

Reproductive Phenology of Woody Species in a North Australian Tropical Savanna¹

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ABSTRACT

Interspecific and interannual variation in reproductive phenology was quantified for 50 common species of trees and shrubs from a mesic savanna near Darwin, northern Australia. The presence of buds, flowers, and fruit was noted over a 30-month period, from September 1992 to February 1995. Surveys were undertaken at monthly intervals for the less common species, and at bimonthly intervals for ten of the common trees and tall shrubs. The majority of species flowered each year at about the same time. There was no evidence of sub-annual or continuous regimes of reproductive phenology. There was no supra-annual carryover of seed-bearing fruit in the canopy of any species. The peak flowering periods were the mid to late dry season (July–August) and the transition between the dry season and the wet season (October–November). The two dominant trees—*Eucalyptus miniata* and *E. tetradonta*—flowered during the dry season, thereby providing resources for some elements of the vertebrate fauna. Flowering and fruiting were uncommon at the end of the wet season (February/March), although two species that flower and fruit at this time (*E. porrecta* and *Terminalia ferdinandiana*) may provide resources to consumers at a time when floral or fruit resources are otherwise scarce. Because the peak of reproductive activity takes place during the late dry season, fruit maturity and seed dispersal have occurred prior to the onset of the rainy season for most species, and germination and seedling establishment potentially may take effect in response to the first rains. Late dry season fires, which tend to be extensive and intense, are a potential threat to the floral and fruit reserves within these savannas.

Key words: Eucalyptus; fire; northern Australia; phenology; savanna; serotiny; synchrony; trees; wet-dry tropics.

GROWTH AND REPRODUCTION OF TREES in the seasonally dry tropics is periodic rather than continuous because of the highly seasonal annual rainfall regime (Sarmiento 1984, Bullock 1995, Reich 1995). In the forests and savannas of the seasonal tropics, considerable effort has been devoted to documenting the interannual and interspecific variation in the major phenological events. Knowledge of plant phenology is fundamental to understanding the community dynamics of these ecosystems. The timing, duration, and degree of synchrony of the various phenological phases have major implications for plant community structure, function, regeneration, and the quantity and quality of resources available for consumer organisms.

In Australia, about one-fifth of the continent is tropical savanna (Mott *et al.* 1985). Despite their virtual domination of northern Australia, there have been few studies of phenology—either vegetative or reproductive—in the savannas (Williams *et al.* 1997). This is in contrast to the numerous

studies of plant phenology in the seasonally dry tropical forests and savannas of Africa, Central and South America, and Asia (Sarmiento & Monasterio 1983, van Schaik *et al.* 1993, Bullock 1995, Reich 1995). In northern Australia, Bowman *et al.* (1991) and Franklin (1998) have presented data on vegetative and reproductive phenology for a number of woody species. Dunlop and Webb (1991) have published data on flowering times in eucalypts. Burrows and Burrows (1992) and Setterfield and Williams (1996) have studied seedfall in several species of savanna eucalypts. Williams *et al.* (1997) have examined the interannual and interspecific patterns of leaf phenology in woody savanna species.

Australian savannas generally are dominated by *Eucalyptus* spp. in the upper story, with a variety of annual and perennial grasses dominating the understory. The structure of the savannas varies from open forest (*sensu* Specht 1981) in the wetter, mesic coastal and sub-coastal regions of the north, to woodlands and low, open woodlands of the more arid interior. Within the woody component, there is a variety of life forms, from ground shrubs to

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trees 30-m tall, and phenological types, from evergreen to deciduous (Wilson *et al.* 1990, Wilson *et al.* 1996, Egan & Williams 1996, Williams *et al.* 1996, 1997).

Rainfall varies from < 500 mm/yr in the arid interior to >1800 mm/yr in the near-coastal, mesic regions of the north. More than 90 percent of the annual rainfall falls during the wet season between November and April (McDonald & McAlpine 1991, Duff *et al.* 1997). In Australian savannas, the occurrence of the wet season is predictable because the monsoon brings rain each year; however, there is interannual variability in the duration and the timing of both the onset and end of the wet season (Taylor & Tulloch 1985).

We present data on the reproductive phenology of 50 woody species in a mesic savanna near Darwin. The leaf phenology of these species was reported in Williams *et al.* (1997). Our goal was to document the seasonal patterns of budding, flowering, and fruiting in these species. Information about these patterns is important with respect to understanding the processes that govern regeneration within savannas, the availability of resources to consumers, and the manner in which various land uses may affect these biological processes. Our major questions were: (1) what is the interannual and interspecific variation, particularly in congeners, in flowering and fruiting?; (2) are the trees and shrubs of this savanna serotinous, retaining seed-bearing fruit for more than one year?; and (3) how synchronous are the reproductive patterns, both between species within years and between years within species?

STUDY SITE AND CLIMATE

The study was carried out in a mesic savanna at Solar Village (12°40'S, 131°10'E), 35 km southeast of Darwin. The Solar Village site has been described in detail by Fensham (1990) and Williams *et al.* (1997). Annual rainfall in the Solar Village region is *ca* 1600 mm (Collard Road, NT, Australian Bureau of Meteorology). Temperatures are high year-round; average January (wet season) maximum and minimum temperatures are 31.8 and 24.8°C respectively, with the corresponding figures for July (dry season) being 30.5 and 20.0°C. The vegetation is open forest (*sensu* Specht 1981) dominated by *Eucalyptus miniata* and *E. tetradonta*, with trees such as *Erythrophloeum chlorostachys*, *Xanthostemon paradoxus*, and *Terminalia ferdinandiana* as subdominants. The understorey is sparse, consisting of perennial and annual grasses such as *Sor-*

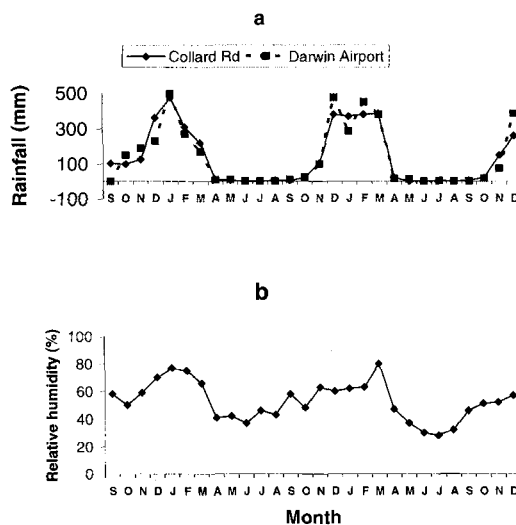


FIGURE 1. Local and regional climatic data for Solar Village and Darwin. (a) Monthly rainfall totals from September 1992 to December 1994 at the Collard Road Bureau of Meteorology rainfall recording station (5 km from the study site; diamonds) and Darwin Airport (35 km from the site; squares). (b) Average daily relative humidity (at 1500 h) for each month of the study; Darwin Airport data.

ghum, *Chrysopogon*, and *Eriachne* spp., and small shrubs. The soil is a sandy loam, overlying lateritic hardpan layers 0.5–1.5 m beneath the surface. This vegetation–soil alliance is typical for the higher rainfall areas in the Darwin region (Wilson *et al.* 1990, 1996; Williams *et al.* 1996). The site has not been burnt since 1978, a fire-free period unusual for Australian savannas in which the typical fire return interval is one to two years (Braithwaite & Estbergs 1985, Williams *et al.* 1998).

Monthly rainfall data for the study period (September 1992–February 1995) were compiled from records collected at two Australian Bureau of Meteorology rainfall stations: Collard Road, 5 km from the site, and Darwin Airport, 35 km from the site. Mean monthly values for relative humidity (at 1500 h) for the study period were calculated from the climatic data set (Darwin Airport, NT, Australian Bureau of Meteorology).

Annual rainfall in each of the two complete wet seasons (1992/1993 and 1993/1994) were *ca* 1600 and 1800 mm, respectively (Fig. 1a). The first major rains (>25mm) occurred in September 1992; in both 1993 and 1994, such rains did not come until October. No rain fell during the June–August period in either year. Variation in relative humidity (RH at 1500 h) from Darwin Airport is given in

Figure 1b. RH was highest during the January–March period, after which there was a rapid decline to seasonal minima in the June–July period. RH increased during the July–September period in each year, prior to the occurrence of any rains. The late dry season increase in RH, and the high humidity that occurs in the transitional period between dry and wet seasons is typical of the climate in the Darwin region (McDonald & McAlpine 1991, Duff *et al.* 1997). In northern Australia, this transition period between seasons is called the “build-up.”

METHODS

Within an *ca* 2-ha area, reproductively mature individuals of 50 woody species (trees and tall shrubs) were selected and tagged. Nomenclature followed Brooker and Kleinig (1994) for *Eucalyptus*. We used the generic term *Eucalyptus* to include several species in this study (*e.g.*, *E. porrecta*) that belong to the “bloodwood” group of eucalypts, which Hill and Johnson (1995) have included in the new genus, *Corymbia*. Dunlop *et al.* (1990) was the authority for all non-eucalypt species.

The number of individuals tagged ranged from two to three for the less common species and ten for the most common species. These ten species included: two evergreen species; *E. miniata* and *E. tetradonta* (Myrtaceae); five brevi- or semi-deciduous species, *E. porrecta*, *E. polysiada*, *Xanthostemon paradoxus* (Myrtaceae), *Erythrophleum chlorostachys* (Caesalpiniaceae), and *Buchanania obovata* (Anacardiaceae); and three fully deciduous species, *Cochlospermum fraseri* (Bixaceae), *Planchonia careya* (Lecythidiaceae), and *Terminalia ferdinandiana* (Combretaceae). These ten species constituted > 95 percent of the tree basal area at the site (Williams *et al.* 1997), as they do for most savannas in the Darwin region (Wilson *et al.* 1990).

Over the period September 1992–February 1995, the vegetative and reproductive state of each individual was recorded at the beginning of each month for the less common species and twice per month (beginning and middle) for the ten common species. The presence of reproductive structures (buds, flowers, or fruits) was recorded for each individual, but we did not quantify their abundance. The number of species in any month exhibiting buds, flowers, or fruits was calculated and expressed as a percentage of the total number of species. For the ten common species (with ten replicate individuals) the percentage of trees with floral buds, flowers, and fruits was calculated for

each assessment date. The timing of the initiation of budding or flowering was assessed by calculating the mean sample time of when these events commenced, with sample periods assigned numerical values such that 1 = January 1, 1.5 = January 15, 12 = December 1, 12.5 = December 15, and so on.

The duration of fruit retention on each tree also was determined, and mean values per species per year calculated. Because we did not quantify the abundance per tree of the reproductive structures, and because we used only one sample block, statistical tests of the significance of interannual variation in the proportion of individuals exhibiting buds, flowers, and fruits were not possible. Interspecific and interannual variation in the timing of initiation of the phenological phases was assessed by split plot ANOVA, with year as the split factor and species as a fixed factor. In these analyses, species differences were tested against replicate trees within species, and year differences and the species X year interaction were tested against the residual variation. This methodology was used by Williams *et al.* (1997) to assess temporal variation in the timing of leaf phenological events (*e.g.*, leaf flushing and leaf fall). In all analyses, the assumption of homogeneity of variance was satisfied without needing to transform the data; analyses were performed using GENSTAT 5.

RESULTS

A summary of the annual pattern of budding, flowering, and fruiting based on all months during which reproductive activity was observed in each of the 50 target species is shown in Table 1. Species are arranged in increasing order of deciduousness (evergreen, brevi-, semi-, and fully deciduous) and decreasing order of basal area in each class. Considerable seasonality in the patterns of budding, flowering, and fruiting is apparent. Most species (34/50) flowered and fruited in each year and did so in roughly the same month each year. Fourteen species flowered and fruited only once during the 30-month study period. Three species did not flower during the survey period: *Maranthes corymbosa*, *Canarium australianum*, and *Dodonea oxypetala*.

There was no supra-annual carryover of fruit in any of the target species, and for most species, fruit was present for one to three months. Our methodology precluded precise estimation of fruit longevity; however, of the 47 species that flowered and fruited, 39 had lost all fruit by the early part of the wet season (January) in at least one year of

the study. Nine species completed fruitfall by the mid to late wet season (February–March).

There was considerable seasonality in this community-wide pattern of budding, flowering, or fruiting (Fig. 2). Flowering and fruiting occurred year-round, although the peak periods of flowering and fruiting were the mid dry season months of July and August, and the build-up months of October and November. In each year there was a substantial decline in the number of species flowering and fruiting between the dry season peak and the second peak. In both 1993 and 1994, the nadir of activity was in the late wet season months of February and March.

The bimonthly patterns of reproductive phenology in nine of the ten common species are shown in Figure 3 (reproductive structures in *E. chlorostachys* were rare and patterns for this species have been omitted). The timing of budding, flowering, and fruiting varied between eucalypt species. *Eucalyptus miniata* and *E. tetradonta* commenced flowering in the early to mid dry season (May–July). Both species showed a mid dry season peak in budding and flowering: June and July for *E. miniata* and July and August for *E. tetradonta*. This interspecific difference in the timing of the initiation of budding (*ca* 2–3 wk) was significant in 1993; the timing of initial flowering was significantly different among species in both 1993 and 1994 (Table 2). Peak abundance in flowering was usually < 100 percent of individuals in any one month for both *E. miniata* and *E. tetradonta*; however, while not all individuals were in bud, flower, or fruit at any one time, all individuals of *E. miniata* flowered and fruited in each year of the study. For *E. tetradonta*, only 60–80 percent of individuals flowered during a given year.

The two semi-deciduous eucalypts, *E. polysciada* and *E. porrecta*, were well separated in the timing of budding and flowering (Figs. 3c, d). *E. polysciada* commenced budding and flowering in the late dry season (September), prior to any rain. *E. porrecta* commenced budding and flowering significantly later (2–6 wk; Table 2). Most individuals of *E. porrecta* flowered after the first rains. In both species, buds appeared after the first flush of new leaves, but the delay was greater in *E. porrecta*.

Among the eucalypts, there was interannual variation in the number of individuals flowering and fruiting. For *E. miniata*, 1994 was the peak year for flowering and fruiting; in the other species, the peak year was 1992/1993. There was also interannual variation in the timing of the initiation of budding and flowering, but this varied among

species. Interannual variation in the timing of initial budding and flowering events was nonsignificant in *E. tetradonta*, *E. miniata*, and *E. polysciada*. In contrast, *E. porrecta* showed significant interannual variation in the timing of initial budding and flowering (Fig. 3a, Table 2). Budding started in mid-September during 1992 and 1994, but was five to six weeks later in 1993.

The seasonality of flowering and fruiting in the two non-eucalypt semi-deciduous species is shown in Figures 3e and 3f. *Xanthostemon paradoxus* was the only common species not to flower and fruit each year (Fig. 3e). *Xanthostemon* flowered and fruited profusely in 1993/1994, but failed to flower in subsequent years. *Buchanania* flowered regularly at about the same time each year, but only *ca* 50 percent of individuals flowered in any one year (Fig. 3f). The semi-deciduous species all tended to flower in conjunction with or soon after leaf flush. In *Buchanania*, the initial flowering occurred before the arrival of rain. In *Xanthostemon*, flowering followed the first rains of the wet season.

The three fully deciduous species (*C. fraseri*, *P. careya*, and *T. ferdinandiana*) all flowered annually (Figs. 3g–i). There was little interannual variation in *Cochlospermum* (Fig. 3g; Table 2). Peak flowering and fruiting in this species was in the mid to late dry season of each year, with no significant difference between years in the timing of the pattern (Table 2). *Cochlospermum* flowered on leafless stems, soon after dry season leaf fall. *Planchonia* showed some interannual variation in flowering and fruiting (Fig. 3h), but there was no significant interannual variation in the timing of events. *Planchonia* flowered at about the time of leaf flush in the late dry season to build-up period, but prior to any rain. *Terminalia*, in contrast, showed significant interannual variation in the timing of events. Flowering and fruiting in 1992/1993 was earlier than in 1993/1994 (Fig. 3i). Fruiting was more abundant, and the period of fruit retention was also much longer in 1992/3 than 1993/4 (Table 2). In *Terminalia*, budding and flowering consistently occurred after the initial rains of the wet season had commenced. Budding took place more or less synchronously with leaf flush.

DISCUSSION

SEASONALITY.—The majority of woody species in this tropical savanna exhibited strong seasonality in their patterns of budding, flowering, and fruiting. Such seasonality is a feature of woody species in both seasonally dry tropical forests and in moist

TABLE 1. Summary abundance and phenological data for 50 woody species (trees and tall shrubs) at Solar Village, northern Australia. Species have been classified according to leaf phenology as: evergreen, brevi-deciduous, semi-deciduous, and fully deciduous after Williams et al. (1997). Columns are: tree basal area (m²/ha); months of minimum canopy cover (specifically months in which canopy <50% for semi- and fully deciduous species); the major period of leaf flush (months in which new foliage >25% of canopy cover); budding; flowering; and fruiting. Records are for a 2.5-year period (September 1992–February 1995).

	Family	Basal area	Canopy minimum	Leaf flush	Buds	Flowering	Fruiting
Evergreen species							
<i>Eucalyptus miniata</i> Cunn. ex Schauer	Myrtaceae	4.40	Sep.–Oct.	June–Dec.	May–Aug.	May–Aug.	June–Nov.
<i>Eucalyptus tetradonta</i> F. Muell.	Myrtaceae	4.00	Sep.–Nov.	June–Dec.	May–Aug.	June–Oct.	July–Dec.
<i>Acacia curculiformis</i> Cunn. ex Benth	Mimosaceae	1.40	Sep.–Nov.	June–Sep.	Apr.	Apr.–June	July–Aug.
<i>Acacia mimula</i> Pedley	Mimosaceae	0.10	Sep.–Nov.	June–Oct.	Apr.–May	May–June	May–Sep.
<i>Denhamia obscura</i> (A. Rich) Meisner ex Walp.	Celastraceae	0.01	Sep.–Nov.	June–Feb.	Jan.	Jan.	Jan.–Feb.
<i>Acacia dimidiata</i> Benth.	Mimosaceae	0.01	Sep.–Nov.	June–Nov.	Mar.–July	May–June	July–Sep.
<i>Acacia oncinocarpa</i> Benth.	Mimosaceae	0.01	Sep.–Nov.	July–Oct.	Apr.–May	May–July	June–Sep.
<i>Exocarpos latifolius</i> R. Br.	Santalaceae	0.01	Sep.–Nov.	Oct.	Dec.	Jan.	Jan.
<i>Livistona humilis</i> R. Br.	Araceae	0.01	Sep.–Nov.	July–Nov.	Jan.	Jan.–Feb.	Jan.–Feb.
<i>Maranthos corymbosa</i> Blume	Chrysobalanaceae	0.01	Sep.–Nov.	July–Oct.	NR	NR	NR
<i>Opilia amentacea</i> Roxb.	Opiliaceae	0.01	Sep.–Nov.	July–Nov.	July–Sep.	Aug.–Dec.	Aug.–Jan.
<i>Pandanus spiralis</i> R. Br.	Pandanaceae	0.01	Sep.–Nov.	Dec.–Feb.	NR	NR	Aug.–Oct.
Brevi-deciduous species							
<i>Eucalyptus porrecta</i> S. T. Blake	Myrtaceae	0.30	July–Oct.	Sep.–Nov.	Sep.–Feb.	Sep.–Apr.	Jan.–Aug.
<i>Acacia aulacocarpa</i> Cunn. ex Benth.	Mimosaceae	0.10	July–Aug.	Sep.–Nov.	Mar.–June	May–July	June–Sep.
<i>Persoonia falcata</i> R. Br.	Proteaceae	0.04	July–Aug.	July–Nov.	June–Nov.	July–Nov.	Sep.–Dec.
<i>Calytrix exstipulata</i> DC.	Myrtaceae	0.01	Aug.–Nov.	Oct.–Dec.	May–Sep.	June–Sep.	Aug.–Nov.
<i>Acacia holosericea</i> Cunn. ex G. Don	Mimosaceae	0.01	Sep.–Nov.	Oct.–Dec.	Apr.–July	June–Sep.	May–Sep.
<i>Alsonia actinophylla</i> (Cunn.) Schum.	Apocynaceae	0.01	July–Aug.	Oct.–Dec.	Sep.–Nov.	Sep.–Nov.	Sep.–Nov.
<i>Dodonaea oxyptera</i> F. Muell.	Sapindaceae	0.01	Aug.	Sep.–Dec.	NR	NR	NR
<i>Eucalyptus bleeseri</i> Blakely	Myrtaceae	0.01	Aug.–Sep.	Oct.–Nov.	Sep.–Nov.	Oct.–Dec.	Oct.–Jan.
<i>Grevillea pteridifolia</i> Knight	Myrtaceae	0.01	Aug.–Oct.	Nov.–Feb.	May–June	June	June–July
<i>Pittosporum melanospermum</i> F. Muell.	Pitrosporaceae	0.01	Aug.–Nov.	Sep.–Dec.	Jan.–Feb.	Jan.–Feb.	Jan.–Feb.
Semi-deciduous species							
<i>Erythrophleum chlorostachys</i> (F. Muell.) Baillon	Caesalpiniaceae	3.40	Sep.	Sep.–Nov.	Oct.	Oct.–Nov.	Dec.
<i>Xanthostemon paradoxus</i> F. Muell.	Myrtaceae	2.00	Sep.–Nov.	Oct.–Dec.	Nov.–Feb.	Nov.–Feb.	Dec.–July
<i>Buchanania obovata</i> Engl.	Anacardiaceae	0.40	July–Aug.	Sep.–Nov.	Sep.–Nov.	Sep.–Dec.	Oct.–Feb.
<i>Eucalyptus polyciada</i> F. Muell.	Myrtaceae	0.30	July–Sep.	Aug.–Oct.	July–Oct.	July–Nov.	Sep.–Dec.
<i>Eucalyptus foelschiana</i> F. Muell.	Myrtaceae	0.01	Aug.–Oct.	Sep.–Nov.	Oct.–Dec.	Jan.	Jan.–Feb.
<i>Alphitonia excelsa</i> (Fenzl) Benth.	Rhamnaceae	0.10	Aug.–Nov.	June–Nov.	Dec.–Apr.	Feb.–Apr.	Mar.–Apr.
<i>Canarium australianum</i> F. Muell.	Burseraceae	0.02	Aug.–Sep.	Oct.–Dec.	NR	NR	NR
<i>Timonius timon</i> (Sprengel) Merr.	Rubiaceae	0.01	July–Oct.	Oct.–Dec.	Dec.	Dec.	Dec.–Feb.
<i>Dolichandrone filiformis</i> (Fenzl) F. Muell.	Bignoniaceae	0.01	June–Aug.	Sep.–Dec.	Dec.	Dec.	Jan.

TABLE 1. Continued.

	Family	Basal area	Canopy minimum	Leaf flush	Buds	Flowering	Fruiting
<i>Grevillea decurrens</i> Ewart & Davies	Proteaceae	0.01	Aug.–Nov.	Oct.–Dec.	Mar.–Apr.	Mar.–May	Apr.–Sep.
<i>Petalostigma pubescens</i> Domin	Euphorbiaceae	0.01	Sep.–Nov.	Oct.–Dec.	Oct.–Nov.	Oct.–Jan.	Dec.–Apr.
<i>Planchonella pohlmanniana</i> (F. Muell.) Burkill	Sapotaceae	0.01	Sep.–Nov.	Oct.–Dec.	Dec.	Jan.	Jan.–Feb.
<i>Pogonolobus reticulatus</i> (F. Muell.) Benth.	Rubiaceae	0.01	Sep.–Oct.	Oct.–Nov.	Nov.–Feb.	Nov.–Feb.	Nov.–Feb.
<i>Strychnos lucida</i> R. Br.	Loganiaceae	0.01	Aug.–Sep.	Oct.–Dec.	Nov.	Nov.–Dec.	Jan.
<i>Syzygium eucalyptoides</i> ssp. <i>bleeseri</i> (O. Schwartz) B. Hyland	Myrtaceae	0.01	June–Nov.	Aug.–Jan.	Sep.–Nov.	Oct.–Dec.	Oct.–Jan.
Fully-deciduous species							
<i>Teminidia ferdinandiana</i> Exell	Combrretaceae	2.00	June–Nov.	Oct.–Dec.	Oct.–Jan.	Oct.–Feb.	Nov.–July
<i>Planchonia careya</i> (F. Muell.) Kunth	Lecythidaceae	0.60	July–Oct.	Sep.–Dec.	July–Nov.	July–Nov.	July–Dec.
<i>Brachychiton diversifolius</i> R. Br.	Sterculiaceae	0.30	May–Oct.	Sep.–Nov.	July–Sep.	July–Sep.	Aug.–Oct.
<i>Brachychiton megaphyllus</i> Guymet	Sterculiaceae	0.10	May–Oct.	Sep.–Oct.	May–July	June–Aug.	July–Sep.
<i>Cycas armstrongii</i> Miq.	Cycadaceae	0.20	May–Sep.	July–Nov.	NR	NR	Jan.–Dec.
<i>Croton arrhemicus</i> Muell. Arg.	Euphorbiaceae	0.10	May–Oct.	Oct.–Dec.	Oct.–Dec.	Oct.–Jan.	Nov.–Jan.
<i>Cochlospermum fraseri</i> Planchon	Bixaceae	0.02	June–Nov.	Oct.–Dec.	Oct.–Oct.	June–Oct.	July–Dec.
<i>Ficus scobina</i> Benth.	Moraceae	0.02	July–Oct.	Oct.–Dec.	NR	Aug.–Dec.	Aug.–Dec.
<i>Breynia cernua</i> (Poirct) Muell.	Euphorbiaceae	0.01	May–Oct.	Oct.–Dec.	Oct.–Nov.	Nov.	Dec.–Feb.
<i>Anidema ghaesembilla</i> Gaertn.	Euphorbiaceae	0.01	Apr.–Oct.	Oct.–Dec.	Nov.	Nov.–Jan.	Nov.–Feb.
<i>Clerodendrum floribundum</i> R. Br.	Verbenaceae	0.01	June–Nov.	Oct.–Dec.	Dec.–Feb.	Dec.–Feb.	Jan.–Mar.
<i>Gardenia megasperma</i> F. Muell.	Rubiaceae	0.01	July–Nov.	Oct.–Dec.	Aug.–Oct.	Oct.–Dec.	Nov.–Dec.
<i>Vriex glabrata</i> R. Br.	Verbenaceae	0.01	July–Oct.	Oct.–Dec.	Sep.–Oct.	Sep.–Nov.	Nov.–Feb.

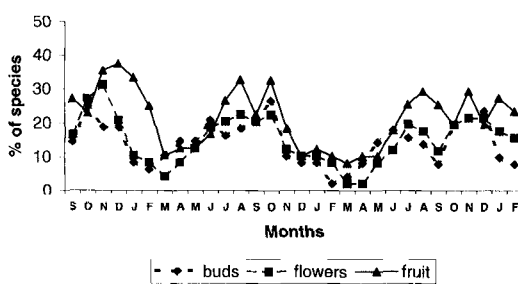


FIGURE 2. Seasonal abundance pattern of buds, flowers, and fruit in 50 species of woody plants at Solar Village, northern Australia. Y-axis: percentage of species in a particular phenological phase from September 1992 to February 1995.

tropical forests with a more equitable distribution of rainfall (Daubenmire 1972, Lieberman 1982, Sarmiento 1984, Koptur *et al.* 1988, Murali & Sukumur 1994, White 1994, Bullock 1995, Reich 1995, Borchert 1996, Muchado *et al.* 1997).

Most species surveyed flowered and set fruit in each year of the study. These species also tended to flower at about the same time each year, and flowered only once per year. In the terms of Newstrom

et al. (1994), such species displayed the "regular and annual" pattern of flowering. Other species, for example *E. chlorostachys* and *X. paradoxus*, flowered infrequently and/or irregularly. These may therefore be "supra-annual," although our period of record is too short to permit definite conclusions on this matter. Two of the three species that did not flower during the study period, *Maranthes* and *Canarium*, are typically components of monsoon rain forest rather than savanna. Both species were represented by only two individuals each, and usually flower regularly in the rain forest habitat (J. C. Z. Woinarski, pers. comm.) No species displayed the "continuous" or "sub-annual" patterns of Newstrom *et al.* (1994).

The transition between dry and wet seasons (the "build-up") was the period in which the majority of woody species were budding, flowering, or fruiting. Such peaks in flowering or fruiting in the late dry season to early wet season have been described for seasonal tropical forests in India (Shukla & Ramakrishnan 1982, Singh & Singh 1992), Mexico (Bullock & Magellanes 1990), Venezuela (de Lampe *et al.* 1992), and Brazil (Muchado *et al.* 1997). The build-up also has been identified as a

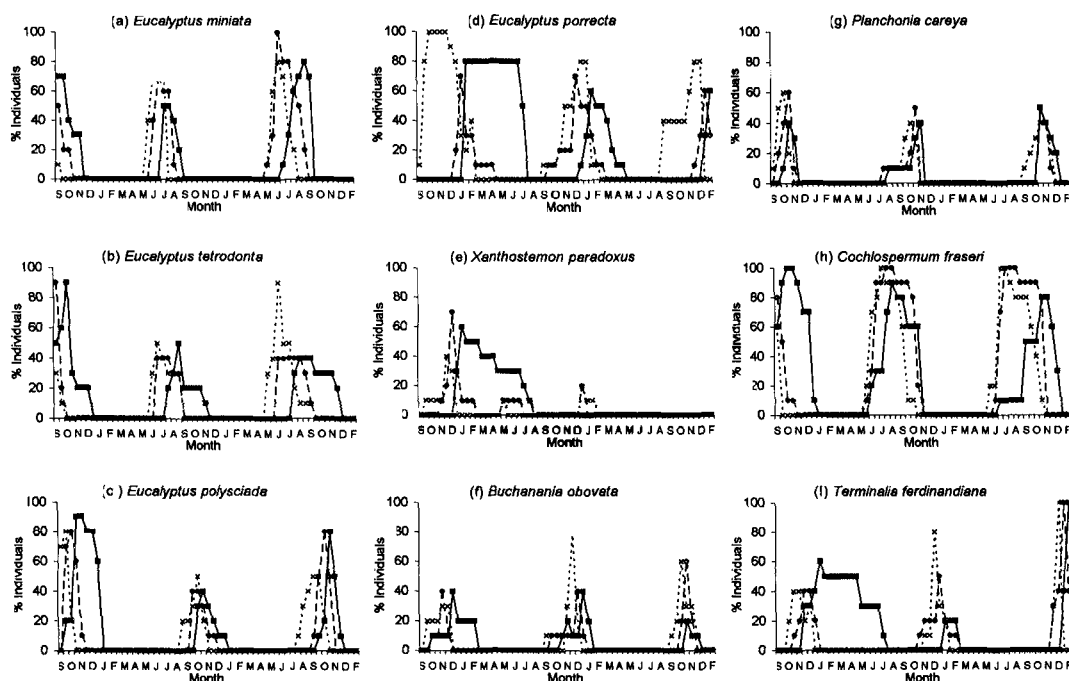


FIGURE 3. Percentage of individuals in nine species of common trees exhibiting buds, flowers, and fruit at Solar Village, northern Australia, from September 1992 to February 1995. Symbols are as for Figure 2. Species are *Eucalyptus miniata* (a), *E. tetradonta* (b), *E. polyciada* (c), *E. porrecta* (d), *Xanthostemon paradoxus* (e), *Buchanania obovata* (f), *Planchonia careya* (g), *Cochlospermum fraseri* (h), and *Terminalia ferdinandiana* (i).

TABLE 2. Mean time of initiation budding and flowering and the duration of fruiting (1992–1994) in six tree species from a savanna near Darwin, northern Australia. The time of first leaf flush (leaf93, leaf94) in the semi- and fully deciduous species (1993 and 1994) is indicated; data from Williams *et al.* (1997). Months have been expressed numerically: 1 = January 1; 1.5 = January 15; 2 = February 1; 2.5 = February 15 and so on. Bud = budding; flw = flowering; frt = fruit; 92, 93, 94 = 1992, 1993, 1994, respectively. Superscripted letters indicate significance of the difference among eucalypt species in the commencement of budding or flowering; eucalypts in the one column sharing the same letter are not significantly different. NA = not calculated, as bud or floral initiation began prior to the study, or fruit fall had not been completed by the end of the study; EG = evergreen species; Species: *Eucalyptus miniata*, *E. tetradonta*, *E. polysciada*, *E. porrecta*, *Cochlospermum fraseri*, *Terminalia ferdinandiana*.

	bud92	bud93	bud94	flw92	flw93	leaf93	flw94	leaf94	frt92	frt93	frt94
<i>Eucalyptus</i> spp.											
<i>E. miniata</i>	NA	5.8 ^a	5.7 ^a	NA	6.2 ^a	EG	5.9 ^a	EG	NA	0.9	1.8
<i>E. tetradonta</i>	NA	6.6 ^b	5.6 ^a	NA	7.0 ^b	EG	6.6 ^b	EG	NA	0.9	1.7
<i>E. polysciada</i>	NA	9.3 ^c	8.7 ^b	9.7	9.8 ^c	8.4	9.7 ^c	7.5	2.3	0.9	0.9
<i>E. porrecta</i>	9.6	11.1 ^d	9.4 ^c	12.7	11.4 ^d	8.3	12.0 ^d	7.8	5.3	1.8	NA
Deciduous trees/shrubs											
<i>C. fraseri</i>	NA	6.1	6.2	NA	6.4	9.9	6.6	10.4	NA	3.0	2.3
<i>T. ferdinandiana</i>	10.6	11.9	11.9	11.3	11.5	10.6	12.4	10.4	3.0	0.3	NA

period of peak leaf flushing activity in all leaf phenological types of woody species—evergreen, semi-deciduous, and fully deciduous—in mesic Australian savannas (Wilson *et al.* 1996, Duff *et al.* 1997, Williams *et al.* 1997).

The mid to late dry season was the peak period for the two dominant trees, *E. miniata* and *E. tetradonta*. Such dry season flowering has been reported elsewhere in the seasonal tropics (Daubenmire 1972, Sarmiento & Monasterio 1983, Sarmiento 1984, Borchert 1996, Patel 1997). A bimodal peak in activity—mid-dry season and build-up/early wet—was also noted by Brennan (1997) in a survey of 93 woody species in Kakadu, 250 km east of Solar Village. Dry season flowering of the dominant eucalypts is also important for consumer organisms in the savanna. The floral reserves of the dominant eucalypts represent an important resource, especially for mobile elements of the vertebrate fauna such as mobile nectarivorous birds (Franklin 1997, Franklin & Noske 1999).

Other studies in the seasonal tropics have reported wet season peaks in flowering and fruiting for woody species. (e.g., Lieberman 1982, White 1994, Wright & van Schaik 1994, Seghieri *et al.* 1995). In this study, however, the wet season (especially the late wet season) was characterized by a low in phenological activity. The late wet season was also a low period for leaf flush and growth at the Solar Village site (Williams *et al.* 1997). Late wet season lows in flowering and fruiting have been demonstrated by other studies in the seasonal tropics (e.g., in India, Patel 1997). In those Neotropical areas in which there is an early wet season peak in

flowering (Bullock & Magallanes 1990, de Lampe *et al.* 1992, Muchado *et al.* 1997), fruiting tended to peak in the mid to late wet season.

Despite the low level of phenological activity during the wet season in our study, other measures of plant growth in the suite of dominant species are typically at maximum levels. Stomatal conductance is typically high during the mid to late wet season in the dominant species of this savanna type (Myers *et al.* 1997) as is assimilation (Prior *et al.* 1997a, b). Stem expansion also occurs during the mid to late wet season (Myers *et al.* 1998). The wet season low in both leaf growth and reproductive activity in this savanna type may thus be a function of resources being directed to other regions of the tree, such as stems and roots, at the height of the wet season. The paucity of flowering in the mid to late wet season also may protect floral structures from the potentially ill effects of the heavy, monsoonal rains that characterize the mid to late wet season.

Despite this consistent, community wide low in phenological activity during the wet season, there were several species (e.g., *E. porrecta* and *T. ferdinandiana*) that flowered and fruited consistently. These two species, because they are common in mesic eucalypt savannas of the Darwin region (Wilson *et al.* 1990) may be keystone reserves—those resources available to consumers at a time when floral or fruit resources are generally low. For example, frugivorous mammals such as tree rats (Friend 1987) may depend on *Terminalia* fruit at this time of year.

SEROTINY.—The lack of serotiny appears to be a general phenomenon in trees from the mesic savannas (Bowman *et al.* 1991, Seghieri *et al.* 1995, Brennan 1997). Non-serotiny in *E. miniata* and *E. tetradonta* was demonstrated by Setterfield and Williams (1996) and Wilson *et al.* (1996) in a similar vegetation formation in Kakadu. The fruiting phenology of the tropical eucalypts thus is in stark contrast to the temperate eucalypts, with fruit held in the canopy for up to four years (Cremer *et al.* 1978, House 1997). The residence time of fruits and time from flower to seed dispersal were not measured in this study; however, other studies have indicated that in *E. miniata* and *E. tetradonta*, seed is shed within eight weeks of ovule formation (Setterfield & Williams 1996) and that in *E. polysiada*, the time from flowering to seed shed is about four weeks (Dunlop & Webb 1991).

Such community wide non-serotiny, combined with the general late dry season peak in flowering and fruiting (38/50 studied had completed fruit dispersal by January) means that in most species, including the community dominants, seed has dispersed by the onset of the wet season. Depending on dormancy characteristics of the seed, seedlings of these species therefore may be able to emerge early in the wet season, take rapid advantage of the initial rains, and establish over the entire wet season.

The strategy of late dry season/early wet season seed dispersal may leave this plant community at risk from late dry season fires. These fires are the most intense of the year (Williams *et al.* 1998) and have become more common in northern Australia over the past 50–100 years (Braithwaite 1991, Russell-Smith *et al.* 1997). Setterfield (1997) indicated that late dry season fires could cause substantial reductions in seed output of *E. miniata* and *E. tetradonta*. Even in those species with a wet season peak in flowering and fruiting (*e.g.*, *Terminalia* and *E. porrecta*) late dry season fires could reduce flowering and fruiting via heat damage to the nascent buds.

SYNCHRONY.—We have demonstrated significant interspecific differences in the timing of flowering and fruiting in this savanna. The four species of eucalypt were all separated in the timing of the main phenological phases. In our previous study on leaf phenology (Williams *et al.* 1997) we demonstrated significant interannual and interspecific differences in the timing of leaf phenological phases. Using the leafing and reproductive phenological data for the ten dominant species studied, six patterns in relation to the degree of deciduousness and

the synchrony of flowering and leafing are recognized:

Deciduous species: (1) Flowering occurred on leafless stems in the mid dry season, after the completion of leaf fall. Leaf flush occurred subsequent to fruiting, after the first rains in build-up early wet season (*e.g.*, *C. fraseri*). Other less common species clearly exhibiting this pattern were *B. megaphyllus* and *B. diversifolius*. (2) Flowering and leaf flush was more or less synchronous in the late dry season, prior to any rain (*e.g.*, *Planchonia careya*). (3) Flowering and leaf flush occurred more or less synchronously, both occurring soon after the first rains in build-up early wet season (*e.g.*, *Terminalia ferdinandiana*). Inter-annual variation in the commencement of leaf flush and flowering may be substantial, depending on when the first rains fall. Other less common species from this study exhibiting this pattern include *Breynia cernua* and *Croton arnhemicus*.

Semi-deciduous species: (4) Flowering occurred after or with the main flush of new foliage, during the late dry season/build-up period. Flowering never took place before the new flush, but did so prior to any rain (*e.g.*, *E. polysiada*, *B. obovata*, and *E. chlorostachys*). (5) Flowering occurred with or after the main flush of new foliage, but subsequent to the initial rains (*e.g.*, *E. porrecta* and *Xanthostemon*).

Evergreen species: (6) Flowering occurred in the dry season (*e.g.*, *E. miniata* and *E. tetradonta*). *Eucalyptus polysiada* and *E. porrecta*, although both members of the bloodwood group of eucalypts, are members of different subgenera (*Blakella* and *Corymbia*, *sensu* Pryor & Johnson 1971). The phenological phases of these species are well separated in time, with no overlap in flowering times. *E. porrecta* appears to exhibit considerable variation in flowering times. This species flowered one to two months earlier at Solar Village than in stands 200 km east in Kakadu (R.J. Williams, pers. obs.). Spatial variation in the timing of flowering in this species may be important, given that *E. porrecta* flowers when few other tree species are flowering (Brennan 1997).

In conclusion, the preponderance of the regular and annual patterns of flowering and fruiting in the trees of this Australian savanna appears to be in accordance with other savannas and dry tropical forests of the world. No species was serotinous, which in the case of the eucalypts, is in stark contrast to the eucalypt forests of southern temperate Australia. The late dry season is an important time for flowering and fruiting in this savanna. This strategy may allow seed of the community domi-

nants to germinate early, and allow seedlings to develop over the full course of the wet season. The species that flower in the dry season provide resources for mobile elements of the fauna. Late dry season fires, however, may be detrimental to the regeneration processes within this savanna type, and may also reduce the abundance of resources available to consumers.

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