

Dioecy, self-compatibility and vegetative reproduction in Australian subtropical rainforest trees and shrubs

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Australian subtropical rainforests and plant populations have become increasingly fragmented since European settlement. Managing relict populations and remnants within the landscape matrix is dependent upon our understanding of plant reproductive biology. The incidence of autogamous self-compatibility and dioecy was investigated in subtropical rainforests, near Taree, in the Manning Valley (northern New South Wales). The proportion of dioecious species in rainforests of the region is high (~17%), but varies among sites. The potential for hermaphroditic species to self-pollinate was examined by bagging inflorescences in the field. Of the > 30 species (in 14 families) studied, nine species exhibited high levels of self-compatibility. These were predominantly pioneer and edge species, but other pioneer species were self-incompatible. Different behaviour occurred within families. Twenty species (in 13 families) regenerated from basal coppice or root suckers following bushfire. The significance of knowledge of reproductive biology for management is discussed.

Introduction

Many tropical and subtropical trees and shrubs are characterised by wide geographical distributions, but at individual sites species often have low population densities. During the Tertiary subtropical rainforest was very extensive in Australia (Adam 1992). In recent geological time its distribution has become limited and fragmented, as much of Australia became arid, with fluctuations in extent driven by climatic change during glacial-interglacial cycles. In the last 200 years, since European settlement, distributions have become further fragmented because of clearance, and stand integrity impaired by weed invasion. Local populations of many species are now very small, in some cases reduced to single individuals per stand.

A knowledge of the reproductive biology of species is an important prerequisite to understanding their resilience to environmental change. Whether or not a species has the ability to self-fertilise, and whether there is plasticity in requirements for pollinators, have particular importance to the ability of species to successfully colonise new sites, and are highly relevant to the management and preservation of remnant rainforest stands.

An ability to self-fertilise reduces vulnerability to extinction (Bond 1994) but, historically, the level of self-incompatibility and requirement for out-crossing in tropical rainforest trees has been a contentious topic (Adam 1992). Federov (1966), discussing the structure of tropical rainforest and speciation in the humid tropics, suggested that out-crossing was rare (due to the spatial isolation of species in complex tropical rainforests) and that self-compatibility was general among rainforest trees. Corner (1954) had earlier argued that 'selfing' is the tendency of all trees even though this will tend to reduce heterozygosity in populations. Ashton (1969) partly summarised Federov's case, taking into account the low densities of rainforest species, as 'given the lack of marked seasonality which leads to irregularity and lack of coincidence in flowering', and assuming that pollen dispersal in temperate and tropical regions was equally efficient, 'then the effective populations in tropical tree species must contain on average fewer individuals than their temperate counterparts, and indeed, self-fertilisation must be the rule.' Ashton (1969) argued that, if Federov and Corner were correct, then dioecism and other breeding systems promoting outcrossing would be eliminated but showed that a significant proportion (26%) of tree species in a Sarawak mixed dipterocarp forest were dioecious, and thus obligate out-crossers. Ashton argued on the basis of plant sexual systems, as indicated by floral morphology, but he had no data on the potential for self-compatibility in non-dioecious species.

Here we present data on the incidence of self-compatibility in more than 30 species of Australian subtropical rainforest trees and large shrubs and give an indication of the proportion of dioecious, and occasionally dioecious, woody rainforest plants. While viable seed production is essential for long distance dispersal, and colonisation of new sites, survival of established populations in the face of disturbance may be enhanced by ability to reproduce vegetatively. An important disturbance factor at the edge of rainforest stands and in rainforest/wet sclerophyll forest ecotones is fire. Observations are reported on the recovery of rainforest edge species following a 1994 bushfire in the Manning Valley.

Methods

The study was largely undertaken during 1991–1993 in lowland rainforest remnants near Taree, in the Manning Valley on the north coast of New South Wales, as part of a larger investigation of the pollination ecology of lowland subtropical rainforest communities (Williams 1995). The majority of tree and shrub species studied displayed the general entomophilous flower syndrome, possessing numerous small actinomorphic flowers. An exception was *Hibiscus splendens* which possessed large (> 7 cm diameter) flowers.

Information on plant sexuality was obtained from Floyd (1989), Beadle, Evans and Carolin (1972), Harden (1990–93), and supplemented by direct observation (Williams 1995).

Potential self-compatibility and the influence of pollination vectors on reproductive success/fruit set were investigated by a series of bagging and open pollination

comparisons. The majority of the bagging experiments was undertaken in subtropical rainforest and wet sclerophyll forest at Lorien Wildlife Refuge (31°45'00"S, 152°32'30"E), and a smaller set of observations was carried out in littoral rainforest at Harrington (31°52'30"S, 152°41'00"E), floodplain rainforest at Lansdowne Reserve (31°32'30"S, 152°32'30"E), and mixed rainforest-wet sclerophyll forest at Kenwood Wildlife Refuge (31°44'45"S, 152°31'30"E).

Unopened flower buds were counted and inflorescences, or groups of flowers, assigned individually numbered tags. Flower buds were counted by marking them with a coloured marker pen. This minimised recounting or the overlooking of buds. On very large inflorescences, individual sections were designated with coloured thread and these bud sub-sets were then counted and marked as above.

Fine nylon bags with a mesh diameter of < 0.1 mm. were placed over inflorescences and individual or small clusters of flowers and secured with woollen yarn to obstruct insect entry into the bag. Bagged inflorescences were located on at least two plants of each species in most cases. Occasionally large orthopterans chewed through the cloth and thrips gained entry. Data from these were discarded and new inflorescences were bagged. Several bagged inflorescences were snapped in strong wind and had to be duplicated. The bags were very conspicuous and the choice of sites, and to a degree, the choice of plants, was dictated by the availability of locations where disturbance was likely to be minimal. All bags were removed upon the conclusion of flowering.

Artificial manipulation of pollen receipt may reveal self-compatibility in species that cannot automatically self (see Gross 1993). However, no attempt was made to undertake hand pollinations because the large numbers of small sized flowers in inflorescences of mass-flowering tree species (e.g., *Euroschinus falcata*, *Alphitonia excelsa*) do not open all at once (i.e. staggered receptivity) and would have required a very long time to pollinate by hand. The time consuming nature of the manipulations would have required repeated and relatively long periods of bag removal with subsequent vulnerability of stigmas to uncontrolled extraneous pollen deposition. In addition, in small, generally entomophilous flowers the stigma may be enclosed and difficult of access, making hand pollination impractical.

Bagging of flowers, in itself, does not provide a rigorous assessment of the degree of self-compatibility likely to occur in the field but it does give an indication of automatic self-pollination (autogamy) and the potential to 'self'.

Massed inflorescences presented problems of counting due to the large number of buds, difficulty in counting very small buds, the inability to adequately assess and identify abortion of buds, and the difficulty in differentiating male and female flowers in some monoecious taxa (particularly Sapindaceae). Plants in this later group were bagged without counting individual buds and scored as self-compatible if development of ovaries occurred.

Fieldwork was undertaken during years in which moderate to severe drought conditions were experienced and this potentially influenced results.

Observations on species capable of regrowing by vegetative coppicing were made after a bushfire on 7 January 1994 in Lansdowne State Forest, adjacent to the Lorien Wildlife Refuge (Williams 1995). This fire occurred towards the end of a prolonged drought (1992–late 1994), and air temperatures during the fire exceeded 35°C.

Plant nomenclature follows Harden (1990–93).

Table 1. Dioecious and occasionally dioecious species occurring at study sites.

1 = Floyd 1989, 2 = Beadle et al. 1972, 3 = Harden 1990, 4 = Harden 1991, 5 = Williams 1995.

Ebenaceae		
<i>Diospyros australis</i>	dioecious	3
<i>D. pentamera</i>	dioecious	3
Euphorbiaceae		
<i>Claoxylon australe</i>	usually dioecious	3
<i>Drypetes australasica</i>	dioecious	3
<i>Mallotus philippensis</i>	usually dioecious	3
Icacinaeae		
<i>Citronella moorei</i>	dioecious	1
Lauraceae		
<i>Litsea australis</i>	dioecious	3
<i>L. reticulata</i>	dioecious	3
<i>Neolitsea australiensis</i>	dioecious	3
<i>N. dealbata</i>	dioecious	3
Meliaceae		
<i>Dysoxylum fraserianum</i>	bisexual or dioecious	4
<i>D. rufum</i>	bisexual or dioecious	4
Monimiaceae		
<i>Wilkiea huegeliana</i>	dioecious, monoecious	1, 2, 3, 5
Moraceae		
<i>Ficus coronata</i>	dioecious or monoecious	3
<i>F. fraseri</i>	dioecious or monoecious	3
<i>F. macrophylla</i>	dioecious or monoecious	3
<i>F. obliqua</i>	dioecious or monoecious	3
<i>F. rubiginosa</i>	dioecious or monoecious	3
<i>F. superba</i> var. <i>henniana</i>	dioecious or monoecious	3
<i>F. watkinsiana</i>	dioecious or monoecious	3
<i>Streblus brunonianus</i>	dioecious	3
Sapindaceae		
<i>Cupaniopsis</i>		
<i>anacardioides</i>	monoecious or dioecious	4
<i>C. parvifolia</i>	monoecious or dioecious	4
Urticaceae		
<i>Dendrocnide excelsa</i>	dioecious	3
<i>D. photinophylla</i>	dioecious	3
Winteraceae		
<i>Tasmania insipida</i>	usually dioecious	3

Results

A total of 152 species of dicotyledonous trees and shrubs was recorded from the study sites including 92 species believed to be bisexual, or facultatively bisexual species, and 26 dioecious, or occasionally dioecious, species (~17 %) (Floyd 1989, Beadle et al. 1972, Harden 1990–93) (Table 1). The incidence of dioecy is probably an underestimate because several species are described in floras as being either dioecious or monoecious. Dioecious species are obligate out-breeders; constraints on the breeding systems of the remaining species are largely unknown.

Most sites possessed fragmented or highly clustered populations or isolated flowering plants of species with low abundances. While this spatial disjunction or isolation may assist the identification of self-compatibility (i.e. where the absence of flowering conspecifics negates the possibility of pollen entry onto bagged flowers), for open-pollinated flowers, the proportion of successfully developing fruit may not represent 'normal' fecundity levels. However, inadequate receipt of pollen and commensurate limitation of female success may be common (Burd 1994).

Fruit set in bagged and open flowers is listed in Table 2. In the open pollinated flowers the percentage of flowers with developing fruit was highly variable, but in many cases was low. Whether these low rates are 'normal' for the species concerned is not known.

The results from the bagged flowers indicate that 16 of the studied species (in 14 families) have the ability to automatically self. This number may be fewer if those species with very low percentages, which may represent contamination, are discounted. Nine species demonstrated relatively high levels of selfing: *Abrophyllum ornans*, *Acradenia euodiiformis*, *Cupaniopsis anacardioides*, *Cryptocarya glaucescens*, *Elaeocarpus reticulatus*, *Eupomatia laurina*, *Hibiscus splendens*, *Scolopia braunii* and *Tasmannia insipida*. These are predominantly pioneer or edge species. Reproductively, *Eupomatia laurina* and *Hibiscus splendens* are specialist species, pollinated by one or a small number of pollinators (Armstrong & Irvine 1990, Williams 1993, 1995). Their ability to self may have important consequences for the maintenance of populations in the absence of pollinators.

The species with no apparent capacity for automatic selfing also include pioneers (e.g. *Alphitonia excelsa*, *Rhodomyrtus psidioides*). In *Alphitonia excelsa* self-incompatibility may be a consequence of protandry, as the stamens, encapsulated by the petals, are carried away from the latter developing gynoecium as the petals recurve (Williams 1995).

Within a family, species exhibit different behaviour (Table 2 — compare *Cryptocarya glaucescens* and *Cryptocarya rigida*; *Acradenia euodiiformis* and *Acronychia imperforata*, *Geijera salicifolia*). The two members of the Escalloniaceae studied (*Abrophyllum ornans*, *Cuttsia viburnea*) showed very high fecundity in open pollinated flowers, but gave contrasting results in the bagging experiment. *Cuttsia viburnea* is apparently an obligate out-breeder, being self-incompatible, while *Abrophyllum ornans* exhibits high levels of self-compatibility.

Table 2. Autogamy (automatic self-pollination) and open pollination results in lowland rainforest species.

Species	Bagged flower buds			Open pollinated flowers		
	flower buds	developing fruit at conclusion of flowering		flower buds	developing fruit at conclusion of flowering	
	#	#	%	#	#	%
Anacardiaceae						
<i>Euroschinus falcata</i> ¹	508	3	0.6	414	83	20.1
Celastraceae						
<i>Denhamia celastroides</i> ¹	1281	0	0	569	41	7.2
Ebenaceae						
<i>Diospyros australis</i> ¹	147	3	2	179	44	24.6
Elaeocarpaceae						
<i>Elaeocarpus reticulatus</i> ¹	223	86	36.9	304	49	16.1
Epacridaceae						
<i>Trochocarpa laurina</i> ¹	433	0	0	605	55	9.1
Escalloniaceae						
<i>Abrophyllum ornans</i> ¹						
- bagging in 1991-92	404	65	16.1	327	307	93.9
- bagging in 1992-93*	201	59	29.4	-	-	-
<i>Cuttsia viburnea</i> ¹	449	0	0	629	521	82.9
Eupomatiaceae						
<i>Eupomatia laurina</i> ¹	31	3	9.7	66	39	59.1
Flacourtiaceae						
<i>Scolopia braunii</i> ¹	415	74	17.8	297	83	28.0
Lauraceae						
<i>Cryptocarya glaucescens</i> ¹	647	117	18.1	766	189	24.7
<i>Cryptocarya rigida</i> ¹	261	0	0	236	9	3.8
Malvaceae						
<i>Hibiscus splendens</i> ¹	22	2	9.1	38	11	29.0
Monimiaceae						
<i>Daphnandra micrantha</i> ¹	533	11	2.1	538	38	7.1
Myrsinaceae						
<i>Rapanea howittiana</i> ¹	127	0	0	179	0	0 ⁷
Myrtaceae						
<i>Acmena smithii</i> ¹	360	13	3.6	276	11	4.0
<i>Archirhodomyrtus beckleri</i> ¹	263	0	0	307	96	31.3
<i>Rhodomyrtus psidioides</i> ¹	182	0	0	413	9	2.2
<i>Tristaniopsis laurina</i> ¹	189	0	0	210	40	19.1
<i>Waterhousea floribunda</i> ¹	634	5	0.8	673	135	20.1
Pittosporaceae						
<i>Hymenosporum flavum</i> ¹	45	0	0	95	2	2.1
Rhamnaceae						
<i>Alphitonia excelsa</i> ²	1778	0	0	1826	99	5.4

	#	#	%	#	#	%
Rutaceae						
<i>Acradenia euodiiformis</i> ¹	583	60	10.3	906	36	4.0
<i>Acronychia imperforata</i> ²	317	0	0	652	0	0 ^{5,7}
<i>Geijera salicifolia</i> ³	783	0	0	1040	131	8.9
Sapindaceae						
<i>Alectryon coriaceus</i> ²						
- bagging in 1991–92	228	0	0	80	0	0 ^{6,7}
- bagging in 1992–93 ^{**}	-	-	-	619	48	7.8 ⁶
<i>Cupaniopsis anacardioides</i> ²	185	17	9.2	590	117	19.8
<i>Guioa semiglaucula</i> ^{2***}	-	-	-	474	42	8.9 ⁶
<i>Guioa semiglaucula</i> ¹	536	4	0.8	-	-	-
<i>Mischocarpus pyriformis</i> ⁴	1112	0	0	1280	124	9.7 ⁶
Verbenaceae						
<i>Clerodendrum tomentosum</i> ²	561	3	0.5	331	4	1.2
Winteraceae						
<i>Tasmannia insipida</i> ¹	46	27	58.7	44	43	97.7

1 location = Lorien Wildlife Refuge, **2** Harrington, **3** Kenwood Wildlife Refuge, **4** Lansdowne Reserve; **5** < 0.001 % of population flowered (buds opened); **6** monoecious sp., bud count includes male and female flowers, therefore 'selfing' is only the proportion of unknown number of female flowers that were present in the bagged inflorescences; **7** did not develop fruit; '*****' bagging repeated in second season to confirm high 1991–92 'selfing' level; '******' repeated in 1992–93 due to zero selfing levels in 1991–92 open pollinated flowers; '*******' bags damaged, repeated at Lorien site in same year.

There may be variation in the reproductive success of species both within and between years. For example, bagging was carried out in 1992 on a single isolated tree of *Rapanea howittiana* at Lorien Wildlife Refuge. This plant set no seed, though a cluster of trees > 100 m distant, and a second population at the Lansdowne Reserve site did. A single small *Rapanea variabilis* flowered (but was not bagged) at Lorien in 1994 and set numerous seed. The tree had not been previously observed to flower over nine years of observations and thrips (*Thrips setipennis*) were the only flower visitors. No other flowering *Rapanea variabilis* were located in the neighbourhood, suggesting self-compatibility or fertilisation via agamospermy.

Failure to set seed in some years has been observed in *Acronychia imperforata*, *Alectryon coriaceus* and *Rhodomyrtus psidioides*, although *Abrophyllum ornans*, *Acmena smithii*, *Alphitonia excelsa*, *Cuttsia viburnea*, *Tasmannia insipida* and *Waterhousea floribunda* populations at Lorien Wildlife Refuge have set large numbers of seed every year, over 14 years of observations, regardless of variation in climatic conditions.

Opportunistic observation allows additions to be made to the list of self-compatible species in Table 2. *Endiandra discolor* (Lauraceae) is regionally rare (Williams 1993) and occurs at the Lansdowne Reserve site as a single mature tree. This tree set seed during April–May 1994, and a germination trial of collected seed demonstrated viability. A single planted tree of *Hicksbeachia pinnatifolia* (Proteaceae), which is not native to the region, set viable seed at Lorien during each year of the study, although no other local ornamental plantings are known.

In *Elaeocarpus reticulatus*, more bagged flowers developed fruit than did open pollinated ones. There are no obvious explanations of this and further observations are required to determine whether this is atypical.

Twenty species of rainforest trees and shrubs, in 13 families, were observed to regenerate from basal coppice following the January 1994 bushfire (Table 3). *Melia azedarach* also regenerated from root suckers. No woody 'rainforest' species present at the site failed to coppice. Two of the species, *Diospyros australis* and *Mallotus philippensis*, are dioecious or usually dioecious (Table 1). The range of species regenerating vegetatively is similar to that recorded by Chesterfield et al. (1990) from burnt rainforest in Victoria.

Table 3. Rainforest trees and shrubs regenerating by coppice growth following bushfire in Lansdowne State Forest, 7 January 1994.

Family	Species
Cunoniaceae	<i>Schizomeria ovata</i>
Ebenaceae	<i>Diospyros australis</i>
Euphorbiaceae	<i>Croton verreauxii</i> <i>Glochidion ferdinandi</i> <i>Mallotus philippensis</i>
Eupomatiaceae	<i>Eupomatia laurina</i>
Lauraceae	<i>Cryptocarya microneura</i> <i>Cryptocarya rigida</i>
Meliaceae	<i>Melia azedarach</i> var. <i>australasica</i> <i>Synoum glandulosum</i>
Myrsinaceae	<i>Rapanea variabilis</i>
Myrtaceae	<i>Acmena smithii</i> <i>Lophostemon confertus</i> <i>Rhodamnia rubescens</i>
Oleaceae	<i>Notelaea longifolia</i>
Pittosporaceae	<i>Hymenosporum flavum</i>
Rutaceae	<i>Acronychia oblongifolia</i> <i>Melicope micrococca</i>
Sapindaceae	<i>Guioa semiglauca</i>
Solanaceae	<i>Duboisia myoporoides</i>

Discussion

Plant reproductive strategies strongly influence the ability of species to colonise and survive in rainforest stands.

Rainforest plants that cannot reproduce vegetatively, and obligate out-crossers that are incapable of producing seed by selfing, are unable to establish colonies from single recruits. Populations reduced to single individuals, and isolated from external pollen sources, are functionally extinct within individual remnants.

Dioecious species would appear to be at a particular disadvantage because reproductive success is linked to the receipt of pollen from male plants. Dioecy is uncommon amongst flowering plants, being found in between 4 and 6% of species (Barrett 1998, Renner & Ricklefs 1995, Richards 1997). The condition is found in many different families, and appears to have evolved independently on a number of occasions (Richards 1997). Some angiosperms may be functionally dioecious, for example where androdioecious plants (with males and hermaphrodites) possess hermaphrodites with nonfunctional pollen (Kearns & Inouye 1993). Muenchow (1987) has suggested that, in general, dioecious species have flowers characteristic of the general entomophilous syndrome. This is the case in our study.

Although dioecy is generally uncommon the incidence is higher amongst trees than herbs (Arroyo & Uslar 1993, Richards 1997, Schatz 1990, Waller 1988) and also in certain habitats — notably rainforest and on oceanic islands (Richards 1997).

The high incidence of dioecy in rainforest has been documented by a number of authors (see Bawa 1980, 1990, Richards 1997). In Sarawak mixed dipterocarp forest Ashton (1969) recorded 26% of trees with girth exceeding 1 foot (~30.5 cm) as dioecious. Russell-Smith and Lee (1992) recorded 16 dioecious species out of a total of 84 (19%) in isolated monsoonal rainforest patches in the Northern Territory. Twenty-one percent of Jamaican montane species, 23% of Costa Rican tropical lowland rainforest species and 31% of Venezuelan montane forest species are documented as dioecious by Bawa (1990).

In our study region the overall incidence of dioecy in rainforest is 17%, but the proportion varies among sites (Table 4).

Table 4. Number of dioecious rainforest tree and shrub species at sites in the Manning Valley.

Site	No. of dioecious spp.	% of total flora
littoral rainforests		
Crowdy Head	9	21
Harrington	16	27
Manning Point	11	36
Saltwater Reserve	9	23
Red Head	13	24
Black Head	14	19
floodplain rainforests		
Wingham Brush Nature Reserve	17	22
Coocumbac Is. Nature Reserve	11	28
Lansdowne Reserve	13	24
montane rainforest		
Dingo Tops (Tapin Tops National Park)	10	12

The evolutionary explanation for the high incidence of dioecy in rainforest is unclear, and various hypotheses are discussed in Richards (1997). Bawa (1980) has argued that female flowers, with no investment in male function may be able to make a high investment in female function, and that in the rainforest environment there is an

advantage to producing large seeds. Richards (1997) suggested that within rainforest, individuals of a species may occur at low density with large distances between them. In consequence self-compatible hermaphrodites may be largely self-pollinated, with a loss of vigour and viability. If dioecious variants arise in such species rare long distance cross pollination may result in higher quality offspring, and hence a long term evolutionary advantage despite lower fecundity than in self-compatible hermaphrodites.

Regardless of the original advantages of dioecy the consequence when rainforest stands are very highly fragmented is a high risk of local extinction for dioecious taxa (Bond 1994) and little capacity for successful colonisation of new sites.

While continued selfing by self-compatible hermaphrodites may result in a decline in offspring 'quality' (Richards 1997), selfing may permit the local survival of species in fragmented stands where individual populations are severely reduced (we did not attempt to test the viability of seeds from self-pollinated flowers - but such a study would provide important information about the long term viability of isolated populations).

Studies in various overseas rainforests have indicated that, generally, outcrossing predominates (e.g., Bawa et al. 1985, Murawski et al. 1994, Murawski & Hamrick, 1991, O'Malley & Bawa 1987, Proenca & Gibbs 1994), although the spatial isolation of trees may influence the degree of outbreeding and fecundity (House 1985, 1992, 1993, Appanah & Chan 1981, Murawski et al. 1990). Our results are comparable with those from elsewhere, but many hermaphroditic species retain some capacity for self-pollination. This ability may be important for survival of biodiversity in the face of continuing disturbance to rainforest, and may also explain survival during periods of natural rapid change.

Once established, the ability to survive disturbance will be aided by an ability for vegetative regrowth. A considerable number of rainforest species in New South Wales and in monsoon forest (Floyd 1990, Bowman 1991) have this facility, and our observations of regeneration from the 1994 fire demonstrate that rainforest recovery from a single intense fire is possible, although the effects of repeated burning may be more serious.

Our observations suggest that in developing management and rehabilitation plans for fragmented rainforest stands particular attention should be given to dioecious species, which may form a large proportion of the flora at some sites.

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