

Reproductive ecology of invasive *Ochna serrulata* (Ochnaceae) in south-eastern Queensland

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Abstract. We investigated aspects of the reproductive ecology of *Ochna serrulata* (Hochst.) Walp., an invasive plant in eastern Australia. *O. serrulata* drupes were similar in size to fleshy fruits of other local invasive plants, but showed some distinct differences in quality, with a very high pulp lipid content (32.8% of dry weight), and little sugar and water. Seeds were dispersed by figbirds, *Sphecotheres viridis* Vieillot, a locally abundant frugivore, and comprised between 10 and 50% of all non-*Ficus* spp. fruit consumed during October and November. The rate of removal of *O. serrulata* drupes was greater in bushland than suburban habitats, indicating that control in bushland habitats should be a priority, but also that suburban habitats are likely to act as significant seed sources for reinvasion of bushland. Germination occurred under all seed-processing treatments (with and without pulp, and figbird gut passage), suggesting that although frugivores are important for dispersal, they are not essential for germination. Recruitment of buried and surface-sown seed differed between greenhouse and field experiments, with minimal recruitment of surface-sown seed in the field. Seed persistence was low, particularly under field conditions, with 0.75% seed viability after 6 months and 0% at 12 months. This provides an opportunity to target control efforts in south-eastern Queensland in spring before fruit set, when there is predicted to be few viable seeds in the soil.

Introduction

Ochna serrulata (Hochst.) Walp. (Ochnaceae) (mickey mouse bush) is an emerging invasive plant in subtropical eastern Australia. It is a perennial shrub introduced as a garden ornamental and is widely planted in Brisbane. The first naturalised specimens in the Queensland Herbarium were collected in 1932 (Batianoff and Butler 2003). *O. serrulata* naturally occurs on the subtropical east coast of southern Africa, from sea level to an altitude of 1800 m, in evergreen forests, scrub forests, rocky hill slopes, bushveld and grasslands (Mbambezi and Notten 2002).

In Australia, *O. serrulata* has invaded rainforests, dry sclerophyll forests and riparian vegetation in coastal districts from Sydney to south-eastern Queensland (Williams *et al.* 1984; Csurhes and Edwards 1998), where it can dominate the shrub layer. In south-eastern Queensland, the species is ranked as one of the 25 most significant invasive plants, on the basis of both perceived detrimental environmental impacts (Batianoff and Butler 2003) and invasiveness and frequency (Batianoff and Butler 2002). *O. serrulata* is also invasive on Lord Howe Island (Swarbrick and Skarratt 1994), Hawai'i (Starr *et al.* 2003) and in Northland, New Zealand, where regionally it is a priority for control (McCluggage 2004).

Little is known of the reproductive ecology of *O. serrulata*, either in its invasive or natural range. We found no descriptions of the breeding system. Dispersal vectors are thought to include animals, water and human activities (Mbambezi and Notten 2002; Batianoff and Butler 2003). Galetti (2002) regards *O. atropurpurea* (a synonym of *O. serrulata*) fruit as mimetic, i.e. providing no nutritional reward for frugivores, but deceiving them into swallowing the seeds. Mimetic fruit have colourful seeds that resemble fleshy ornithochorous (bird-dispersed) fruit (Galetti 2002). In south-eastern Queensland, birds are probably the main dispersal vectors, with at least 12 species consuming drupes (Stansbury and Vivian-Smith 2003).

We found little information on the effect of seed processing (i.e. gut passage through birds, or manual pulp removal) on seed viability or germination, or the persistence of *O. serrulata* seed banks. Mbambezi and Notten (2002) recommend the use of cleaned, fresh seed for germination and noted that the seed does not keep. Morton (1998) also suggested the seed bank may be transient, as she found no *O. serrulata* seedlings germinating in soil samples taken from beneath infestations in a forest remnant in Brisbane.

Birds disperse the seeds of many invasive plant species in south-eastern Queensland (Stansbury and Vivian-Smith 2003) and elsewhere (Richardson *et al.* 2000). A better understanding of invasive plant traits (e.g. phenology, fruit crop characteristics, fruit nutrient quality and germination requirements), their relationships with vertebrate dispersers (e.g. dietary importance, fruit-removal rates and effects of gut passage on germination) and how they differ with landscape setting is likely to provide greater predictive ability in relation to seed-dispersal patterns, invasive plant spread and associated management opportunities (Sallabanks 1993; Vila and D'Antonio 1998; Richardson *et al.* 2000; Gosper *et al.* 2005). The aim of this research was to study the reproductive ecology of *O. serrulata* in its invasive range in south-eastern Queensland, in order to identify features that contribute to invasiveness and opportunities for improving current management practices. This study examines a broad range of aspects of reproduction, from flowering through dispersal to recruitment. Specifically, we focussed on the following questions:

- (1) What are the seasonal patterns of flower and fruit production for *O. serrulata*? Phenology can affect invasiveness through determining the timing and reliability of seed availability (Richardson *et al.* 2000; Gosper 2004a).
- (2) Do *O. serrulata* drupes provide a food reward, and how does drupe morphology and pulp nutrient content compare with those of fruits of co-occurring species in south-eastern Queensland? These fruit characteristics can influence fruit choice by frugivores (Murray *et al.* 1993; Stiles 1993) and may affect dispersal distributions of seeds of invasive plants (Vila and D'Antonio 1998).
- (3) Do *O. serrulata* drupe-removal patterns vary between habitats (suburban and bushland)? Differential rates of fruit removal for invasive species have been recorded between habitats (Gosper 2004b), and may provide opportunities to direct control efforts to habitats that act as a greater source of propagules.
- (4) Do *O. serrulata* drupes form an important food for any frugivorous birds in south-eastern Queensland? Specifically, what is the role of figbirds, *Sphecotheres viridis* Vieillot? Figbirds consume *O. serrulata* drupes (Stansbury and Vivian-Smith 2003) and are among the most abundant and widespread frugivores in disturbed rainforest and urban habitats in south-eastern Queensland (Sewell and Catterall 1998; Moran *et al.* 2004), and hence may be an important dispersal agent.
- (5) What conditions promote recruitment of *O. serrulata*? How do different seed-processing treatments (pulp removal, gut passage) and environmental conditions (light, burial, watering) affect recruitment?
- (6) Does *O. serrulata* have a transient seed bank? How do seedling emergence and seed viability vary in response to a range of environmental conditions?

Materials and methods

Study area

The study was conducted in Brisbane, south-eastern Queensland, Australia. The climate is subtropical, with a summer peak in precipitation (average annual precipitation = 1146 mm). Over most of the study, rainfall was less than average, with winter and spring 2004 particularly dry, but large rainfall events occurred in January and November 2004.

Flower and fruit characteristics

For phenology measurements, we selected two bushland reserves with riparian and dry sclerophyll-forest communities and populations of *O. serrulata*: Whipbird Park, Macgregor (27°34'17.4"S, 153°04'36.1"E), and Minnippi Parklands, Tingalpa (27°29'15.1"S, 153°06'49.6"E). Sites were visited once per month, and five mature (>1 m in height and not overgrown with other vegetation) *O. serrulata* plants were randomly selected from fixed transects along paths. The total number of open flowers, infructescences (referring to the whole fruit structure of the red receptacle and attached drupes) with green drupes and the number of ripe drupes (referring to individual pulp-covered seeds) per plant were counted. From these measurements, the mean numbers of flowers, infructescences and drupes per month were calculated. Plants were sampled for 19 months from September 2003 to February 2005, covering two flowering/fruitlet seasons.

Morphology measurements were made from a sample of 60 drupes, which were collected from multiple individuals of *O. serrulata* at three Brisbane locations: Chelmer (27°30'55.4"S, 152°58'05.2"E), Oxley (27°32'47.4"S, 152°58'07.9"E) and Brookfield (27°29'35.4"S, 152°55'35.0"E). For each drupe, we measured drupe length, drupe width, whole-drupe weight, pulp wet weight, seed wet weight, seed number, seed length and seed width. The separated pulp and seeds of 30 drupes were oven-dried at 60°C to a constant weight. Dry weights of pulp and seed were then measured and the water content of pulp and seed calculated. We also calculated wet and dry weight ratios of pulp to seed and the relative yield (RY, the ratio of dry pulp to drupe wet weight; Izhaki 2002) (for birds that pass seeds intact).

Pulp was separated from seeds for analysis of nutritional content. The pulp is the expected digestible portion of drupes for frugivores that ingest drupes and act as legitimate seed dispersers. Drupes were collected from many plants at several different locations around Brisbane. Pulp from all drupes was combined to make up a single bulk sample for analysis. The Centre for Food Technology (Agency for Food and Fibre Services, Queensland Department of Primary Industries) and Symbio Laboratories carried out the nutritional analyses. Methods of the Association of Official Analytical Chemists (2000) were used for moisture (AOAC 934.06), fat (AOAC 960.39), protein (AOAC 920.152), ash (AOAC 940.26), total sugars and sugar profile (AOAC 982.14). Protein was not measured directly, but was calculated by multiplying total nitrogen by a conversion factor of 6.25. The remainder was assumed to be carbohydrates. Energy content was estimated by using Food Standards Australia New Zealand (2005) fixed conversions for fats (37 kJ per unit weight), protein (17 kJ per unit weight) and carbohydrates (17 kJ per unit weight). Content of manganese, copper, iron, zinc, sodium, phosphorus, potassium, calcium and magnesium was measured by microwave assisted nitric acid digestion (ESIH2). We recognise that these nutrient analyses are simplistic (see Levey and Martínez del Río 2001; Izhaki 2002); however, they do provide a guide to the relative quality of pulp.

To place our results within the context of other fleshy-fruited plants in south-eastern Queensland, we compared drupe morphology and pulp nutrient content of *O. serrulata* with the average of those of other bird-dispersed invasive plants that fruit concurrently, at least in part ($n = 30$ for morphology, $n = 15$ for nutrient content), from Gosper (2004a) and

C. R. Gosper and G. Vivian-Smith (unpubl. data). Comparable data for co-occurring native species are not available.

Drupe removal

Three sites were selected in suburban areas of Brisbane: Taringa 1 (27°30'09.5"S, 152°59'21.4"E), Taringa 2 (27°29'36.8"S, 152°59'19.6"E) and Corinda (27°32'57.6"S, 152°58'24.4"E); and three in nearby bushland reserves: Brisbane Forest Park 1 (27°28'33.3"S, 152°57'43.8"E), Brisbane Forest Park 2 (27°28'48.8"S, 152°58'33.5"E) and Oxley (27°32'54.8"S, 152°58'00.4"E). Suburban sites had *O. serrulata* infestations along roads adjoining houses or a grassy recreational park and had a scattered canopy of *Eucalyptus* spp. and/or ornamental trees. The bushland sites had *O. serrulata* as a co-dominant component of the understorey, with *Eucalyptus* and *Lophostemon* spp. in the canopy.

Transects, 30 m long, were run through each site, placed in a random direction. Fifteen plants with ripe drupes were randomly selected, and on each, a portion with five ripe drupes was marked with a numbered wooden peg. Any other ripe or green drupes were removed. At two of the sites (one bushland and one suburban), there were insufficient drupes to follow this methodology on all plants. At these sites, when drupes could not be located, we attached a small branch with five drupes to an *O. serrulata* plant with green twist ties by using similar methods to Gosper (2004b), who also describes some potential biases of this method. The artificially attached drupes were replaced every 2 days to avoid drupe drop because of desiccation. The number of drupes remaining per plant was recorded daily at each site for 4 days, and again at Day 7. Missing drupes were assumed to have been taken by frugivores, based on the outcome of a pilot study conducted at two sites. Gauze litter traps were placed beneath a sample of tagged branches with fruit. Over the 6-day trial, 12% of drupes were captured in litter traps. The remainder were either retained on the plant or removed beyond the parent plant, indicating dispersal (C. R. Gosper, G. Vivian-Smith and K. Hoed, unpubl. data). Captured drupes may also include the results of bird foraging activities, such as when drupes are accidentally dislodged or dropped, or deliberately discarded after being picked. At each site, the density of ripe drupes was measured in 0.25-m² plots placed every 2 m along the 30-m transect.

Drupe-removal data were analysed with the survival analysis module of Systat 9 (Steinberg *et al.* 1999). Survival analysis is ideally suited to these kinds of data, where the end of the experiment may be reached before all drupes are removed. After testing that the assumption of proportional hazards was not violated, we compared drupe-removal (survival) curves between bushland and suburban sites by comparing Kaplan–Myer estimates by using the Cox proportional hazard model, with habitat (bushland/suburban) as a covariate.

Seed dispersal by figbirds

In Sherwood Forest Park, Brisbane (27°31'57.7"S, 152°58'28.3"E), groups of figbirds regularly congregated after feeding in isolated trees over asphalt roads (termed a 'roost'). In excess of 20 birds occurred in and around the park throughout the year, although smaller numbers (0–10, plus fledged young after breeding) used the roost at any one time. A lightly wooded park, suburban areas and remnant natural and weedy vegetation along the Brisbane River surrounded the roost. We swept a section of the road (~1 × 3 m) beneath three roost trees before each collection. Between 2 and 5 days later, depending on the deposition rate, we collected all defecated, dropped or regurgitated food. A set sampling period was not considered appropriate because of variation in the number of roosting birds and the time spent at the roost, between collection periods. For the purpose of this paper, we assumed figbirds deposited all material. However, other birds may have contributed small portions. For example, occasional olive-backed orioles, *Oriolus sagittatus* Latham, also used the roost.

Three samples (collected from beneath different trees) were collected per month throughout the period October 2003 to February 2005. Over the main fruiting period of *O. serrulata* (October–January), collections were made more frequently, i.e. every 3 weeks. Samples were then sorted, with seeds of each type counted. Fig (*Ficus* spp.) seeds were not counted, as we were unable to identify these to species or convert seed number to an estimate of the number of whole fruit consumed. Unidentified seed samples were placed in potting mix in a polythene tunnel greenhouse for germination and later identification, with another sample kept for comparison with other collected seeds. A seed herbarium was established for the comparison of sample seeds with those collected from fruit of known identity.

The number of seeds in the samples and any other identifiable material (e.g. pieces of exocarp) were used to estimate the number of fruit consumed. For invasive species we used prior measurements of seed number per fruit (described above). For native species we obtained values from the literature or from inspection of a small sample of fruit.

Nearby *O. serrulata* populations were in planted hedges, self-colonising individuals in gardens and small patches of invasive plants in the park. The nearest plants were 100 m from the centre of the roost area in a garden.

Germination, recruitment and persistence

Several experiments investigated germination, seedling recruitment and seed-bank persistence characteristics of *O. serrulata*. Seeds used in these experiments were collected from plants at four Brisbane sites (Brookfield, Macgregor, Oxley and Taringa 1), with the exception of seeds passed by figbirds that were collected from the Sherwood roost. Seeds were collected between 5 and 11 November 2003. Manual pulp removal was undertaken by scraping seeds between two wooden blocks covered with wire insect mesh that stripped the pulp from the seeds. To prevent seed damage, *O. serrulata* seeds were considered depulped once ~70% of the pulp had been removed.

Germination was investigated in an incomplete randomised factorial experiment that tested responses to either a 12-h photoperiod or continuous darkness for different seed treatments (intact drupes, seeds with pulp manually removed and figbird gut passage). Germination response to figbird gut passage was tested only under light conditions. Ten seeds were placed on filter paper (Advantec 2) within each of 10 Petri dishes (or replicates) under a 15/25°C alternating thermoperiod with 6 mL of tap water added. Dark treatments involved wrapping Petri dishes in two layers of aluminium foil. All Petri dishes were randomly placed in clear, sealed plastic bags to create similar conditions of humidity for both light and dark (wrapped) Petri dishes. Additional water was added to each Petri dish on a weekly basis as required. Germination was recorded when the radicle protruded >3 mm. The experiment began on 17 November 2003, with germination monitored weekly for 91 days.

Two emergence-response experiments were conducted, one under regular irrigation within a polythene greenhouse tunnel (tunnel emergence experiment) and a second under field conditions of natural rainfall (field emergence experiment) by using methods adapted from Panetta (2000). The tunnel experiment was an incomplete factorial design, measuring emergence responses under non-limiting moisture conditions to seed burial (0 cm, 1 cm) and different seed-processing treatments (intact drupes, manual pulp removal and figbird gut passage). All treatment combinations were utilised with the exception of the 'figbird gut passage × 1 cm burial' treatment. This combination was not incorporated for the following two reasons: gut-passed seeds were in limited supply and burial following defecation was considered a less likely scenario for *O. serrulata* seeds. There were 10 replicates per treatment for all treatment combinations except figbird gut passage, where only five replicates were used. Each experimental unit consisted of a 12-cm pot filled with a commercial sandy loam mix containing

20 seeds. Emergence was monitored (seedlings counted and then removed) every 14 days for the first 6 weeks and then monthly for 12 months.

The field emergence experiment was a completely randomised factorial design ($n=30$ replicates per treatment) that investigated responses to seed burial (0 cm, 1 cm) and pulp removal (intact drupes and manual pulp removal). Pots (12 cm in diameter) were filled with the sandy loam mix and sunk into the soil down to 11 cm, with 1 cm of the pot protruding above the soil surface. A wooden lattice (4-cm wooden battens spaced at 4.5×4.5 cm) was placed 18 cm above the soil surface and covered with 50% shade cloth. Field conditions aimed to simulate those likely to be experienced by seeds landing below a suitable perch tree or low canopy. Plots were located within a rodent-proof fence to reduce the likelihood of seed predation. Emerging seedlings were recorded and then removed from pots at monthly intervals for 12 months. Both field and tunnel emergence experiments commenced on 18 November 2003 and ran until 14 December 2004, at the Alan Fletcher Research Station, Sherwood (AFRS).

Seed persistence was determined for seeds exposed to the same sowing and pulp-removal treatments (except figbird gut passage) and watering conditions as in the field and tunnel emergence experiments. Squares of nylon-mesh insect screen were buried 1 cm below the seeds to reduce the amount of soil from which the propagules were later extracted. Persistence was determined by retrieving subsamples of five replicates ($n=20$ seeds per replicate) of each sowing treatment at 6 months, and 10 replicates ($n=20$ seeds per replicate) at 12 months and testing the seeds for viability. Viable seeds included seeds that were germinable as well as those that were assessed as dormant. Passing the soil containing seeds through a 1-mm sieve assisted retrieval of seeds. Decayed seeds (those that disintegrated when gently rubbed between thumb and forefinger) were counted and discarded. The remaining seeds were then placed in Petri dishes and subjected to germination tests using the same methods as described for the germination experiment (15/25°C alternating 12-h thermoperiod and a 12-h photoperiod). When no further germination was recorded after 32 days, the remaining seeds were dissected and embryos were visually assessed for viability. Seeds decayed, or containing a decayed, shrivelled or discoloured (brown) embryo were considered non-viable. Seeds containing an embryo that was firm and cream, green or pale yellow were considered viable.

Owing to non-normality in both germination and emergence data, we used non-parametric tests (Kruskal–Wallis one-way analysis of variance and Mann–Whitney U -test) to analyse both germination and emergence data.

Results

Flower and fruit characteristics

Ochna serrulata flowered in spring (August–November) in south-eastern Queensland. Flowers were open only for a short period; hence peak flowering was not always recorded in the monthly surveys, making comparisons among sites and years difficult. Green drupes were abundant from September to December, and remained present in smaller quantities through to February (Fig. 1). Ripe drupes were present from September to March, although there were consistently few ripe drupes from January onwards (Fig. 1). The month of peak availability varied slightly among sites and years, although in most cases it was in December. No flowers or fruit were recorded in other months.

Individual *O. serrulata* drupes were glossy black, with a small yellow to brown spot where the drupe was attached

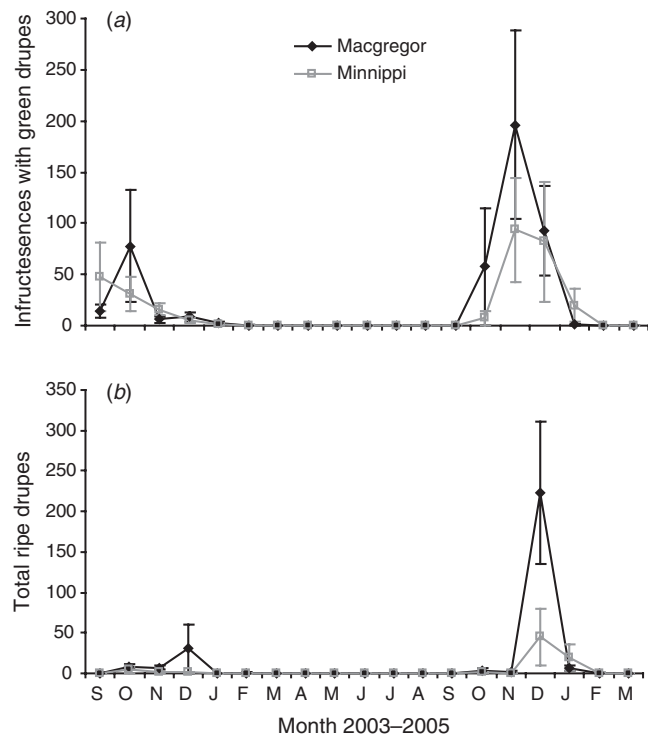


Fig. 1. (a) Monthly counts of infructescences with green drupes and (b) total ripe drupes per *Ochna serrulata* plant in Brisbane, south-eastern Queensland. Each point is the mean of five plants, with standard error.

to the receptacle, and slightly asymmetrically oval in shape. The drupe contained a single oval seed, which was green and had a fibrous covering. The pulp was oily, and could only be removed from the seed with force. Drupes were slightly smaller in dimensions and weight than the average for other invasive fleshy-fruited plants in south-eastern Queensland that fruited concurrently, whereas seed dimensions were close to average, and seed and pulp weights smaller (Table 1). The ratio of digestible pulp to seed was much lower for *O. serrulata* than for most other invasive plants, but as a consequence of the low water content of the pulp (Table 2), the RY of *O. serrulata* was much higher than average.

The nutrient content of *O. serrulata* pulp was substantially different from that of other invasive plants (Table 2). It had comparatively low water and sugar content, but very high lipid content. Assuming total digestion of the pulp, *O. serrulata* provides a much higher than average energy gain per drupe. In terms of micronutrients, *O. serrulata* was particularly low in calcium, potassium and sodium, but high in manganese, copper and iron. These nutrient values are presented as a percentage of dry weight of pulp. As *O. serrulata* has low pulp water content, on a per drupe basis these nutrients are proportionally higher in *O. serrulata* than in the other fruits.

Table 1. Drupe morphology of *Ochna serrulata*

Characteristic	<i>Ochna serrulata</i> ^A	Other invasive plants ^B
Drupe/fruit		
Length (mm)	7.53 ± 0.12	12.29 ± 2.06
Width (mm)	6.05 ± 0.08	11.71 ± 1.76
Wet weight (g)	0.127 ± 0.006	4.18 ± 2.39
Seed		
Length (mm)	6.64 ± 0.16	5.59 ± 0.82
Width (mm)	4.97 ± 0.10	4.55 ± 0.61
Wet weight (g)	0.081 ± 0.005	0.62 ± 0.26
Dry weight (g)	0.059 ± 0.006	0.38 ± 0.15
Pulp		
Wet weight (g)	0.048 ± 0.002	3.55 ± 2.14
Dry weight (g)	0.025 ± 0.001	0.49 ± 0.26
Wet weight ratio pulp : seed	0.72 ± 0.05	3.28 ± 0.40
Dry weight ratio pulp : seed	0.57 ± 0.06	1.03 ± 0.08
RY (dry pulp weight : drupe wet weight)	0.21 ± 0.01	0.15 ± 0.01

^AMean ± standard error from a sample of 60 (30 for dry weights).

^BMean ± standard error from 30 other invasive plant species that fruit concurrently with *O. serrulata* (at least in part) in south-eastern Queensland: *Asparagus aethiopicus* cv. Sprengeri, *A. africanus*, *A. virgatus*, *Celtis sinensis*, *Cestrum parqui*, *Chrysanthemoides monilifera* spp. *rotundata*, *Cinnamomum camphora*, *Duranta erecta*, *Eriobotrya japonica*, *Eugenia uniflora*, *Lantana camara* var. *camara*, *Ligustrum lucidum*, *L. sinense*, *Murraya paniculata* cv. *Exotica*, *Opuntia tomentosa*, *Passiflora foetida*, *P. suberosa*, *Phytolacca octandra*, *Psidium guajava*, *Rhaphiolepis indica*, *Rivina humilis*, *Sambucus canadensis*, *Sansevieria trifasciata*, *Schefflera actinophylla*, *Schinus terebinthifolius*, *Solanum americanum*, *S. hispidum*, *S. mauritanium*, *S. seaforthianum* and *Syagrus romanzoffiana*.

Drupe removal

Drupe removal was monitored at all sites over the duration of the experiment. Significant differences between drupe survival functions in the two habitat types were detected (likelihood test statistic = 9.014, d.f. = 1, $P = 0.003$). At the end of the 7-day monitoring period, more drupes had been removed from bushland sites ($n = 198$) than suburban sites ($n = 169$) (Fig. 2), with bushland drupes having a mean survival probability after 7 days of 17.1%, compared with 38% for suburban drupes. Marginally significant differences in survival functions between sites within habitats were detected (likelihood test statistic = 3.704, d.f. = 1, $P = 0.054$). Ripe-drupe density averaged 20.8 m^{-2} at bushland sites and 10.3 m^{-2} at suburban sites.

Seed dispersal by figbirds

The population of figbirds sampled in this study used *O. serrulata* drupes extensively. In October and November, on average between 10 and 50% of all fruit consumed of non-*Ficus* spp. were drupes of *O. serrulata* (Fig. 3). *O. serrulata* drupes formed a lower proportion of the diet of figbirds over

Table 2. Pulp nutrient content of *Ochna serrulata*

Characteristic ^A	<i>Ochna serrulata</i>	Other invasive plants ^B
Water (g per 100 g wet weight)	47.6	76.1 ± 4.2
Lipid (g per 100 g)	32.8	2.4 ± 1.1
Protein (g per 100 g)	9.4	9.8 ± 1.7
Total carbohydrates (g per 100 g)	55.9	80.3 ± 2.3
Total sugars (g per 100 g)	2.9	35.7 ± 4.2
Fructose (g per 100 g)	1.0	19.2 ± 2.3
Glucose (g per 100 g)	1.9	16.2 ± 2.9
Sucrose (g per 100 g)	0.0	0.2 ± 0.2
Energy (kJ per 100 g)	2324	1623 ± 28
Ash (g per 100 g)	1.9	7.4 ± 0.7
Manganese (mg per kg)	92.5	38.4 ± 13.8
Copper (mg per kg)	18.8	11.5 ± 1.9
Iron (mg per kg)	69.4	47.2 ± 7.6
Zinc (mg per kg)	30.3	44.3 ± 15.9
Sodium (mg per kg)	28.9	2400 ± 973
Phosphorus (mg per kg)	1590	2094 ± 273
Potassium (mg per kg)	7225	30 585 ± 3484
Calcium (mg per kg)	809	2558 ± 536
Magnesium (mg per kg)	1387	2135 ± 595

^AAll measures except for water content are per dry weight of pulp.

^BMean ± standard error from 15 other invasive plant species that fruit concurrently with *O. serrulata* (at least in part) in south-eastern Queensland: *Asparagus aethiopicus* cv. Sprengeri, *A. africanus*, *Celtis sinensis*, *Chrysanthemoides monilifera* spp. *rotundata*, *Cinnamomum camphora*, *Duranta erecta*, *Eugenia uniflora*, *Lantana camara* var. *camara*, *Ligustrum lucidum*, *Murraya paniculata* cv. *Exotica*, *Opuntia tomentosa*, *Passiflora suberosa*, *Rivina humilis*, *Solanum mauritanium* and *S. seaforthianum*.

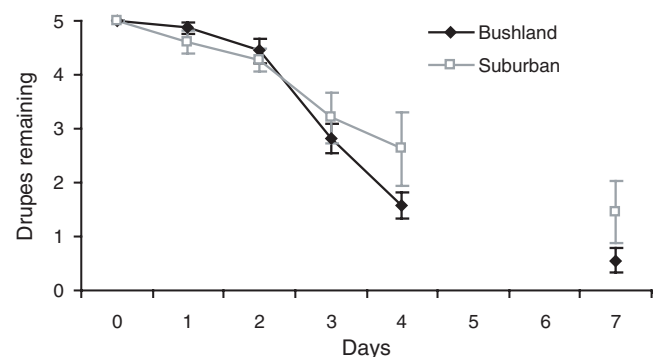


Fig. 2. Survival curves for the removal of *Ochna serrulata* drupes in suburban and bushland habitats. Each point is the mean of three sites per habitat, with standard error.

the remainder of the fruiting season. Fruit material of non-*Ficus* spp. formed 63 and 66%, respectively, of the total dried mass of material collected over the two *O. serrulata* fruiting seasons. The other fruits used by figbirds over this period were from a range of other invasive plants, indigenous plants and cultivated non-indigenous but as yet non-invasive plants. The indigenous fruits used included *Ficus* spp.,

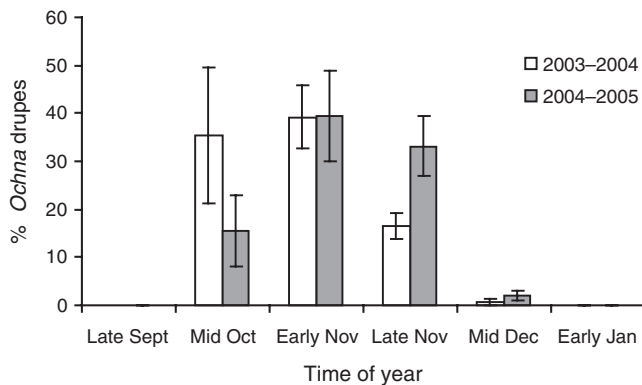


Fig. 3. The proportion of *Ochna serrulata* drupes of all the non-*Ficus* spp. fruit consumed by figbirds at Sherwood, Brisbane. Bars show the means of three samples per time period in each year with standard error.

Archontophoenix cunninghamiana (H.Wendl.) H.Wendl. et Drude, *Cordyline* spp., *Cupaniopsis anacardioides* (A.Rich.) Radlk. and *Dianella* spp. (C. R. Gosper, unpubl. data).

Although figbirds readily consumed *O. serrulata* drupes, the nutritional benefit derived from these was less apparent. Passed *O. serrulata* drupes appeared relatively intact, and certainly the pulp appeared little changed after defecation.

Germination and recruitment

Germination commenced between 6 and 10 days, peaking between 10 and 24 days after the start of the experiment. Only a single germination was recorded between 66 and 91 days, when the experiment was terminated. Germination rates ranged from 2.0 to 18.0%, with greater germination under light conditions (Mann-Whitney $U = 308.0$, d.f. = 1, $P = 0.002$) (Table 3). No significant

Table 3. Final germination/emergence percentage (mean \pm s.e.) of *Ochna serrulata* seeds in response to different light/burial and seed processing treatments

Experiment	Light/burial and seed-processing treatment combination	Germination/emergence (%)
Germination	Dark + pulp	7.0 \pm 3.0
	Dark - pulp	2.0 \pm 1.3
	Light + pulp	18.0 \pm 5.3
	Light - pulp	18.0 \pm 4.7
	Light figbird gut passage	10.0 \pm 4.2
Tunnel emergence	1 cm + pulp	3.0 \pm 1.5
	1 cm - pulp	3.0 \pm 1.3
	0 cm + pulp	25.0 \pm 2.8
	0 cm - pulp	23.5 \pm 3.1
	0 cm figbird gut passage	18.0 \pm 2.5
Field emergence	1 cm + pulp	18.7 \pm 2.5
	1 cm - pulp	9.7 \pm 1.7
	0 cm + pulp	0.2 \pm 0.2
	0 cm - pulp	0.0 \pm 0.0

differences in germination rates were detected among the three seed-processing treatments (with and without pulp and gut passage) (Kruskal-Wallis test: $H = 2.04$, d.f. = 2, $P = 0.361$).

Emergence rates in the tunnel experiment were somewhat greater than in the growth cabinet, with means ranging from 3.0 to 25.0%, depending on the treatment. Under these conditions of regular watering, emergence was significantly lower in the 1-cm than in the 0-cm sowing treatment (Mann-Whitney $U = 396.5$, d.f. = 1, $P < 0.001$) (Table 3). We were again unable to detect any significant differences in emergence among the three seed-processing treatments (Kruskal-Wallis test: $H = 2.107$, d.f. = 2, $P = 0.349$).

Emergence rates from the field experiment were lowest, with means ranging from 0.0 to 18.7%. They showed significant responses to both burial (Mann-Whitney $U = 310.5$, d.f. = 1, $P < 0.001$) and seed-processing treatments (Mann-Whitney $U = 268.0$, d.f. = 1, $P = 0.006$). Emergence from the 0-cm treatment was virtually non-existent. Of the buried seeds, emergence from seeds with pulp was almost double that from seeds with pulp manually removed (Table 3). In both the field and tunnel experiments, emergence peaked strongly between 27 and 56 days, with no further emergence recorded after 118 days although monitoring continued for a total of 391 days.

Seed-bank persistence

At 6 months, viability of seeds was very low (0.75%) for seeds retrieved from field conditions, with only 3 of the 400 seeds used in the experiment considered viable. These seeds did not germinate during tests, but appeared viable following more detailed visual inspection on dissection at the termination of the germination test after 32 days. Seeds from the tunnel at six months showed greater viability on visual inspection, with no significant differences between any of the treatment combinations (Kruskal-Wallis test: $H = 1.032$, d.f. = 3, $P = 0.793$). Again, there was no germination when tested, yet a final viability assessment following seed dissection indicated viability of $11.2\% \pm 1.8$ (mean \pm s.e.). At 12 months, no viable seeds were identified from seeds retrieved from either the tunnel ($n = 400$ seeds) or the field ($n = 800$ seeds).

Discussion

Flower and fruit characteristics

Ochna serrulata flowered and fruited over a similar period of the year in its invasive range in south-eastern Queensland as in its native range in Africa (Mbambuzeli and Notten 2002). The between-year variation in flowering and fruiting times in this study might have resulted from water limitation in spring 2004, when south-eastern Queensland was unusually dry.

Ochna serrulata drupes have several characteristics that render them particularly attractive to bird consumers. First, the drupes and seeds are relatively small. More bird species and individuals usually visit plants with smaller fruits and/or seeds than with larger fruits and seeds (Herrera 1985; Green 1993). Less desirable for dispersers, however, is the small pulp return per drupe. Second, pulp of *O. serrulata* is high in lipids, but has little water and sugar. Pulp high in lipids is preferred by some bird species (Stiles 1993; Levey and Martínez del Rio 2001). *O. serrulata* pulp nutrient characteristics appear to be unusual, and no other invasive species in south-eastern Queensland that we have studied, is similar. Moreover, similar pulp content is rare among native species in Australia (French 1991) and overseas (Snow 1981; Wheelwright *et al.* 1984; Johnson *et al.* 1985; Herrera 1987). Other pulp that has such high lipid content usually has greater water content. Pulp rich in lipids often have low sugar content (as in *O. serrulata*), and this relationship may be related to the digestive strategies of some birds for efficient lipid use (Levey and Martínez del Rio 2001). As lipids are assimilated more slowly than carbohydrates, birds that specialise on these fruits have relatively long digestion times (Levey and Martínez del Rio 2001). Although no effort was made to determine the digestive times of figbirds feeding on *O. serrulata* drupes, the amount of the pulp digested indicates that gut retention time may be short and that the high pulp lipid content was not being fully used. The other invasive plant fruits consumed concurrently by figbirds (C. R. Gosper, unpubl. data) also indicated that they were not specialising in lipid-rich fruits. *O. serrulata* pulp provides a poor source of several micronutrients that are generally in short supply in fruit but are important in vertebrate metabolism, including calcium, phosphorus (O'Brien *et al.* 1998) and sodium (Levey and Martínez del Rio 2001).

Drupe removal

The rate of drupe removal differed between the two habitat types, suburban areas and bushland. The reason(s) for this difference is unclear, although it may be related to differences in frugivore abundance, composition (Sewell and Catterall 1998) or behaviour (Fernández-Juricic and Tellería 2000), or in response to different habitat features (Hutchinson and Vankat 1998). Although we did not survey the frugivores at our study sites, Sewell and Catterall (1998) found figbirds to be more abundant in suburban areas with well established planted gardens than in patches of natural vegetation. This does not match the lower rate of removal of drupes in suburban areas in this study, and suggests that other frugivores (see Stansbury and Vivian-Smith 2003) also contributed to removal. Suburban sites are likely to have suffered more disturbance (by people, domestic animals and cars) than those in bushland, which may have affected bird behaviour (Fernández-Juricic and Tellería 2000) and contributed to the lower removal rates.

Frugivores could be responding to the greater average fruit density at bushland sites. Greater crops can contribute to greater rates of removal of fruits (Sallabanks 1993), although in this study, high rates of removal still occurred at a bushland site with few ripe drupes. No measurements of other fruit food sources at sites were made.

Seed dispersal by figbirds

Figbirds consumed and dispersed substantial quantities of viable *O. serrulata* seeds. Interestingly, the peak in ripe-drupe availability did not match the peak of consumption (Fig. 1 cf. Fig. 3). Figbirds ate proportionally more *O. serrulata* drupes in October and November than in December, even though drupe availability was generally greater in December. There are at least four possible factors contributing to this result.

First, it is possible that *O. serrulata* plants in the foraging range of figbirds at Sherwood fruited earlier. The areas near the roost are predominantly suburban gardens, compared with the bushland areas where phenology was measured. Second, the ripe drupes counted at plants in this study represent the total ripe drupes produced per plant, less those removed, such as by frugivores and other factors (e.g. accidental dislodgement, plant damage and fruit abortion). Frugivores could have been exploiting drupe crops intensively early in the fruiting season (as evidenced by the figbird study) and this may have been sufficient to remove ripe drupes before they could be counted in our phenology assessments. Third, frugivores may use more *O. serrulata* drupes earlier in the fruiting season because of greater scarcity of other fruit foods. *O. serrulata* produces fruit at the end of the period of the most restricted diversity of native fleshy fruit sources in eastern Australian rainforests (July–October; Holmes 1987; Innis 1989). Fourth, if pulp nutrients are not readily accessible for figbirds, decreasing use of *O. serrulata* over time could show birds learning to avoid *O. serrulata* drupes. We did not determine whether figbirds were assimilating nutrients (and hence test whether *O. serrulata* drupes were mimetic (see Galetti 2002) for figbirds). Other birds, however, feed on *O. serrulata* drupes in such a way as to suggest that nutritional rewards can be gathered from the pulp. Pale-headed rosellas, *Platycercus adscitus* Latham, scrape off some of the thin layer of pulp with their bill, and then discard the seed without ingestion, usually with some remaining pulp attached (C. R. Gosper, pers. obs.). This behaviour suggests that the drupes are not mimetic in this case, as the birds separate a nutritionally valuable part of the drupe from the seed before ingestion (nor are the seeds likely to be predated, cf. Stansbury and Vivian-Smith 2003).

The figbirds sampled in this study moved viable seeds to a site largely unsuitable for *O. serrulata* recruitment, i.e. asphalt roads and adjoining managed lawns and gardens. Hence, these birds were not 'directing' (Wenny and Levey

1998) seeds to suitable microsites for recruitment. However, germination of *O. serrulata* was noted beneath the roost, and recruitment is frequent beneath other sites often used by figbirds, particularly large *Ficus* spp. trees and prominent perches. It is not possible to estimate how far figbirds might disperse seeds, although in natural habitats they are mobile, nomadic and forage over distances exceeding 1 km (Price *et al.* 1999).

Germination and recruitment

The germination and emergence experiments indicated that *O. serrulata* recruitment is likely to occur across a range of microsite conditions, providing moisture levels are not limiting. *O. serrulata* demonstrated a preference, but not a requirement, for light conditions in the germination experiment, and surface sowing in the tunnel emergence experiment where moisture was not limiting. Under field conditions of sporadic rainfall the emergence of buried seeds was greatest. Although not measured, we believe this response may be due to greater moisture availability and less desiccating conditions for seed buried at 1-cm depth in the field, particularly given the low moisture-holding capacity of the sandy loam used. However, it should be noted that regular rainfall was received at AFRS during the initial months of this experiment when emergence was recorded. Further field studies of seedling establishment in populations with different soil types, and levels of disturbance (e.g. fire or herbivory) and plant competition would improve our understanding of population establishment and spread of *O. serrulata*.

Passage of seeds through the gut of frugivores can promote germination above levels achieved with either intact fruits or seeds with the surrounding tissues manually removed (depulped) (Izhaki and Safriel 1990). In other species, depulping has a similar effect on germination as gut passage, such as in the invasive *Schinus terebinthifolius* Raddi (Panetta and McKee 1997). In other cases, gut passage can decrease germination rates (Traveset and Verdú 2002). Only in the field experiment were differences in germination between seed-processing treatments recorded, with greater germination of seeds with the pulp still attached than for depulped seeds (gut passage was not tested under field conditions). This result is unusual, as most fleshy fruit respond positively to pulp removal. In a field situation, we suggest that the pulp might play a role in reducing desiccation of the seed and delay decay. Pulp in *O. serrulata* is firmly attached to the seed and not easily removed manually or via gut passage (seeds passed by figbirds looked very similar to unpassed seeds, suggesting gut passage may have a limited effect in figbirds at least). Hence, it is not surprising that there were no differences in germination of gut-passed seeds compared with seeds with pulp. This study indicates that *O. serrulata* is not dependent on frugivory for recruitment, but that dispersers may facilitate movement of viable propagules to new locations.

Our results suggest that regular summer rainfall, combined with a substrate of a reasonable moisture-holding capacity, is likely to provide conditions suitable for *O. serrulata* recruitment in natural environments. No data on recruitment rates in natural conditions are available; however, seedling densities are often high (Morton 1998). Extrapolation of these results suggests that *O. serrulata* is likely to be most invasive in regions with summer rainfall, which is where it has been recorded in Australia.

Ochna serrulata appears to have a non-persistent seed bank, with no germinable seeds remaining after 6 months and no viable seeds present at 12 months under either field or irrigated tunnel conditions. This conclusion is supported by an absence of further emergence events recorded beyond 118 days in both tunnel and field emergence experiments. These results are consistent with those of other studies demonstrating transient seed banks in other bird-dispersed weed species in south-eastern Queensland (e.g. Panetta and McKee 1997; Panetta 2000, 2001).

Management implications

These findings suggest several management opportunities to reduce seed dispersal, recruitment and re-colonisation following control of *O. serrulata*. Two significant findings are the short period of viability of *O. serrulata* seeds and a single, well defined fruiting season (spring–summer). Together, these provide an opportunity to schedule *O. serrulata* control measures 6–12 months after seed production has ceased. At this time there is minimal viable seed in the soil from last season, and new seed inputs can be largely prevented. Re-invasion could occur through dispersed seed, so it would be necessary to target other local sources of *O. serrulata* seed. Our results also suggest that recruitment may be lower during dry conditions, indicating that dry periods could also be a useful time to undertake control.

The drupe removal experiment suggests that habitats differ in importance as seed sources. *O. serrulata* could be controlled in bushland habitats as a priority over suburban habitats, as more drupes were removed and presumably dispersed. Whether this difference in removal rates is biologically meaningful is less clear, as substantial removal of *O. serrulata* drupes also occurred in suburban areas, and these are potential source plants for re-invasion of bushland. This is especially likely, given the mobility of figbirds and their ability to use scattered food sources (Price *et al.* 1999).

When invasive plants provide a food resource for native wildlife, the impacts of any large-scale control efforts on food availability should be considered carefully. One option to minimise the impacts of control or redirect dietary preferences, is the provision of alternative food resources of a similar quality and season to the invasive plant resource. Our observations (at the suburban Sherwood site) of figbird diets showed that fruits of several native species are used concurrently with *O. serrulata*.

We have identified two areas of future research that would further improve *O. serrulata* management. First, control programs could be manipulated to determine reinvasion patterns and their relative importance. Contributions to reinvasion from different sources could be quantified; sources would include new seed inputs from dispersers, recruitment from the seed bank (which could be minimised if control is undertaken at the recommended time) and the colonisation by other invasive plants (e.g. other bird-dispersed weeds) or natives. The effectiveness of removing seed sources from surrounding areas could also be tested experimentally. Second, traits of native fruits other than phenology could be measured, to determine their suitability as replacement foods for figbirds for use in revegetation and to provide a better understanding of native-bird dietary requirements. The nutritional composition of native fruit, in particular, is poorly known.

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