Gap-dependence in mangrove life-history strategies: a consideration of the entire life cycle and patch dynamics

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Summary

1. Tropical rain forest trees have been classified according to the importance of canopy disturbances for their life histories. To assess gap-dependence vs. shade tolerance, we propose using demographic analysis of the degree to which gaps are critical for population growth.

2. Population growth is the composite of the successes and failures of individuals experiencing different life-cycle pathways (i.e. gap, building, and mature forest patches). To assess the contribution of each pathway, it is necessary to study patch dynamics.

3. We use stage and patch structured matrix models and loop analysis to assess the life-history strategies of two Neotropical mangrove trees, *Avicennia germinans* and *Rhizophora mangle*. We use data from field studies in Lake Maracaibo, Venezuela, that were specifically designed to parameterize these models.

4. In *R. mangle*, seedling to juvenile progression was limited to high light patches (> 20% canopy openness), even though they comprised < 10% of the area, and population growth depended entirely on gaps. *A. germinans* seedlings progressed to juveniles from all light patches, and progression rates increased with light level. However, low and medium light patches (< 20% openness) were most important to population growth because they were most frequent. We suggest that *R. mangle* is gap-dependent while *A. germinans* is shade-promoted (i.e. shaded patches are demographically more important to *A. germinans* population growth even though seedling progression rates increase with canopy openness).

5. Previous studies considered *R. mangle* shade-tolerant because its propagules can establish and initially survive in the shade, but our classification was based on its entire life cycle. For *A. germinans*, the important measure was not the growth response to light, but the frequency and demographic importance of different light patches.

6. *Synthesis*: These examples show that observations of a plant's germination biology or photosynthetic/growth response to light do not necessarily translate into demographic behaviour because physiology can be decoupled from demography by patch dynamics. Thus, it is critical to consider the entire life cycle in the context of forest patch dynamics when assessing the life-history strategies of tropical trees.

Key-words: *Avicennia germinans*, canopy gap, disturbance, gap dynamics, Markov model, matrix model, patch, population projection matrix, *Rhizophora mangle*, tropical forest, Venezuela

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Introduction

Tropical rain forest trees have been divided into two broad categories, gap-dependent vs. shade-tolerant,

according to the importance of canopy gaps for their life histories (Denslow 1987; Swaine & Whitmore 1988). A number of parameters have been used to place species into these life-history categories, including seedling germination, establishment and growth (Swaine & Whitmore 1988; Clark & Clark 1992), leaf-level photosynthetic traits (Kitajima 1994), leaf and seedling morphology and biomass allocation (Osunkoya *et al.* 1994), and seed size (Foster & Janson 1985). While these parameters are useful for understanding shade-tolerance on a physiological basis, they may not fully explain the importance of gaps vs. shade conditions in a demographic context. For example, classifications based on seedling performance do not consider the possibility that successful seedling colonization and initial growth may be followed by differential survivorship and progression to the juvenile stage (Martínez-Ramos *et al.* 1989). Furthermore, plant performance in response to light may depend on plant size (Clark & Clark 1992). Here, we propose using demographic analysis of the degree to which gaps are critical for population growth when classifying tropical tree life-history strategies.

To assess the role of canopy gaps in the population dynamics and life histories of forest tree species, it is necessary to consider the different life-cycle pathways (gap, building, and mature forest patches) that individuals may experience (*sensu* Caswell 1989). The population growth rate is the composite of the successes and failures of individuals experiencing different life-cycle routes (van Groenendael *et al.* 1994). For example, a seedling of a gap-dependent species that spends its entire life in the understorey may never reach reproductive maturity, making no contribution to population growth. On the other hand, a seedling that initially establishes in the understorey and subsequently experiences a gap opening may be able to progress successfully to the juvenile stage, reach maturity, and reproduce. To assess the contribution of each life-cycle route to population growth, it is necessary to estimate: (i) the frequency, and changes in frequency, of patch types; (ii) the probability that an individual will experience each patch type; and (iii) the associated patch-specific vital rates (Álvarez-Buylla 1994).

Patch-structured models have been used to compare the relative importance of gaps vs. closed canopy for the population growth of several species that spend their entire life cycle in the forest understorey. These include the tropical herb *Calathea ovandensis* (Horvitz & Schemske 1986), the temperate herb *Primula vulgaris* (Valverde & Silvertown 1997), and the understorey tropical long-lived palm *Astrocaryum mexicanum* (Martínez-Ramos *et al.* 1988). However, studies exploring gap dependence in canopy-level tree species using a whole life cycle and patch-structured approach are currently lacking.

The purpose of this study is to assess the life-history strategies of tropical trees using a quantitative analysis of the entire life cycle and patch dynamics. We use mangroves as our study system because even though gaps are considered important for mangrove forest dynamics (Smith *et al.* 1994; Duke 2001), population-level studies of mangrove life-history strategies are lacking. We studied *Avicennia germinans* and *Rhizophora mangle* because they are the dominant mangrove tree species in the Neotropics and in our field sites in Lake Maracaibo, Venezuela (Narváez 1998).

Mangrove seedlings typically increase assimilation and growth with increased light (Ball & Critchley 1982; Krauss & Allen 2003; López-Hoffman *et al.* 2006). In field and glasshouse experiments on *A. germinans*, seedling assimilation and growth rates increase significantly with an increase in light level (López-Hoffman *et al.* 2007). Numerous field studies have examined the effects of canopy gaps on mangrove seedling performance (Ellison & Farnsworth 1993; McKee 1995; McGuinness 1997). Some studies report higher seedling establishment and growth in gaps (Putz & Chan 1986). Others report similar seedling establishment and survival rates in gaps and non-gaps, but higher seedling growth rates, and higher sapling densities, in gaps (Clarke & Allaway 1993; Clarke & Kerrigan 2000). In particular, several studies report higher *R. mangle* juvenile densities in gaps than non-gaps (Smith *et al.* 1994; Sousa *et al.* 2003b; Whelan 2005), leading Whelan (2005) to suggest that *R. mangle* may be a gap-dependent species. Historically, *R. mangle* has been considered a shade-tolerant species (Ball 1980) on the basis that its seedlings are frequently observed under a range of canopy conditions.

Methods

To evaluate population dynamics, we used stage-based projection matrices where seedling demography was light patch-specific (Álvarez-Buylla 1994). Juveniles and adults were not assigned to distinct light patches. The relatively simple mangrove forest canopy and lack of horizontal layers means that light levels vary little for the adult size classes, although this may not be true for juveniles (see Discussion). We used loop analysis (van Groenendael *et al.* 1994) to identify the most important life-history routes (i.e. the light patches critical for seedling to juvenile progression). To characterize the life-history strategies of *A. germinans* and *R. mangle*, we combined insights from patch-structured models of population dynamics with studies of seedling performance along a range of light levels, an analysis of forest size structure, and simulations of juvenile and adult size-time growth trajectories (Lieberman & Lieberman 1985).

STUDY SITE, SPECIES SELECTION AND PLOT SIZE

The study was conducted in the Río Limón mangrove forest of Lake Maracaibo, western Venezuela (10°96′70″ N, 71°73′24″ W). There are three mangrove tree species; we studied *R. mangle* and *A. germinans* because they

are most common (Narváez 1998). All study sites were in low salinity, low intertidal areas subject to approximately the same inundation and salinity regimes; salinity varied seasonally between 0 and 15% full seawater (López-Hoffman 2003). We established eight permanent plots (60 × 40 m) in sites that were between 0.5 and 2 km from one another.

FOREST PATCH DYNAMICS

To understand gap dynamics, it is necessary to (i) determine the range and frequency of forest light levels, and (ii) follow changes in light levels over time. We superimposed a 10 × 10 m grid system upon each permanent plot. In June 2000 and June 2001, we measured canopy openness (%CO) at each grid point (one reading in each cardinal direction). Ten metres was the minimum distance at which there was no spatial autocorrelation in light level (López-Hoffman 2003). We used canopy densiometers to measure canopy openness (Forestry Suppliers, Jackson, MS, USA).

We classified three light patch levels of %CO (i.e. patch types): Low (0–9.9%), Medium (10–19.9%) and High (≥ 20%). High light patches were large gaps formed by tree falls. Medium patches were either gaps in the process of closing, or small gaps created by branch falls. Low light patches represented the mature forest understorey. We quantified the probability that a patch at a given light level would, over the course of the year, stay the same, increase, or decrease, by comparing %CO at each grid point in June 2000 and 2001 (one transition year/period). These data were used to parameterize a Markov chain model of light patch dynamics (see below).

MANGROVE SPECIES DEMOGRAPHY

We defined five stages: seedlings (S, < 70 cm height), juveniles (J, ≥ 70 cm height and < 2 cm diameter at breast height, d.b.h.), small adults (A1, 2–14.9 cm d.b.h.), medium adults (A2, 15–29.9 cm d.b.h.) and large adults (A3, 30+ cm d.b.h.). Previous mangrove studies have also used cut-off values between 50 and 100 cm height as the division between seedling and juvenile (Clarke & Allaway 1993; Clarke & Kerrigan 2000). The division between juveniles and small adults (2 cm d.b.h.) was the smallest size at which individuals were observed to reproduce. The definition of adult size classes was an optimization between the number of size classes and the number of individuals per class (Caswell 2001). The seedling stage was subdivided into three categories: seedlings in Low, Medium and High light patches. The average vital rates for each life stage were determined as follows.

Adult and juvenile transition rates

In June 1999, 2000 and 2001 (two transition years/periods), we measured the heights and stem diameters of adults and juveniles in the permanent plots (Table 1). For *A. germinans*, we measured diameter at 1.3 m above ground (d.b.h.). For *R. mangle*, due to prominent adventitious roots, diameter was measured 1.3 m above the point at which trunk diameter became uniform. For juveniles, we measured diameter at ground level, and also at breast height if the juvenile stem was ≥ 1.3 m tall. We determined that an individual had progressed/retrogressed to another size class if its diameter increased/decreased enough to qualify for that class. Juveniles that were not relocated on subsequent censuses were considered dead. Adults were determined to be dead if they were uprooted and/or their entire crown was dry.

Seedling transition rates

We used two approaches to estimate seedling vital rates along a range of light levels: (i) from May 1999 to May 2000 we conducted a field experiment of seedling growth; and (ii) from June 2000 to June 2001 we followed the performance of naturally established seedlings. These data represent two transition periods/years (Table 1).

(i) *Field experiment*. In our study area, we identified nine spots along a gradient of light levels, ranging from closed canopy to forest gaps of different sizes. At each spot, we established a 5 × 5 m plot; two, three and four plots at Low, Medium and High light, respectively. Canopy openness was measured with a densiometer. Each plot was cleared of low-stature vegetation and debris. Mature *R. mangle* and *A. germinans* propagules were collected from nearby trees. For 6 weeks prior to the experiment, *A. germinans* propagules were germinated in 10 cm, sand-filled plastic cups. *R. mangle* propagules were not germinated prior to the experiment. Between 5 and 7 May 1999, 50 *A germinans* seedlings (between 25 and 30 cm tall) and 50 *R. mangle* propagules (between 25 and 30 cm long) were planted into each plot. The *R. mangle* propagules were inserted 5 cm into the soil. Two weeks after transplanting, we thinned the plots to 25 seedlings per species, and measured the height of all remaining seedlings. The seedlings were re-measured in May 2000. At the end of the year, if a seedling had grown taller than 70 cm, we considered that it had progressed to the juvenile class. Seedling mortality was determined by absence at the final census.

(ii) *Field demography of naturally established seedlings*. In June 2000, we marked all seedlings in 32 3.14-m² plots (1 m radius) randomly located at different light levels within the 60 × 40 m permanent plots. We established 12 seedling plots each at Low and Medium light, and 8 at High light; we had fewer High light plots because large gaps were infrequent. In June 2001, we re-censused the plots; unmarked seedlings were considered to have established in the intervening year. For seedling growth and survival rates, in June 2000 we measured the height of a maximum of 15 randomly chosen seedlings per plot. These seedlings were re-measured in

June 2001. Seedling mortality and progression to juvenile were estimated as above.

Seedling establishment and fecundity rates

We used the annual rate of seedling establishment in the seedling plots to estimate adult fecundity per light patch level (it should be noted that mangroves do not form a seed bank). Fecundity was quantified as the average number of new seedlings produced per adult per light patch per year. It was calculated as follows: (i) we estimated an allometric relationship between tree crown area and trunk d.b.h. (López-Hoffman 2003); (ii) we assumed that an individual's fecundity was proportional to its crown area; (iii) we estimated each tree's percentage of the total canopy area in the permanent plots; (iv) we estimated total annual seedling establishment in the permanent plots (independent of light level); (v) we multiplied each tree's proportion of total permanent plot crown area by the total annual seedling establishment in the permanent plots to estimate each tree's annual fecundity; (vi) we apportioned each tree's annual fecundity to each light patch level according to the frequency of that light level (see previous section); and (vii) we averaged the contributions of trees in each size class to each light patch type to obtain size and patch-specific fecundity rates.

The probabilities of survivorship and progression were analysed using general linear models (GLIM 3.77, Royal Statistical Society, London, UK). We used a logit link function and a binomial error. Rescaled procedure was applied when over-dispersion was detected (Crawley 1993). ANOVAs of growth and seedling establishment rates were analysed with Data Desk 6.1 (Data Description Inc., 1997; Ithaca, NY, USA). We simulated size-time growth trajectories for juveniles and adults using a method based on annual growth increment data proposed by Lieberman & Lieberman (1985). For this analysis, we used adult d.b.h. growth. Because some juveniles were shorter than breast height, we simulated their growth trajectories using ground-level diameter growth from 0 to 4 cm. Given the species' allometry, a ground-level diameter of 4 cm roughly translates to a d.b.h. of 2 cm.

MODEL DESCRIPTION

To integrate seedling demography with patch dynamics, we used projection models where the seedling transition probabilities were patch-specific and discrete Markov chain models to describe forest light patch dynamics. The Markov model has the form:

$$\alpha^k(t) = \sum_{l=1}^{r} d^{kl} \alpha^l(t-1) \qquad \text{eqn 1}$$

where, $\alpha^k(t)$ defines the area per forest patch type k at time t, d^{kl} is the probability of patch type l changing to patch type k, α^l is the area in light patch type l at time $t-1$, and r is the number of forest patch types.

Population projection matrices have the form: $v_{t+1} = M \times v_t$ where v_t is a vector representing the population stage structure at time t, v_{t+1} is the population stage structure after one unit of time, and M is a square matrix containing the transition rate averages for each stage class. The elements of M, p_{ji}, are the contributions per individual in stage i to stage j in the next time step. The population growth rate, λ, is the largest positive eigenvalue of M (Caswell 2001).

In non-matrix form, the population projection equation for juvenile and adult individuals in stage i, assumed to be independent of patch dynamics, is:

$$n_i(t+1) = \sum_{j=1}^{s} p_{ij} n_i(t) \qquad \text{eqn 2}$$

where $n_i(t+1)$ and $n_i(t)$ are densities of juvenile or adult individuals in stage i at times $t+1$ and t, respectively, and s denotes the number of stages or size classes.

The population projection equation for seedlings that considers patch dynamics, is:

$$n_i^k(t+1) = \sum_{j,l=1}^{s,r} (d^{kl} p_{ji}^l) n_i^l(t) + \left(\frac{[a^k(t)][f_{ij}]}{a_{tot}} \right) n_j(t) \qquad \text{eqn 3}$$

where $n_i^k(t+1)$ is the number of seedlings (stage i) and in patch type k at time $t+1$. The first part of the term models the forest patch dynamics of already established seedlings; d^{kl} describes the probabilities of change among patch types, p_{ij}^l is the probability that a seedling (stage i) in light patch l progresses to the juvenile stage j. Note that if $j = i$ there is no seedling to juvenile progression and if $k = l$ there is no change between patch types. The number of seedlings in patch type l at time t is $n_i^l(t)$. The second part of the term considers the adults' contributions of new seedlings to specific forest patch types. The area per patch type, $\alpha^k(t)$, is given by the Markov chain (eqn 1) and α_{tot} is the total area where the population grows. The contribution of an adult in stage j to new established seedlings is f_{ij} (i.e. the stage-specific fecundity rate). The number of adults in class j at time t is $n_j(t)$.

Our model makes several important assumptions. First is that annual seedling survival was determined by initial patch type, and that all patch changes occurred at the end of year. Secondly, we assumed that the contribution of new seedlings to each patch type was proportional to the amount of forest occupied by the patch type. This was reasonable because there were no statistically significant differences in seedling establishment rates between light patches (see Results). Thirdly, our model assumes that population dynamics are independent of population densities; future versions should consider density-dependent dynamics. Finally, we assumed that the small-scale disturbances we model are the principal gap creating events in the system; this may be reasonable given that our study sites lie south of the Caribbean hurricane belt.

Table 1. For each species, the sample size used to estimate the average vital rates for each life-cycle stage and the transition years are noted. The data source for seedlings is noted (either the field experiment or the field demography of naturally established seedlings). For all life stages, there are a total of two transition periods

|	Data source	Transition year/s	*A. germinans* (*n*)	*R. mangle* (*n*)
Sd-Low	Field experiment	1999–2000	100	100
Sd-Medium	Field experiment	1999–2000	150	150
Sd-High	Field experiment	1999–2000	200	200
Sd-Low	Field demography	2000–2001	80	74
Sd-Medium	Field demography	2000–2001	121	92
Sd-High	Field demography	2000–2001	69	71
Juveniles	NA	1999–2000 2000–2001	73	59
Adult 1	NA	1999–2000 2000–2001	31	36
Adult 2	NA	1999–2000 2000–2001	17	30
Adult 3	NA	1999–2000 2000–2001	53	29

MATRIX MODEL ANALYSIS

The matrix models were parameterized using annualized demographic and patch dynamics rates. For seedlings, we used the arithmetic mean vital rates from the field experiment and the study of naturally established seedlings (representing two transition periods/years). For juveniles and adults, which we followed for 2 years, we used the geometric mean vital rate over the two transition years/periods. Standard, numerical, iterative techniques for estimating λ were used (512 iterations; Caswell 2001). Elasticity values for each matrix element were obtained following de Kroon *et al.* (2000).

We used loop analysis to determine the relative importance of light patch levels for seedling to juvenile progression. Loop analysis, which is based on elasticity analysis, identifies all possible life-cycle pathways and assigns them a value based on their relative importance for the population growth rate (van Groenendael *et al.* 1994). Using loop analysis allows us to consider the possibility that a seedling in a given forest patch type might need to experience a change in light level before progressing to the juvenile stage. We report pooled values for self and retrogression loops. In order to highlight the importance of different patch types for seedling to juvenile progression, we pooled reproductive loops with the same seedling to juvenile pathways, regardless of the adult stages. For example, the loops 'Low light seedling to Juvenile to Adult 1' and 'Low light seedling to Juvenile to Adult 1 to Adult 2' are pooled together. However, the loops 'Low light seedling to Medium light seedling to Juvenile to Adult 1' and 'Low light seedling to Juvenile to Adult 1' are not pooled together because they have different seedling to juvenile pathways.

Results

FOREST PATCH DYNAMICS

The observed frequency of light levels in the forest was 74% of the forest at Low light, 21% at Medium, and 5%
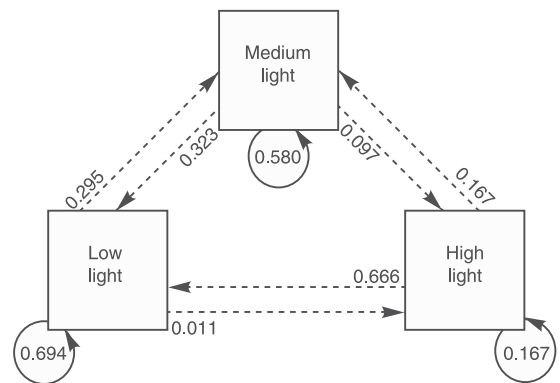

Fig. 1. Diagram of the Markov matrix of annual transition probabilities between light patches (see text for further details).

Table 2. (a) ANOVA of the effect of light patch type and species on seedling establishment. There were no significant effects of species or patch type on establishment rates. (b) ANOVA of effects of size and species on adult tree growth rates. There were no significant differences between the two species

	d.f.	Sums of squares	*F*-ratio	*P*
(a) Seedling establishment (individual m^{-2})				
Light	2	79.69	1.48	0.24
Species	1	25.90	5.23	0.15
Light × Species	2	9.91	0.18	0.83
Error	59	1588.43		
(b) Average adult girth (d.b.h.) growth (cm year^{-1})				
Size	3	19.46	13.70	≤ 0.01
Species	1	1.38	2.91	0.09
Size × Species	3	2.67	1.88	0.13
Error	268	126.89		

at High. Most Low light patches stayed at Low, with only a 1% annual probability of experiencing a gap opening and changing to High light. Most High light patches reverted to lower light levels (Fig. 1). The stable stage distribution of the Markov matrix, the steady state frequency of patch types, was 54% Low, 40% at Medium, and 6% at High light. Both the stable
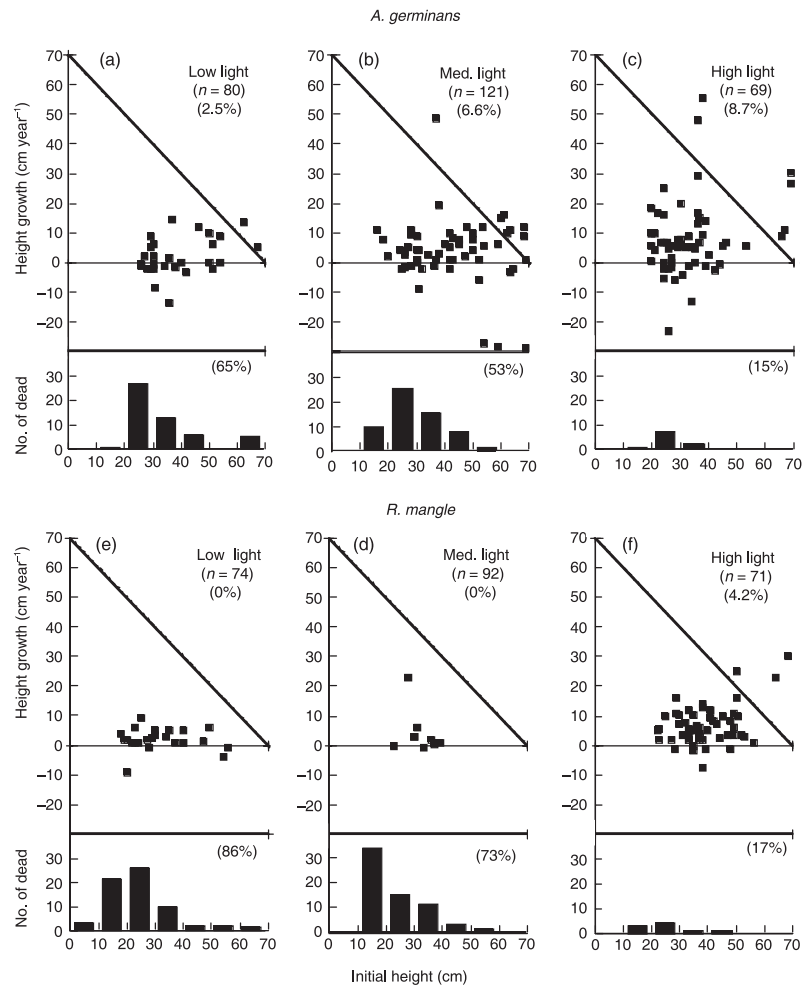
Fig. 2. Based on data from the field demography study of naturally established seedlings. The top panel of each figure shows seedling growth and progression to juvenile rates as a function of initial size. Progression occurs when a seedling (< 70 cm in height) grows enough in 1 year to be at least 70 cm tall. Points above the diagonal dashed line represent individuals that progressed. In the top panel, the numbers in parentheses indicate sample size and the percentage of seedlings that progressed to juvenile. The bottom panels depict seedling mortality as a function of initial size, with percentage mortality in parentheses.

and observed light frequencies indicate a low disturbance regime during the study years.

SEEDLING ESTABLISHMENT, SURVIVORSHIP, AND GROWTH

There were no statistically significant species or patch type effects on seedling establishment rates (Table 2a). Based on the field data of naturally established seedlings, for each patch type, Fig. 2 shows mortality, growth, and seedling to juvenile progression as a function of initial height. For both species, the probability of mortality significantly decreased with increased light level; overall, *R. mangle* seedlings had significantly higher probability of mortality (Fig. 2; Table 3a). *A. germinans* seedlings progressed from all patch types, and the probability of progression increased with light level ($P \leq 0.05$). *R. mangle*, however, experienced progression only at the highest light level (Fig. 2). Overall, *A. germinans* had higher rates of seedling to juvenile progression than *R. mangle* ($P \leq 0.01$;

Table 3b). The results of the field experiment were similar; seedling progression rates increased with light ($P \leq 0.05$; Table 3c). *A. germinans* experienced seedling progression from all light levels (4, 3 and 12% from Low, Medium and High, respectively). However, *R. mangle* experienced progression only from High light patches (0% from Low and Medium, and 11% from High light). In the field experiment there were no significant effects of light patch type or species on mortality.

JUVENILE AND ADULT SIZE-TIME GROWTH TRAJECTORIES AND VITAL RATES

R. mangle juveniles reached 4 cm ground-level diameter (about 2 cm d.b.h., the size division between juveniles and adults) in about 12 years, vs. 35+ years for *A. germinans*. Thus, on average, *R. mangle* grew to adulthood three times more rapidly than *A. germinans* (Fig. 3). *A. germinans* was longer-lived, reaching 110 cm d.b.h. in about 350 years. *R. mangle*'s maximum observed diameter and lifespan were 50 cm d.b.h. and 75 years, respectively

Table 3. General linear models of seedling probability of mortality and seedling to juvenile progression as a function of patch type and species. The data source for seedlings is noted (either the field experiment or the field demography of naturally established seedlings)

	d.f.	Deviance χ²	P
(a) Field demography			
Seedling mortality probability (ind./ind./year)			
Light	2	138.00	≤ 0.001
Species	1	15.65	≤ 0.001
Light × Species	2	4.25	NS
(b) Field demography			
Seedling-juvenile progression (ind./ind./year)			
Light	2	6.10	< 0.05
Species	1	8.83	< 0.01
Light × Species	2	4.28	NS
(c) Field experiment			
Seedling-juvenile progression (ind./ind./year)			
Light	2	7.36	< 0.05
Species	1	0.35	NS
Light × Species	2	1.64	NS
(d) Field experiment			
Seedling mortality probability (ind./ind./year)			
Light	2	1.36	NS
Species	1	0.15	NS
Light × Species	2	4.12	NS

(Fig. 4). There were no significant species differences in growth rates (Table 2b) or adult probability of mortality.

POPULATION SIZE STRUCTURE

In *A. germinans*, the number of individuals per size class steadily declined from the small to large classes (Fig. 5). *R. mangle* had a more irregular structure, with

peaks and valleys and an eventual numerical decline, suggesting that recruitment, mortality and/or growth rates changed across time (Fig. 5).

SPECIES LIFE CYCLES

Fig. 6 depicts life-cycle flux diagrams for the two species and incorporates the effects of forest patch dynamics on seedling demography. For both species, yearly mortality rates and population density declined as individuals passed from seedlings to adults. Annually, only 0.67% of all *R. mangle* seedlings progressed per year to the juvenile stage; all progression was from High light patches (Fig. 6a). Juveniles had a 20% probability of reaching the small adult stage. This fast growth period in the *R. mangle* life cycle declined in the next stages (Fig. 6a). There was an *A. germinans* seedling to juvenile progression from all patch types and the rate increased with light level. Over all patch types, 5% of seedlings progressed to juvenile each year (Fig. 6b). Annually, juveniles had a 5.4% probability of progression, but there was also 3% retrogression from A1 to juvenile (Fig. 6b), suggesting that the juvenile-A1 transition may be the greatest bottleneck in the *A. germinans* life cycle. The mean population growth rate, λ, of the *R. mangle* population was 1.043. Mean λ for *A. germinans* was 1.148.

LOOP ANALYSIS

Loop analysis identified three *R. mangle* pathways for seedling to juvenile progression; in all three, seedlings had to experience a High light patch before progression (Table 4). For *A. germinans*, loop analysis identified eight pathways. Each of the three light patch types was the final stage before progression to juveniles for at least one of the eight identified pathways (Table 4). For *A. germinans*
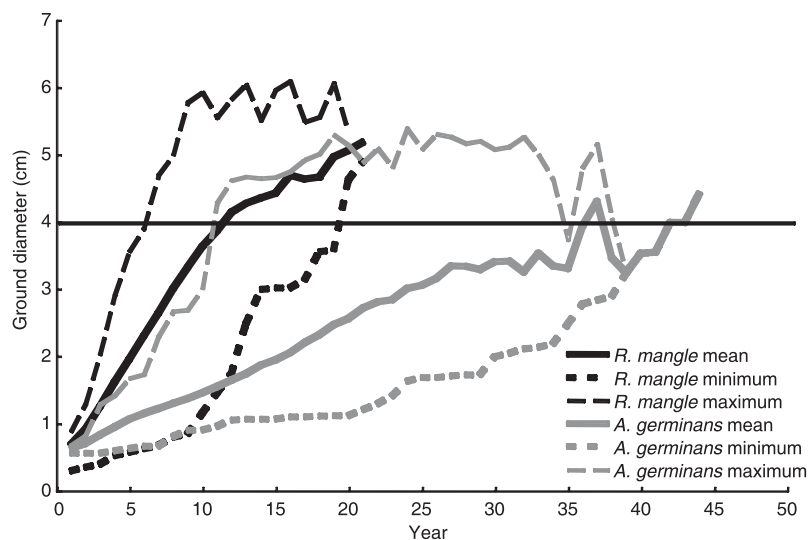
Fig. 3. Simulation of juvenile *R. mangle* and *A. germinans* size-time growth trajectories based on their periodic diameter ground-level growth increments. For each species, the mean, maximum and minimum trajectories are graphed. The horizontal line at 4 cm represents the division between juvenile and Adult 1. Four cm at ground-level is about 2 cm d.b.h., the division between juveniles and adults. On average, *R. mangle* juveniles reach adulthood in about 12 years, vs. over 35 years for *A. germinans*.
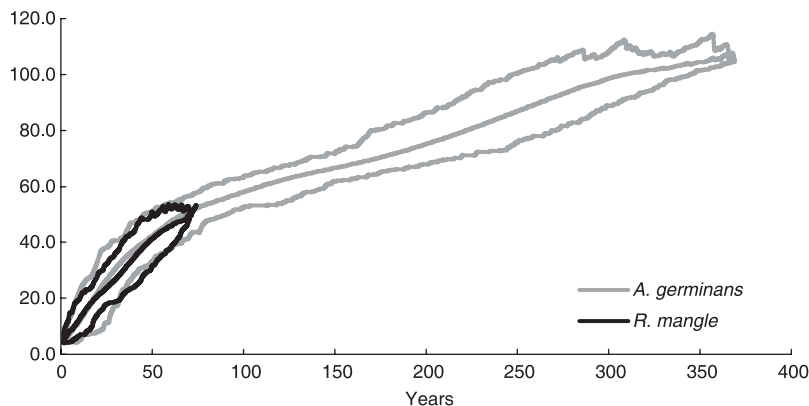
Fig. 4. Simulation of adult *R. mangle* and *A. germinans* size-time growth trajectories based on their annual d.b.h. growth increments. For each species, the mean, maximum and minimum growth trajectories are graphed.
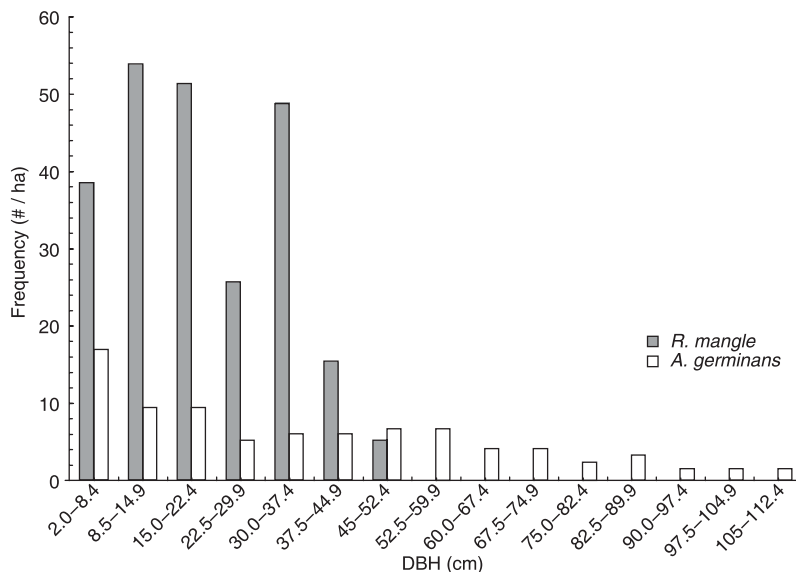
Fig. 5. Size structure of the adult classes. The diameter classes are more finely subdivided than the classes used for matrix analysis in order to highlight the population structure.

the order of the demographic importance of forest light patches was Medium > Low > High (Table 4).

Discussion

This study demonstrates that it is critical to consider both the entire life cycle and patch dynamics when assessing the life-history strategies of tropical trees. Using this approach, we conclude that *R. mangle* may be a gap-dependent species. In our study, *R. mangle* population dynamics relied entirely on disturbance and regeneration in canopy gaps. All observed *R. mangle* seedling to juvenile progression occurred from High light patches even though those patches comprised < 10% of the forest. According to loop analysis, the only way a seedling initially in a Low or Medium patch could contribute to population growth was if the patch happened to change to High light during the course of the year.

We used two approaches to estimate seedling vital rates, a field experiment and observations of naturally established seedlings. Seedling to juvenile progression could have been influenced by the seedlings' initial heights. The naturally established *R. mangle* seedlings at Low and Medium light were slightly shorter than those at High light. However, the seedlings were randomly selected, so the shorter initial heights were most likely a function of intrinsically lower seedling growth rates. Furthermore, in the field experiment, where we transplanted uniformly sized seedlings, there was no seedling to juvenile progression at Low and Medium light; all progression occurred at High light. This strongly indicates that *R. mangle* seedlings depend critically on high light levels and gaps for recruitment to the juvenile stage.

Some authors have suggested that *R. mangle* seedlings are 'just sitting there' waiting for gaps to open (Rabinowitz 1978), similar to the 'sit and wait'
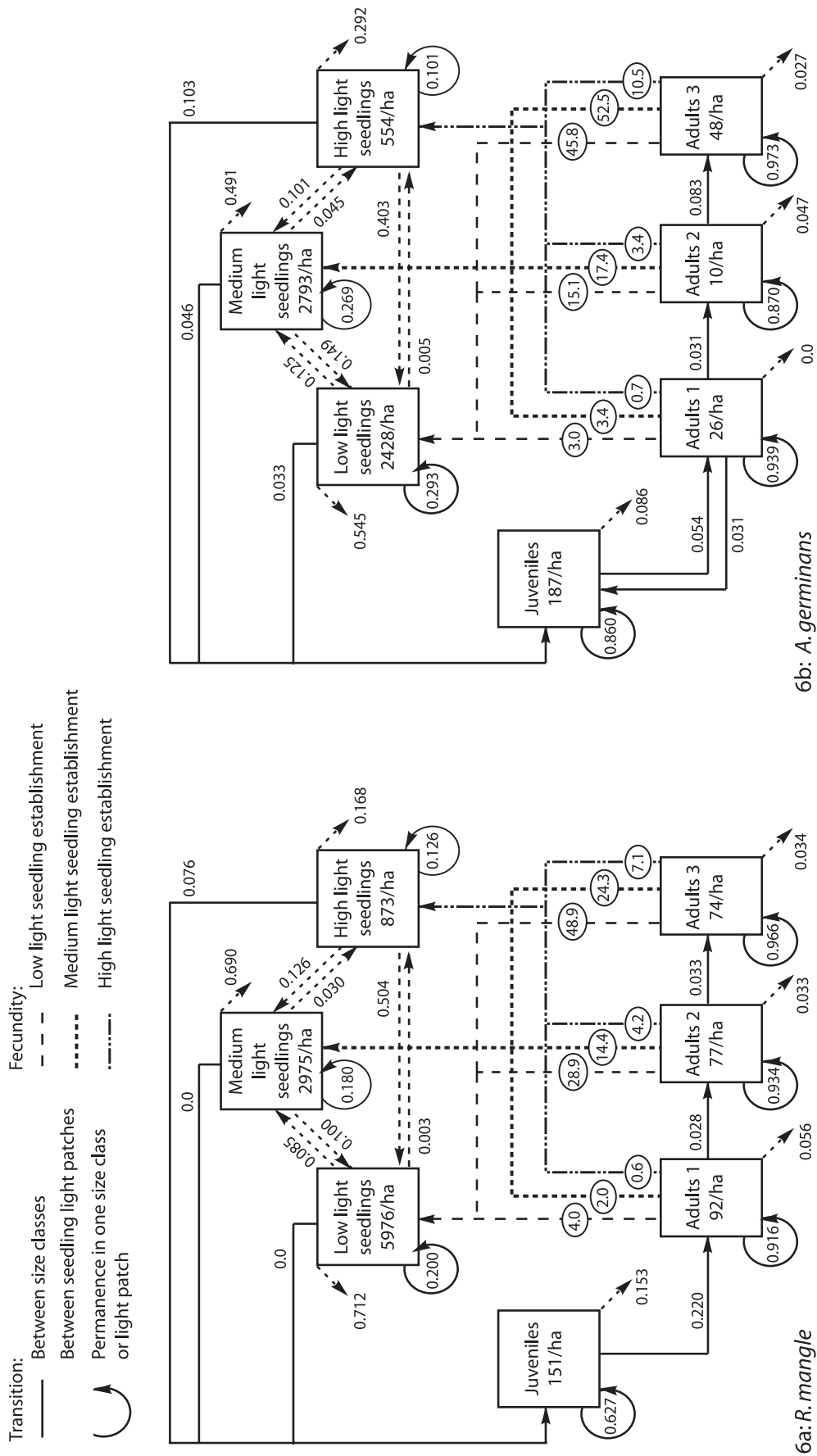
Fig. 6. This life-cycle flux diagram for (a) *R. mangle* and (b) *A. germinans*. The diagrams include details of seedling growth and light patch dynamics. *A. germinans* shows all vital rates necessary to construct the matrix models. For juveniles and adults, the density of individuals per class per hectare, transition rates between classes, mortality and permanence rates per class, and adult fecundity values are shown. For seedlings, the density of individuals per patch type per hectare, transition rates between patch types, and seedling to juvenile progression rates per patch type are shown. All values are the mean vital rates of data from two transition years/periods. The seedling values are the mean of the field experiment and field demography data sets.

Table 4. Loop analysis to determine the relative importance of light patch levels for seedling to juvenile progression. Pooled values for self and retrogression loops are reported. Reproductive loops with the same seedling to juvenile pathways, regardless of the adult stages, are pooled (see Methods). The letters L, M and H refer to seedlings in Low, Medium and High light patches, respectively, and J refers to the juvenile stage. The table is organized according to last patch type before progression to juvenile. The patch type subtotals represent the relative importance of each patch type. For *R. mangle*, there were four pathways for progression to juvenile; in all cases, seedlings had to experience a High light patch before progression. *A. germinans* had eight pathways for progression to juvenile, originating from light levels. For *A. germinans* the order of the demographic importance of light patches was Medium > Low > High

Loop type	Final patch	Loop value *A. germinans*	*R. mangle*
Reproductive	Low light:		
	L to J	8.74	–
	Subtotal	**8.74**	–
	Medium light:		
	M to J	9.72	–
	L to M to J	2.15	–
	L to H to M to J	0.09	–
	Subtotal	**11.96**	–
	Hight light:		
	H to J	3.63	14.74
	M to H to J	1.22	2.19
	L to H to J	0.06	0.57
	L to M to H to J	0.20	0.48
	Subtotal	**5.11**	**17.98**
Retrogression		**0.34**	–
Self loops		**73.61**	**82.02**
Total		99.75	100.00

approach observed in other tropical trees (Brienen & Zuidema 2006). For example, the rain forest tree *Nectandra ambigens* forms dense seedlings carpets from which juveniles emerge only when canopy gaps open (Córdova 1985). Here, we quantitatively test the notion that *R. mangle* exhibits a 'sit and wait' strategy. At our field site, we estimated a 1% transition probability from Low to High light gaps, indicating that the forest turnover rate is 100 years (the inverse of 0.01). Given that forests are a mosaic of different disturbance ages, the mean time for an average seedling in Low light to experience a High light gap is 50 years. The annual survivorship rate of *R. mangle* seedlings at Low light was 0.220. Thus, the probability of a seedling surviving 50 years is 1.322E-33, implying there is almost no chance of a seedling 'waiting' for a gap. It is possible that *R. mangle*'s strategy is to constantly produce a large number of seedlings so that at least some are likely to directly colonize a canopy gap.

The shade intolerance of *R. mangle* seedlings could be the result of a physiological trade-off promoting high growth rates in gaps while allowing herbivory in the shade. Although we did not document herbivory, studies have found higher mangrove seedling mortality

and herbivory under closed canopies (Osborne & Smith 1990; Sousa *et al.* 2003a; Lindquist & Carroll 2004). In a study of tropical rainforest trees, Kitajima (1994) showed that species with higher growth rates in gaps have lower survivorship in the shade because of herbivory. Physiological adaptations promoting high growth in gaps preclude energetically costly morphological protections against herbivores in the shade (Kitajima 1994).

Juvenile and adult growth rates and life span further suggest that *R. mangle* is gap-demanding (*sensu* Whitmore 1989). *R. mangle* was faster growing and much shorter-lived than *A. germinans*. *R. mangle* juveniles grew to adulthood about three times more rapidly than *A. germinans* juveniles. Disturbance-dependent species have size structures like *R. mangle*'s, with valleys reflecting mortality caused by perturbations, followed by peaks of regeneration (Sprugel 1976). Individual-based model simulations of mangrove population dynamics also indicate that *R. mangle* is dependent on light gaps (Chen & Twilley 1998) and that under high disturbance regimes out-competes *A. germinans* (Berger & Hildenbrandt 2000; Berger *et al.* 2002).

Our observations on *R. mangle* do not differ from previous observations. For example, Sousa *et al.* (2003b) and Whelan (2005) also note that *R. mangle* seedlings can establish at all light levels and that juvenile density is higher in gaps. Our significant contribution is to place these observations in a demographic context; by considering the complete life cycle, we clearly demonstrate that *R. mangle* is demographically a gap-dependent species, not a shade-tolerant species as suggested (Ball 1980). This strongly suggests that life-history classifications of tropical tree species should be based on an analysis of the entire life cycle.

The *A. germinans* example emphasizes the importance of considering patch dynamics when assessing the demographic importance of gaps for tropical trees. In both field and glasshouse experiments, *A. germinans* seedlings respond to increased light with increased assimilation and growth (López-Hoffman *et al.* 2007). Indeed, in this study, rates of *A. germinans* seedling to juvenile progression significantly increased with increase in light level, and population growth benefited from seedling to juvenile progression from all forest patch types. This would seem to suggest that *A. germinans* is a light demanding species, dependent on gaps for population growth. Nonetheless, according to the loop analysis, the order of demographic importance of light patches for population growth was Medium > Low > High. Seedling to juvenile progression in Medium and Low light patches was demographically more important than in High light patches because Medium and Low light patch levels were more frequent in the forest. We suggest that *A. germinans* should be considered a shade-promoted species because shaded patches were demographically most important to its population growth even though seedling progression rates increased with canopy openness.

This result strongly indicates that a species' growth and photosynthetic response to increased light levels may not reflect the importance of gaps in its life-history strategy. In fact, many rain forest shade species respond to increased light with increased growth (Popma & Bongers 1988; Poorter 1999). The important metric is not the growth response to light, but the demographic importance of different light patches. If the patch condition that produces the highest growth rates is not frequent, the patch type may not be important for overall population growth. Thus, it is critically important to consider patch dynamics (the frequency, and changes in frequency, of patch types) when assessing the relative importance of different patch types for tropical tree life-history strategies.

Conclusion

In this study, we have suggested using demographic analysis of the degree to which gaps are critical for population growth when assessing tree life-history strategies. We proposed that the most robust way to determine the importance of gaps in a species' life history is to evaluate the entire life cycle and consider patch dynamics. We suggest that species whose population growth rate critically depends on growth and survival in gaps are indeed demographically gap-dependent, even if some seedlings are able to survive in shade. Species whose population growth rate benefits most from seedling to juvenile progression under shade conditions, even though individual growth rates may increase with light availability, may be considered demographically shade-promoted. Through the examples of the Neotropical mangroves, *R. mangle* and *A. germinans*, we have shown that observations of a plant's germination biology or seedling photosynthetic/growth response to light do not necessarily translate into its demographic behaviour because physiology and demography can be decoupled by patch dynamics.

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