

## The population dynamics of the mangrove *Avicennia marina*; demographic synthesis and predictive modelling

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### Abstract

Population dynamics of the widespread mangrove *Avicennia marina* was studied over the complete life-history from zygotes through to adults in southeastern Australia. Zygote survival, propagule dispersal, seedling establishment, seedling recruitment and sapling recruitment were examined by demographic censuses over a range of spatial and temporal scales. Hypotheses about factors regulating survival were tested by manipulative field experiments. Life table statistics for survival and fecundity were used to calculate transition probabilities and their variance for seven stages of life history. These parameters were used as the basis of a stochastic model that predicts population structure after small and large scale perturbations.

### Introduction

Modelling the population dynamics of long-lived species, such as mangroves, has been frustrated by problems of complexity related to spatial heterogeneity of populations and the stochastic nature of their dynamics. A useful conceptual model of the spatial and temporal components of a mangrove forest or metapopulation is the 'shifting mosaic' model (Shugart & Urban, 1988). A mangrove forest consists of a mosaic of smaller cohorts, often of differing species, each having a history that depends on episodic recruitment of seedlings (Fig. 1a). The uneven size distributions of mangrove populations in southeastern Australia suggests that episodic mass mortality and/or regeneration occurs at two spatial scales (Fig. 1a). Smaller scale disturbances (type a) result from the death of a few individuals and create gaps of a few crown diameters, whereas larger scale disturbances resulting from storms, and pathogen attack create regeneration sites >0.1 ha.

In many mangrove forests propagules regularly establish because they contain precociously developed embryos, but the recruitment of the established seedlings to older cohorts (saplings) depends on the episodic availability of a 'regeneration niche' (Clarke

& Allaway, 1993). Often such opportunities arise after small scale disturbances such as tree fall, which free up sediment and light resources, or larger scale events such as sedimentation or mass mortality (Fig. 1). It is this event driven component of the wider and more complex metapopulation dynamics of mangrove forests containing *Avicennia marina* (Forsk.) Vierh. that this paper addresses.

Life table statistics can be used for demographic modelling of a population, *i.e.* to simulate population change using mathematical algorithms. In particular, matrix population models have been used to project what would happen to the population if demographic attributes remain unchanged, *i.e.* exponential growth (Caswell, 1989). For predictive modelling such assumptions are mostly untenable, but Caswell (1989) argues that they 'reveal something about the present population'. For example, the various indices generated from a deterministic model can be used for interspecific comparison (Harcombe, 1987; Silvertown *et al.*, 1992). While matrix models may be useful for comparative purposes their use as predictors of future population size and structure is limited (e.g. see Burns & Ogden, 1985) because mangrove populations are limited by environmental filtering and competition. Non-linear models can, however, be developed from

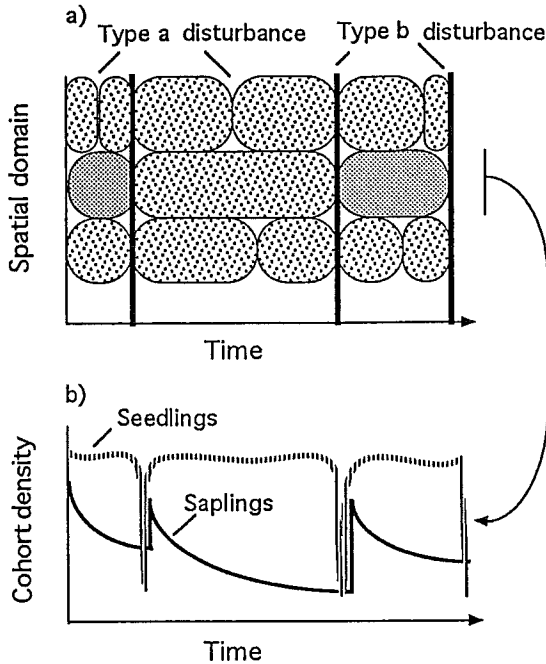


Fig. 1. a) Shifting mosaic model with two types of disturbance. Small scale disturbance type a, and larger scale disturbance type b. b) Sapling recruitment and mortality after disturbance, seedlings constantly present in the understorey.

life table statistics together with information about how environmental filtering and competition influence demographic rates.

The purpose of this paper is firstly to present a demographic synthesis of the life history of the mangrove *Avicennia marina* var *australasica* Walp. Moldenke (Duke, 1991) in south-eastern Australia, and secondly to present a predictive population model for population growth after a regeneration niche has been created.

**Demographic synthesis**

*The life cycle*

The life cycle of *Avicennia marina* starts with the potential zygote population in the form of female gametophytes. After fertilisation the population consists of precociously developing embryos that are partially dependent on maternal support. Once dispersed, the propagule must chance on a favourable place to establish, grow and recruit to older age classes. The cycle is complete when offspring are produced by

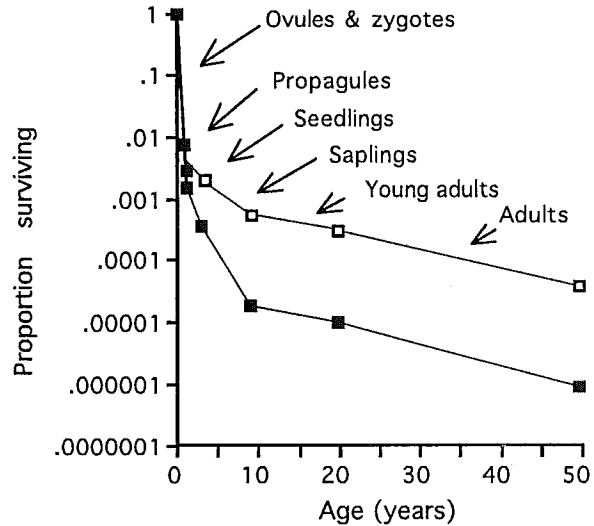


Fig. 2. Survivorship throughout the life history. Closed symbol type a disturbance, open symbol type b disturbance, e.g. colonisation. Error terms available on request to author.

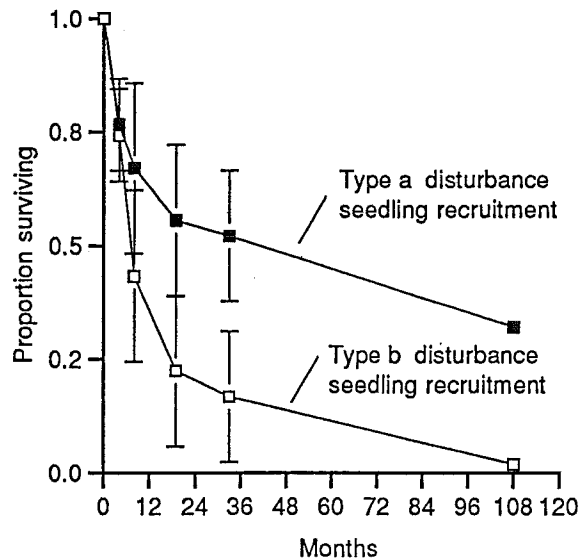


Fig. 3. Survival of seedlings and saplings under type a and type b disturbance. (See Clarke & Allaway, 1993).

either reproduction forming genets or by growth forming independent clones or ramets.

*Predispersal mortality*

About one third of flower primordia, each containing four ovules, survive to become open flowers but only 3% (0.75% of ovules) survive to become viable fruits some ten months after the initiation of flower buds

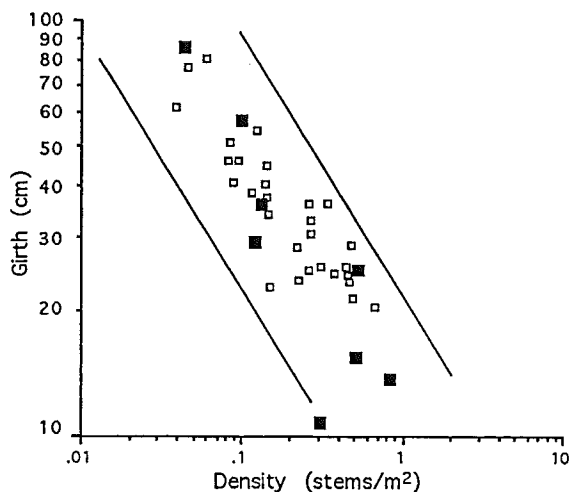


Fig. 4. Correlation of girth and density of trees. Solid symbol *Avicennia marina*. Open symbol data from Jimenez *et al.*, 1985. Thinning slope shown as solid line.

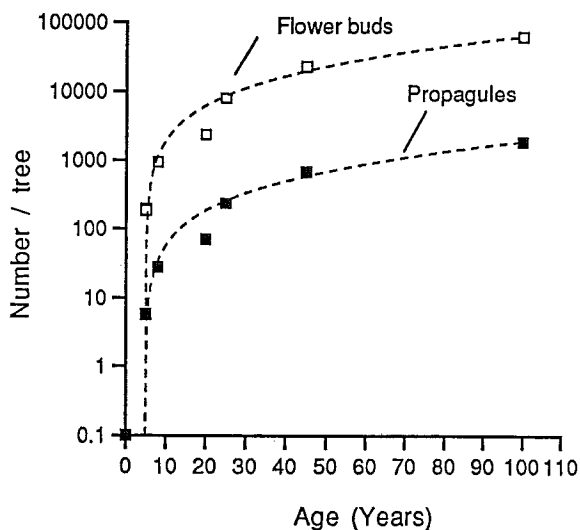


Fig. 5. Fecundity schedule for potential fecundity (flower buds) and realised fecundity (propagules). Details of fecundity errors presented in Clarke & Myerscough, 1991.

(Clarke & Myerscough, 1991) (Fig. 2). Insect herbivores can influence the viability of propagules, but the size of the effect is small in south-eastern Australia (Clarke, 1992). In contrast, rare climatic events, such as hail storms, may reduce predispersal survival close to zero (Clarke, 1992).

#### Dispersal and establishment

Once released from maternal support propagules have an obligate phase of dispersal about one week, although

the dispersal phase may extend over many months (Clarke, 1993). During this period there appears to be little mortality, except for stranding outside the normal habitat range of mangroves (Clarke & Myerscough, 1993). To estimate establishment accurately many thousands of propagules need to be followed over a wide range of conditions. Of these about half of the propagules that strand establish over a wide range of salinity, light and nutrient conditions (Clarke & Myerscough, 1993) (Fig. 2). Some mortality is due to predation (Clarke & Myerscough, 1993), although this mortality is far less than that reported for tropical populations of *Avicennia marina* (Smith, 1987). Apart from predation the main factor inhibiting establishment appears to be tidal and wave buffering.

#### Seedling growth and survival

Once propagules establish seedling survival is independent of light, nutrient and salinity conditions for during the phase while the cotyledons are attached (Clarke & Myerscough, 1993; Clarke & Allaway, 1993). In contrast, survival of seedlings after the post-cotyledonary phase appears to be largely resource dependent. Seedlings require a combination of light and sediment resources for enhanced growth and survival, *i.e.* recruitment to a reproductive phase (Clarke & Allaway, 1993). About 25% of established seedlings can recruit to a sapling stage (*ca* 10 years) if the regeneration niche is large, *i.e.* after gross canopy and sediment disturbance, whereas after small gap disturbance about 10% recruit to this stage (Clarke & Allaway, 1993) (Fig. 2, Fig. 3).

#### Sapling and tree survival

In crowded stands populations of saplings appear to thin because of interspecific competition (Fig. 4), but as growth slows the cause of mortality probably shifts towards disturbance effects. One of the problems in predicting the effects of differing environmental conditions of thinning rates is the difficulty in deriving estimates of growth under particular environmental conditions (Landsberg, 1986). Mortality rates change with the age of the tree population (Fig. 2); those in crowded populations have higher natural annual mortality, and this decreases as trees thin and other factors influence mortality. At some stage, however, this rate must increase as older plants appear to be more prone to tree fall and pathogens.

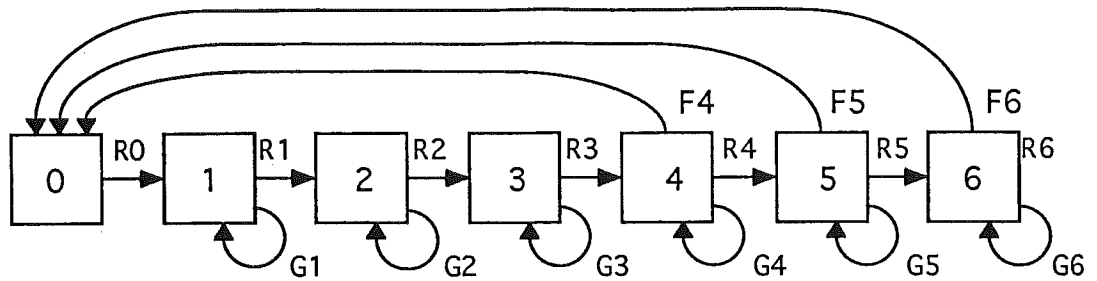


Fig. 6. Life cycle model based on seven life history stages. 0 = propagules, 1 = cotyledonary seedlings, 2 = seedlings, 3 = saplings, 4 = young trees, 5 = trees, 6 = older trees. F = fecundity, R = probability of growth to next stage, G = probability of remaining in stage (mortality =  $1 - R - G$ ).

### Reproduction and fecundity

Plants as young as 5 years can produce viable propagules, but under conditions of crowding and rapid growth most of the plants appear not to be fecund until they become a small tree (*ca* 20y) (Fig. 5) (Clarke, 1992). Fecundity of a tree increases with size and age until maturity where the potential annual fecundity is large (Fig. 5). Mature trees, however, are only fecund every few years, hence averaged over an estimated lifetime of about a century an individual produces about 250 propagules each year (Clarke, 1992).

### Modelling

A simple stage-structured model of *A. marina* incorporating the life history outlined above shows seven stages and the probabilities of recruiting to the next stage, the probability of remaining in a stage and at each stage its fecundity (Fig. 6) (Table 1). The transition probabilities differ depending on the type of regeneration niche created and subsequent environmental filtering. The latter effect can, however, be taken into account by incorporating the variance about mean values. The transition probabilities for two types of regeneration are shown in Table 1. Type a is a regeneration sequence after small scale disturbance the size of a few tree crown areas and type b is a sequence following the creation of a new niche (e.g. sedimentation) or the disturbance on the scale of  $>0.1$  ha (e.g. storms, disease, clearing, oil spills). The transition probabilities of recruitment or growth to the next stage, the probability of remaining in a stage and the fecundity rates can be used in Lefkovich matrices to project population growth (Caswell, 1989).

Clearly, it is unrealistic, in a predictive sense, to assume that the transition probabilities remain

unchanged through time such that population growth is exponential *i.e.* deterministic (Fig. 7). Instead, a non-linear component to the model can be introduced so that the transition probabilities decrease as populations become crowded and the canopy closes (Fig. 8). It should be noted that this non-linear projection is stochastic, but for clear presentation of the mean trend the error terms have been excluded from Fig 8. When the maximum density is reached for saplings the transition probabilities for the previous stages are reduced to zero (Table 1). A non-linear modelling projection was made after initialising the population with 1000 propagules that disperse in from surrounding cohorts or sown. The modelled area of the population would be about  $100 \text{ m}^2$  *i.e.* 1 propagule per  $\text{m}^2$  and the initial transition probabilities used assume regeneration following a large scale disturbance such as an oil spill and smaller scale disturbances such as the formation of a canopy gap. Initial seedling numbers ensure rapid recruitment of saplings, but as they reach maximum density after about a decade further recruitment is restricted as transition probabilities for seedlings reach zero (Fig. 8). Thereafter numbers of saplings decrease as thinning, and recruitment to older stages, occur. After about 20 years very few saplings are left in the understorey and canopy trees stabilise in density at about  $0.05\text{--}0.1$  trees  $\text{m}^{-2}$ . The predictions the present model makes about the population structure of *Avicennia marina* stands in south-eastern Australia have been verified from stands of known age, but its ability to predict dynamics needs to be tested by observations of sites with a known disturbance history.

### Discussion

Much research in mangrove ecology, and plant ecology in general, has been essentially descriptive. Distribu-

Table 1. Annual transition probabilities and fecundity for a stage-based model. Mortality = 1 - Recruitment - Remaining. type a disturbance, small scale; type b disturbance, large scale. Variance values available on request to author.

Rates	Disturbance	Stage						
		0 Propagules	1 Cotyledonary seedlings	2 Seedlings	3 Saplings	4 Young tree	5 Tree	6 Older tree
Fecundity (F)	Type a	0	0	0	0	0	500	1000
	Type b	0	0	0	0	100	500	1000
Mortality	Type a	0.800	0.250	0.165	0.018	0.029	0.008	0.001
	Type b	0.600	0.104	0.122	0.045	0.029	0.008	0.001
Recruitment (R)	Type a	0.200	0.083	0.010	0.073	0.008	0.012	0.000
	Type b	0.400	0.230	0.045	0.045	0.008	0.012	0.000
Remaining (G)	Type a	0.000	0.666	0.825	0.909	0.963	0.980	0.999
	Type b	0.000	0.666	0.825	0.909	0.963	0.980	0.999

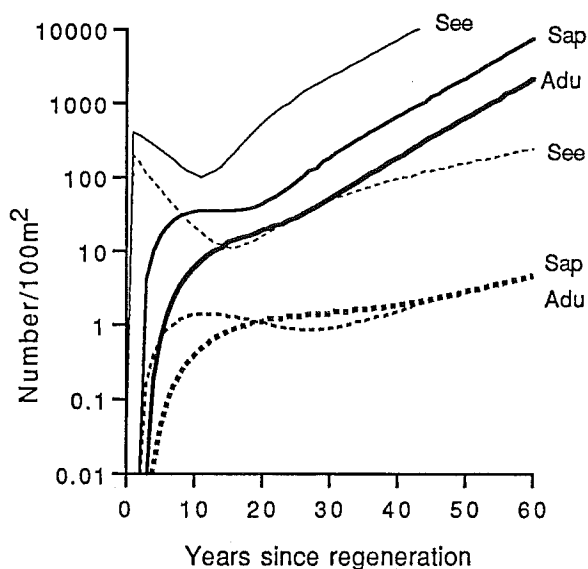


Fig. 7. Deterministic model of population growth after disturbance. Broken line type a disturbance, solid line type b disturbance. Model initialised with 1000 dispersed propagules. See seedlings, Sap saplings, Adu Adults. Confidence limits removed for ease of interpretation.

tions of taxa and patterns of zonation have occupied a plethora of studies and there is now an adequate descriptive background against which hypotheses can be framed. Generality at the landscape scale (geomorphic studies) and precision at the individual scale (ecophysiology) have characterised correlative approaches in attempts to provide explanations and predictions of mangrove distributions, abundance and performance.

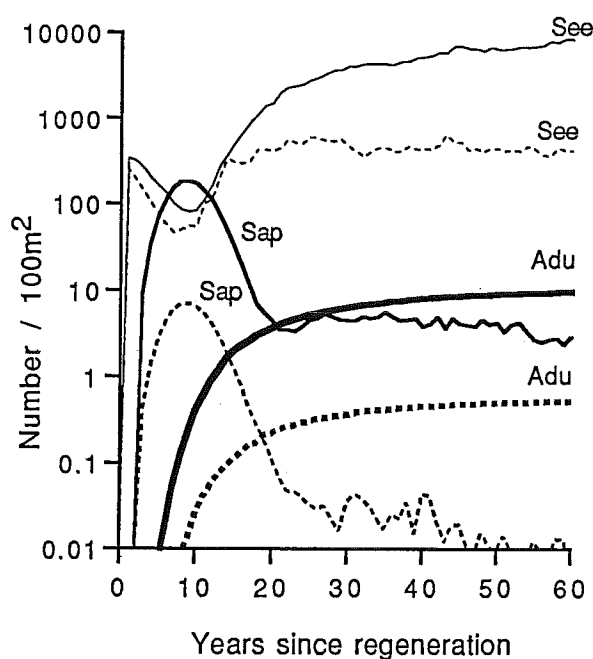


Fig. 8. Non-linear model of population growth after disturbance. Broken line type a disturbance, solid line type b disturbance. Model initialised with 1000 dispersed propagules. See seedlings, Sap saplings, Adu Adults. Confidence limits removed for ease of interpretation.

More recent trends focus on plant populations and experimental manipulation to test specific hypotheses about mangrove processes. These studies seem to provide a conceptual link between the extreme scales of space and time inherent in studies of mangrove vege-

tation by focussing on the fundamental unit of natural selection.

Population studies of mangrove species, and most other long-lived plants, often concentrate on components of the life cycle to explain present distribution and abundance. In mangroves, propagule predation (e.g. Robertson *et al.*, 1990), dispersal (e.g. Rabinowitz, 1978), seedling growth (e.g. Ball, 1988) and seedling predation (e.g. Smith, 1987) have been studied to explain distribution and abundance. Alone, these explanations may be inadequate because other life history stages may influence the overall population process. The present study shows that it is logistically possible to construct life tables for mangrove species and at the same time test hypotheses about regulation of survival, growth and fecundity. Clearly, the spatial and temporal variances are large when dealing with field population data; however adequate spatial and temporal replication will increase the precision and generality of the results. These data are not easy to collect in an often inaccessible and difficult working environment; nevertheless, they form an important basis for understanding and predicting the gap and regeneration dynamics of mangrove forests (see e.g. Grant *et al.*, 1993). Predictions from these models should be tested either by large scale experimental manipulations or by closer analysis of natural or human induced perturbations rather than stand structure analysis, given the problems of determining the age structure of mangroves. Simple stochastic models that incorporate transition probabilities to predict population size may, in the future, be incorporated into more complex shifting mosaic models to assess broader scale effects such as climate change or resource utilisation.

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