many".

Consistently, sites and trees were selected and data recorded by DCF, diameters measured by TAB, and reproductive state assessed by AW.

Data analysis

From our field data, the phenological state of a tree is rated in three classes representing buds, flowers and spent flowers [fruit] respectively. For example, a tree with a phenological state of >25%, 0 and 0 is entirely in bud. It follows from our scoring system that at least one, but possibly two or even three, of the three classes must be greater than 25%. These ratings were converted to a phenological score for each tree (trees with no reproductive organs excluded) as follows:

- ratings of 0 were weighted 0, ratings of less than 25% weighted as 0.125 (median of 0-25%) and ratings of more than 25% weighted as the remainder of a total of 1 divided by the number of classes that scored greater than 25%. Thus, the sum of weights is 1.0; and
- the weighted scores were then summed as buds x 1, flowers x 2, spent flowers x 3.

Examples of the process are provided in Table 1. The resulting phenological score describes progression from all buds (score 1) to all spent flowers or fruit (score 3).

For each site, an index of reproductive effort was calculated as 100 times the sum of the individual reproductive effort classes divided by the sum of potential efforts (number of individuals x 4).

Table 1. Example calculations of the phenological score of a tree.

Each row represents a hypothetical tree. Reproductive categories separated by backslashes are: buds / flowers / spent flowers[fruit]. See Methods section for weightings. Calculations are: $\text{weighting}_{\text{buds}} * 1 + \text{weighting}_{\text{flowers}} * 2 + \text{weighting}_{\text{spent}} * 3$. The resulting phenological score measures progress through the flowering cycle from 1 (= all organs were buds) to 3 (all organs were spent flowers or fruit).

Abundance	Weighting	Calculation	Phenological score
>25% / 0 / 0	1 / 0 / 0	$1 * 1 + 0 * 2 + 0 * 3$	1
>25% / <25% / 0	0.875 / 0.125 / 0	$0.875 * 1 + 0.125 * 2 + 0 * 3$	1.125
>25% / >25% / <25%	0.4385 / 0.4385 / 0.125	$0.4385 * 1 + 0.4385 * 2 + 0.125 * 3$	1.6875
<25% / >25% / <25%	0.125 / 0.75 / 0.125	$0.125 * 1 + 0.75 * 2 + 0.125 * 3$	2
>25% / >25% / >25%	0.333 / 0.333 / 0.333	$0.333 * 1 + 0.333 * 2 + 0.333 * 3$	2
0 / >25% / >25%	0 / 0.5 / 0.5	$0 * 1 + 0.5 * 2 + 0.5 * 3$	2.5
0 / 0 / >25%	0 / 0 / 1	$0 * 1 + 0 * 2 + 1 * 3$	3

As phenology scores and the abundance of old fruit had strongly skewed distributions, i.e. values were very frequently at the extreme of low and high values, and old fruit in particular had few abundance classes (three), all statistical tests were conducted non-parametrically – with Kruskal-Wallis tests to compare median values of classes (variously sites or the abundance of old fruit in three classes) and Spearman rank tests to examine correlations.

To evaluate whether the timing of reproduction in individual trees was more strongly related to site than expected from broader patterns of reproduction, we tested whether phenology scores differed significantly between sites assessed on the same day. Trees showing no reproductive activity were excluded.

To evaluate whether reproduction in years when only a few individuals flower was related to tree vigour, we tested the proposition that the abundance of old fruit was correlated with tree diameter. To evaluate whether trees with old fruit were spatially aggregated, we tested whether the abundance of old fruit on individual trees varied between sites.

We tested whether reproductive effort scores varied between sites. Further, to evaluate whether reproductive effort in 2013-14 was influenced by reproductive effort in preceding years, we grouped trees by their abundance of old fruit and tested for a group effect on 2013-14 effort.

Because site-level effects may complicate any relationship between previous and current reproductive effort (e.g. some sites may be better watered and thus trees more able to flower twice), we attempted analysis of this dataset with site included as a random effect using permutational statistics. However, the test was precluded because many sites had no variance with respect to old fruit.

Results

Phenology

Inland White Mahogany was photographed in flower on 25 Nov. 2013 when it was noted that flowering was moderately widespread and had been underway for at least a week. By early December it was evident that a mass-flowering event was underway. Three “late” sites in which most trees were in bud on the second last day of the quantitative survey (2 Jan. 2014) were revisited on 30 Jan. 2014 and found to contain a range of states including some buds, numerous flowers and many developing fruit, with the median state at the sites judged subjectively to be flowering, spent flowers and between flowering and spent flowers respectively, but widespread flowering had ceased by that date. Flowering thus occurred over at least a 12-week period.

On five of six survey days, the phenological score of trees was strongly dependent on site (Table 2), indicating that there was greater synchrony among trees within than between sites. There was no

Table 2. Phenological scores compared among sites for each of the six survey days.

H is Kruskal-Wallis H; P is the probability. Phenological scores have been averaged across trees to produce a site mean.

Date	No. of sites	No. of trees	H	P	Mean site score \pm SD
21 Dec. 2013	10	134	65.6	<0.0001	2.1 \pm 0.74
27 Dec. 2013	6	90	15.9	0.007	1.9 \pm 0.92
29 Dec. 2013	6	90	33.9	<0.0001	1.6 \pm 0.65
31 Dec. 2013	6	90	27.5	<0.0001	2.5 \pm 0.43
2 Jan. 2014	6	90	62.5	<0.0001	1.7 \pm 0.71
4 Jan. 2014	3	45	0.9	0.64	2.0 \pm 0.46

progression of phenological scores with date (Table 2), indicating that sub-regional synchrony was greater than regional synchrony. There are insufficient data from any one day to evaluate possible effects of elevational or rainfall gradients, but it was our impression that no such gradients in phenological scores existed.

Reproductive effort

Most healthy mature *E. mediocris* flowered (97.4%), and most of these flowered heavily (75.0% flowered on more than 75% of available leafy shoots) (Fig. 3A). Of the 14 trees that did not flower, only three were 15 cm diameter or less and had no old fruit (out of 81 trees 15 cm diameter or less), suggesting that our threshold for maturity of 10 cm diameter rarely if ever included trees too small to flower. Most trees had no old fruits, 11.5% had some old fruit and 2.6% had many old fruit. There was no significant correlation between tree diameter and the abundance of old fruit ($r_s = 0.004$, $n = 549$, $P > 0.5$). Trees with old fruit tended strongly to be aggregated at certain sites (Kruskal-Wallis $H_{35,549} = 115.2$, $P < 0.0001$) but these were widely dispersed through the survey area.

There was a strong effect of site on the reproductive effort of individual trees (Kruskal-Wallis $H_{35,549} = 114.5$, $P < 0.0001$). Most sites had reproductive effort indices (which potentially range from zero to 100) of 90 or greater and no site had an index of less than 40 (Fig. 4). Two of the three sites with reproductive effort indices of less than 70 were at the geographical and elevational extremity of the survey area (Fig. 2: A10 & C5 cf C6). Only three sites had no internal variation between trees in reproductive effort – in these cases, all were scored as 76–100% for effort.

Flowering effort varied with the abundance of old fruits (Kruskal-Wallis $H_{2,549} = 16.4$, $P = 0.0003$). Post-hoc multiple comparisons revealed no difference between trees with no old fruit and those with a little old fruit ($P = 1.0$), but significant differences between each of these categories and those with a lot of old fruit ($P = 0.007$ and $P = 0.03$ respectively). Trees with a lot of old fruit had notably lower flowering effort during this event than other trees, though most still flowered (Fig. 3B-D).

Historical records of flowering of Inland White Mahogany in the Herberton area

Saeed de Ridder (pers. comm. to DCF, 31 Dec. 2013) commenced revegetation work around Herberton just over 20 years ago, and has been actively engaged with local vegetation ever since*. He noted mass-flowering of *E. mediocris* the year after he commenced this work (and collected seed from it), and again about 10 years later, though neither event rivalled the 2013/14 event in intensity.

Kate Prout (pers. comm. to DCF, 12 Dec. 2013) has lived on a bush block on the fringe of Herberton township for the last 13 years. *Eucalyptus mediocris* is the dominant tree on the block (DCF pers. obs.). In marked contrast to 2013/14, she reports not previously having seen a major flowering of the species.

Consistent with the above, DCF noted that only a small minority of *E. mediocris* trees flowered in 2012/13.

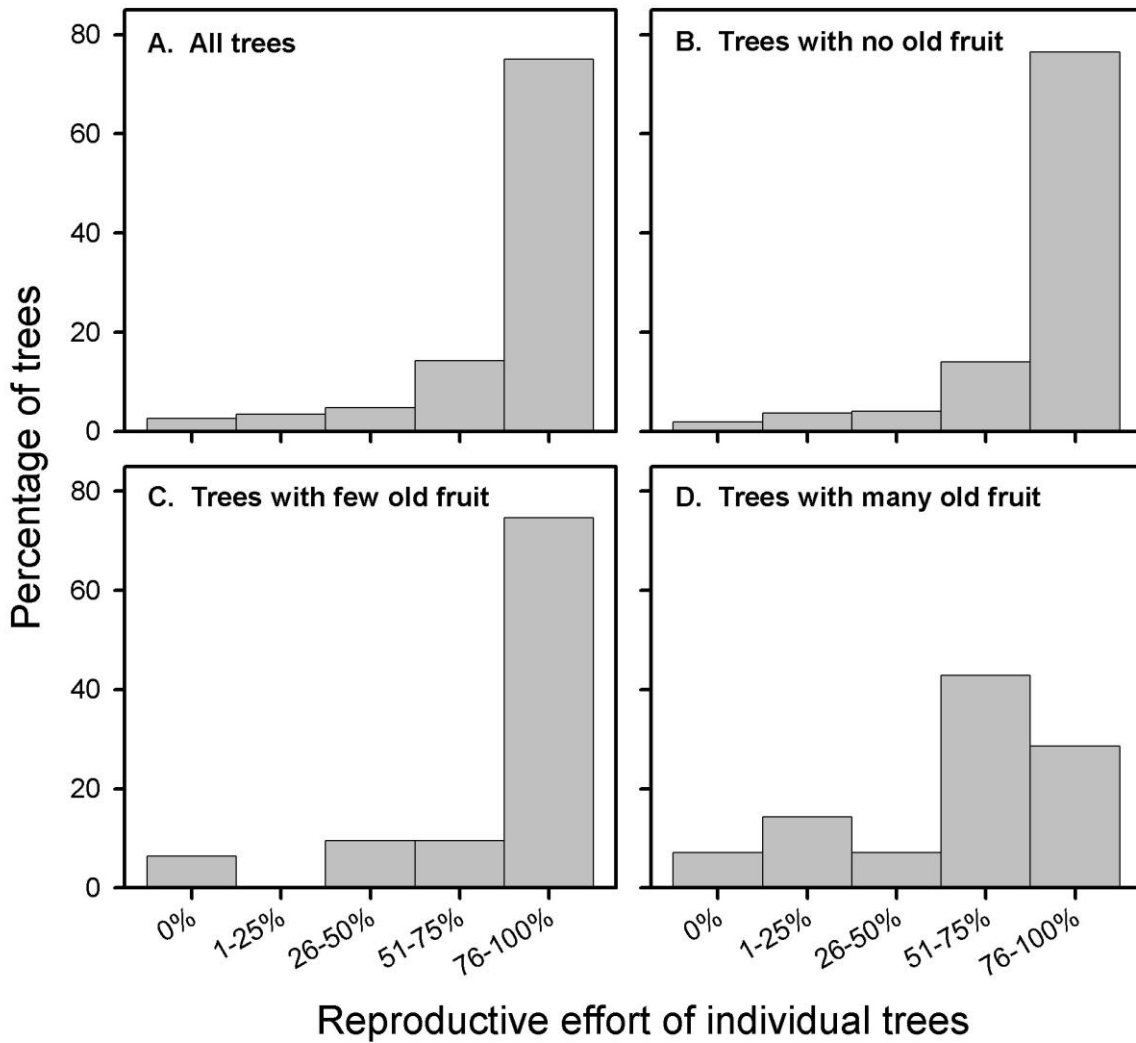


Figure 3. Reproductive effort (% of potential) of *Eucalyptus mediocris* trees in the Herberton area of north Queensland during the 2013/14 mass-flowering event. Sample sizes are n = 549, 472, 63 & 14 trees respectively.

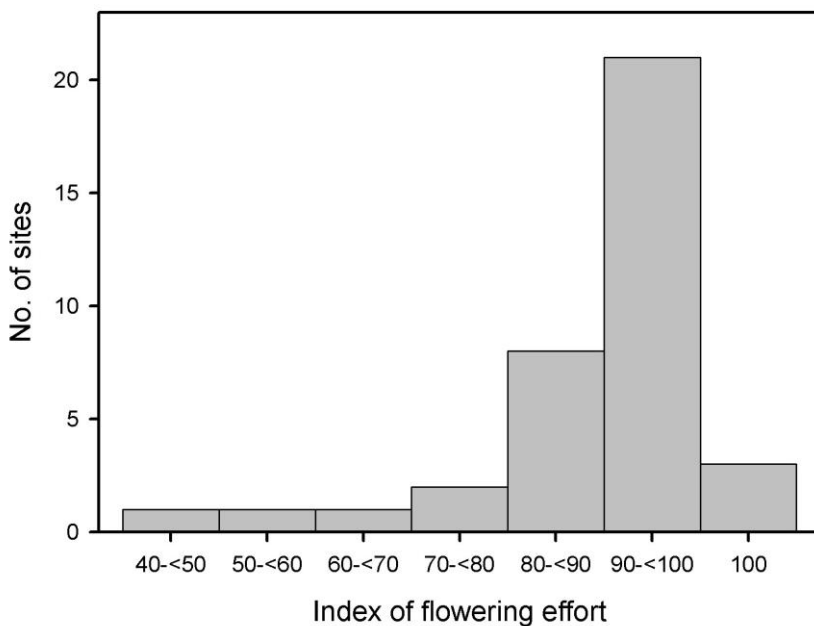


Figure 4. Frequency distribution of sites by flowering indices. Site indices potentially range from 0 (no trees flowering in 2013/14) to 100 (all trees flowering in 2013/14 and all with an effort class of 76-100%).

Discussion

Over about a 12-week period, almost every Inland White Mahogany tree flowered in an area in which it is abundant and which exceeded 100 km², and most trees flowered intensely. We do not know what happened to individuals outside our study area, but our data provides a hint that sites at the edge of our study area may have flowered less intensely. Within our study area, there was some evidence of internal structuring to the event in the form of greater synchrony within than between sites, and spatial aggregation of trees that had flowered in recent year(s) as shown by the presence of old fruit. Trees with evidence of having flowered in recent year(s) showed limited depression of flowering intensity but little depression of propensity to flower at all, suggesting resource depletion in what are well-weathered, shallow and infertile soils of granitic, rhyolitic or metamorphic origin.

Anecdotal evidence over 20 years suggests that flowering in *E. mediocris* stands is strongly bimodal – sharply divided between *much* and *few* – and thus meets the definition of a masting species (Kelly 1994). It seems implausible that this variation is a direct response to year-to-year variation in the environment (the “resource-matching” hypothesis of Kelly 1994), for example rainfall, as even the scant evidence shows that the year-to-year variation in flowering grossly exceeds variation in rainfall. Further, other trees and shrubs that co-occur with *E. mediocris* (for example many species of *Acacia*) flower annually. Depression in the extent of flowering by trees carrying fruit from a previous flowering suggests a limited role for resource depletion in the deferral of flowering by individuals. However it does not, in itself, suggest a reason for synchronised flowering among many individuals.

Nevertheless, climatic events may be the proximal drivers of masting events (Kelly 1994; Kelly and Sork 2002; Williamson and Ickes 2002). Remarkably little is known about the drivers of flowering in eucalypts. Trade-offs between allocation of resources to flowering (including flower budding and fruiting) and leaf growth have been demonstrated in eucalypts (reviewed by House 1997). In southern Australia, wet cool weather that enables photosynthesis but precludes growth may prompt diversion of resources into flower buds,

the development of which to flowering may take many months or even several years (Porter 1978; Law *et al.* 2000). However, mean monthly daytime maximum temperatures in Herberton exceed 20°C throughout the year (Herberton climate data downloaded from www.bom.gov.au, 10 Jan. 2012) so growth of foliage is unlikely ever to be precluded by low temperatures.

In the case of the event described in this paper, it is noteworthy that Inland White Mahogany was not the only species to flower prolifically at about this time. As the flowering of Inland Mahogany waned, Pink Bloodwood (*Corymbia intermedia*) flowered heavily though this may not be so unusual. Shortly thereafter (early in 2014), Lemon-scented Gum (*C. citriodora*) flowered massively and in marked contrast to flowering over the previous two years (DCF pers. obs.). Herberton Ironbark (*E. atrata*) also flowered heavily. This is a striking parallel to the staggered mass-flowering of dipterocarps in peninsular Malaysia which Ashton *et al.* (1988) reported as adaptive by reducing competition for pollinators.

In view of mass-flowering by multiple eucalypt species, it seems appropriate to seek a common climatic driver of these events, as also noted for Asian dipterocarps (Ashton *et al.* 1988). We speculate that rainfall was the key driver and note the following sequence of events (Fig. 5):

- the dry season of 2012 was extended with below average rainfall for six of seven months from June to December including severe depression of rainfall in the hot months of November and December. The dry spell continued until mid-January 2013.
- the dry spell was broken by sustained, soaking rain from a low pressure system (ex-TC Oswald). Although rainfall for February and March was well below average, it was sufficient to maintain moisture levels and was followed by sufficient rain at no greater than two-month intervals throughout the dry season, including good rains in November as Inland White Mahogany commenced flowering, to sustain sub-soil moisture levels.

Towards the end of the dry spell in late 2012, a number of patches of Inland White Mahogany defoliated, some dying and others subsequently re-

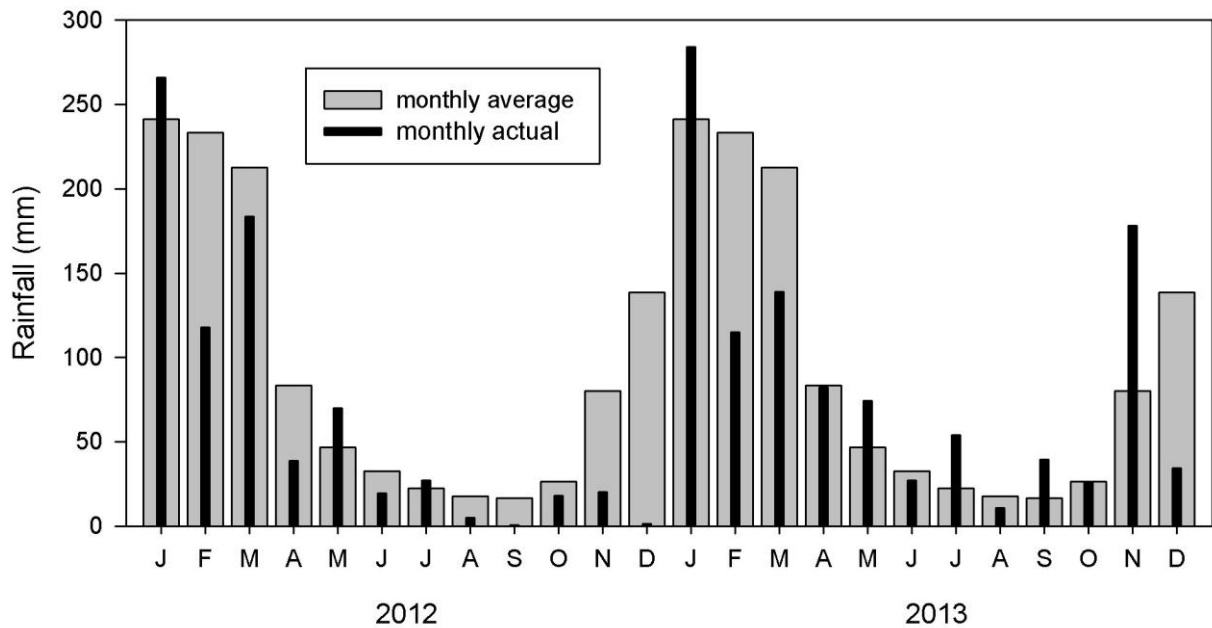


Figure 5. Monthly rainfall in Herberton for the two years prior to the mass-flowering of Inland White Mahogany overlain on long-term monthly average rainfall.

Data are for the Herberton (Mowbray Road) gauge, download progressively over time from www.bom.gov.au.

shooting epicormically from major branches only. We propose that stress associated with the dry spell induced many trees (not showing obvious signs of stress) to enter a state of vegetative dormancy from which they emerged synchronously with the heavy rain associated with ex-TC Oswald, developing floral buds, and that reasonable subsequent conditions allowed development of these buds through to flowering. This hypothesis could explain the unusually strong synchrony of events, though we acknowledge it does not explain why the response was one of flowering and not of growth.

Thoughts about the evolutionary drivers of masting in *E. mediocris* are necessarily speculative. As general candidates, one could consider improvements to pollination efficiency (the “wind pollination” and “animal pollination” hypotheses of Kelly 1994) and/or satiation of seed or seedling predators (the “predator satiation” hypothesis) (see also Kelly and Sork 2002); both seem plausible in this case. The only relevant evidence we have is that this mass-flowering event (including the associated eucalypt species mentioned above) was strongly associated with the arrival, persistence and departure of a very large aggregation (many

tens of thousands) of a likely key pollination agent, the Little Red Flying-fox (*Pteropus scapulatus*) in Herberton (Franklin and Barnes, unpublished data).

Longer-term studies of this phenomenon in eucalypts would self-evidently lead to greater understanding of the nature and evolutionary and proximal drivers of it. That eucalypts are key elements of Australian ecosystems, and that the floral and seed resources they supply are key resources for a wide range of Australian fauna, argues that such studies should be a priority.

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* Saeed de Ridder passed away on 20 Sept. 2015