Floral abortion and pollination in four species of tropical mangroves from northern Australia

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Abstract

We assessed natural rates of floral abortion in four common mangrove species from northern Australia and subsequently manipulated pollination experimentally. *Sonneratia alba* J. Smith exhibited the highest rate of fruit set of the four species (23%), indicating this mangrove was best able to utilise the natural pollination opportunities provided. Fruit set in *S. alba* appeared, however, to be pollinator limited, as large increases in fruit set occurred after manual cross-pollination of flowers. *Avicennia marina* (Forsk.) Vierh. had the highest rate of natural pollination, but fruit set was lower (15%) and appeared to be impeded by resource limitations. Although a range of insects visited *Ceriops australis* (C.T. White) Ballment, T.J. Sm & Stoddart, the rate of fruit set was low (3%) and the capacity for flower fertilisation limited, despite evidence of autogamy in this species. There was an indication of both resource and pollinator limitation in *C. australis*. *Rhizophora stylosa* Griff. exhibited limited fruit set (0.5%), possibly due to limiting maternal resources and the lack of adaptation of flowers to either animal or wind pollination. Large increases in fruit set were recorded after manual cross-pollination of *R. stylosa* flowers. *R. stylosa* and *C. australis*, characterised by resource rich propagules with long periods of development, both aborted a large proportion of propagules during the fruit maturation process.
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1. Introduction

The reproductive biology of mangroves has often been regarded with interest due to the unusual breeding mechanisms, including vivipary, exhibited by many of these plants (Tomlinson, 1986). In fact, the focus of research on mangrove reproductive biology has almost exclusively been on the fruit dispersal stage (Primack et al., 1981). Surprisingly little is known of their pollination biology, with limited emphasis on the processes and success rate of propagule production. Many terrestrial studies have investigated the influence of pollinator and resource limitations on the reproductive output of angiosperms (Horvitz and Schemske, 1988; Campbell and Halama, 1993; Corbet, 1998). Few studies have assessed how successful mangroves are at utilising pollinators, how much reproductive effort is required to produce a single propagule, and whether propagule production is limited by resources or by pollinators. A more complete understanding of the reproductive biology of mangroves is useful, particularly due to the growing pressures on mangrove environments from coastal development, and for effective mangrove rehabilitation programmes.

The aim of this study was to investigate the reproductive biology of four mangrove species, *Avicennia marina*, *Ceriops australis*, *Rhizophora stylosa* and *Sonneratia alba*. Specifically, we assessed rates of pollination and floral abortion. To gauge the relative success of each mangrove's reproductive technique, we monitored the extent of floral abortion, in which the rate of successful maturation of flower buds, rates of floral fertilisation and the relative success rate of fruit and propagule production was determined. The role of pollinators and maternal resources in the reproduction of the four mangroves was tested by a manipulative experiment that involved four treatments, three of which involved bagging flowers and manipulating pollination.

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2. Methods

2.1. Study site and plant species

The study site was situated in the mangrove community opposite Channel Island, located in the middle arm of Darwin Harbour, in the tropical north of Australia (12°26′S, 130°51′E). 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 May–September. The transition between dry and wet season, the 'build-up', occurs during October/November and is characterised by increasing humidity and thunderstorm activity. 'Build-down' occurs in April/May with a corresponding decrease in humidity and limited rainfall. Darwin Harbour is a macrotidal habitat (up to 8 m), with a semi-diurnal inequality.

Mangrove communities in Darwin Harbour are diverse, comprising about 24 mangroves species, with *C. australis* and *R. stylosa* the most widely distributed. These two mangroves, in combination with *A. marina* and *S. alba*, were investigated between 1999 and 2001, during the reproductive periods of each species (Coupland et al., 2005). Within a typical Darwin Harbour mangrove community, *A. marina* is generally located at the terrestrial fringe of the mangrove community, followed by regions of *C. australis*. Mixed regions of *Bruguiera exaristata* Ding Hou and *R. stylosa* are located adjacent to *C. australis*, followed by pure stands of *R. stylosa* and finally *S. alba* is located at the lowest intertidal level.

Fruit are produced in all four of the mangrove species, however, in *A. marina*, *C. australis* and *R. stylosa*, germination of the fruit occurs while it is still attached to the parent tree. The process is termed vivipary (Tomlinson, 1986). The structure at this stage is a propagule, which is actually a seedling and often quite large, representing a considerable resource investment on the part of the parent tree. *Avicennia* propagules are, however, crypto-viviparous. They do not exhibit the more advanced vivipary of *Ceriops* and *Rhizophora*, as the hypocotyl (embryo) does not penetrate the pericarp. *Sonneratia* is a non-viviparous genus, producing fruit that contain numerous seeds (Tomlinson, 1986).

2.2. Assessment of natural rates of floral abortion and fertilisation

Ten reproductive trees of each species were haphazardly selected and two reproductive branches tagged on each of these plants (totalling 20 reproductive shoots for each species). To determine natural rates of floral abortion and fertilisation, the number of young buds, mature buds, flowers, fruit and propagules on each shoot were counted during the reproductive period of each species (with daily observations during peak periods). For *C. australis* observations required up to 14 months for a single reproductive cycle, for *A. marina* and *S. alba* 3 months, and for *R. stylosa* up to 8 months. Record was made of any predation of reproductive units. The percentage of buds that reached floral maturity and developed into fruit and propagules was calculated. Chi-square analyses were used to test for differences among species at different stages in the development of fruit/propagules (i.e. overall conversion of buds to propagules; conversion of buds to flowers; flowers to fertilised flowers; fertilised flowers to propagules). Chi-squared analyses were used as the number of flowers contained within each replicate often varied among replicates. For the purpose of the analysis only the reproductive categories of bud, flower, fertilised flower (or dormant fruit for *C. australis*) and propagule (or fruit for *S. alba*) were used. Categories were homogenised in this way to enable analyses to be conducted.

2.3. Manipulative experiment

Ten trees of each of each species were haphazardly selected and on each plant four reproductive shoots were allocated to one of the four treatments below.

2.3.1. Bagged cross-pollinated

A reproductive branch on each tree was enclosed in a bag of mesh fabric (0.25 mm mesh size) preventing insects, birds and bats from entering, and limiting penetration by wind borne pollen. Bags had a wire loop sewn to the outside to ensure the mesh fabric did not come into contact with the flowers. When flowers opened and the stigma was receptive, they were manually cross-pollinated with pollen from another tree using a paintbrush. This treatment was to establish whether cross-pollination was required for fertilisation.

2.3.2. Bagged closed

A reproductive shoot was enclosed using the same type of mesh fabric bag but the bag remained permanently closed until after the flowering period of the reproductive shoot. These bags also had a wire loop sewn to the outside. This treatment was to establish whether self-fertilisation was occurring.

2.3.3. Bagged open

A reproductive shoot was enclosed in a mesh fabric bag with the distal end held open with a wire loop, allowing animals and wind access to the flower. This treatment was a control for any artefacts created by placing the bag around the reproductive shoots. Bagging experiments in the past have not included a control for the effect of containing the flower, but it is possible that bagging may produce micro-climatic conditions that inhibit seed production (Whelan and Goldingay, 1986).

2.3.4. Unbagged control

A reproductive shoot was tagged at the base but remained un-bagged to determine the outcome under natural conditions.

Bagged and unbagged flowers were checked frequently (daily for some species during peak reproductive periods, or weekly during less productive times) to determine the status of the reproductive units. Following flowering, reproductive units were examined to determine if they had been fertilized – this was apparent from changes in appearance – but left attached to the tree to determine the extent of abortion. The experiment occurred over 3 months for *A. marina* and *S. alba*, up to 7 months for *C. australis* and up to 8 months for *R. stylosa*.

Results were analysed within species using chi-squared analyses to test for differences in fertilisation success for each treatment, and hence the necessity for cross-fertilisation and the presence of autogamy. Chi-squared analyses were used as the number of flowers contained within each bag often varied among replicates and the number of replicates that were able to be cross-pollinated was not consistent.

3. Results

3.1. Natural rates of floral abortion and fertilisation

A small proportion of *A. marina* buds developed into propagules (15%) (Fig. 1a). Nearly all buds developed into flowers (98%) and most of these flowers were fertilised (83%). The number of fertilised flowers that developed into propagules was, however, considerably lower (18%).

Ceriops australis exhibited a low success rate in conversion of buds to propagules (3%) (Fig. 1b) despite the large numbers of buds produced on each reproductive branch. A large proportion of buds developed to maturity (93.5%), and of these, most became flowers (82%). There was a sharp decline in survival of reproductive units, with only a small proportion of flowers fertilised (7%) and becoming dormant fruit. Following 8 months of dormancy, 66% of these fruit began to develop, with most of these finally becoming propagules (93%).

Rhizophora stylosa produced large numbers of buds, however, most buds failed to develop into propagules (99.5%, Fig. 1c). A large proportion of young buds became mature buds (99%), with most mature buds becoming flowers (93%). There was a sharp decline in survival of reproductive units, with very few of flowers fertilised (3%). Conversion of fertilised flowers into fruit was greater than half (57%), although transition of fruit to propagules was less successful (25%).

In *S. alba* almost a quarter of buds developed into fruit (23%) (Fig. 1d). There was considerable loss of buds between the young and mature stage of development (36%), primarily due to predation. Of buds that reached maturity, a large proportion became flowers (73%). Successful fertilisation occurred in 59% of these flowers. Once fertilised, the success rate of fruit production was high (85%). Unlike *C. australis* and *R. stylosa* there was a gradual decline in the survival of reproductive units.

Mangrove species differed significantly in the successful development of buds to fruit/propagules (d.f. = 3, χ^2 = 61.88, $P < 0.001$), with *A. marina* showing the highest success rate and *R. stylosa* the lowest (d.f. = 2, Am = Sa > Ca > Rs, where significant $P < 0.001$, except Ca > Rs, $P < 0.05$). Upon closer investigation of the propagule/fruit production process, different patterns were apparent among species. The successful transition of buds to flowers varied significantly among species (d.f. = 3, χ^2 = 70.37, $P < 0.001$), with *A. marina* and *R. stylosa* exhibiting the highest conversion rate (d.f. = 2, Am = Rs > Ca > Sa; where significant $P < 0.001$). A similar pattern was apparent among species in the progression of flowers to fertilised flowers (d.f. = 3, χ^2 = 261.14, $P < 0.001$). There were significantly higher numbers of *A. marina* flowers
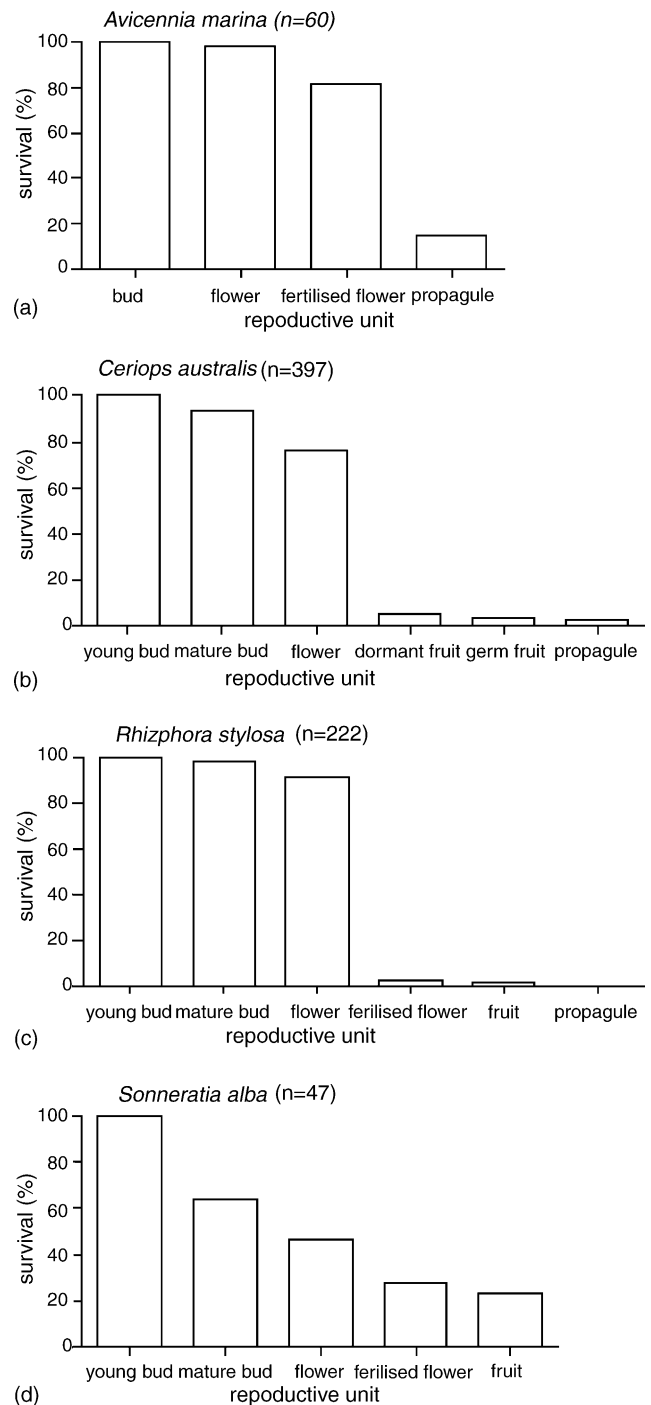

Fig. 1. Survival (%) of reproductive units of four species of mangroves (a) *A. marina* ($n = 60$), (b) *C. australis* ($n = 397$), (c) *R. stylosa* ($n = 222$) and (d) *S. alba* ($n = 47$). NB: 'germ fruit' represents germinating fruit, the point at which the hypocotyl starts to extend; propagule is the stage at which the hypocotyl is fully extended.

fertilised than for the other three species (d.f. = 2, Am > Sa > Ca = Rs; where significant $P < 0.001$; except Am > Sa, $P < 0.05$). With the transition of fertilised flowers to fruit/propagules, the differences among species were also significant (d.f. = 3, χ^2 = 26.83, $P < 0.001$), but were distinct from the above pattern: *S. alba* and *C. australis* showed the highest conversion rate of fertilised flower to propagule/fruit
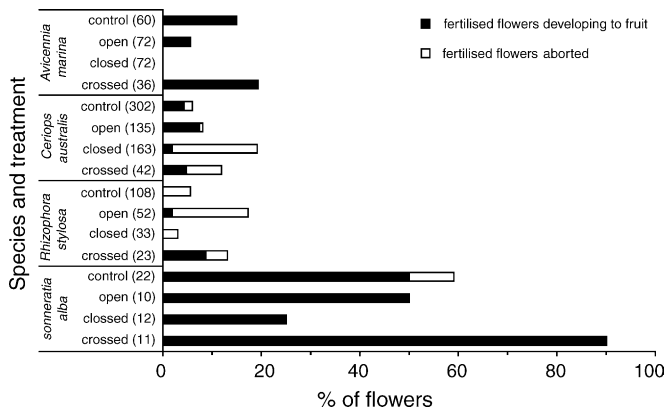
Fig. 2. *A. marina*, *C. australis* and *R. stylosa* flowers that developed into fruit (not propagules) and *S. alba* flowers that developed into fruit for unbagged control, bagged open, bagged closed and bagged cross-pollinated treatments. White sections of bars indicate flowers that were fertilised and began to develop but were subsequently aborted. Numbers in parentheses after treatment names indicate the sample size for that treatment.

and *A. marina* the lowest (d.f. = 2, Sa = Ca > Rs = Am, with Sa > Am $P < 0.001$; Ca > Rs $P < 0.05$; Ca > Am, $P < 0.01$).

3.2. Manipulative experiment

In no species did unbagged control and bagged open differ significantly, indicating that the process of bagging flowers was unlikely to have a confounding effect upon the results.

A. marina treatments differed significantly in the relative number of flowers developing into fruit (d.f. = 3, $\chi^2 = 16.58$, $P < 0.001$). Flowers in the bagged closed treatment produced significantly fewer fruit relative to flowers than the unbagged control (d.f. = 1, $\chi^2 = 11.59$, $P < 0.001$) and the bagged open treatments (d.f. = 1, $\chi^2 = 4.11$, $P < 0.05$). Flowers in the bagged cross-pollinated treatment produced significantly more fruit relative to flowers than either bagged open (d.f. = 1, $\chi^2 = 5.06$, $P < 0.05$) or closed treatments (d.f. = 1, $\chi^2 = 14.97$, $P < 0.001$; Fig. 2).

The number of flowers developing into fruit in *C. australis* did not differ significantly among treatments (d.f. = 3, $\chi^2 = 5.50$, $P > 0.05$; Fig. 2). There was, however, a large proportion of aborted flowers in the bagged closed treatment.

R. stylosa exhibited very little fruit set in any treatment. Chi-squared analyses could not be performed on the data due to the low expected values for all treatments. The bagged cross-pollinated treatment did exhibit higher fruit set than the other treatments, however, the bagged open treatment had the highest proportion of flower fertilisation but a large number of these flowers were aborted (Fig. 2).

The relative number of flowers developing into fruit in *S. alba* differed significantly among treatments (d.f. = 3, $\chi^2 = 10.23$, $P < 0.05$; Fig. 2). Flowers in the bagged cross-pollinated treatment produced a significantly higher number of fruit than the bagged open (d.f. = 1, $\chi^2 = 7.36$, $P < 0.01$), bagged closed (d.f. = 1, $\chi^2 = 10.14$, $P < 0.01$) and the unbagged control treatments (d.f. = 1, $\chi^2 = 5.30$, $P < 0.05$; Fig. 2).

4. Discussion

The capacity of mangroves to convert floral visitation to flower fertilisation and fruit set is an important step in the recruitment process and ultimately to the maintenance of existing mangrove communities. A wide variety of potential pollinators visit flowers of the four species investigated (Coupland, 2002), including a range of insects, as well as birds and bats in *S. alba*. Yet the four species differed in their ability to utilise the potential pollen vectors, illustrated in part by their varying rates of fertilisation and fruit set. Disparity in fruit/propagule size among the mangroves, and the associated differences in maternal resources required to produce the fruit/propagules is likely to have an impact on fruit set.

4.1. Avicennia marina

Avicennia marina had the second highest fruit set of the four species investigated (15%). Few buds appeared to be predated by insects, perhaps due to the fact that buds are small and the rewards greater once flowers have opened. Of these flowers, a vast majority was fertilised (83%), giving this species the highest rate of fertilisation of all the species examined. Fruit set in Darwin Harbour was considerably higher than reported for *A. marina* in southern Australia, in which only an average of 21% of flowers survived to form immature fruit and only 3% to form propagules (Clarke, 1992). The high rate of fertilisation reported in this study, and similarity in fruit set between unbagged control and cross-pollinated treatments in the pollination experiment, indicates that the fruit set was not pollinator limited, that is, the observed insect flower visitors were likely to be in sufficient number and range, and were effective pollinators. Clarke (1992) reported similar conclusions for *A. marina* in south eastern Australia.

Reduced success in transition from fertilised flower to fruit (18% success), and similarity in fruit set between cross-pollinated treatments and unbagged controls indicates that fruit set in *A. marina* was likely to be resource limited (see Whelan and Goldingay, 1986; Corbet, 1998; Fleming and Holland, 1998). Clarke (1992) and Hutchings and Saenger (1987) reported that some of the decline in viable fruit production in *Avicennia* was a result of insect attack on developing fruit, but more importantly, that approximately 75% of the mortality may have been due to maternal regulation. *A. marina* propagules are resource rich (mean weight 2.3 g ± 0.2 S.E.; Coupland, 2002) and therefore would be metabolically expensive to produce. As they are a rich source of nutrients, there is an abundant and diverse range of insect propagule predators (McAlpine, 1965; Hockey and De Baar, 1991; Clarke, 1992; Minchinton and Dalby-Ball, 2001; Coupland, 2002) and these predators influence the rate of propagule maturation. Resource constraints and insect predation on developing fruit and propagules in *A. marina* may both act to reduce fruit set.

Fruit was not produced in the bagged closed treatment (nor was there any fruit that began to develop but were later aborted) indicating self-fertilisation was unlikely to be occurring in *A. marina* in Darwin Harbour, emphasising the importance of

pollen vectors to the reproductive process. In contrast, Clarke and Myerscough (1991) reported fruit set in bagged *A. marina* in south eastern Australia, indicating partial self-compatibility in that region. Bagged *A. marina* flowers that set fruit in south eastern Australia, however, showed a higher rate of maternal abortion than in unbagged control flowers, which may reflect an inbreeding depression (Clarke and Myerscough, 1991).

4.2. Ceriops australis

Ceriops australis had a low rate of propagule production from buds (3%). Few buds were lost during the developmental stage to flower. The greatest obstacle to successful fruit set in *C. australis* was the step from flower to dormant fruit (7% success), indicating that pollination was limited, a consequence of either limited pollinators or ineffectual floral pollination mechanisms, or that maternal regulation of fruit set was occurring. Given that many moths were observed visiting flowers of this species, as well as a range of other small insect vectors (Coupland, 2002), it seems unlikely that there is an insufficient number or range of pollen vectors, particularly as previous studies have reported that moths and other small flying insects are capable of triggering the delicate pollen release mechanisms characteristic of this species (Tomlinson et al., 1979; Tomlinson, 1986). Confirming that there was a sufficient supply of pollinators for *C. australis* flowers, the cross-pollination treatment in the pollination experiment proved as effective as the unbagged control in pollinating flowers. Therefore, despite the presence of numerous insect vectors and their capacity to release and transport pollen, it may be the capacity of flowers themselves to utilise the pollination opportunities that limited successful pollination. The fact that the cross-pollination treatment did not produce more fruit than the unbagged control tends to support this suggestion. There was, however, a high proportion of aborted fertilised flowers in the cross-pollination treatment indicating that maternal regulation of fruit set is also likely to be a factor limiting fruit set.

Autogamy has been proposed to be associated with high levels of fruit set (Primack et al., 1981), presumably as it is an effective method of ensuring pollination. There was, however, evidence of autogamy in *C. australis* and this mangrove had low fruit set. Almost 2% of flowers set fruit in the bagged closed treatment. Fruit set in the closed treatment was not significantly different to the unbagged control, indicating that *C. australis*, although potentially limited in its capacity for successful fertilisation, may rely more on self-pollination, in comparison to insect vectors, than has previously been believed. Autogamy did appear to cause a high rate of abortion, as a large proportion of developing fruit produced in the bagged closed treatment were aborted. As with *A. marina*, this may be due to inbreeding depression.

Even with successful fertilisation in *C. australis*, there was considerable loss of fruit at the fruit germination stage (34% loss), perhaps due to maternal resource limitations. Propagules of *C. australis* are large (mean wet weight 1.2 g ± 0.1S.E.; Coupland, 2002), energy rich relative to the size of the plants in Darwin Harbour, and are produced in abundance. Consequently, considerable resources would be required for their production. The period of propagule development (when the hypocotyl penetrates the pericarp) coincided with the commencement of the flowering period (Coupland et al., 2005) with its associated energy requirements, potentially restricting resource availability. Resource limited abortions have also been reported in studies investigating fertilisation and seed production in terrestrial species (Chaplin and Walker, 1982; Corbet, 1998; Fleming and Holland, 1998). Chaplin and Walker (1982) suggested that smaller individuals may be unable to produce seeds/fruit due to energy constraints, and must accumulate sufficient energy reserves prior to becoming functionally hermaphroditic, that is, contributing more than pollen to the reproductive process. This may be the case in *C. australis*.

4.3. Rhizophora stylosa

Rhizophora stylosa had a very low rate of fruit-set (0.3%), lowest of the three species. There was very little bud loss during the maturation process despite the fact that buds developed on the tree over a number of months and were exposed to insect predation (0.4% loss). Most buds actually developed into flowers (93%), with successful fertilisation the greatest impediment to fruit set. Only 3% of flowers were fertilised, which contrasts significantly with *A. marina* and *S. alba*. The very low rate of fertilisation reported in this study is lower than that estimated in *R. mangle* (7%) and *R. apiculata* (13%) (Hogarth, 1999), but similar to that for *R. stylosa* in north eastern Australia (4%) (Duke et al., 1984). This indicates that animal visitors of *R. stylosa* flowers observed in Darwin Harbour (Coupland, 2002), and in other regions, may be restricted in their ability to pollinate flowers. Insects were most commonly observed entering flowers that still had petals, possibly seeking a pollen reward. At this stage the stigma was not receptive and thus pollination could not occur. Once the petals had fallen, and presuming the flowers were still attached to the tree, a small exudate (nectar) reward was produced. Only ants were observed utilising this secretion. Ants have often been viewed as pollen thieves rather than pollinators (Fægri and van der Pijl, 1979; Buckley, 1982), although ants have been reported to be effective pollinators in a number of studies (Peakall et al., 1991; Gómez and Zamora, 1992; Garcia et al., 1995; Ramsey, 1995; Gómez et al., 1996; Puterbaugh, 1998; Gómez, 2000). As ants tended only to visit *R. stylosa* flowers that had already lost their petals, and with them their pollen, ant pollen transport between flowers is unlikely. It is possible that ants are encouraged to visit the flowers at this stage to prevent herbivores from attacking flowers, as has been reported in terrestrial plant species (Apple and Feener, 2001).

When *R. stylosa* flowers were manually cross-pollinated in the bagging experiment, the rate of successful fertilisation and subsequent fruit set was much higher than the other treatments (although the limited numbers meant that statistical comparisons were unreliable). The fact that relative rates of fruit set were higher in the cross-pollinated treatment indicates that

pollinators may be the limiting factor in successful fruit set for *R. stylosa*. There may have been an insufficient number of flower visitors or visitors were not capable of fertilising flowers, contrary to the situation observed in *C. australis*. Wind also appears to have limited success as a pollen vector. Floral features of *R. stylosa* may not be sufficiently well adapted to utilise this mode of pollination, illustrated by the lack of modification of the stigma for capturing wind-borne pollen.

Autogamy is limited in *R. stylosa* in Darwin Harbour, evident by the bagged closed treatment failing to produce any fruit, although some flowers were fertilised but later aborted. The difference in timing of pollen release and stigma receptivity (flowers are protandrous) limits the capacity for self-fertilisation. Successful fertilisation in *R. stylosa* is consequently dependent upon pollination by cross-fertilisation mechanisms, which have been shown to be limited in this species.

Abortion of fertilised flowers was also common in *R. stylosa*, with just under half of the failing to develop (43%). Abortion of reproductive units was much higher with the transition from fruit to propagules (75% abortion). High abortion rates were also apparent in the bagging experiment. Flowers in bagged open treatment showed the highest rate of fertilisation of the four treatments, with the same potential to set fruit as *A. marina*, but the vast majority of them were aborted before fruit set. Low conversion of flowers to fruit is a feature common in tropical trees with comparatively large fruits (Duke et al., 1984). *R. stylosa* propagules are the largest of the four species investigated (mean wet weight 36.6 g ± 1.7S.E.; Coupland, 2002). Consequently, the low rate of fruit set recorded in this study may be a reflection not only of restricted pollination, but also of resource limitation, e.g. see terrestrial studies on resource limitation by Chaplin and Walker (1982), Corbet (1998) and Fleming and Holland (1998). As the large propagules characteristic of *R. stylosa* are likely to be metabolically expensive to produce, trees may limit their output per reproductive season, or abort developing propagules when energy reserves are restricted.

4.4. Sonneratia alba

In *S. alba* there was an incremental decline in the number of reproductive units at each stage of the reproductive process. Fruit set occurred in approximately one quarter of initial buds (23%), considerably lower than reported in Queensland, Australia (89%) (Primack et al., 1981). In Darwin Harbour, just under half (47%) the young buds reached anthesis, significantly lower than in the other three mangrove species, indicating that bud development was a limiting factor in *S. alba* reproduction. Buds were often bored by insects (a weevil, possibly an Attelabidae, Rhynchitinae), and bored buds generally fell prior to anthesis. Flower predation was also apparent, at times resulting in loss of large pieces of the flower, with the resulting damaged flowers often not being fertilised. Marks on the flowers indicated that possums, rats and/or parrots may have been responsible. Overall, a large proportion of flowers were not fertilised (59%), indicating that aside from

damage to flowers, there might be an insufficient number of suitable pollen vectors. For example, even though birds were often observed perching on the branch behind the flower, reaching around to access the floral resources, the position of birds limited their potential contact with the stigma.

When flower fertilisation actually occurred, a large proportion became fruit (82%), indicating that pollinator rather than resource limitations were influencing fruit set. This was reinforced in the bagging experiment by significantly higher fruit set in the cross-pollinated treatment compared to the unbagged control, and no evidence of floral abortion. Insect predation on buds and limited flower fertilisation appear to be the greatest hindrance to fruit set in *S. alba*. A greater abundance of the observed visitors are required for a higher rate of flower fertilisation in this species.

High rates of fruit set in *S. alba* in other regions of Australia have been proposed to indicate self-compatibility (Primack et al., 1981). The bagging experiment revealed that perhaps 25% of fruit set in Darwin Harbour *S. alba* was a consequence of self-pollination, as about one quarter of flowers in the bagged closed treatments set fruit. Similarity in fruit set in the unbagged control and bagged closed treatment indicated that self-pollination occurs as a regular part of the *S. alba* reproductive process.

References

Apple, J.L., Feener Jr., D.H., 2001. Ant visitation of extrafloral nectaries of *Passiflora*: the effects of nectary attributes and ant behavior on patterns in facultative ant–plant mutualisms. Oecologia 127, 409–416.

Buckley, R.C., 1982. Ant–plant interactions: a world review. In: Buckley, R.C. (Ed.), Ant–Plant Interactions in Australia. DR W Junk Publishers, London, pp. 111–162.

Campbell, D.R., Halama, K.J., 1993. Resource and pollinator limitations to lifetime seed production in a natural plant population. Ecology 74, 1043–1051.

Chaplin, S.J., Walker, J.L., 1982. Energetic constraints and adaptive significance of the floral display of a forest milkweed. Ecology 63, 1857–1870.

Clarke, P.J., 1992. Predispersal mortality and fecundity in the grey mangrove (*Avicennia marina*) in southeastern Australia. Aust. J. Entom. 17, 161–168.

Clarke, P.J., Myerscough, P.J., 1991. Floral biology and reproductive phenology of *Avicennia marina* in south-eastern Australia. Aust. J. Bot. 39, 283–293.

Corbet, S.A., 1998. Fruit and seed production in relation to pollination and resources in bluebell. *Hyacinthoides non-scripta*. Oecologia 114, 349–360.

Coupland, G.T., 2002. The ecological interaction between insects and mangroves in Darwin Harbour, Australia. Ph.D. Thesis, Charles Darwin University.

Coupland, G.T., Paling, E.I., McGuinness, K.A., 2005. Vegetative and reproductive phenologies of four mangrove species from northern Australia. Aust. J. Bot. 53, 109–117.

Duke, N.C., Bunt, J.S., Williams, W.T., 1984. Observations on the floral and vegetative phenologies of north-eastern Australian mangroves. Aust. J. Bot. 32, 87–99.

Fægri, K., van der Pijl, L., 1979. The Principles of Pollination Ecology. Pergamon Press, Oxford.

Fleming, T.H., Holland, J.N., 1998. The evolution of obligate pollination mutualisms: senita cactus and senita moth. Oecologia 114, 368–375.

Garcia, M.B., Antor, R.J., Espadaler, X., 1995. Ant pollination of the paleoend-mic dioecious Borderea pyrenaica (Dioscoriaceae). Plant Syst. Evol. 198, 17–27.

Gómez, J.M., 2000. Effectiveness of ants as pollinators of *Lobularia maritima*: effects on main sequential fitness components of the host plant. Oecologia 12, 90–97.

Gómez, J.M., Zamora, R., 1992. Pollination by ants: consequences of the quantitative effects on a mutualistic system. Oecologia 91, 410–418.

Gómez, J.M., Zamora, R., Hódar, J.A., García, D., 1996. Experimental study of pollination by ants in Mediterranean high mountain and arid habitats. Oecologia 105, 236–242.

Hockey, M.J., De Baar, M., 1991. Some records of moths (Lepidoptera) from mangroves in southern Queensland. Aust. Entomol. Mag. 18, 99–128.

Hogarth, P.J., 1999. The Biology of Mangroves. Oxford University Press, Oxford.

Horvitz, C.C., Schemske, D.W., 1988. A test of the pollinator limitation hypothesis for a neotropical herb. Ecology 69, 200–206.

Hutchings, P., Saenger, P., 1987. Ecology of Mangroves. University of Queensland Press, St. Lucia.

McAlpine, D.K., 1965. New fruit-fly found on mangroves. Aust. Nat. Hist. 15, 60.

Minchinton, T.E., Dalby-Ball, M., 2001. Frugivory by insects on mangrove propagules: effects on the early life history of *Avicennia marina*. Oecologia 129, 243–252.

Peakall, R., Handel, S.N., Beattie, A.J., 1991. The Evidence for, and Importance of, Ant Pollination. In Ant–Plant Interactions. Oxford University Press, Oxford, pp. 421–428.

Primack, R.B., Duke, N.C., Tomlinson, P.B., 1981. Floral morphology in relation to pollination ecology of five Queensland coastal plants. Austrabaileya 4, 346–355.

Puterbaugh, M.N., 1998. The roles of ants as flower visitors, experimental analysis in three alpine species. Oikos 83, 36–46.

Ramsey, M., 1995. Ant pollination of the perennial herb *Blandfordia grandiflora* (Liliaceae). Oikos 74, 265–272.

Tomlinson, P.B., 1986. The Botany of Mangroves. Cambridge University Press, Cambridge.

Tomlinson, P.B., Primack, R.B., Bunt, J.S., 1979. Preliminary observations in the floral biology in mangrove Rhizophoraceae. Biotropica 11, 256–277.

Whelan, R.J., Goldingay, R.L., 1986. Do pollinators influence seed-set in *Banksia paludosa* Sm. and *Banksia spinulosa* R. Br. ? Aust. J. Ecol. 11, 181–186.