Vegetative and reproductive phenologies of four mangrove species from northern Australia

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Abstract. Mangrove communities in the tropical north of Australia are some of the most species rich in the world, yet surprisingly little is known of their reproductive and vegetative phenology. This study investigated the phenology of four mangrove species: Avicennia marina (Forsk.) Vierh., Ceriops australis (C.T. White) Ballment, T.J.Sm & Stoddart, Rhizophora stylosa Griff. and Sonneratia alba J. Smith, in Darwin Harbour over 24 months. Investigations included documenting the flowering and fruiting phenology, periods of leaf flush and leaf longevity. Flowering in these mangroves generally occurred during the dry season (June–October), with the exception of R. stylosa in which flowering occurred in the middle of the wet (December–February). Fruits and propagules were released in the dry and ‘build up’ periods (August–November), with the exception of A. marina, which released propagules in the middle of the wet season. Fruit and/or propagule maturation took less than 2 months in A. marina and S. alba, whereas in C. australis and R. stylosa maturation took 12 and 11 months, respectively. Timing of new leaf production generally coincided with the flowering and fruiting periods of each of the four species. Periods of leaf flush and leaf fall were often closely linked, and species with longer-lived leaves produced fewer leaves at each period of leaf flush. Maximum leaf longevity varied considerably among mangroves, ranging from 8 months in the lower canopy of S. alba to more than 24 months in C. australis. There was also large variability in leaf longevity among different regions of the canopy, with shade leaves generally living longer than sun leaves, and leaves in the upper canopy (3–7 m) longer than those in the lower regions (0–3 m).

Introduction

Mangroves are often important contributors to the primary production of near-shore environments, providing a food source for a range of organisms (Lugo and Snedaker 1974; Odum and Heal 1975; Robertson et al. 1992). Much of the leaf material produced by mangroves directly enters the detrital food web, with comparatively little consumed by herbivores (Robertson and Duke 1987; Farnsworth and Ellison 1991; Coupland 2002). In contrast, mangrove flowers and propagules are often a valuable food source for a host of animals, including insects and crabs (Robertson et al. 1990; Clarke 1992; Minchinton and Dalby-Ball 2001; Clarke and Kerrigan 2002).

Patterns in the production of leaves and timing of flowering and fruiting have been linked to seasonal variation in environmental conditions, including temperature and rainfall, for plants in upland biomes, such as tropical rainforest (e.g. Wright 1996; Bach 2002), and in tropical mangrove communities (e.g. Fernandes 1999; Gwada et al. 2000; Ochieng and Erfemeijer 2002). Consequently, it has been suggested that plant phenologies develop that are synchronised to local or regional environmental conditions (Fernandes 1999). Unlike upland forests, mangrove systems are also influenced by tidal inundation. The position of mangroves within the community in part determines the height of tidal waters to which they are subjected, and the associated fluctuations in salinity. Wium-Andersen (1981) suggested that leaf production in mangroves is influenced by the frequency of tidal inundation. As a result, mangroves at the lowest intertidal level may be expected to show different leaf phenologies from mangroves at the terrestrial fringe of the community.

Many studies have documented mangrove litter fall to assess mangrove productivity; however, fewer studies have documented mangrove phenology, particularly reproductive phenology. Knowledge of mangrove phenology is important for understanding both mangrove contribution to near-shore productivity and the plant-animal interactions within the community.
community itself. In the northern region of Australia, which contains some of the most diverse mangrove communities in the world, very few studies have documented the phenological aspect of mangrove biology. Beyond the small-scale (local) importance of documenting mangrove phenology is the relevance of the information at regional and global scales, and to the field of mangrove macroecology (see Ellison 2002). Ellison (2002) suggested that leaf-level traits could be used to predict the response of mangrove ecosystems to global-scale environmental changes, such as rising sea levels and temperature, and that there was a requirement for more detailed information on functional traits of mangroves.

In an effort to increase our understanding of mangrove processes and to contribute information relevant to mangrove macroecology, this paper describes the vegetative and reproductive phenologies of four mangrove species (Avicennia marina, Ceriops australis, Rhizophora stylosa and Sonneratia alba) from Darwin Harbour, northern Australia, over 2 years. This paper addresses the following questions: (1) are there seasonal patterns in the production of leaves and reproductive parts, and is there interrelated co-ordination in the leaf flush and the reproductive cycle; (2) how long-lived are mangrove leaves, and does the position of leaves within the canopy influence leaf longevity, i.e. through exposure to direct sunlight and/or tidal inundation?

Methods
Site descriptions and plant species
The study site was situated in the mangrove communities of Darwin Harbour, northern Australia (12°26′ S, 130°51′ E). The site was in the middle arm of the harbour, separated by a narrow band of water from Channel Island (Fig. 1), and was characterised by its open exposure to the main water body of the harbour.

The mangrove communities of Darwin Harbour are diverse, comprising about 24 of the 70 mangrove species recognised world-wide (for recognised list refer to Duke et al. 1998). Four mangrove species were selected for the purpose of this study, Avicennia marina is often located immediately adjacent to the terrestrial environment in Darwin Harbour and occupies approximately 7% of the mangrove habitat (Brocklehurst and Edmeades 1996). A. marina grows up to 12 m at the study site and is only inundated on high spring tides, so the upper canopy is rarely, if ever, immersed. Ceriops australis and Rhizophora stylosa are the most widely distributed mangroves in Darwin Harbour, occupying 40 and 33%, respectively, of the mangrove habitat. C. australis trees rarely grow above 3 m at the study site and are inundated only on high spring tides; consequently, the canopy is infrequently immersed. R. stylosa is located at the lower intertidal level and as a result is inundated with every tide; however, the length of immersion decreases with increasing distance inland. R. stylosa grows up to 12 m at the study site and the prop roots associated with this species often form an impenetrable barrier. S. alba is less abundant within the harbour, occupying only 5% of the mangrove habitat. This mangrove occurs at the lowest intertidal level at the study site and is inundated at every tide. Trees grow up to 9 m at the study site and at spring tides more than half the tree canopy can be immersed.

Darwin Harbour experiences a tropical humid climate with two major seasons: a wet summer season, described as monsoonal, between November and March, and a dry winter season spanning from May to September (Fig. 2). The transition between the dry and wet seasons, the 'build-up', occurs during October–November and is characterised by increasing humidity and thunderstorm activity. 'Build-down' occurs during April–May, with a corresponding decrease in humidity and limited rainfall. Darwin Harbour itself is a macro-tidal habitat (up to 8 m) with a semi-diurnal inequality.

Phenological monitoring
The study site was visited monthly over 24 months, from May 1999 to April 2001. To determine periods of leaf fall and leaf flush (vegetative phenology), three trees were haphazardly selected for each species. Eight branchlets, four below 3 m (0–3 m) and four above 3 m (3–7 m),
were tagged on each tree, with branchlets equally divided between the sun and shade regions of the canopy. Only four branchlets were tagged for *C. australis* because this species did not grow above 3 m at the study site. Leaves were numbered consecutively on the adaxial surface with a xylene-free permanent marker and branchlets were checked monthly to document the loss of leaves and the production of new leaves. As new leaves appeared on the branchlet, they were numbered following the numbering pattern on the branchlet. Leaf longevity was compared within the canopy (with height and aspect) for each species by a two-factor ANOVA (height and aspect fixed factors) (probability level 0.05).

To determine the reproductive phenology (flowering and fruiting periods), 10 trees for each of the four species were haphazardly selected and marked with flagging tape. Twenty branchlets were haphazardly selected for observation on each tree every month between November 1999 and October 2001, and the presence/absence of reproductive activity (i.e. presence of buds, flowers, old flowers, fruit and propagules) was recorded. The percentage of branches bearing reproductive structures was calculated monthly.

**Results**

**Vegetative phenology**

Leaf production in the four species corresponded broadly to seasonal changes. New leaves were often produced during the ‘build-up’ and wet season (September–March). Production of leaves in *A. marina*, however, generally occurred towards the end of the wet season and the beginning of the dry (February–March) (Fig. 3). *A. marina* and *S. alba* exhibited unimodal leaf production. In contrast, leaf production in *C. australis* and *R. stylosa* fluctuated throughout the year, but overall there was greater production during the wet season. Periods of leaf production and leaf fall were closely linked. This was particularly apparent in *A. marina* in which peak fall often occurred in the month following initiation of new leaves (Fig. 3). Leaf longevity varied considerably among the four mangroves and with the location of the leaves within the canopy. Leaves of *C. australis* were the longest-lived (Table 1), with many leaves in the shade regions of the canopy living beyond the 24-month monitoring period (Fig. 4).

Reflecting this, shade leaves were significantly longer-lived than their sun counterparts (*F*$_{1,65} = 10.88$, *P* < 0.01). Leaves of *R. stylosa* were shorter-lived (Fig. 4), with the longest lifespan recorded in the upper shade regions of the canopy (18 months, Table 1). Upper regions of the canopy were significantly longer-lived than lower regions (*F*$_{1,186} = 13.75$, *P* < 0.001). Similarly, for *S. alba* the upper regions of the canopy were significantly longer-lived (*F*$_{1,45} = 60.78$, *P* < 0.0001), although on average leaves of *S. alba* were the shortest-lived leaves of the four species, few living beyond 12 months (Table 1, Fig. 4). Leaves of *A. marina* lived on average only slightly longer than those of *S. alba*, with leaves in the lower shade regions exhibiting the longest lifespan for this species (Table 1). There was an interaction between height and aspect in *A. marina* (*F*$_{1,1065} = 71.04$, *P* < 0.05), owing to the shorter leaf longevity in the sun region of the lower canopy than in the rest of the tree (Table 1).

**Reproductive phenology**

*Avicennia marina* had a consistent flowering pattern, with buds forming in September–October during the humid ‘build-up’ period. Bud development was rapid, with flowering beginning in October. The flowering period was relatively short, ending in December during the wet season (Fig. 5a). The brown and hard old flowers that did not develop into fruit remained on the trees for many months and did not appear to serve any particular function. Fruiting occurred from December to February, with a peak between December and January (Fig. 5a). Propagule development in this species was rapid (2 months from flower to propagule), with no dormancy period observed.

The reproductive cycle of *C. australis* was very regular in periodicity (Fig. 5b), with buds developing on trees in May, during the ‘build down’ period and into the start of the dry season. These started as small primordial buds, green in colour, which developed over the course of months into the more rounded and longer burgundy form characteristic of mature buds. Flowering commenced slowly in this species,
starting in August, reaching a peak in October during the ‘build-up’, and finishing abruptly in late October–early November. Old flowers often remained attached to the plant for a few months after the flowering period. Flower fertilisation produced a small fruit that exhibited a long dormancy period before extension of the hypocotyl and development into a mature propagule. The dormant fruit were observed on trees in January and remained dormant
until August. At this time, the hypocotyl penetrated the pericarp and began to extend. Fully mature propagules were first observed in October during the peak flowering period (12 months from flower to propagule), and most fell from trees before January (Fig. 5b).

The reproductive cycle of *R. stylosa* was generally seasonal (Fig. 5c), although green primordial buds were observed on trees throughout the year. Over the course of a few months, the green buds developed into the yellow mature buds characteristic of this species. Bud maturation peaked in December, with flowers most abundant between December and February (the wet season). If flowers were not fertilised, they fell from the tree within a few days. The timing of fruit and propagule development was variable. Fruit were observed developing after the peak flowering period in January and were also evident up until August in some individuals. Mature propagules were observed on trees from April to November, although this was also variable (11 months from flower to propagule) (Fig. 5c).

*Sonnerratia alba* exhibited a seasonal reproductive cycle (Fig. 5d). Buds developed rapidly and were seen on the trees only in the month before and during the flowering period. Peak flowering occurred between the months of May and July, the period of the ‘build-down’ and the dry season, but also occurred less extensively during the wet season in January and February. Fruit matured rapidly (less than 2 months from flower to fruit) and fell from trees during July–September, with smaller-scale fruiting events also observed in December and January (Fig. 5d).

**Discussion**

**Vegetative phenology**

Leaf production in *R. stylosa*, although seemingly erratic, was greater during the wet season (December–May), broadly consistent with *R. stylosa* from north-eastern Australia (Duke *et al*. 1984). Timing of leaf flush during the wet season was also reported in *Rhizophora apiculata* in southern Thailand (Christensen and Wium-Andersen 1977). Leaf production in *C. australis* also fluctuated throughout the year (but was highest in October–November and February), consistent with *C. australis* on the mid-eastern coast of Australia (Saenger and Moverley 1985) and with *Ceriops* in Thailand (Christensen and Wium-Andersen 1977). In contrast, Duke *et al*. (1984) reported that the canopy of *C. australis* in north-eastern Australia was effectively dormant for 6 months of the year during the dry season.

Leaf flush in *A. marina* and *S. alba* corresponded with increased humidity and rainfall associated with the ‘build up’ and wet seasons (October–May). Unlike *A. marina* on the eastern coast of Australia (Saenger and Moverley 1985), *A. marina* in Darwin Harbour did not exhibit bimodal leaf production: only one peak of leaf production was observed during the wet season, consistent with *A. marina* in nearby...
Papua New Guinea (Duke 1990). Wium-Andersen (1981) suggested that bimodality in leaf production is characteristic of species in areas subjected to frequent tidal inundation. In contrast, mangroves growing at higher inter-tidal areas of the community were suggested to exhibit unimodal growth patterns as a result of large seasonal fluctuations in groundwater salinity (Wium-Andersen 1981). *A. marina* in Darwin Harbour is located at highest intertidal area of the mangrove community investigated, and patterns of leaf production and leaf fall in *A. marina* were perhaps the most consistent and distinctly unimodal of the four mangroves investigated. However, *S. alba*, located at the
lowest intertidal level of the mangrove community, also
appeared to exhibit largely unimodal leaf production, with
the peak of leaf production occurring during the wet season.
Unlike A. marina, S. alba does not experience the same
extreme fluctuations in salinity because of regular and
frequent tidal inundation, indicating that other factors, such
as temperature, are likely to be influencing leaf initiation.

Saenger and Moverley (1985) suggested that leaf
production in mangroves was closely tied to changes
in temperature, with seasonal increases in temperature
associated with leaf initiation. In the Japanese Kandela;
candel, the environmental factors most closely linked to leaf
flush were temperature and humidity, the two factors being
closely interdependent (Gwada et al. 2000). Duke (1990)
also suggested that changes in temperature, rainfall and
general moisture levels are likely to control mangrove leaf
production. Although leaf production in C. australis and
R. stylosa appeared erratic, there was a broad seasonal decline
in production during the dry season, possibly associated with
changes in humidity and temperature. For all four species,
the increases in humidity and precipitation occurring during
the ‘build-up’ and wet seasons in Darwin Harbour are likely
to be the triggers for the leaf production. The timing of the
reproductive cycle also appears to be linked to the vegetative
phenology of the four species (see below).

According to estimates of leaf longevity by Duke
et al. (1984), R. stylosa leaves in north-eastern Australia
live longer (13-23 months) than those in Darwin Harbour
(mean 11 months, maximum 18 months). In contrast, leaf
longevity of R. apiculata in Thailand was reported to be
15 months (Christensen and Wium-Andersen (1977),
recalculated by Duke et al. (1984) because of arithmetical
error) and 18 months in Gladstone (24°S, 151°E), north-
eastern Australia (Saenger 2002). Contrary to the variability
exhibited in Rhizophora, A. marina leaf longevity was very
similar among Darwin Harbour, Thailand (Wium-Andersen
and Christensen 1978), north-eastern Australia (Duke 1990;
Saenger 2002) and south-eastern Australia (Clarke 1994),
the exception being 23-month leaf longevity recorded in
Ballina (29°S, 154°E), central-eastern Australia (Saenger
2002). There was also similarity in S. alba leaf longevity
between Halmahera Island (02°N, 128°E), Indonesia (mean
7 months) (Moraya et al. 1988), and Darwin Harbour.

Species with longer-lived leaves (C. australis and
R. stylosa) produced fewer leaves at each period of leaf
flush (Figs 3, 4). C. australis had the greatest leaf longevity
of the four species investigated, with a small proportion
of C. australis leaves living longer than the 24 months of
the present study (0.4%) (Fig. 4). As a result, maximum
longevity of C. australis leaves in Darwin Harbour could
determined. In Thailand, C. tagal leaf longevity was
estimated to be 18 months (Wium-Andersen and Christensen
(1978), recalculated by Duke et al. (1984) because of an
arithmetical error). Estimates of 30-54 (mean 42) months for
C. tagal in north-eastern Australia (Duke et al. 1984) seem
extensive in comparison, even to the 22–36 months recorded
for C. tagal in South Africa (Steinke and Rajh 1995) and
the 27 months in Prosperine (23°S, 149°E), north-eastern
Australia (Saenger 2002). It is unlikely that leaf longevity of
C. australis in Darwin Harbour would be so lengthy, given
that only a small proportion of leaves lived beyond 24 months
in this study. It should be noted that estimates of maximum
longevity are very much dependent on sample size: the larger
the sample size the greater the maximum values will be.

There was spatial variation in leaf longevity among
regions of the tree canopies, with leaves in shade regions
of the canopy living longer than those in the sun, and those in
the upper canopy living significantly longer than those in the
lower regions (with the exception of A. marina). Variations
in longevity are likely to reflect differences in damage to the
leaves from solar radiation, tidal inundation (with associated
damage by debris) and herbivory (see Coupland 2002), with
exposed and/or damaged leaves falling earlier. The effect of
leaf height in the canopy on leaf longevity was particularly
apparent in S. alba and R. stylosa, the mangroves subjected
to the greatest degree of tidal immersion. The mean lifespan
of leaves in the lower canopy (0-3 m) was up to 2 months less
than that in the upper canopy (3-7 m) (maximum longevity
S. alba: 9 months v. 14 months; R. stylosa: 15 months v.
18 months; Table 1). Shading also significantly influenced
longevity; for example, 14% of C. australis shade leaves lived
beyond the 24 months of this study, compared with none in
the sun regions of the canopy (Table 1). Shade leaves also
lived longer than sun leaves in South African C. tagal, a small
proportion living up to 50 months (Steinke and Rajh 1995).

Reproductive phenology

October flowering of A. marina in Darwin Harbour is
consistent with that reported by Wightman (1989), but not
with that by Woodroffe et al. (1988) (December), both studies
from Darwin Harbour. Woodroffe et al. (1988), however,
based their timing of flowering on litter collections, and
as such did not directly measure the peak abundance of
flowers or their first appearance (Primack 1985). Flowering
of A. marina is earlier in Darwin Harbour than the closely
situated populations in Port Moresby (9°32'S, 147°17'E),
and Semeniuk et al. (1978), flowering in A. marina occurs
earlier in lower latitudes, and as such, these authors predicted
that flowering in A. marina should commence in December at
the latitude occupied by Darwin Harbour. The earlier timing
of the reproductive cycle in Darwin Harbour may be triggered
by climate conditions unique to the Darwin Harbour region;
for example, differences in the timing of peak annual air
temperatures and timing of the wet season start.

Bud initiation in C. australis was recorded in the dry
season in Darwin Harbour, with flowering occurring during
the ‘build up’, similar to Western Australia (Semeniuk et al.
In southern Thailand, buds were observed on C. tagal in April and May, and flowers in June, consistent with the commencement of the wet season in that region (Wium-Andersen and Christensen 1978). Sonneratia alba also flowers during the dry season in Darwin Harbour, similar to the same species in Western Australia (June–August) (Semeniuk et al. 1978). There is a lag in flowering of S. alba at a higher latitude in north-eastern Queensland (18°05′S), with flowering occurring between November and December, at the start of the wet season (Duke 1988).

Peak flowering in R. stylosa also occurs in the wet season in Darwin Harbour, although bud production occurs throughout the year. Bud primordia are also produced throughout the year in Rhizophora apiculata in southern Thailand, although flowering occurs during the dry season (Christensen and Wium-Andersen 1977), as it does in Western Australia (April–August, Semeniuk et al. 1978). As with A. marina, the differences in timing of flowering among locations may be influenced by climatic factors.

In all species in Darwin Harbour, with the exception of R. stylosa, peak flowering occurs during the dry season through to the start of the wet, consistent with that reported by Duke et al. (1984). The dry conditions are likely to facilitate pollinators and pollination. According to Duke et al. (1984), the release of mature propagules during the wet season, with the associated increased river flow, occurs at a time that is beneficial for seedling establishment. With the exception of A. marina, however, the timing of propagule release in Darwin Harbour is not consistent with the period of increased rainfall. C. australis releases propagules in the ‘build-up’ before the wet season, whereas S. alba and R. stylosa release propagules during the dry season. The reason for these obvious differences in the timing of fruit and propagule release is likely to be linked to variations in the occurrence of favourable conditions in the Darwin region.

Faster developmental rates of S. alba fruit and A. marina propagules in the Darwin Harbour mangroves than in populations at higher latitudes can be related to climatic differences with latitude, particularly temperature regimes as described by Duke (1988, 1990). In contrast with the 2 months required for propagule maturation in tropical Darwin Harbour, in higher-latitude, temperate regions of Australia, A. marina propagules may take up to 9 months to mature following flowering (Clarke and Myrescough 1991). Fruit maturation time was also more rapid for S. alba fruit in Darwin Harbour than for the same species in the higher latitude of north-eastern Queensland (Duke et al. 1984).

**References**


In summary, patterns in reproductive and vegetative phenology are repeated each year in the four mangroves, although they are more distinct in some species than in others. The timing of these patterns is likely to coincide with specific climatic conditions, such as rainfall and temperature. The short time between production of bud primordia and development of mature fruit and/or propagule in the tropical Darwin Harbour mangroves, compared with those occurring in temperate mangrove communities, is noteworthy and consistent with that reported by Duke (1990). The periodicity of reproductive and vegetative phenology for the Darwin Harbour mangroves is not expected to be consistent for the entire northern Australian region as different monsoonal regimes within this large biogeographic region are likely to result in intraspecific variations in phenology.

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