DISTRIBUTIONAL CONSTRAINTS ON AN INVASIVE NEOTROPICAL SHRUB, *CLIDEMIA HIRTA*, IN A MALAYSIAN DIPTEROCARP FOREST.

DISTRIBUCIÓN CONTRASTANTE DE UN ARBUSTO INVASOR NEOTROPICAL *CLIDEMIA HIRTA,* EN UN BOSQUE DE DIPTEROCARPACEAS EN MALASIA

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ABSTRACT

Clidemia hirta, a pantropical invasive shrub of the family Melastomataceae, originates in humid tropical Central and South America, extending from southern Mexico to Argentina, including Venezuela. *C. hirta* is distinct among the many invasive plant species of the Malay Peninsula because of its ability to invade anthropogenically undisturbed primary and tall secondary forests. In order to gain insights into the conservation threat posed by this invasive shrub in intact Malaysian dipterocarp rainforests, factors known to limit the distribution and abundance of *C. hirta* in its native range were quantitatively assessed at an invasive site in Malaysia – the Pasoh Forest Reserve. Furthermore, plant characters often thought to convey invasive potential, plant size and herbivore damage levels, were assessed in Malaysia, and at two sites in Venezuela, where *C. hirta* is native. This study determined that the *C. hirta* population at Pasoh is largely confined to a narrow band of the light availability gradient. The comparison between native and invasive populations revealed that plant size and herbivory levels in Malaysia were similar to those found among Venezuelan populations.

Key Words: *Clidemia hirta*, enemy release hypothesis, light-gap specialist, plant invasion, tropical forest, Caparo Forest Reserve, La Mucuy, Parque Nacional Sierra Nevada, Pasoh Forest Reserve.

RESUMEN

Clidemia hirta es un arbusto invasor pantropical de la familia Melastomataceae, originario del trópico húmedo de América Central y del Sur, cuya distribución abarca desde el sur de México hasta Argentina, incluyendo a Venezuela. *C. hirta* se diferencia de otras plantas invasoras de la península Malaya por su habilidad de invadir tanto bosques primarios como bosques secundarios altos y perturbados antropogénicamente. Para determinar el estado en que este arbusto invasor se encuentra en las selvas húmedas primarias de dipterocarpaceas en Malasia, se estudiaron factores que limitan su distribución y abundancia tanto en su rango nativo como en un sitio donde es invasor en la Reserva Forestal de Pasoh, en Malasia. Además, caracteres de la planta que la convierten en invasora potencial, altura de la planta y daños por herbívoros, fueron medidos en Malasia, y en dos localidades en Venezuela, de donde es nativa. Este estudio determinó que la población de *C. hirta* de Pasoh está confinada principalmente a una banda estrecha en un gradiente de disponibilidad lumínica. La comparación entre las poblaciones nativas e invasoras revelan que el tamaño de la planta y los niveles de herbívoria fueron similares a los encontrados en las poblaciones de Venezuela.

Palabras clave: *Clidemia hirta,* especialista en claros, invasión de plantas, selvas tropicales, Reserva de Caparo, La Mucuy, Parque Nacional Sierra Nevada, Reserva de Pasoh

INTRODUCTION

The introduction of non-indigenous plant species into natural communities constitutes a serious threat to the preservation of biodiversity (Vitousek *et al.* 1996), and can fundamentally alter the structure and functioning of ecosystems (e.g. Vitousek *et al.* 1987, Gordon 1998). Because of their high conservation value, the extent to which anthropogenically undisturbed continental tropical forests are susceptible to invasion by non-native plants is an issue of longstanding concern to ecologists and conservation biologists (Rejmánek 1996, Lonsdale 1999). Nevertheless, few studies of plant invasion have been undertaken in continental tropical forests, making it difficult to understand the consequences of exotic introductions on the structure and composition of native plant assemblages.

The Neotropical shrub *Clidemia hirta* (L.) D. Don (Melastomataceae) is unusual among exotic plant species on the Malay Peninsula. Of the hundreds of non-native plant species in Singapore, only *C. hirta* has so far become established in closed-canopy primary and tall secondary forests (Corlett 1988, Teo *et al.* 2003). The small size of the forest fragments considered in these studies (0.03 to 2.0 ha) underscores the tendency for even small patches of primary forest to resist invasion by exotic plants, and suggests that the mechanisms facilitating *C. hirta* invasion may be unique. A recent study documented the unexpected invasion of *C. hirta* into an anthropogenically undisturbed (i.e. naturally disturbed) species-rich dipterocarp forest in Peninsular Malaysia (Peters 2001). *C. hirta* is an aggressive invader of Hawaiian forests, and may be displacing formerly prevalent plant species there (Wester and Wood 1977). The causes and consequences of *C. hirta* invasion in this biologically important Malaysian forest are poorly characterized, making it difficult to assess whether *C. hirta* is a uniquely proficient invader, or merely a forerunner of other invasive plant species.

The introduction of non-native plants may alter the availability of resources critical for establishment, growth, and reproduction. Determining the conservation threat of plant invasions thus requires an understanding of the factors influencing the distribution and abundance of non-native plants. Previous work has shown that both light availability and leaf herbivory influence the distribution of *C. hirta* in its native range (Taylor 1928, Cook 1929, DeWalt *et al.* 2004a, 2004b). Light availability often limits recruitment in tropical forests understorys (Clark and Clark 1992, Chazdon *et al.* 1996), and even shade tolerant plant species may require extended periods in high-light environments for successful regeneration (Weldon *et al.* 1991, Brown and Whitmore 1992). Leaf herbivores may influence tropical forest composition by selectively lowering plant fitness (Marquis and Braker 1994). Escape from herbivory has often been implicated as a mechanism allowing non-native plant species to proliferate in introduced ranges (Keane and Crawley 2002).

The purpose of this study was primarily to assess the distribution of *C. hirta* relative to the available light microsites in a species-rich dipterocarp forest of Southeast Asia. Secondarily this study ascertained whether herbivore damage on *C. hirta* is lower in this introduced site than in part of its native range, and addresses the recent prediction that herbivory on *C. hirta* in invasive sites with high species richness and closely related native flora will be high relative to herbivory on *C. hirta* in species-poor sites where this plant is invasive (DeWalt 2004b).

MATERIALS AND METHODS

Study Species

C. hirta is a densely branching perennial shrub native to tropical Central and South America. It has invaded wet and dry regions of the tropics and subtropics including Hawaii, Fiji, and the Malay Peninsula (Wester and Wood 1977, Cronk and Fuller 1995). *C. hirta* produces fruit continuously (Melo 1999), and local dispersal is performed by frugivorous birds, mongooses (*Herpestes auropunctatus*), pigs, and humans (Wester and Wood 1977, Smith 1992). Long-distance dispersal is probably inadvertently facilitated by humans (Cronk and Fuller 1995). *C. hirta* is omnipresent in the oil palm and rubber plantations that constitute over one quarter of the land area of Peninsular Malaysia.

Study Sites

In August 1997 the *C. hirta* population was sampled at the Pasoh Forest Reserve, about 140 km southeast of Kuala Lumpur, Peninsular

Malaysia (2°58'N, 102°19'E). The reserve consists of a core of 650 ha of evergreen primary lowland dipterocarp forest surrounded by 2000 ha of regenerating forests that were logged in the 1950s. At the time of the study the entire reserve was bordered by oil palm plantations on three sides and adjacent to 600-1000 ha of primary hill dipterocarp forest. Annual precipitation at Pasoh is approximately 1800 mm with two distinct peaks in April/May and November/December, but with every month receiving more than 100 mm rainfall. In January 1999 *C. hirta* populations were censused in two sites where the plant is native. The first site was La Mucuy site in the Parque Nacional Sierra Nevada, Venezuela (8°37' N, 71° W), a montane tropical rain forest (elevation ~2200 m a.s.l.) receiving approximately 1800 mm of precipitation annually, with 4 dry months from December to March. *C. hirta* is one of four *Clidemia* species at this site (Steyermark and Huber 1978). The second site was the Caparo Forest Reserve, in West-Llanos, State of Barinas, Venezuela (7°20'-7°40 N, 70°30'-71°W). The site is a semideciduous lowland tropical forest (elevation ~10 m a.s.l.) with 14% evergreen tree species. Annual precipitation at Caparo is approximately 1750 mm per year, with 5.5 dry months from December to mid-April (Worbes 1999).

Canopy Light Conditions

The light environments of 242 haphazardly selected *C. hirta* plants were assessed at Pasoh using hemispherical photographs of the forest canopy taken from a point just above the apical meristem of each plant. For plants with multiple fruiting branches, photographs were taken above the apical meristem of each primary branch with reproductive structures and averaged. In order to assess the range of available light conditions in the Pasoh Forest, hemispherical photographs were taken along the transition from closed canopy understory to the center of treefall gaps. Using a previously assembled map of the gaps in the 50-ha forest dynamics plot at Pasoh (Peters 2001), four gaps were randomly chosen without consideration for gap location or size. In each gap, two parallel transects oriented in a randomly selected direction were established such that they passed through the approximate center of the gap and extended 10 m from the gap edge into the understory in both directions. Photographs were acquired at 5 m

intervals along each transect at 0.5, 1.0, and 1.5 m aboveground. Light availability measures were averaged across parallel transects.

Canopy photos were acquired with a system utilizing an equiangular "fisheye" lens with a wide-angle (160 degrees field of view) entry viewer mounted on a digital camera (QuickCam, Connectix Inc., San Mateo, California, USA). Grayscale images were converted to black and white and analyzed using the computer programs NIH Image 1.57 (National Institutes of Health, Washington D.C., USA) and SOLARCALC v6.1.1 (Chazdon and Field 1987, Ackerly and Bazzaz 1995). Diffuse light was calculated based on percent canopy openness and direct light was calculated by integrating solar tracks across canopy openings over the period of a year. This method assumes no seasonal changes in canopy cover, and no cloud cover. Estimates of daily photosynthetic photon flux density (PPFD) obtained in this manner therefore represent maximum potential values of PPFD ($PPFD_{potential}$).

Stature and Herbivore Damage

Plant size at Pasoh, La Mucuy and Caparo was assessed by measuring the maximum stem length of a subset of haphazardly selected individuals that were at least 3 cm tall (n = 248, 100, and 18 at Pasoh, La Mucuy and Caparo, respectively). In terms of nearest neighbor distance and density variability the spatial distribution of haphazardly selected plants at Pasoh did not differ from the distribution expected by randomly selecting the same number of individuals from the entire Pasoh population, indicating that the haphazard selection of individuals was effectively random. A previous allometric investigation found that maximum stem length was the non-destructive metric most closely correlated with whole plant biomass (Peters 2001). Herbivory was assessed on the top six leaves (or all leaves if fewer than six were present) by making a one-time determination of leaf sizes and the proportion of leaf area missing (*sensu* Lowman 1984). Because individual leaves were not followed through time, estimates of herbivore leaf damage are conservative. Venezuelan and Malaysian populations of *C. hirta* were identified in the field from reproductive characters. The veracity of *C. hirta* individuals at each site was ascertained through examination of numerous *C. hirta* specimens in the Harvard University Herbaria (Cambridge, Massachusetts, USA).

RESULTS

As expected, both canopy openness and $PPFD_{potential}$ decreased monotonically from the center of forest gaps to the understory, and increased with increasing height aboveground. Canopy openness measured 1 m aboveground ranged from 0.25% in the understory to a maximum of 13.04% in the center of a large gap, while total daily $PPFD_{potential}$ ranged from 0.02 to 15.34 mol m^{-2} d^{-1}. The heterogeneity in light availability also varied predictably. It was lowest under closed canopies, which were uniformly dark, higher in gap edges, and highest in the very center of gaps.

C. hirta at Pasoh was present along the entire transition from fully-enclosed understorys to the center of large treefall gaps, but was most prevalent in partially-shaded gap edges. Both reproductive (55%) and non-reproductive (53%) individuals were disproportionately concentrated within a narrow band of this light availability gradient, between 2 and 4.5% canopy openness (Figure 1). Reproductive *C. hirta* plants (as indicated by the presence of fruits or flowers at any developmental stage) consistently received more light than non-reproductive individuals.

$PPFD_{potential}$ above reproductive individuals, 6.78 ± 0.57 (mean ± 1 S.E.), was almost 40% greater than that above non-reproductive plants, 4.93 ± 0.21. Furthermore, reproductive plants received significantly less of their daily $PPFD_{potential}$ as sunflecks. Although some immature plants were found under completely closed canopies, no reproductive individuals were in areas with less than 2% canopy openness. This higher light availability above reproductive individuals was largely due to their greater height; daily $PPFD_{potential}$ increased significantly with stem length ($P < 0.005$). Of the 20 reproductive *C. hirta* plants included in this census, all had stem lengths exceeding 0.85 m. When plants of similar size were compared (i.e. stem length = 0.85 m), there were no differences between reproductive and non-reproductive individuals in terms of light availability (canopy openness: $P = 0.713$; $PPFD_{potential}$: $P = 0.928$).

Standing herbivore damage levels were similar at all three sites, with no significant differences among herbivore damage levels (Figure 2). Stem length varied among the three populations, but there were not consistent trends between the Malaysian and Venezuelan populations (Figure 2).
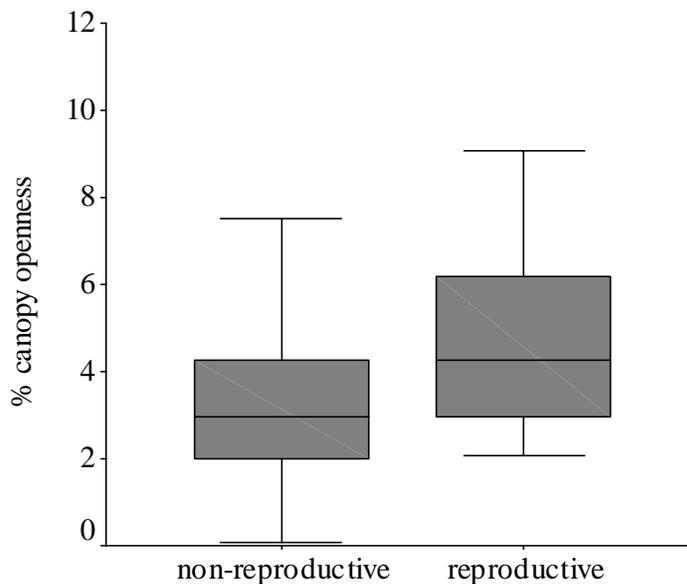
Figure 1. The mean canopy openness above reproductive individuals was significantly greater than the openness above all other individuals (t test: $P = 0.012$). These box-and-whiskers plots summarize the distribution of canopy openness above non-reproductive (n = 222) and reproductive (n = 20) *C. hirta* plants. The box length is the interquartile range, which contains 50% of the values. The whiskers extend from the box to the highest and lowest values, excluding outliers. The line across the box indicates the median. Outliers are cases with values more than 1.5 box lengths from the upper or lower edge of the box.
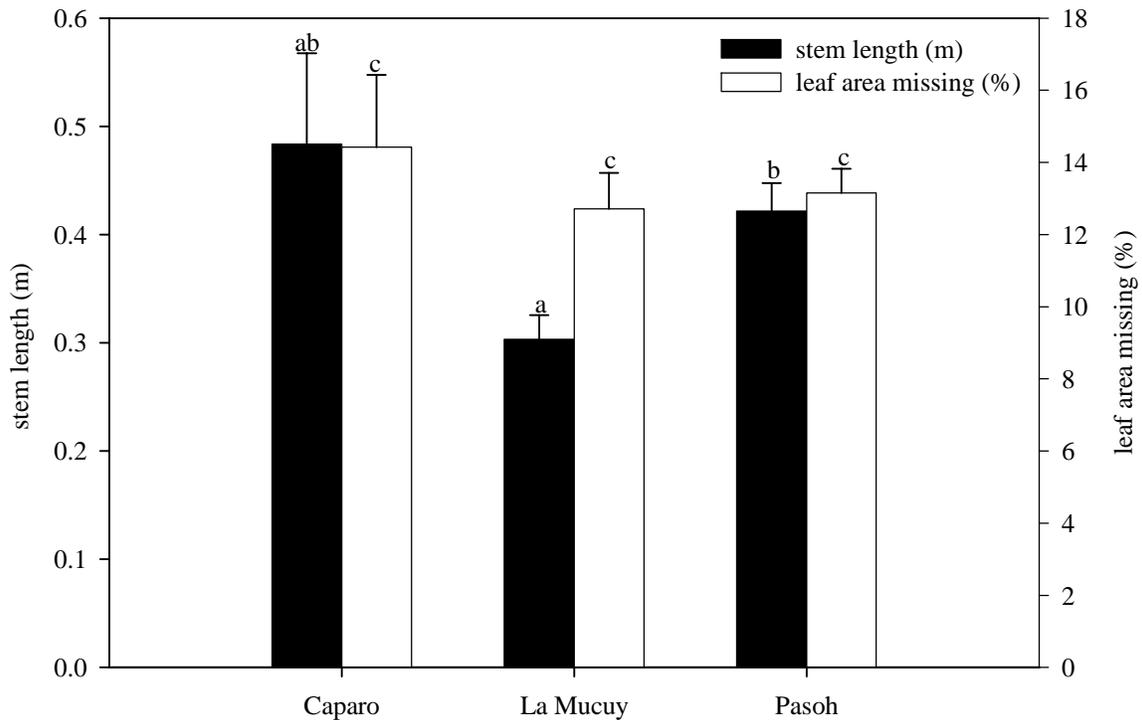
Figure 2. Stem length and leaf area missing to herbivory (mean + 1 S.E.) did not differ consistently between *C. hirta* populations in Pasoh and Venezuela. Bars with different letters are marginally significantly different (P = 0.10) from one another (Tukey's HSD test).

DISCUSSION

Both total daily $PPFD_{potential}$ and canopy openness were found to increase monotonically from the understory to the center of gaps. Total daily $PPFD_{potential}$ in the center of gaps was 5.8 to 15.4 times greater than in the understory. These results contradict the findings of a previous study recently conducted at Pasoh that reported that total daily PPFD in a small (*ca* 50 m^2) gap was not significantly higher than in the understory (Tang *et al.* 1999). Although the source of the discrepancy is unclear, it may be due to the small size of the single gap considered in the previous study or the lack of replication of gap sites. In general, undersorey light availability increases with the size of the overhead canopy opening (Barton *et al.* 1989, Chazdon 1992, Dirzo *et al.* 1992, Brown 1993). Within gaps there may be considerable

variation in light availability over very small spatial scales (Chazdon *et al.* 1988, Raich 1989, Brown 1993, Dalling *et al.* 1998). The range of light availability reported in the present study is not unusual. In a hill dipterocarp forest of Penang Island, Malaysia, mean PPFD reaching the understory varied by more than 10 fold along a transect from gap center to forest understory (Raich 1989). Fluctuations of similar magnitude were found for a large gap in a Costa Rican forest (Chazdon *et al.* 1996). This study and other investigations indicate that there can be substantial microsite heterogeneity within gaps of dipterocarp forests (Brown 1993, Dalling *et al.* 1998).

The results of this study indicate that *C. hirta* at Pasoh is disproportionately concentrated in a narrow band of this light availability gradient. A recent demographic study of the *C. hirta* population at Pasoh found that it is almost exclusively

associated with gaps and gap edges, often coincident with pig disturbance (Peters 2001). These observations are consistent with the results of a recent experiment conducted at the nearby Serting ulu experimental forest in Negeri Sembilan, Peninsular Malaysia. There, *C. hirta* was found to readily recruit into artificially-created gaps, and recruitment was substantially increased by soil disturbance that simulated pig rooting. In contrast, neither soil disturbance, manual seed addition, nor their combination could induce *C. hirta* seedling establishment under closed canopies at that site (Seidler 2003). It thus appears that *C. hirta* is confined to relatively high-light environments in the dipterocarp forests of Peninsular Malaysia.

Greenhouse experiments have demonstrated the ability of both Hawaiian and Costa Rica populations to establish and thrive in low light conditions, but natural enemies probably exclude *C. hirta* from low light forest understorys in Costa Rica (DeWalt 2004b). Substantially lower herbivory levels were observed in Hawaii, where the escape from natural enemies is apparently responsible for the species' widespread occurrence in both high and low light environments. Possible explanations for this escape from enemies on the island of Hawaii include the short period since *C. hirta* introduction (30 years) and the absence of closely related native plant species, leading to the prediction that herbivory on invasive *C. hirta* would be higher in the presence of native Melastomataceae (DeWalt 2004b). This prediction was supported by the results of the present study. Standing herbivory levels at Pasoh, where the *C. hirta* introduction is apparently less than 30 years old (Peters 2001) and the flora of native Melastomataceae is rich, were comparable to those measured among two populations in Venezuela.

These results suggest that the *C. hirta* invasion in Pasoh may be progressing very differently than the well-documented invasion in Hawaii. Naturally-occurring populations of invasive plants have frequently been found to be taller and more fecund outside of their native ranges (Crawley 1987, Noble 1989, Juvik and Juvik 1992). In Hawaii, *C. hirta* is taller, denser, and more fruitful than where the species is native (Wester and Wood 1977). This pattern was not observed at Pasoh, where *C. hirta* was no taller than in Venezuela, and had similar levels of standing leaf damage. The evolution of increased competitive ability (EICA) hypothesis predicts that under identical growing conditions,

individuals of a species taken from introduced sites will grow taller and produce more biomass than individuals taken from the native range (Blossey and Nötzold 1995, Willis *et al.* 2000). A recent experiment using *C. hirta* found little support for the EICA prediction; when grown in a common garden, Hawaiian populations were no different than Costa Rican populations in terms of their stature or growth (DeWalt 2004a). No common garden data are available for Malaysian or Venezuelan populations, and determining the extent to which physiological, morphological, and environmental parameters associated with *C. hirta* vary between native and invasive sites is difficult because the critical parameters have been quantitatively assessed in only a small number of populations. Nevertheless, the totality of these results suggests that distinctions between the two invasions may be due to differences among sites, such as, for instance, the depauperate Hawaiian biota, rather than any physiological differentiation between the populations.

A demographic study conducted at Pasoh between 1997 and 1999 suggests that the three- to five-fold increase in *C. hirta* density expected in the decade from 1999 to 2009 may hinder the recruitment of gap-dependent native species in the foreseeable future (Seidler 2003), although recent land use modification in the vicinity of the reserve may mitigate this increase. In lowland mixed-dipterocarp forest of Sri Lanka, *C. hirta* is thought to be displacing *Melastoma malabathricum*, a closely related native species with apparently similar autecology (Singhakumara *et al.* 2000). Because the regeneration of biologically and economically important dipterocarp species are dependent upon access to high-light canopy openings, identifying species dependent upon the narrow range of light microsites dominated by *C. hirta* is critical to understanding the conservation implications of this invasion.

ACKNOWLEDGEMENTS

LITERATURE CITED

ACKERLY, D. D. and F. A. BAZZAZ. 1995. Seedling crown orientation and interception of diffuse radiation in tropical forest gaps. Ecology 76: 1134-1146.

BARTON, A. M., N. FETCHER and S. REDHEAD. 1989. The relationship between treefall gap size and light flux in a neotropical rain forest in Costa Rica. Journal of Tropical Ecology 5: 437-439.

BLOSSEY, B. and R. NÖTZOLD 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. Journal of Ecology 83: 887-889.

BROWN, N. D. and T. C. WHITMORE. 1992. Do dipterocarp seedlings really partition tropical rain-forest gaps? Philosophical Transactions of the Royal Society of London B 335: 369-378.

BROWN, N. 1993. The implications of climate and gap microclimate for seedling growth conditions in a Bornean lowland rain forest. Journal of Tropical Ecology 9: 153-168.

CHAZDON, R. L. 1992. Photosynthetic plasticity of two rainforest shrubs across natural gap transects. Oecologia 92: 586-595.

CHAZDON, R. L. and C. B. FIELD. 1987. Photographic estimation of photosynthetically active radiation: evaluation of a computerized technique. Oecologia 73: 525-532.

CHAZDON, R. L., K. WILLIAMS and C. B. FIELD. 1988. Interactions between crown structure and light environment in five rain forest *Piper* species. American Journal of Botany 75: 1459-1471.

CHAZDON, R. L., R. W. PEARCY, D. W. LEE and N. FETCHER. 1996. Photosynthetic responses of tropical forest plants to contrasting light environments. Pp. 5-51, *in* S. S. Mulkey, R. L. Chazdon and A. L. Smith (eds.): Tropical Forest Plant Ecophysiology. Chapman & Hall, New York.

CLARK, D. A. and D. B. CLARK. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. Ecological Monographs 62: 315-344.

COOK, B. A. 1929. Some notes on the plant associates and habitat of *Clidemia hirta* (L.) D. Don in Trinidad. Fiji Agricultural Journal 2: 92-93.

CORLETT, R. T. 1988. The naturalized flora of Singapore. Journal of Biogeography 15: 657-663.

CRAWLEY, M. J. 1987. What makes a community invasible? Pp. 429-453, *in* A. J. Gray, M. J. Crawley and P. J. Edwards (eds.): Colonization, Succession and Stability Blackwell Scientific Publications, Oxford.

CRONK, Q. C. B. and J. L. FULLER. 1995. Plant Invaders: the Threat to Natural Ecosystems. Chapman & Hall, New York.

DALLING, J. W., S. P. HUBBELL & K. SILVERA. 1998. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. Journal of Ecology 86: 674-689.

DEWALT, S. J., J. S. DENSLOW, J. L. HAMRICK. 2004a. Biomass allocation, growth, and photosynthesis of genotypes from the native and introduced ranges of the tropical shrub *Clidemia hirta*. Oecologia 138: 521-531.

DEWALT, S. J., J. S. DENSLOW and K. ICKES. 2004b. Natural-enemy release facilitates habitat expansion of an invasive shrub, *Clidemia hirta*. Ecology 85: 471-483.

DIRZO, R., C. C. HORVITZ, H. QUEVEDO and M. A. LÓPEZ. 1992. The effects of gap size and age on the understorey herb community of a tropical Mexican rain-forest. Journal of Ecology 80: 809-822.

GORDON, D. R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. Ecological Applications. 8: 975-989.

JUVIK, J. O. and S. P. JUVIK. 1992. Mullen (*Verbascum thapsus*): the spread and adaptation of a temperate weed in the montane tropics. Pp. 254-270, *in* C. P. Stone, C. W. Smith and J. T. Tunison (eds.): Alien Plant Invasions in Native Ecosystems of Hawai'i: Management and Research. University of Hawaii Press, Honolulu.

KEANE, R. M. and M. J. CRAWLEY. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution 17: 164-170.

LONSDALE, W. M. 1999 Global patterns of plant invasions and the concept of invasibility. Ecology 80: 1522-1536.

LOWMAN, M. D. 1984. An assessment of the techniques for measuring herbivory: is rainforest defoliation more intense than we thought? Biotropica 16: 264-268.

MARQUIS, R. J. and H. E. BRAKER. 1994. Plant-herbivore interactions: diversity, specificity, and impact. Pp 261-280, *in* L. A. McDade, K. S. Bawa, H. A. Hespenheide and G. S. Hartshorn (eds.): La Selva: Ecology and Natural History of a Neotropical Rain Forest. University of Chicago Press, Chicago.

MELO, G. F., I. C. MACHADO and M. LUCENO. 1999. Reproduction of three *Clidemia* (Melastomataceae) species in Brasil. Revista de Biologia Tropical 47: 359-363.

NOBLE, I. R. 1989. Attributes of invaders and the invading process: terrestrial and vascular plants. Pp. 301-313, *in* J. A. Drake, H. A. Mooney, F. diCastri, R. H. Groves, F. J. Kruger, M. Rejmánek and M. Williamson (eds.): Biological Invasions: a Global Perspective. John Wiley & Sons, New York.

PETERS, H. A. 2001. *Clidemia hirta* invasion at the Pasoh Forest Reserve: an unexpected plant invasion in an undisturbed tropical forest. Biotropica 33: 60-68.

RAICH, J. W. 1989. Seasonal and spatial variation in the light environment in a tropical dipterocarp forest and gaps. Biotropica 21: 299-302.

REJMÄNEK, M. 1996. Species richness and resistance to invasion. Pp. 153-172, *in* G. H. Orians, R. Dirzo and J. H. Cushman (eds): Biodiversity and ecosystem processes in tropical forest. Springer-Verlag, New York.

SEIDLER, T. G. 2003. Spatial and demographic consequences

of seed dispersal in a tropical forest. Ph.D. thesis, Harvard University, Cambridge, MA.

SINGHAKUMARA, B. M. P., R. S. J. P. UDUPORUWA and P. M. S. ASHTON. 2000. Soil seed banks in relation to light and topographic position of a hill dipterocarp forest in Sri Lanka. Biotropica 32: 190-196.

SMITH, C. W. 1992. Distribution, status, phenology, rate of spread, and management of *Clidemia* in Hawai'i. Pp. 241-253, *in* C. P. Stone, C. W. Smith and J. T. Tunison (eds.): Alien Plant Invasions in Native Ecosystems of Hawai'i: Management and Research. University of Hawaii Press, Honolulu.

STEYERMARK, J. A. and O. HUBER. 1978. Flora del Avila: Flora y Vegetación de las Montanas del Avila, de la Silla y del Maiguata. Sociedad Venezolana de Ciencias Naturales y Ministerio del Ambiente y de los Recursos Naturales Renovables, Caracas.

TANG, Y., N. KACHI, A. FURUKAWA and M. B. AWANG. 1999. Heterogeneity of light availability and its effects on simulated carbon gain of tree leaves in a small gap and the understory in a tropical rain forest. Biotropica 31: 268-278.

TAYLOR, T. H. C. 1928. Investigations in Trinidad on a parasite for "*Clidemia hirta*." Fiji Agricultural Journal 2: 2-8.

TEO, D. H. L., H. T. W. TAN, R. T. CORLETT, C. M. WONG and S. K. Y. LUM. 2003. Continental rain forest fragments in Singapore resist invasion by exotic plants. Journal of Biogeography 30: 305-310.

VITOUSEK, P. M., C. M. D'ANTONIO, L. L. LOOPE and R. WESTBROOKS. 1996. Biological invasions as global environmental change. American Scientist 84: 468-478.

VITOUSEK, P. M., L. R. WALKER, L. D. WHITEAKER, D. MUELLER-DOMBOIS and P. A. MATSON. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science 238: 802-804.

WELDEN, C. W., S. W. HEWETT, S. P. HUBBELL and R. B. FOSTER. 1991. Sapling survival, growth, and recruitment - relationship to canopy height in a Neotropical forest. Ecology 72: 35-50.

WESTER, L. L. and H. B. WOOD. 1977. Koster's Curse (*Clidemia hirta*), a weed pest in Hawaiian forests. Environmental Conservation 4: 35-41.

WILLIS, A. J., J. MEMMOTT and R. I. FORRESTER. 2000. Is there any evidence for the post-invasion evolution of increased size among invasive plant species? Ecology Letters 3: 275-283.

WORBES, M. 1999. Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo Forest Reserve in Venezuela. Journal of Ecology 87: 391-403.