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Seed production, germinability and seedling growth for a bird-pollinated shrub in fragments of kwongan in south-west Australia

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ABSTRACT

In this study we investigate the effect of population size on the proportion of flowers that produce a fruit (fruit set), the number of seeds per fruit (seed set), seed germinability, seedling mortality and growth in a range of population fragments for the bird-pollinated mixed mating system shrub *Calothamnus quadrifidus* R. Br. (Myrtaceae). We found no significant linear relationship ($p < 0.05$) between population fragment size and fruit set in any of the three years reproduction was studied. In contrast, we found a very strong positive correlation between the number of seeds produced per fruit and increasing population fragment size for each of the three years. We found no significant linear relationships between population fragment size and seed germination, or seedling growth and mortality. The most plausible explanation for the decline in seed set is increased inbreeding in smaller populations. Although a previous mating system analysis with allozymes did not reflect the above, we present evidence from other lines of inquiry to indicate that inbreeding does increase in smaller populations, but is masked by post-zygotic lethal systems that eliminate genetically incompetent homozygous embryos. We found no evidence that highly mobile pollinators transporting pollen among fragments rescue small fragments from inbreeding. We discuss the implications of our findings for the conservation of plant diversity in fragments of species rich Mediterranean climate shrublands.

1. Introduction

Fragments of native vegetation scattered across agricultural and urban landscapes are common throughout the world. For plant species in these fragments, populations are typically smaller and more isolated than they were historically, the abundances of their interacting species have changed, new species have been added, and the abiotic conditions and resources necessary for growth and reproduction have been altered. For sexually reproducing plant species, changes to the pollinator community and mate availability may have a number of important consequences for pollen flow, the mating system, seed production, and offspring fitness, factors all of which influence population vital rates and viability (Whelan et al., 2000; Young et al., 2000; Hobbs and Yates, 2003; Aguilar et al., 2006).

For self-compatible but preferentially outcrossing plants with generalized pollination systems, changes in the pollinator community are unlikely to impact on plant reproduction (Bond, 1994; Donaldson et al., 2002; Yates and Ladd, 2005; Yates et al., 2007). However, as plant populations become smaller and mates become fewer, selfing and/or mating

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between closely related individuals (bi-parental inbreeding) is more likely, producing offspring that are more homozygous than their parents. Increases in inbreeding may lead to the expression of lethal or harmful recessive mutations that lower seed production, reduce germination, increase seedling mortality, and reduce rates of growth and flowering (Dudash and Fenster, 2000).

The fragmentation of Mediterranean climate southwestern Australia's floristically rich heath and shrub-lands (kwongan) is relatively recent with most clearing occurring between 1949 and 1969 (Burvill, 1979). Many small fragments still contain significant amounts of plant diversity (Gibson et al., 2000; Obbens et al., 2001). However, sufficient time may not have passed for the negative consequences of fragmentation to have a substantial effect on the composition of the remaining vegetation. Plant populations that are too small to be viable may persist for long periods because of the longevity of individuals, or because a residual soil seed-bank buffers the population against declines in seed production and offspring performance (Saunders et al., 1991; Turner et al., 1996). Consequently, the further loss of plant diversity from habitat fragments could be reasonably expected, but because basic information on population responses is skewed towards a small number of functionally equivalent groups, especially self-incompatible perennial herbs, there is still considerable uncertainty about which species are most at risk (Hobbs and Yates, 2003; Aguilar et al., 2006). Moreover, to date, 80% of investigations into plant reproductive susceptibility to habitat fragmentation have evaluated the effects for a single flowering season (Aguilar et al., 2006). Studies that include more than one year frequently find contradictory results among years indicating that temporal variability in factors affecting reproduction is likely to be extremely important (Hobbs and Yates, 2003). Further empirical studies that integrate studies of pollinator visitation, pollination, mating systems and fecundity for a range of species encompassing different life-history traits over multiple flowering seasons are needed (Whelan et al., 2000; Hobbs and Yates, 2003; Aguilar et al., 2006).

In 2001, we began a study investigating the pollinator community, pollination, the mating system, seed production and progeny fitness among population fragments of the bird-pollinated species *Calothamnus quadrifidus* R. Br. (Myrtaceae). We chose *C. quadrifidus* because there is still much to be learnt about the viability of population fragments of mixed-mating system, bird-pollinated shrubs (Hobbs and Yates, 2003); a functional group of plants well represented in the diverse Mediterranean climate shrub- and heath-lands (kwongan) of south-west Australia (Whelan and Burbidge, 1980; Hopper, 1981; Keighery, 1982; Brown et al., 1997). Detailed examination of the system for one species may give suitable management directions for many species.

In an another paper (Yates et al., 2007), we reported that the composition of the honeyeater pollinator community was similar across population fragments, and there was no correlation between the number of birds visiting plants and population fragment size. Honeyeaters were most commonly observed visiting numerous inflorescences within single plants in all populations, but as population fragments became larger, movements between plants were more commonly observed. Levels of pollination were high across all fragments and unrelated to population size. Contrary to expectations based on assumptions of mixed-mating in *C. quadrifidus*, levels of outcrossing and bi-parental inbreeding did not decline as population fragments became smaller. This result could theoretically be due to self-incompatibility maintaining outcrossing rates in small populations. However, we can be confident that self-incompatibility is not a factor in the mating system of *C. quadrifidus* since paternity analysis with exclusion probability has unambiguously identified self-pollination in progeny arrays (Byrne et al., 2007).

One explanation for our findings is that transport of pollen among population fragments by highly mobile honeyeaters may considerably extend the mating pool beyond the individual fragment, rescuing small populations from inbreeding. The honeyeaters we observed foraging on *C. quadrifidus* (Yates et al., 2007) can fly long distances, for example Brown-headed honeyeaters (*Melithreptus brevirostris*) have been recorded moving between fragments 3.1 km apart, singing honeyeaters (*Lichenostomus virescens*) 10.5 km and brown honeyeaters (*Lichmera indisticta*) 12.5 km (Saunders and de Rebeira, 1991). Indeed, some authors have argued that bird-pollination has been selected in the south-west flora to promote outcrossing in species characterized by small, naturally dissected populations that are a consequence of historical fragmentation (Hopper, 1981). In a companion study, we measured pollen immigration into *C. quadrifidus* population fragments isolated by 2–5 km indicating that pollen dispersal is occurring in this landscape (Byrne et al., 2007). If this extensive pollen flow among fragments is rescuing small populations from inbreeding we would expect to see no correlation between population fragment size and fecundity (fruit set, the number of seeds per fruit), and progeny fitness (seed germinability, seedling mortality, seedling growth).

Alternatively, selfing and bi-parental inbreeding may be higher in smaller population fragments, but post-zygotic seed abortion mechanisms involving deleterious recessive genes are masking their effects. Such mechanisms can significantly influence the outcomes of a mating system study if embryos arising through self-fertilization and bi-parental inbreeding are aborted before they can be assessed in the mating system analysis (Kennington and James, 1997). As a consequence, inbreeding in smaller population fragments may well be higher than in larger population fragments, but not detected by a mating system analysis. If post-zygotic lethal systems are operating in *C. quadrifidus*, and inbreeding is higher in small populations than in larger populations, we would expect to see the number of seeds per fruit decrease as population fragment size decreases.

In this paper, we continue our studies of the genetic and ecological factors affecting the viability of *C. quadrifidus* population fragments. Specifically we investigate fruit set, the number of seeds per fruit, seed germinability, seedling mortality and growth. We hypothesize that if highly mobile honeyeaters considerably extend the mating pool beyond the individual fragment rescuing small populations from the expected effects of inbreeding, as suggested by our gene-flow study, then fruit set, seed production, seed germinability, seedling mortality and seedling growth will be unrelated to population fragment size. We discuss what our results mean