Interregional comparison of the size-structure of populations of *Melaleuca quinquenervia* in its native and exotic range, with and without biocontrol agents

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Summary We compare size structure and rates of recruitment and mortality in populations of *Melaleuca quinquenervia* in its native and exotic ranges. In the exotic range study sites were chosen to include contrasts in presence and abundance of two biological control agents. We tagged and measured (DBH) all the individuals in permanent plots and revisited them annually to record growth, mortality and recruitment. DBH varied among sites, the largest trees were found in the native populations. Per capita mortality (% deaths between years) was highest in Florida, where both insects are present; and lowest in the Bahamas where no insects are present. In Australia, even though the full range of natural enemies comprising approximately 450 species is present, death rate on average, and recruitment were quite low. Annual per capita recruitment is difficult to quantify in our study plots because it is episodic and mostly restricted to newly colonised sites. Since observed mortality was nonzero and recruitment was low, local populations seem to be declining.

Keywords *Melaleuca quinquenervia*, regional comparison, population parameters, biocontrol.

INTRODUCTION

Comparative demographic studies of invasive species in their exotic and native ranges may provide new insights into differential population dynamics (Hierro *et al.* 2005). We are investigating the impacts of two biocontrol agents on population growth of *Melaleuca quinquenervia* (Cav.) Blake (Myrtaceae). The first step, which we present here, is to describe the size structure and vital rates in native and exotic ranges, including areas with and without biological control agents. Specific objectives of this paper are to: 1) characterise the size structure 2) estimate individual growth rates; and 3) quantify population-level death and birth rates of *M. quinquenervia* populations in its native and exotic ranges.

MATERIALS AND METHODS

Study system *Melaleuca quinquenervia* is a tree native to sub-tropical Australia currently invading southern Florida, Puerto Rico, and the Bahamas (Serbesoff-King 2003). Melaleuca produces serotinous fruits (capsules) that may remain attached to the tree for several years. An adult tree can produce millions of seeds per year, with massive seed release episodically occurring after stress (Woodall 1982). For example, seed dispersal and seedling establishment is favoured by frequent fires in both native and exotic ranges. Periodic massive seed release, after a disturbance event, into a previously unoccupied area favours the formation of even-aged stands (Turner *et al.* 1998). Two insects, both native to Australia, have been introduced to Florida as biological control agents: the leaf-eating weevil *Oxyops vitiosa* Pascoe (Coleoptera: Curculionidae), and the sap-sucking psyllid *Boreioglycaspis melaleucae* Moore (Homoptera: Psyllidae). Approximately 450 species of insect herbivores have been reported on *Melaleuca* in its native range (Balciunas *et al.* 1995). In Puerto Rico and the Bahamas, *Melaleuca* invasion is in its early stages and no biocontrol program has been implemented. However, in 2006 *B. melaleucae* were occasionally found in *Melaleuca* populations in Puerto Rico (Pratt *et al.* 2006).

Demographic plots In 2003, we set up demographic plots in South Florida, and in the native range of *M. quinquenervia*, the east coast of Australia. In 2005 additional plots were established in northeast Puerto Rico and in the northern Bahamas. Plots were laid out to include patches with different size classes to capture demographic rates by size within each region. The initial sampling effort in Australia included: two sites, seven plots, 533 individuals <1.3 m, and 1510 individuals ≥1.3 m. Florida included seven sites, 39 plots, 3567 individuals <1.3 m, and 4267 individuals ≥1.3 m. Puerto Rico included one site, six plots, 1492 individuals <1.3 m, and 707 individuals ≥1.3 m. The Bahamas included three sites, 13 plots, 430 individuals <1.3 m, and 868 individuals ≥1.3 m. We subsequently lost three plots in Florida due to herbicide application and urban development. Initially, we tagged all Melaleuca plants in the plots, recording size and reproductive status of each. We recorded mortality, recruitment and size every year until 2007 (except in Australia where the last census was carried out in 2006). For plants <1.3 m in height (hereafter denoted 'seedlings'), diameter of the stem 5 cm above the ground was recorded. For plants ≥1.3 m in height (hereafter denoted 'larger plants'), the diameter at breast height (DBH) (1.3 m) was recorded. All new seedlings that appeared in each plot every year were tagged and followed.

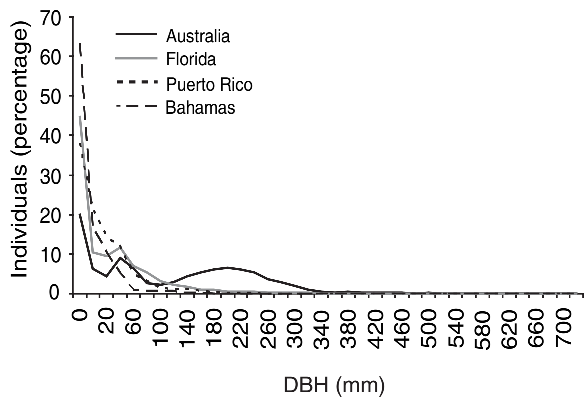

Figure 1. Mean percentage of the size distribution of *M. quinquenervia* populations across years in Australia (2003–2006, 1903 individuals), Florida (2003–2007, 4213 individuals), Puerto Rico (2005–2007, 2240 individuals), and the Bahamas (2006–2007, 1200 individuals). Size is reported as diameter at breast height (DBH) in categories of 20 mm (20–720); category 0 includes individuals <1.3 m; category 10 includes individuals ≥1.3 m and ≤10 mm DBH; categories 20–720 include individuals >1.3 m and its corresponding DBH cut-off.

Data analyses Size distributions among geographic regions were compared using a chi-square test. Growth of individuals was calculated as the proportional change in diameter using the formula: [(final – initial)/initial]. Differences in growth rates among regions were compared using Kruskal-Wallis tests and P values were calculated based on Chi-square distributions (JMP 4.0).

RESULTS

Size structure In all regions, the shape of the size distribution (i.e. the proportion of individuals in each size class) was very similar across years, with the most variation in Florida (not shown). The shape of the size distribution differs between Australia and the exotic regions, and further differences exist among exotic regions ($\chi^2_{(111)}$ = 7591.4, P <0.001) (Figure 1). The biggest contrast is in the large adults which distinctly made up a larger proportion of the native populations than the exotic populations. In Australia, 49% of the individuals were large adults while in Florida this figure was only 9%. In Puerto Rico and the Bahamas, the percentage of large adults was even lower (4% and 2%, respectively). The seedling portion of the population also varied. In the native region, on average 20% of the individuals were seedlings across years (min: 14% in 2006; max: 26% in 2003). In contrast, most of the individuals in the three exotic regions were seedlings. In Florida seedlings comprised 43% of the individuals (min: 27% in 2006; max: 59% in 2005). In Puerto Rico seedlings were 37% of the individuals (min: 32% in 2005; max: 52% in 2007); and in the Bahamas, seedlings were 63% of the individuals (min: 59% in 2007; max: 67% in 2006).

Vital rates Individual growth was significantly different among regions for both seedlings ($\chi^2_{(3)}$ = 764.19, P <0.0001) and larger plants ($\chi^2_{(3)}$ = 186.34, P <0.0001). The Bahamas had the highest seedling growth (median = 27%) while Florida and Puerto Rico were very similar having the lowest growth rate, an order of magnitude lower (median = 2 and 3%, respectively). The Bahamas also had the highest growth of larger plants (median = 11%), while Australia had the slowest growth rate (median = 0.3%), nearly two orders of magnitude lower. Mortality was highest in Florida and lowest in Australia (Table 1). Recruitment was highest in Puerto Rico and lowest in Australia (Table 1).

DISCUSSION

The greatest difference in size structure of *M. quinquenervia* is between Australia and the three exotic regions, but there are also differences between Florida and the other two regions. In Puerto Rico and the Bahamas populations are in earlier phases of invasion, while in Florida populations have had more time to mature so that small adults are also common. Australian populations are in a mature phase; there are many large adults (100–300 mm DBH). Even though the whole community of natural enemies is present in Australia, per capita mortality is very low. Mortality was highest in Florida, where populations are very dense. Biological controls have the potential to

Table 1. Number of individuals of *M. quinquenervia* marked at the beginning of each year in each geographic region, and per capita mortality and recruitment throughout the study (n/a: not available). Per capita mortality and recruitment were calculated as the number of deaths and of new seedlings at time t + 1, respectively, divided by the number of individuals alive at time t.

	No. individuals				Per capita mortality				Per capita recruitment			
	2003	2004	2005	2006	2003–04	2004–05	2005–06	2006–07	2003–04	2004–05	2006–07	2006–07
AUS	2037	1935	1850	1780	0.04	0.03	0.03	n/a	0.0005	0.0005	0.001	n/a
FL	7815	5045	4230	1948	0.26	0.10	0.54	0.42	0.05	0.37	0	0.31
PR	n/a	n/a	2201	2068	n/a	n/a	0.04	0.37	n/a	n/a	0	0.55
BAH	n/a	n/a	n/a	1298	n/a	n/a	n/a	0.08	n/a	n/a	n/a	0.07

negatively impact survival (Franks *et al.* 2006), but so does intraspecific competition (Rayamajhi *et al.* 2006). For populations in Puerto Rico and the Bahamas, mortality was relatively lower and, although they are also very dense, insect herbivores are nearly absent. For all regions, mortality was commonly higher than recruitment which suggests that populations are decreasing over time. However, in the Bahamas mortality and recruitment were very similar. In contrast, mortality in Florida was much higher than recruitment, suggesting that populations are decreasing. Recruitment was also very low within our plots, but given that it is episodic and is known to be highest in newly colonised sites, it has been difficult to capture. We observed a recruitment event of a newly colonised site in Florida in 2005. Size-structured demographic models are needed to explore the population dynamics of *Melaleuca* and determine 1) the rate at which populations are growing in each region, and 2) the potential influence of biocontrol on population growth.

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