

Hurricane disturbance accelerates invasion by the alien tree *Pittosporum undulatum* in Jamaican montane rain forests

Bellingham, Peter J.^{1*}; Tanner, Edmund V.J.² & Healey, John R.³

¹Landcare Research, P.O. Box 69, Lincoln 8152, New Zealand; ²Department of Plant Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EA, UK; E-mail evt1@cam.ac.uk; ³School of Agricultural and Forest Sciences, University of Wales, Bangor LL57 2UW, UK; E-mail j.healey@bangor.ac.uk;

*Corresponding author; Fax +64 33252418; E-mail bellingham@landcareresearch.co.nz

Abstract

Questions: Do past disturbance, soil nutrients, or species diversity predict the invasion success of the alien tree *Pittosporum undulatum* in an island montane rain forest? What are the consequences of its invasion for forest composition and species diversity?

Location: Blue Mountains, Jamaica.

Methods: Censuses of trees ≥ 3 cm DBH in permanent plots in four sites within ca. 7 ha; 1974-2004 (intensive sites) and in 16 plots within 250 ha; 1990-2004 (extensive plots).

Results: *Pittosporum* was unrecorded in the intensive sites before a severe hurricane in 1988: by 2004 all four sites were invaded. *Pittosporum* had invaded 25% of the extensive plots in 1990 and 69% in 2004, where its basal area increased from 0.5 ± 0.4 (SEM) $\text{m}^2 \cdot \text{ha}^{-1}$ in 1990 to 2.8 ± 1.3 $\text{m}^2 \cdot \text{ha}^{-1}$ in 2004. It had zero stem mortality and diameter growth rate exceeded that of native species fourfold. *Pittosporum*'s basal area in the extensive plots in 2004 was positively related to the stand basal area damaged in the 1988 hurricane and negatively related to soil N concentrations. *Pittosporum* invasion was unrelated to stand-level tree species diversity in the extensive plots but as its basal area increased over time the basal area of native species and stand-level diversity declined.

Conclusions: There are no obvious functional attributes of *Pittosporum* unrepresented in the native tree flora although it has high photosynthetic efficiency compared with native trees. More widespread invasion of these forests by *Pittosporum* seems inevitable since hurricanes, which accelerated the invasion, affect these forests frequently.

Keywords: Biodiversity; Conservation; Growth rate; Mortality; Oceanic island; Soil N; Species diversity.

Nomenclature: Adams (1972) except where other authorities given.

Introduction

Biological invasions can have major adverse effects on ecosystems, including the reduction of biodiversity (Chapin et al. 2000). Tropical rain forests, amongst the world's most diverse ecosystems, are generally not susceptible to invasions by alien plant species (Whitmore 1991; Fine 2002; Teo et al. 2003). However, an exception appears to be tropical rain forests on oceanic islands, often rich in endemic species, which can be invaded by alien trees (Binggeli 1996; Meyer & Florence 1996; Fleischmann 1997; Mueller-Dombois & Fosberg 1998; Lepš et al. 2002; Wisser et al. 2002; Meyer & Lavergne 2004). When alien trees invade island tropical rain forests, they may alter ecosystem properties and successions (Walker & Vitousek 1991; Rothstein et al. 2004) and after invasion there can be reduction in diversity or recruitment failure of native tree species (Lavergne et al. 1999). For these reasons it is important to understand the factors that determine why alien trees can invade oceanic island tropical rain forests.

Disturbance can be a major factor governing plant invasion (Elton 1958; Hobbs & Huenneke 1992; D'Antonio et al. 1999; De Gruchy et al. 2005), also interacting with site productivity interact such that productive environments are most vulnerable to invasion where there is a high frequency and intensity of disturbance (Huston 1994). Many island ecosystems are subject to frequent natural disturbances, such as hurricanes, and anthropogenic disturbance (D'Antonio & Dudley 1995). Other factors that can influence invasion by alien plant species include nutrient availability (Alpert et al. 2000) and the species richness of the resident plant community (Wisser et al. 1998; Levine & D'Antonio 1999). Stand-level species richness of island forests is often low compared with that on continents; Denslow (2003) hypothesized this may contribute to low levels of resource use, high resource availability and thus greater likelihood of invasion. Additionally, isolated

island ecosystems may be more susceptible to invasion because the resident biota comprises poor competitors (Darwin 1873). In island forests, the resident flora is often characterized by low productivity, and this combined with low diversity, may further render forests susceptible to invasion (Kitayama 1996; Denslow 2003). In search for key determinants of invasion in an island rain forest, we studied the invasion of Jamaican tropical montane forests over time by an introduced Australian tree, *Pittosporum undulatum*. Specifically we considered:

1. Do past disturbance, soil nutrients, or species diversity predict the invasion success of *Pittosporum* in these forests?

2. Are resources in these montane forests under-used or used inefficiently by the native tree species compared with the alien *Pittosporum* and could this explain its successful invasion?

3. What are the consequences of invasion by *Pittosporum* for forest composition and species diversity?

Methods

Study species

Pittosporum undulatum (*Pittosporaceae*) is a long-lived evergreen tree native to forests in southeastern Australia that grows to 15 m (Harden 1992; Cronk & Fuller 1995). In Jamaica it flowers from February to August with ripe fruit available year-round (P.J. Bellingham unpubl.), and its seeds are bird-dispersed (Gleadow 1982). It is invasive outside its native range in Australia (Gleadow & Ashton 1981; Rose & Fairweather 1997) and elsewhere in South Africa, as well as on many islands, including Lord Howe Island, the Azores, Hawaii and Jamaica (Cronk & Fuller 1995).

Study site

We conducted our study in montane rain forests in the western Blue Mountains, Jamaica (18°05' N, 76° 38-40' W). Prevailing trade winds, soils and past disturbance are the predominant influences on composition and structure; canopy heights are 4 - 20 m (Shreve 1914; Grubb & Tanner 1976). Nine canopy tree species occur widely, notably *Podocarpus urbanii* Pilg. and *Cyrilla racemiflora*, with many others locally abundant (Asprey & Robbins 1953). The forests were affected by Hurricane Gilbert in 1988, the most powerful hurricane in the Caribbean in the 20th century. At the start of our study, in 1974, there was no evidence of past hurricane disturbance (the site may have been last affected in 1951) and only Hurricane Gilbert affected the site strongly during the course of our study (1974-2004).

Data collection

We conducted censuses of trees in 16 200-m² plots (extensive plots; Bellingham 1991), in which six plots are located at regular 1-km intervals along the crest of the range (one plot not shown in Bellingham 1991 is 1 km east of plot 13), and ten sample plots on the slopes of the range – five each on the northern (windward) and southern (leeward) slopes of the range. Plots on the slopes were located 250 m down-slope from plots on the crest of the range, along transects located orthogonal to the crest. The plots sample an altitudinal range of 1300-1920 m a.s.l. within 250 ha (Bellingham & Tanner 2000). Censuses of these plots were conducted in 1990 (May-August), in 1994 (August-September) and 2004 (July-August). A comparison was also made between four larger sites (intensive sites), composed of contiguous 10 m × 10 m plots, within ca. 7 ha (18°05' N, 76°39' W, 1580-1600 m a.s.l.) established in 1974 to examine a soil fertility and vegetation composition gradient. These cover a much longer census interval, with censuses in 1974, 1984, 1989, 1991, 1994, and 2004. The four intensive sites were the Col (0.09 ha, previously known as Gap forest), Wet Slope (0.1 ha), Mull Ridge (0.1 ha), and Mor Ridge (0.06 ha) forest sites of Tanner (1977). Understorey light (photosynthetically active radiation, PAR) was quantified in these intensive sites in May 1989, eight months after Hurricane Gilbert, before it declined to pre-hurricane levels (Bellingham et al. 1996).

At each census of the extensive plots and intensive sites, all stems ≥ 3 cm DBH (diameter at breast height, 1.3 m) were identified to species and diameters were measured, i.e. multi-stemmed individuals were treated as separate entities and we also recorded which stems were attached. All stems were labelled to ensure accurate re-identification. A band was painted on each trunk at breast height and all measurements were made on these painted bands. New recruits after the first census (i.e. those that grew to be ≥ 3 cm DBH since the previous census) were labelled and painted similarly. Mortality of stems was confirmed only when stems lacked sprouts and rot had begun above breast height.

Slope, altitude and aspect were measured at the centre of each of the extensive plots. Aspect was transformed into a linear variable ranging from 0.00 to 2.00 using the transformation of Beers et al. (1966). We measured the linear distance (km, using 1:12 500 maps) from each of the extensive plots (positions determined using GPS) to the Cinchona Botanic Gardens (18°04' N, 76°39' W, 1500 m a.s.l.), the point of introduction of *Pittosporum* in ca. 1870 (Healey et al. 1995). In 1990 we measured the DBH of trees killed during the 1988 hurricane and, among surviving stems, noted which stems had been severely damaged during the hurricane,

i.e. those that lost crowns, were uprooted or were completely defoliated (Bellingham 1991; Bellingham et al. 1995). Soils were measured in the extensive plots in 2004. We obtained a mean soil pH (in distilled water) per plot, from six samples of soil collected from 0-15 cm depth beneath the litter layer. Soil nutrients were analysed from a single sample (15 cm depth) at a random point within each plot. Total soil C and N were measured by a CHN analyzer and P using acid digest (Brookside Laboratory Association Inc., Knoxville, Ohio, USA).

Data analysis

We computed the relative diameter increment (R_D , Kohyama 1991) and absolute diameter increment ($\text{cm}\cdot\text{a}^{-1}$) of each stem that remained alive between censuses, excluding tree ferns (*Cyathea* spp.). Comparisons of R_D and absolute diameter increment between species were compared using hierarchical models with plot as a random effect. Logarithmic models were used to calculate annual percentage mortality and recruitment rates of stems for each plot (calculated as in Burslem et al. 2000). All percentage data were arcsine square-root transformed before analysis. Shannon (H') and α index values were computed for tree stems in each extensive plot as measures of diversity (Magurran 1988); *Pittosporum* stems were included in the calculation of these indices.

We used generalized linear models (GLMs, using GenStat 6.1, Payne 2002) to determine relationships between *Pittosporum* basal area in each of the extensive plots in 2004 and: (1) site factors (altitude, slope, aspect, soil pH, C, N, P); (2) stand characteristics (stand basal area, stem density and H' in 1990); (3) disturbance by Hurricane Gilbert (percentage mortality and severe damage to basal area caused by the hurricane in each plot; method of assessment as in Bellingham et al. 1995) and (4) distance to the Cinchona Botanic Gardens. GLMs were fitted using a negative binomial function with a log link.

Results

Invasion dynamics

No *Pittosporum* stems ≥ 3 cm DBH were recorded in censuses of the intensive sites in 1974 and 1984. The first was recorded in 1989 in one of the four sites; by 2004 all four sites had been invaded (Fig. 1a). The invasion of the intensive sites was less advanced than was found in the wider assessment of the forests: the percentage of *Pittosporum* basal area in intensive sites in

2004 was less than the average in the extensive 200-m² plots 14 years earlier (Fig. 1b). *Pittosporum* occurred in four of the 16 extensive plots in 1990, in nine plots in 1994 and in 11 plots in 2004.

In 1990 *Pittosporum* was the species with 14th greatest stem density across all 16 extensive plots (144 ± 118 stems/ha; mean per plot \pm SEM) but by 2004 it had the highest mean stem density (684 ± 348 stems/ha; a significant increase, paired $t_{15} = 2.21$; $P = 0.043$). There were 46 stems across all extensive plots in 1990 and 219 in 2004; a recruitment rate of 10.4%/a over 14 yr. In contrast, the recruitment rate of stems of native species in the extensive plots was $1.8 \pm 0.22\%/a$ (mean per plot) over the same period. There was zero mortality of *Pittosporum* stems in both the extensive plots and the intensive sites while native trees' mortality rate was $2.3 \pm 0.25\%/a$ (extensive plots; 1990-2004).

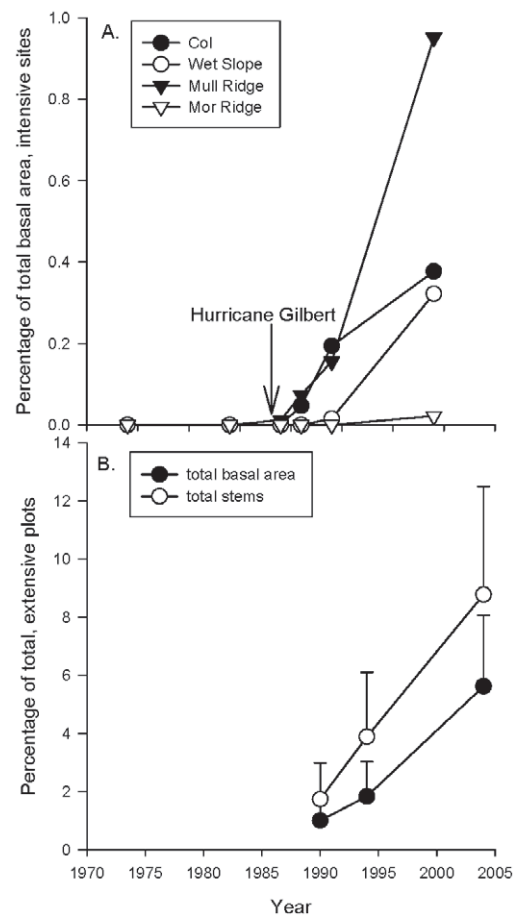


Fig. 1. A. Changes in the percentage of basal area comprised of *Pittosporum undulatum* in four intensive sites within ca. 7 ha in Jamaican montane rain forest over 30 years. Influence of Hurricane Gilbert (1988) denoted. B. Changes in percentage of total basal area and total stems comprised of *Pittosporum undulatum* in 16 extensive plots within 250 ha in Jamaican montane rain forests over 14 years (mean \pm 1 SE). Note different y-axis scales.

Growth

Pittosporum's absolute diameter growth rate across all extensive plots during 1994-2004 was four times greater ($0.3 \pm 0.03 \text{ cm.a}^{-1}$; $n = 104$) than that of all native tree species ($0.07 \pm 0.003 \text{ cm.a}^{-1}$; $n = 1175$; $F_{1238} = 246.4$, $P < 0.001$) and its relative diameter growth rate (R_D ; 0.04 ± 0.003) was five times greater (0.009 ± 0.0003 ; $F_{1238} = 301.4$, $P < 0.001$). This is likely to be an underestimate of how much faster growing were *Pittosporum* stems than native stems because we did not include in the comparison growth rates of native stems

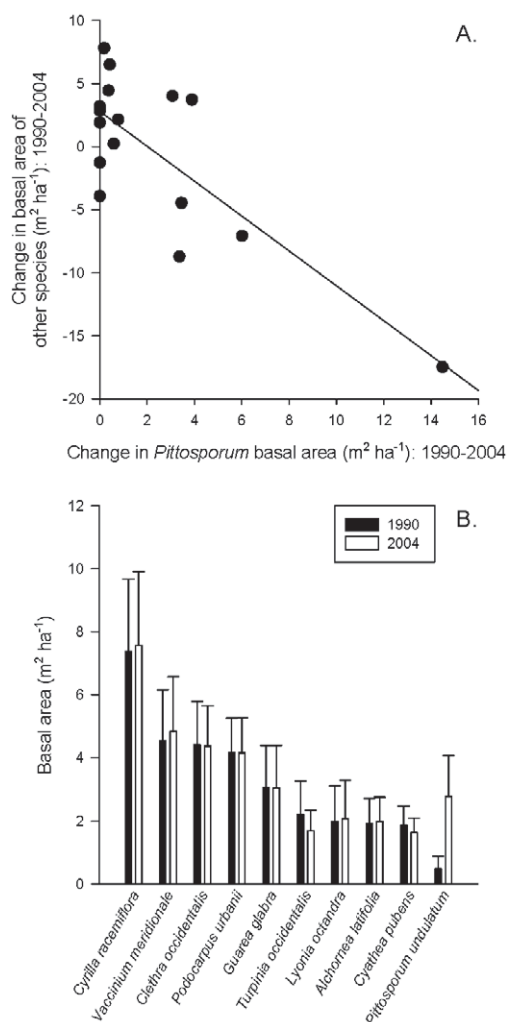


Fig. 2. **A.** Relationship between change in basal area of *Pittosporum undulatum* and change in basal area of other species (all native except *Cinchona officinalis*; $y = 2.79 - 1.38x$; $R^2 = 0.63$, $P < 0.001$) over 14 years in the 16 extensive plots in Jamaican montane rain forests; **B.** Changes in the basal area of ten species that comprised 66% of total 2004 basal area in the same plots (mean ± 1 SE). The change in basal area of *Pittosporum undulatum* was significant ($t_{15} = 2.44$; $P = 0.028$) but not for any of the other species ($t_{15} < 1.53$; $P > 0.149$).

that died; these were likely to have been slow-growing. In the extensive plots only an uncommon native species, *Sapium harrisii* (*Euphorbiaceae*) ($n = 1$) had a growth rate greater than *Pittosporum* (absolute = 0.6 cm.a^{-1} and $R_D = 0.08$; 1994-2004). *Cinchona officinalis* (*Rubiaceae*), the only other alien tree species in these plots, had a growth rate ($R_D = 0.01 \pm 0.002$; $n = 34$) that was not different from native species ($F_{1192} = 0.042$; $P = 0.837$). Absolute diameter growth rates and R_D of *Pittosporum* during 1994-2004 in the intensive sites ($0.3 \pm 0.09 \text{ cm.a}^{-1}$ and 0.04 ± 0.008 respectively, $n = 13$) were very similar to those in the extensive plots (unpaired $t_{57} = 0.43$, $P = 0.673$ for absolute rates; $t_{57} = 0.14$, $P = 0.890$ for R_D).

Pittosporum R_D in the extensive plots was unrelated to soil pH, C, N, P, C:N or C:P but was positively related to soil N:P ($R_D = 0.005 + 0.005 [\text{Soil N:P}]$; $R^2 = 0.40$, $P = 0.039$). Similarly, in the intensive sites *Pittosporum* R_D in the Col (N:P = 15.7; $R_D = 0.02 \pm 0.004$) was lower than in the Mull Ridge (N:P = 23.7; $R_D = 0.08 \pm 0.009$; unpaired $t_9 = 7.06$, $P < 0.001$).

Pittosporum invasion and native species

The invasion of *Pittosporum* (its basal area and stem density in 1990 in the extensive plots) was unrelated to either the stem density or basal area of native species in 1990 ($R^2 < 0.06$; $P < 0.35$). The total basal area of all species in the extensive plots was not different between 1990 ($49.7 \pm 3.98 \text{ m}^2 \text{ ha}^{-1}$) and 2004 ($51.6 \pm 3.98 \text{ m}^2 \text{ ha}^{-1}$; paired $t_{15} = 1.79$; $P = 0.094$) but, at a plot scale, as *Pittosporum* basal area increased between 1990 and 2004 the basal area of native species (and *Cinchona officinalis*) declined (Fig. 2a). While the plot in which *Pittosporum* basal area increased most had large leverage, exclusion of this datum still resulted in a significant negative relationship ($R^2 = 0.28$, $P = 0.044$). The plot in which *Pittosporum* basal area increased most also had high levels of hurricane damage (52% of basal area severely damaged) but two other plots, with much smaller increases in *Pittosporum* basal area, had greater levels of hurricane damage. Although *Pittosporum* basal area increased across the extensive plots, there was no significant decline in the basal area of any of the dominant native species (Fig. 2b) and similarly there was no change in the cumulative basal area of 59 rare species (that constituted 9.6% of basal area across all plots in 1990; $4.9 \pm 0.78 \text{ m}^2 \text{ ha}^{-1}$ in 1990 cf. and $4.7 \pm 0.85 \text{ m}^2 \text{ ha}^{-1}$ in 2004; paired $t_{15} = 1.05$; $P = 0.311$).

At the earlier stage of invasion of the extensive plots in 1990, there was no relationship between *Pittosporum* basal area and H' ($R^2 = 0.008$, $P = 0.75$) or α ($R^2 = 0.003$, $P = 0.84$). By 2004, at a later stage of invasion, H' was weakly negatively related to *Pittosporum* basal area and stem density ($R^2 < 0.24$, $P < 0.07$), but α was not related

to *Pittosporum* basal area. Where H' decreased in plots between 1990 and 2004 *Pittosporum* basal area increased (Fig. 3); while this relationship was driven strongly by the plot most heavily invaded in 1990, which also saw the greatest increase in basal area, there was still a weak negative relationship ($R^2 = 0.20$, $P = 0.10$) when this plot was excluded from analysis. Changes in *Pittosporum* basal area were much more weakly negatively related to changes in α ($R^2 = 0.13$, $P = 0.18$).

What predicts *Pittosporum* invasion?

The best predictors of *Pittosporum* basal area in the extensive plots in 2004 were soil N (negatively related, $P = 0.032$) and the percentage of basal area severely damaged during Hurricane Gilbert (positively related, $P = 0.042$; GLM deviance ratio = 6.92; $P < 0.001$). There was only a weak negative relationship between *Pittosporum* basal area in extensive plots in 2004 (log + 1 transformed data) and plot distances from the Cinchona Botanic Gardens, the point of introduction ($R^2 = 0.18$, $P = 0.097$), suggesting that too much time had elapsed since its introduction and naturalisation (> 100 years) for distance from source to be an important determinant. *Pittosporum* basal area in plots within the intensive sites in 2004 (log + 1 transformed) was unrelated to PAR 8 months after Hurricane Gilbert ($R^2 = 0.022$, $P = 0.52$). Although *Pittosporum* may have responded to canopy openings and damage at a local scale, its recruitment per plot to the ≥ 3 cm DBH size class was presumably chiefly governed by variation in its abundance as seedlings and saplings in the forest understorey, in the soil seed bank or as seed rain.

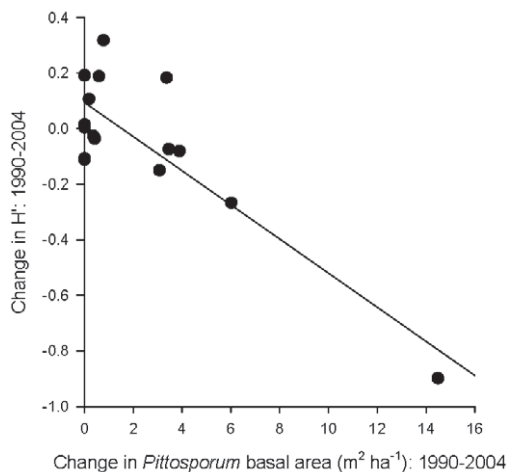


Fig. 3. Relationship between change in basal area of *Pittosporum undulatum* and H' ($y = 0.094 - 0.061x$; $R^2 = 0.71$, $P < 0.001$) over 14 years in the 16 extensive plots in Jamaican montane rain forests.

Discussion

Pittosporum undulatum has become an important invasive tree in Jamaican montane rain forests during the last 30 years. Although introduced near the forest in the late 1800s, it was not reported in the forests in the early 20th century (Shreve 1914). Its presence within the native forests was first noted in 1973, where it had colonized alongside man-made trails (Grubb & Tanner 1976). By 2004 it had become a widespread invader in the forests, found up to 5.9 km from its point of introduction and > 2 km from the nearest trails. Seedlings noted in the early 1970s are now established trees and it is now locally a substantial component of stand basal area (Fig. 1b). Its increasing dominance of stands is apparent in its rapid increase in basal area over 14 years in widespread plots (Fig. 2b; Lundholm & Larson 2004). Successful invaders of islands often have functional characteristics unrepresented in the resident biota (Walker & Vitousek 1991; Simberloff 1995) but there is no obvious functional attribute of *Pittosporum* unrepresented in the resident flora. Dispersed by native birds, it is likely to become more widespread and a more substantial component of these forests with time.

Disturbance and invasion

The invasion of the forests by *Pittosporum* accelerated after widespread disturbance to the forests by Hurricane Gilbert in 1988 (Fig. 1a and GLM). This is consistent with other studies which have shown that past disturbance can predict the likelihood of invasion by alien plants (e.g. Burke & Grime 1996; De Gruchy et al. 2005) although this is not always the case (Wiser et al. 1999). Invasions of other forests by alien trees have accelerated after damage caused by hurricanes and cyclones, e.g. *Miconia calvescens* DC. in Tahitian montane rain forests (Merlin & Juvik 1995). The origin of the individuals accounting for *Pittosporum*'s rapid basal area increase by 1994 (Fig. 1a) is not known. *Pittosporum* can germinate and establish beneath dense canopies in Australia (Gleadow 1982) and in Jamaica there was a seedling bank of *Pittosporum* under intact canopies; it was the twelfth most abundant seedling species in six plots adjacent to the intensive Col site in 1986, long after the last direct hurricane strike (Healey 1990). Growth rates of individuals from this seedling bank accelerated in response to increased light resulting from canopy gaps (Healey 1990) and there were widespread increases in understorey light under canopies defoliated by Hurricane Gilbert (Bellingham et al. 1996). *Pittosporum* can also germinate in large numbers following canopy disturbance: in the Jamaican Col-type forest measured before Hurricane Gilbert; *Pittosporum* was

the fourth most abundantly recruited seedling species in experimental canopy gaps (Healey 1990), though whether from the soil seed bank or from seed rain is not known. After a typhoon damaged forests in the Bonin Islands, another alien tree species, *Bischofia javanica* Blume, showed increased recruitment from an existing seedling bank that showed acceleration of the growth in response to increased light (Shimizu 1988; Yamashita et al. 2000) and the same pattern was evident for several alien tree and liana species that invaded subtropical hardwood forests in Florida after a hurricane (Horwitz et al. 1998). Rapid recruitment and growth after hurricanes of some species already present in the understorey coupled with low levels of adult mortality (the usurper syndrome, Bellingham et al. 1995) has been shown in other forests (Batista & Platt 2003; Ostertag et al. 2005) and *Pittosporum* exhibits characteristics of this syndrome. In addition to hurricanes, landslides also provide sites for *Pittosporum* invasion; it was the fifth most abundant woody species across several landslides > 15 years old (Dalling 1994) and intense hurricanes generate new landslides (Dalling & Tanner 1995) that *Pittosporum* could be expected to colonize.

Past and ongoing anthropogenic disturbance also contributes to invasion patterns of *Pittosporum*, akin to the mode of invasion of rain forests in Réunion by the alien tree *Ligustrum robustum* Thwaites ssp. *walkerii* (Decne.) P.S. Green (Lavergne et al. 1999). In Jamaica, secondary forests have developed after the abandonment of plantations along the native forest's southern boundary and close to the point of *Pittosporum*'s introduction at the Cinchona Botanic Gardens. *Pittosporum* is often a substantial component of these secondary forests (6–28% of basal area; McDonald & Healey 2000), a pattern similar to that at the margins of old-growth forests in southern Australia (Rose 1997). In Jamaica, these secondary forest stands provide a major source of inoculum for more distant invasion.

While *Pittosporum* has invaded forests across a range of soil nutrient status and floristic composition (Tanner 1977) it apparently invades moderately fertile sites more successfully; it is hardly found in the least-fertile Mor Ridge site. In the extensive plots, its invasion (*Pittosporum* basal area in 2004) was negatively related to soil N concentration, and its growth rates were positively related to soil N:P; five of the nine plots from which *Pittosporum* growth data could be calculated had soil N:P that exceeded the Redfield ratio of 16 (above which P is likely to become limiting for biological processes relative to N; Redfield 1958; Wardle et al. 2004). Its lesser invasion, to date, of the Mor Ridge forests (Fig. 1a), in which soils are also highly acidic (mean 0–10 cm soil pH = 3.0; Tanner 1977) suggests that it may be unable to invade very infertile sites.

Invasibility and diversity

Observational and experimental studies are equivocal in determining links between community diversity and invasibility and are often confounded by the influences of disturbance and fertility (Prieur-Richard & Lavorel 2000). We found no link between stand-level tree diversity and the extent of *Pittosporum* invasion (its basal area in 2004): past disturbance and soil nutrients were more important predictors. Although there was no relationship between stand-level tree diversity and the likelihood of *Pittosporum* invasion in Jamaica, the question remains whether Jamaican montane forests in general are more likely to be invaded because of lower diversity at a regional scale. Central American montane rain forests at similar latitudes, with which Jamaican forests have floristic affinities, have not been reported to be invaded by alien tree species (e.g. Kappelle et al. 1996; Williams-Linera 2002). They also appear to be more diverse than Jamaican montane forests (e.g. mean tree H' of 3.3 in Costa Rican rain forest at 2950 m, Kappelle et al. 1996, vs. 2.7 in Jamaican extensive plots). This offers support for Denslow's (2003) suggestion that compared with continental forests, lower diversity forests on oceanic islands have poor resistance to the establishment of new individuals of alien species.

Chronic anthropogenic disturbance and disrupted mutualisms may explain the high level of invasions of oceanic island forests (D'Antonio & Dudley 1995). However, while chronic anthropogenic disturbance is a feature of the Jamaican Blue Mountains (Eyre 1987), Central American montane forests are also subject to widespread deforestation and fragmentation (e.g. Williams-Linera 2002). Chronic natural disturbance is a feature of many island ecosystems invaded by woody plants (Merlin & Juvik 1995; Yamashita et al. 2000) but many Central American forests are also subject to wind disturbances (Whigham et al. 1999) and tectonic activity. Forests on oceanic islands can be exposed more frequently to inputs of alien plant seeds and other propagules than mainland habitats (D'Antonio & Dudley 1995; Denslow 2003). Successful invasions are often a function of introduction effort (e.g. Duncan 1997) and concerted introduction effort for alien plant species, including *Pittosporum*, occurred at a Botanic Garden < 6 km from our study sites. Not only *Pittosporum* but also other alien plants in the forests including *Cinchona officinalis* and *Hedychium gardnerianum* (Grubb & Tanner 1976) derive from introductions to this Botanic Garden. A rare example of invasion of continental montane rain forests, the alien tree *Maesopsis eminii* Engl. in the East Usambara Mountains of Tanzania, derives from extensive adjacent plantations of this

species (Binggeli & Hamilton 1993) which, like *Pittosporum*, is dispersed into native forests by native birds (Cordeiro et al. 2004).

Resource use by native trees vs. Pittosporum

The question is whether resources in these montane forests are under-used or used inefficiently by the native tree species compared with the alien *Pittosporum*. Nutrient supplies are limiting growth in the Jamaican Mull Ridge forest because both N and P fertilization increased trunk growth in this site (Tanner et al. 1990) but trunk growth was also N and P limited in continental montane forest (Tanner et al. 1992). In the shade of Mull-Ridge-type forest, *Pittosporum* seedlings had low leaf nitrogen concentrations (0.9%) compared with seedlings of five native species (1.1 - 1.5%; Ball 2000). Water might limit the growth of seedlings in dry periods in this forest (wilting is occasionally seen in understorey seedlings) but *Pittosporum* seedlings do not have an especially high water use efficiency (Ball 2000).

Light levels in the understorey in the intensive Mull Ridge site long after the previous direct hurricane strike were 4 - 5 % (Aylett 1985), slightly higher than the 1 - 3% commonly recorded in lowland tropical rain forests. Thus light resources may be more available than in lowland rain forests, possibly promoting invasion but it is unknown whether continental montane forests intercept more light than island montane forests. In the understorey of Jamaican montane forest *Pittosporum* seedlings have higher photosynthetic rates than seedlings of the native trees ($A_{\max} = 2.3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ cf. the next highest rate, 1.3, for the native gap-demanding tree *Alchornea latifolia*; Ball 2000). Furthermore their photosynthetic nitrogen use efficiency was $24 \mu\text{mol}\cdot\text{CO}_2\cdot\text{mol}^{-1}\cdot\text{N}^{-1}\cdot\text{s}^{-1}$ vs. 8-17 for five native species. Thus if *Pittosporum* seedlings in the understorey are successful because of resource use it is because they use light or nutrients more efficiently than native species; but it is a matter of degree rather than it being a 'super' species (Fine 2002). *Pittosporum* seedlings in gaps also have higher rates of photosynthesis than their competitors ($A_{\max} = 3.6 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ vs. 3.3 for *Palicourea alpina* and 2.4 for *A. latifolia*; Ball 2000), again a matter of degree. While growth rates of alien plants do not usually exceed those of co-occurring natives (Daehler 2003), the trunk growth rates of *Pittosporum* adults are 4-5 times greater than those of native species. Its trunk growth rates increased as P became more limiting, i.e. they increased with soil N:P, but even in less P-limited sites it still has faster trunk growth rates. For example, where soil N:P was lowest across the intensive sites (Col site; soil N:P =

15.7), *Pittosporum* R_D was twice that of native species. Its higher trunk growth rates can only be partially explained by the higher photosynthetic rate. Another reason may be that *Pittosporum* has a higher than average leaf area index due to its deep, dense crown; this would also be consistent with a global pattern showing alien species usually have greater leaf areas than native species (Daehler 2003). Other relevant factors that might explain *Pittosporum*'s rapid growth might include different biomass allocation patterns in *Pittosporum* and potentially lower rates of herbivory and diseases; the latter may be a reason for its zero tree mortality observed in the plots over 14 years.

Future status of Pittosporum in Jamaica

Invasion of Jamaican montane rain forests by *Pittosporum* resulted in an overall decline in basal area of native species in proportion to increased basal area of the invader. There is some evidence of a decline in tree species diversity (H') occurred along an invasion gradient over 14 years. Thus the current dominance of *Pittosporum* in secondary forests on the southern slopes of the range (McDonald & Healey 2000) could be a result of long-term decline in diversity of communities initially dominated by native trees. Other ecosystem consequences of *Pittosporum* dominance, both above- and below-ground, have yet to be assessed but its foliage contains resins and saponins (Cronk & Fuller 1995) that may have below-ground effects as shown for other invasive alien trees in island forests (Walker & Vitousek 1991; Rothstein et al. 2004). Many of the *Pittosporum* stems we measured in sites up to 6 km from its point of introduction were reproductive and as native birds disperse its seeds to more remote sites it is likely to form a seedling bank throughout these forests. Thus the full extent of the impacts of its invasion on forest structure may take some decades to become apparent. Since hurricanes, which disturb these forests on average every 25 years, appear to accelerate *Pittosporum* invasion and abandonment of cut-over natural forest results in dominance of the regrowth by *Pittosporum*, more widespread invasion of these forests seems inevitable. Efforts to prevent its further spread through control, especially biological control (Healey et al. 1995), will be important to prevent reduction of diversity in these forests which have high endemism (e.g. 41% of the flora, Tanner 1986).

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