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Resistance of island rainforest to invasion by alien plants: influence of microhabitat and herbivory on seedling performance

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Abstract

Experiments have promise in determining mechanisms by which communities resist invasion. Growth and survivorship of transplanted seedlings of introduced tree species (*Leucaena leucocephala*, *Muntingia calabura, Adenanthera pavonia*, and *Clausena excavata*) were used to assess abiotic (light regime) and biotic resistance (herbivory) to invasion of rainforest on Christmas Island (Indian Ocean). At four sites, seedlings were transplanted into the forest edge along roadside verges and into adjacent intact forest; half were caged to prevent access by the dominant seedling consumer, the red land crab (*Gecarcoidea natalis*). Red crab densities did not differ between roadside and forest plots. Red crabs initially reduced survivorship of *Leucaena* in both edge and interior plots but virtually all seedlings in the forest interior were dead after 41 weeks. Survivorship of *Muntingia* was also initially reduced by crabs in the forest edge, but again, all but one seedling died by the end of the experiment. Seedlings of *Adenanthera* and *Clausena* fared much better overall, surviving well in both locations. Red crabs had no overall effect on *Adenanthera* survival but significantly reduced survival of *Clausena* in forest plots. For both species, seedling performance was greater in the forest edge than in the forest interior. Red crabs had no effect on height increment for either species; however, for *Clausena*, red crabs reduced seedling mass in the forest interior. Both *Adenanthera* and *Clausena* were able to persist in the intact forest. *Clausena* is now actively invading intact rainforest, but *Adenanthera* appears dispersal-limited. Resistance factors in intact forest appear hierarchical: biotic resistance afforded by land crabs can impede establishment of some plant invaders but seedling responses to abiotic factors (e.g., the light regime) largely overwhelm its effect. Together, these two community attributes are likely to restrict the range of plant invaders to a small suite of species that can successfully establish in intact rainforest on the island. However, increased propagule pressure from a variety of shade-tolerant species and further declines in the abundance of the dominant seedling consumer may lead to increasing invasion success in this island rainforest.

Introduction

One of the major challenges in invasion biology is predicting the invasiveness of alien species once they arrive at novel sites. Much attention has focussed on properties of the invaders themselves (e.g., Rejmánek 1995; Williamson and Fitter 1996) and considerable progress has been made in identifying common traits of successful invaders (e.g., Rejmánek and Richardson 1996; Rejmánek 2000; Kolar and Lodge 2001). However, far less emphasis has been placed on identifying traits which confer resistance to recipient communities (Mack 1996), and most work to date has examined emergent properties of communities, such as species richness and diversity (e.g., Elton 1958; Simberloff 1995; Rejmánek 1996), and extrinsic factors such as

disturbance (Hobbs and Huenneke 1992; D'Antonio et al. 2001). There remains a clear need to explicitly tease apart, preferably through experimentation, the mechanisms of resistance to invasion (Prieur-Richard and Lavorel 2000). A recent example of this approach is the manipulative work on invasion-resistance of grassland communities (Crawley et al. 1999).

Invasive alien species pose a threat to native plant communities globally, especially where these communities are disturbed (D'Antonio et al. 2001). However, relatively few alien plant species seem to have the capacity to invade undisturbed native plant communities (Rejmánek 1989). Rejmánek (1996), for example, could identify only 42 species worldwide that were invading primary tropical forests. On Christmas Island (Indian Ocean), abundant red land crabs (*Gecarcoidea natalis*) have been shown experimentally to be the primary determinant of rainforest seedling recruitment, by differentially consuming the seeds and seedlings of a wide variety of native plant species (O'Dowd and Lake 1990, 1991; Green et al. 1997). As such, this dominant consumer could play a key role in inhibiting the invasion of rainforest on the island by alien plants. In just over a century of human settlement, Christmas Island has accumulated an impressive list of introduced plant species: 236 of 448 species (52.7%) on the island are aliens (Claussen 2001). Most of these are confined to disturbed areas such as minefields, overburden dumps, and road corridors (Du Puy 1993; Swarbrick 1997), where most are likely to remain as long as the forest canopy remains intact. Nevertheless, some species may have the potential to invade intact rainforest on the island.

In this study, we experimentally assess the relative importance of microhabitat and herbivory by crabs as determinants of invasion by seedlings of four common weed trees on the island. To do this, we transplanted seedlings into roadside vegetation with a relatively open canopy and well-lit understorey, and into adjacent intact rainforest, where the canopy is almost completely closed and light levels in the understorey are very low. Half of the seedlings transplanted into each habitat were caged to protect them from herbivorous land crabs.

Materials and methods

This study was carried out on Christmas Island (10°30′ S, 105°40′ E), an isolated oceanic island in the northeastern Indian Ocean. The climate is monsoonal, with a wet season from November to May, and a total annual rainfall of 2000 mm. The island rises to a central plateau in a series of cliff and terraces, and these formations largely define the three major forest types on the island. Primary rainforest occurs mostly on the plateau, marginal rainforest and scrub forest occur mostly on the drier cliffs and terraces (Du Puy 1993).

Approximately 25% of the island has been cleared; most of these clearings were created over the past several decades for phosphate mining. The access roads to mined areas were often very wide with extensive verges; these verges have now been colonised by a suite of light-demanding species, both native and introduced. Native tree species in these verges include *Claoxylon indicum* and *Macaranga tanarius* (both Euphorbiaceae), *Pipturus argenteus* (Urticacaeae), and *Melochia umbellata* (Sterculiacaeae). The common alien trees include *Leucaena leucocephala* (Mimosaceae), *Muntingia calabura* (Flacourtiaceae), *Ricinus communis* (Euphorbiaceae), *Carica papaya* (Caricaeae), and *Psidium guava* (Myrtaceae).

For this study we selected four recognised weed species common on Christmas Island, all of them trees (Swarbrick 1997): *Adenanthera pavonia* (Mimosaceae), *Clausena excavata* (Rutaceae), *Leucaena*, and *Muntingia*. These species range from the light-demanding *Muntingia* and *Leucaena*, to the more shade-tolerant species *Adenanthera* and *Clausena*. *Muntingia* is native to Central and South America, and is thought to have been introduced to the island during the Japanese occupation of the island 1942–1945 (Swarbrick 1997). *Leucaena* is also Neotropical in origin but now widespread throughout the tropics, and may have been introduced to the island as an ornamental in the 1950s (Swarbrick 1997). *Adenanthera* is native to Southeast Asia, and was probably introduced to Christmas Island as a shade tree. *Clausena* occurs from India to the Philippines (Du Puy 1993), and may have been introduced in error for the similar species *Murraya koenigii* (curry leaf; Swarbrick 1997). However, it is also possible that the species was deliberately introduced, since the leaves, bark, and roots are known to have medicinal properties (Huang et al. 1997; Wu et al. 1998; Nakamura et al. 1998).

Our study was carried out alongside the North–South Baseline, a major haul road in the east of the island. Four pairs of study sites, each separated by 1.0–2.3 km,

were selected randomly from locations outside the boundaries of the Christmas Island National Park. Each site consisted of paired 10 m × 12 m plots, 1 located in the disturbed verges of the haul road, the other set well into the adjacent and intact primary rainforest ('Location', L, in subsequent analyses). Each plot was divided into a grid of 2 m × 2 m cells, for a total of 42 points.

Field-collected seedlings were grown individually in pots in the shadehouse to a mean height of 10.5 cm for *Adenanthera*, 7.5 cm for *Clausena*, 12.1 cm for *Leucaena*, and 6.9 cm for *Muntingia*. Five pairs of seedlings (each matched for height and leaf number) per species were then transplanted into each plot in late November 1998 at randomly selected locations on the grid. Of each pair, 1 seedling was protected from crab attack by a cylindrical poultry netting cage 20 cm in diameter and 30 cm tall ('crab protection', CP, in subsequent analyses). These cages were secured in place with wire pegs. The height of each seedling after transplanting was measured, and two-way ANOVAs for each species showed no significant difference in initial height between the treatments (forest edge vs forest interior, and caged vs open).

The number and condition (evidence of herbivory, etiolation, etc.) of surviving seedlings was recorded after 2, 7, 12, 17, and 41 weeks. At the end of the experiment in September 1999, we recorded the final height of surviving seedlings, uprooted them by hand, and returned them to the laboratory, where we determined the dry mass (70 °C for 48 h) of their above-ground parts. At each morning census, we recorded the number of active red crabs on each plot. The number of active red crab burrows on each plot was recorded at the beginning and end of the experiment.

Treatment differences in plant performance (per cent height increment; November 1998–September 1999, and final mass; September 1999) were analysed with two-way ANOVAs for *Adenanthera* and *Clausena*. For *Muntingia* in both locations and *Leucaena* in the forest interior, too few seedlings survived for analysis. Height increment and mass of *Leucaena* seedlings were compared with *t*-tests. Mean increment or mass values of the survivors in each block were used as replicates. Residuals were plotted against their corresponding estimates to check for homogeneity of variances, and the data transformed where appropriate. Treatment differences in percent survivorship were analysed with an extension of Gehan's generalised Wilcoxon test, Peto and Peto's generalised Wilcoxon test, and the log-rank test (Survival Analysis Package, Statsoft, Inc. 1996). For each species, we pooled data within treatments across pairs of plots. In situations where there are more than two treatments, this test only indicates the presence or absence of a significant difference, not where those differences lie; there are no formal *post hoc* tests comparing all possible treatment pairs. Following a significant test, we performed Cox–Mantel tests on all possible treatment pairs (six; EC vs EO, EC vs FC, EC vs FO, EO vs FC, EO vs FO, and FC vs FO where E = forest edge, F = forest interior, C = caged, O = open). However, in judging the effects of microhabitat alone, we compared EC *versus* FC because the comparison EO *versus* FO is potentially confounded by different levels of crab activity between forest and edge plots. For assessing the effects of crab herbivory on seedling survival, we considered the tests EC *versus* EO, and FC *versus* FO.

Potential differences in the density of red crab burrows between plots in disturbed edge and intact forest in November 1998 and September 1999 were analysed with paired *t*-tests. Differences in the densities of active red crabs during the experiment were analysed with repeated measures ANOVA; no transformation of either data set was required.

The transplant experiment suggested that *Clausena* survived well in shaded conditions. To further investigate the ability of *Clausena* to invade intact rainforest, we randomly chose two roadside locations where *Clausena* was common. In forest adjacent to each location (Phosphate Hill, Rock Crushing Plant), we established a single 100 m × 4 m transect. On each transect we recorded the number and height of all *Clausena* stems, and also the number, height and species of all stems ≤ 2 m in height.

Results

Seedling survivorship

Survivorship of seedlings varied markedly between species, and between treatments. The multisample survival test was significant for all species (*Adenanthera* $\chi^2 = 27.72$, $P < 0.001$; *Clausena* $\chi^2 = 11.55$, $P = 0.009$; *Leucaena* $\chi^2 = 51.09$, $P < 0.001$; *Muntingia* $\chi^2 = 45.30$, $P < 0.001$). Therefore, Cox–Mantel tests on survival were performed for individual treatment pairs for each species (Table 1).

Table 1. Cox–Mantel tests on per cent survivorship of seedlings of four species transplanted into forest edge (E) and forest interior (F) which were either caged (C) or left in the open (O).

	EO	FC	FO
Leucaena			
EC	2.300 (0.021)	6.043 (0.000)	6.359 (0.000)
EO	—	3.779 (0.000)	4.659 (0.000)
FC	—	—	2.403 (0.016)
Muntingia			
EC	3.076 (0.002)	5.369 (0.000)	5.323 (0.000)
EO	—	3.122 (0.002)	3.302 (0.001)
FC	—	—	1.433 (0.152)
Adenanthera			
EC	1.456 (0.146)	3.964 (<0.001)	4.680 (0.000)
EO	—	2.604 (0.009)	3.488 (<0.001)
FC	—	—	1.435 (0.153)
Clausena			
EC	1.447 (0.148)	0.000 (1.000)	2.687 (0.007)
EO	—	−1.447 (0.148)	1.249 (0.212)
FC	—	—	2.687 (0.007)

P-values are in brackets.

Leucaena – Overall, seedlings transplanted into roadside plots survived much better than those transplanted into adjacent intact forest (Figure 1a); 90% of caged seedlings survived for 41 weeks in roadside plots, compared with 5% of caged seedlings in the forest interior over the same period (EC vs FC, Table 1). Red crabs had a significant negative impact on seedling survival on roadside plots (EC vs EO). They also had a significantly negative impact in the forest (FC vs FO), but this effect was most obvious in the first seven weeks, after which only one seedling survived.

Muntingia – For the first 7 weeks, seedlings transplanted on roadside plots survived much better (85%) than seedlings transplanted into the forest (0%). By the end of the experiment, however, only a single *Muntingia* seedling survived in roadside plots (Figure 1b). Overall, these differences were significant (EC vs FC, Table 1). Red crabs had a significant negative impact on seedling survival in roadside plots

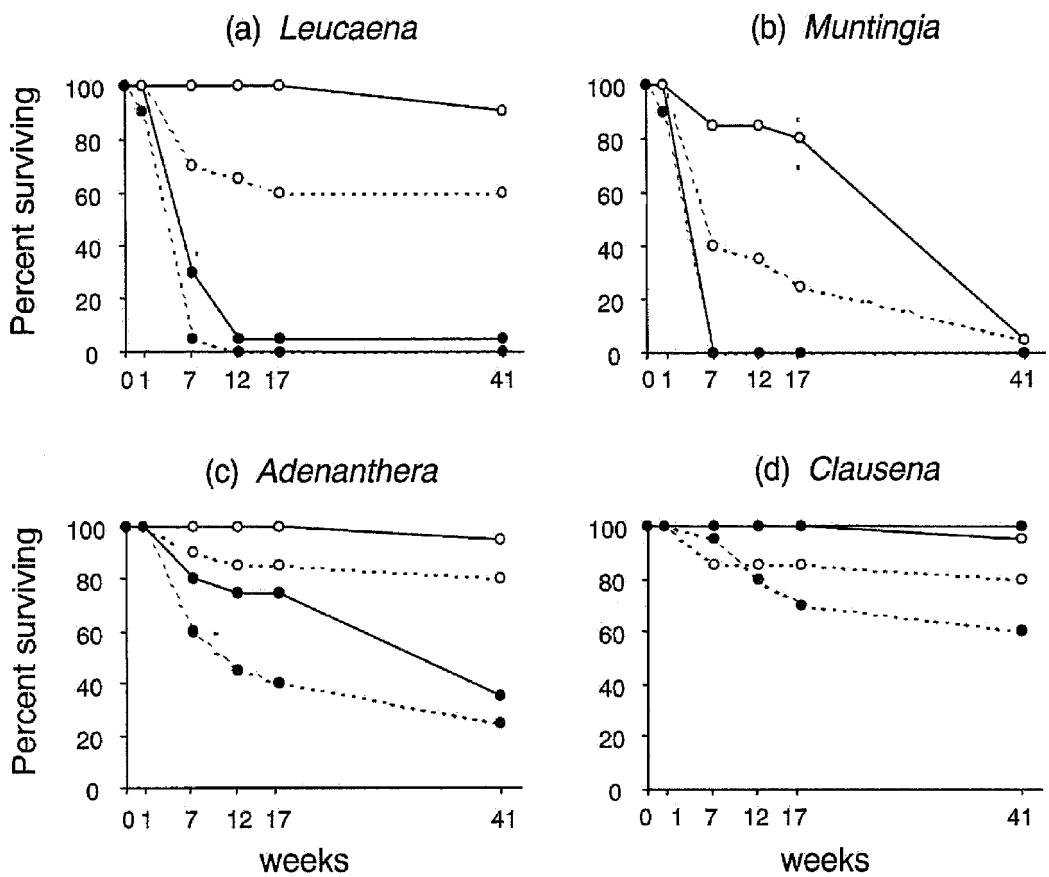

Figure 1. Percent survival of seedlings of (a) *Leucaena*, (b) *Muntingia*, (c) *Adenanthera*, and (d) *Clausena* over 41 weeks in the transplant experiments. Open circles = forest edge; solid circles = forest interior. Solid lines = caged; dashed lines = open.

(EC vs EO), but not in the forest (FC vs FO) where all seedlings were dead by seven weeks.

Adenanthera – The survival of transplanted *Adenanthera* seedlings was 95% in the roadside plots over 41 weeks, which was significantly higher than survival (40%) in the forest (Figure 1c; EC vs FC, Table 1). Red crabs had no significant impact on seedling survival in either roadside plots (EC vs EO), or in the forest interior (FC vs FO).

Clausena – Overall, 93% of caged *Clausena* seedlings survived to the end of the experiment (Figure 1d); there was no significant difference in survival between roadside seedlings and those in the forest (EC vs FC, Table 1). Red crabs had no significant impact on seedling survival on roadside plots (EC vs EO), but did have an impact in the forest (FC vs FO).

Seedling performance

Leucaena – In forest edge plots, height increment increased by 143.2% when seedlings were protected from red crabs compared to a 44.6% increase for seedlings placed in the open ($t_{1,6} = 5.72$, P (two-tailed) $= 0.001$). However, no difference in final seedling mass occurred between caged and uncaged treatments ($t_{1,6} = 0.373$, $P > 0.05$).

Adenanthera – Height increment and final seedling mass were greater on roadside plots than in adjacent intact forest (Figure 2a, b; Table 2; increment L; $P = 0.003$, mass L; $P = 0.003$). On an average, *Adenanthera* seedlings on the forest edge increased in height by 66.5% during the experiment, compared with 4.7% for seedlings transplanted into the forest interior. These trends were reflected in a 7-fold difference in seedling mass between the treatments. Red crabs had no discernible effect on seedling performance (increment CP; $P = 0.595$, mass CP; $P = 0.495$). Further, there was no significant interaction between L and CP for either increment or mass (Ps > 0.400).

Clausena – Height increment and final seedling mass were greater on forest edge plots than in the adjacent forest interior (Figure 2c, d; Table 2; increment L; $P = 0.001$, mass L; $P < 0.001$). *Clausena* seedlings transplanted into roadside plots more than doubled in height during the experiment, whereas seedlings in the forest interior shrunk by several per cent (Figure 2c). This small effect may have been due to a lack of real growth in dim conditions, combined with the accretion of soil around stems through rain splash. Like *Adenanthera*, there was a seven-fold difference in final seedling mass between forest edge and interior plots. Red crabs had no

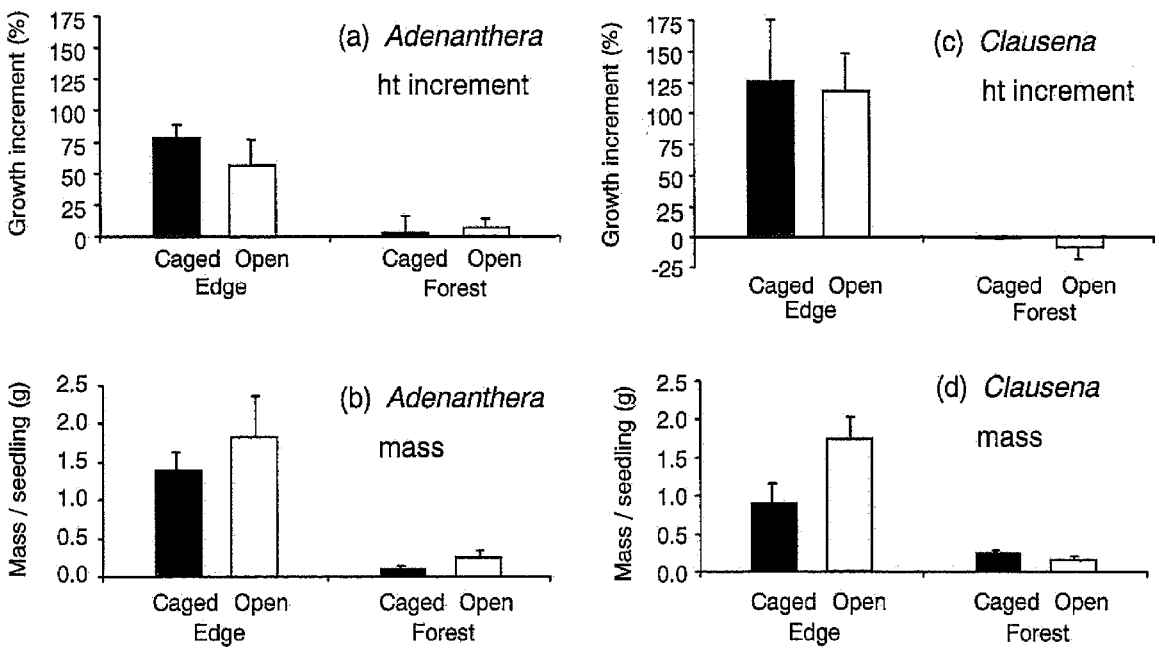

Figure 2. Percent height increment (based on seedling height changes over 41 weeks and final above-ground mass for *Adenanthera* (a, b) and *Clausena* (c, d) seedlings transplanted into roadside edge and forest interior. *Leucaena* and *Muntingia* are not plotted because too few seedlings survived.

Table 2. Two-way ANOVA for height increment and final above-ground dry mass for transplanted seedlings of *Adenanthera* and *Clausena*.

Source	d*f*	MS	*F*	*P*
(a) *Adenanthera* – height increment				
L	1	13137.23	15.803	0.003
CP	1	250.34	0.301	0.595
L × CP	1	585.57	0.704	0.421
Error	10	831.33		
(b) *Adenanthera* – mass				
L	1	6.59	15.791	0.003
CP	1	0.21	0.501	0.495
L × CP	1	0.12	0.290	0.602
Error	10	0.42		
(c) *Clausena* – height increment				
L	1	63309.42	17.345	0.001
CP	1	235.96	0.065	0.804
L × CP	1	0.00	0.000	1.000
Error	12	3650.03		
(d) *Clausena* – mass				
L	1	4.93	30.336	0.000
CP	1	0.61	3.742	0.077
L × CP	1	0.83	5.137	0.043
Error	12	0.16		

L = location, forest edge or forest interior; CP = crab protection, caged or open.

significant impact on seedling performance (increment CP; $P = 0.804$, mass CP; $P = 0.077$). There was no significant interaction between L and CP for height increment ($P = 1.000$), but there was for seedling mass ($P = 0.043$).

Density of active red crabs and burrows

During the experiment, the density of actively foraging red crabs varied from 2 to 44 crabs per plot. There were no significant differences in crab density between roadside and forest interior plots (one-way repeated measures ANOVA, $F_{1,6} = 0.490$, $P = 0.510$). The density of red crab burrows ranged from 8 to 34 burrows per plot at the beginning of the experiment, and between 10 and 25 burrows per plot by the end of the experiment. The differences in red crab burrow density between roadside and forest plots were not significant at either the beginning of the experiment (paired t-test, $t = -1.094$, P (two-tailed) = 0.153), or at the end ($t = 0.890$, $P = 0.439$). Because there was no significant variation in crab density and activity between the plot types, crab density and activity need not be regarded as covariates when interpreting patterns of seedling survival and plant performance.

Clausena *transects*

Transects at both sites showed that *Clausena* can be a major component of the forest understorey. At Phosphate Hill, of the 591 stems ≤ 2 m tall on the transect, 26.4% were *Clausena* (0.39 stems m^{-2}). At Rock Crushing Plant, *Clausena* comprised 70.2% of 1276 stems, and occurred at an average density of 2.24 stems m^{-2}. At both sites, the size structure of the population showed the classic 'reverse J' curve, with many small seedlings (≤ 60 cm tall), and a few stems up to 6 m tall (Figure 3).

Discussion

Red crabs are a widespread and abundant omnivore on Christmas Island and play a major role in structuring rainforest on the island, both by consuming a wide variety of native seeds and seedlings (O'Dowd and Lake 1990, 1991; Green et al. 1997) and by consuming a large fraction of annual litter input (O'Dowd and Lake 1989; Green et al. 1999a). This suggests that red crabs could also play a key role in determining the success of invasive alien species into the rainforest. This is the case for at least one well-known invader; red crabs prevent the invasion of the giant African landsnail (*Achatina fulica*) into island rainforest (Lake and O'Dowd 1991). However, despite their impact on the abundance and composition of native rainforest plants (O'Dowd and Lake 1989, 1990) and their potential widespread role as biotic resistors of invasion, this study has shown that at low densities, (0.07–0.3 crabs m^{-2}), red crabs have little effect on survivorship and performance of seedlings of four widespread introduced plant species transplanted into the understorey of closed rainforest.

However, the survivorship of introduced tree seedlings in rainforest appears dependent on the density of red crabs. In a previous study (O'Dowd and Lake 1990), survival of *Leucaena* and *Muntingia* seedlings was measured in just days at high crab densities (0.8–2.6 crabs m^{-2}). These observations suggest that at sites with higher crab densities, impacts on resistant species (*Clausena* and *Adenanthera*) would have been greater. This example illustrates that biotic resistance to invasion afforded by a single dominant species,

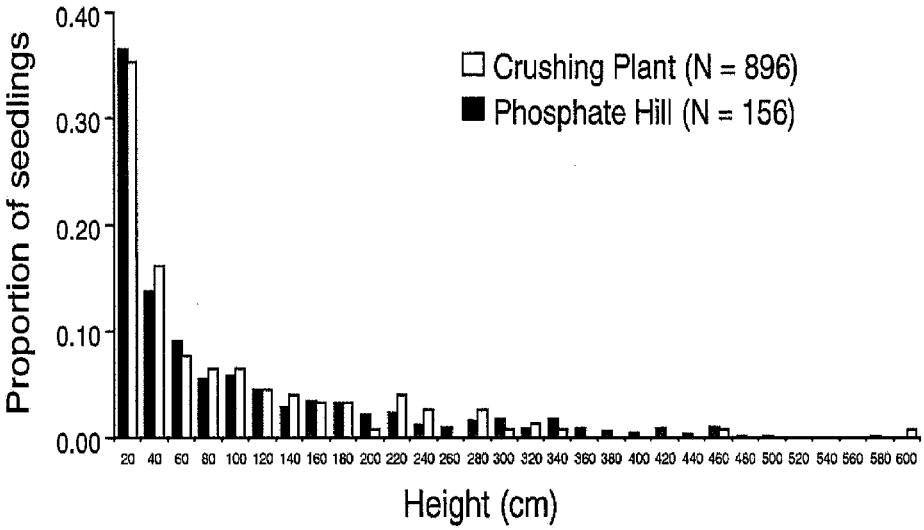

Figure 3. Height–frequency distribution of *Clausena* at Crushing Plant and Phosphate Hill.

even for those species with a demonstrable history of resistance, is conditional.

For *Leucaena* and *Muntingia*, the transplant experiment suggests that these light-demanding species are unable to survive in the long term under the heavy shade of intact rainforest canopy. However, it is possible that other factors, such as soil differences between the edge and forest plots, play a role. Red crabs did have a small but significant effect on the survival of *Leucaena* seedlings transplanted into the rainforest understorey (see also O'Dowd and Lake 1990), but clearly, this effect was eventually overwhelmed by microhabitat differences. *Muntingia* is a well-known pioneer species from Central and South America, where it only establishes in large treefall gaps of least 150 m^2 (Denslow 1980; Fleming et al. 1985). Gaps of this size occur on Christmas Island (Green 1996), and the species is not limited by dispersal since it forms an abundant seed bank under intact rainforest (Green et al. 1999b). However, *Muntingia* remains restricted to disturbed areas and has not been found in large natural gaps in rainforest on the island. This suggests that red land crabs have played a predominant role in preventing this species from invading natural treefall gaps in the forest, which is consistent with the marked caging effect we detected for this species in roadside plots.

In contrast to *Leucaena* and *Muntingia*, both *Adenanthera* and *Clausena* seedlings are able to tolerate conditions in the forest understorey, even though there was a significant reduction in plant performance in both species. Under these conditions, uncaged *Clausena* seedlings survived better (60% over 41 weeks) than those of *Adenanthera* (25%), despite suffering significant mortality due to red crabs. These data suggest that both species should be actively invading intact rainforest on Christmas Island. However, our observations indicate that only *Clausena* is becoming widespread in the forest. The reasons are probably related to the dispersal characteristics of the two species. The diaspores of *Adenanthera* are very hard, shiny red seeds, which are thought to mimic fleshy fruits (McKey 1975; Peres and Vanroosmalen 1996; Foster and Delay 1998). As such, they are nominally vertebrate-dispersed, but on Christmas Island dispersal appears primarily to be through gravity (Swarbrick 1997), and this species has not spread far from areas where it has been planted (however, *Adenanthera* is actively invading several forest communities in the Seychelles; Fleischmann 1997). On the other hand, the diaspore of *Clausena* is a translucent, fleshy pink berry containing one or two seeds, and is highly attractive to pigeons (*Ducula whartoni*) and possibly fruit bats (*Pteropus natalis*; PTG, pers. obs.). This species appears to be spreading across the island from the northeast (J. Claussen, unpublished data), where it is abundant along roadsides and establishing in adjacent rainforest. The reverse J size distribution on the two forest transects suggests that this species is actively recruiting. At Rock Crushing Plant, in particular, taller individuals were of reproductive size.

This study suggests that on Christmas Island, potential plant invaders of intact rainforest must possess two key traits: the ability to establish and grow under heavy shade, and the ability of both seeds and seedlings to tolerate, evade, or resist consumption by red crabs. For example, seedling consumption of native and alien species is inversely related to total fibre and phenolic concentration (O'Dowd and Lake 1990), and seedlings of some species may escape consumption by rapidly reaching a crab-resistant size (Green et al. 1997). Any potential invader will also benefit from effective dispersal once it has arrived at a site (e.g., Rejmánek and Richardson 1996; Rejmánek 2000). From a management point of view, simple transplant experiments like these may be an effective and objective means of determining which species may be robust against perceived forms of resistance offered by the recipient community. The lack of such experiments has only recently been decried (Prieur-Richard and Lavorel 2000).

Although the traits of invading species usually remain constant in ecological time, their recipient communities can be dynamic, changing systems. Consequently, the forms of resistance to invasion offered by them may also change. One major driver of rapid community change is disturbance (Sousa 1984; Pickett and White 1985). An increasingly common form of disturbance is invasion by alien species with the ability to alter the resistance of their recipient community – the 'Invasional Meltdown Hypothesis' (Parker et al. 1999; Simberloff and von Holle 1999). Here, alien species, which are themselves unable to act as the primary invader, can invade in the wake of the impact of a primary invader. Such a scenario is currently unfolding on Christmas Island (O'Dowd et al. 1999, 2003; Green et al. 1999c). Over the last several years, supercolonies of the invasive yellow crazy ant (*Anoplolepis gracilipes*) have established in 25% of the island's rainforest, completely eliminating local red crab populations. In these ant infestations several species of scale insects have also reached extremely high densities, from which the ants derive a large proportion of their diet in the form of honeydew. Together, ants and scale insects appear to be causing canopy dieback, which has increased light availability on the forest floor. In the absence of crabs, and with increased light, several shade-intolerant weed species (*Capsicum frutescens*, *Carica papaya*, *Cordia curassavica*, and *Muntingia*) have now established in the forest.

This study has shown that for tree seedlings to successfully invade intact forest, potential invaders must be shade tolerant and resistant to crab herbivory. As in many other island systems, Christmas Island has no redundant consumers; that is, if a potential invader can tolerate red crabs, there are no other generalist consumers on the island to resist invasion. However, at present we know of only a single species (*Clausena*) which, by virtue of its tolerance to shade and crab herbivory, is actively invading intact forest. As such, the situation on Christmas Island is consistent with Rejmánek's (1996, and references therein) view that in the absence of anthropogenic-induced disturbance, even insular tropical forests are relatively resistant to plant invasion. However, this may change with increased propagule pressure from a variety of shade-tolerant species (Fine 2002) and further declines in the abundance of the dominant seedling consumer on the island.

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