The effect of *Pittosporum undulatum* on the native vegetation of the Blue Mountains of Jamaica

May 1997

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Research supported by the U.K. Overseas Development Administration and the U.K. Department of the Environment *Darwin Initiative* programme

1. Introduction

1.1 Background

The Australian tree *Pittosporum undulatum* Vent. was introduced to the Blue Mountains of Jamaica in 1883. Sixty-six years later this bird-dispersed tree had become "perhaps the commonest tree" in secondary forest around the Cinchona Botanic Gardens, its place of introduction (Bengry & Serrant 1949). Previous research projects have identified its competitive success against native tree species (Healey 1990) and the low density and species richness of native vegetation beneath dense stands of the alien (Goodland 1990). The density of *P. undulatum* seedlings in areas of previously uninvaded forest greatly increased following the disturbance created by Hurricane Gilbert in 1988 (Bellingham 1993), and the species has now spread throughout at least 1,300 ha of primary and secondary montane forest (Healey & Goodland 1995). We have estimated that the area of the potential range of the species in the Blue Mountains could be as high as 44,000 hectares (Goodland & Healey 1996), seriously threatening the high biodiversity of the mountain range. There are about 275 species of flowering plants in the Blue and John Crow Mountains National Park endemic to Jamaica (Grubb & Tanner 1976, Bellingham 1993, Muchoney *et al.* 1994).

These facts have led to concern amongst many scientists that the spread of *P. undulatum* in the Blue Mountains may lead to the competitive exclusion of many native plant species. The former Park Manager considered the need for reliable information about the impact of the invasion to be one of the highest priorities for the national park (D. Lee, pers. comm., 1991). This is because past work had not provided sufficient evidence of the severity of the threat to convince donor agencies of the need to provide necessary funds for a control programme, or to form the basis for a management plan when funding is available.

This report, therefore, investigates the effects of *P. undulatum* on the native plant biodiversity of forests of the Blue Mountains. Given sufficient time (and without man's intervention) it seems probable that all the montane forests of the Blue Mountains would become invaded by *P. undulatum*. The lower altitudinal limit of *P. undulatum* is poorly known (it is probably between 600-1000 m), but most primary, and therefore diverse, forest below 1000 m has been cleared in the last two centuries or so. The report deals only briefly with "time-dependent" issues, (such as the current extent of *P. undulatum*, the rate of spread, population changes in permanent sample plots, possible limiting factors to its range), or the ability of *P. undulatum* to grow outside the forest (on deforested slopes or landslides), subjects dealt with in Goodland & Healey (1996). It concentrates on the immediate and long-term effects of the introduced species once it has already arrived at a site, a small area of forest such as a permanent sample plot.

Possible effects on other aspects of the ecology of the Blue Mountains (non-vascular plants, animals, the nutrient and hydrological cycles), and on humans, were considered in Goodland & Healey (1996).

The factors that determine the effect of *P. undulatum* on native plants in the Blue Mountains can be broken down into the rate of dispersal, the ability of the species to capture land and resources once it arrives at a site (its competitive ability) and its persistence (whether it is eventually replaced by other species at the site).



Figure 1. Factors that determine the success and impact of an invasive plant such as P. undulatum The main factors that control the rate of dispersal of *P. undulatum* are shown in the figure below. In summary:

- P. undulatum was introduced to the Cinchona Botanic Gardens in 1883
- · the species may have been planted by man outside the gardens
- in the few decades after introduction most of the land around Cinchona which had been under coffee and *Cinchona* plantations was gradually abandoned and reverted to secondary forest
- P. undulatum juveniles start to produce seed when about 5-6 years old
- seed production is high, a regression relationship between DBH and seed production in 1992 giving a mean of 37,500 seeds for a 8 cm DBH tree
- seed production has been at least fairly high for every year from 1992 to 1996
- there are at least six common native bird species that eat and presumably disperse P. undulatum seeds
- · vegetative spread, through mechanisms such as suckering or layering, are not important to the rate of invasion
- the species is able to establish itself in all habitat types in the western Blue Mountains, though with difficulty in very
 undisturbed forest, in Mor Ridge forest or on landslides
- Hurricane Gilbert in particular and probably hurricanes in general have played a major role in facilitating the establishment of the species in otherwise undisturbed forest



Figure 2. Factors determining the rate of spread of P. undulatum in the Blue Mountains

This report will focus on the competitive suppression by *P. undulatum* of native plant species, as the competition for light and below-ground resources are the most obvious mechanisms by which *P. undulatum* may affect native species. *P. undulatum* trees have a dense crown, so shade probably accounts for a large part of the suppressive effect of the species (though we cannot determine to what extent the dense canopy has its effect because of a reduction in light or a probable reduction in throughfall). We have some evidence that the below-ground competitive ability of *P. undulatum* is high in comparison with the native species, though we have no

experimental evidence on the relative importance of above- and below-ground competition. We give our best assessment of the persistence of *P. undulatum* in the Discussion chapter at the end.

There are several other possible mechanisms by which *P. undulatum* may affect native plant species, briefly discussed below, though little is known about many of these.

- Allelopathy. Allelopathy has been suggested as a factor depressing the number of native seedlings beneath scattered *P. undulatum* trees in the Blue Mountains where the light levels would have indicated a higher seedling density (J. Dalling, pers. comm., 1991). In Australia, Gleadow and Ashton (1981) found that leachates from *P. undulatum* leaves appeared to inhibit the germination (expressed as a percentage of control) of several *Eucalyptus* species; for example, germination of *E. obliqua, E. melliodora* and *E. gonocalyx* was 47.1, 8.1 and 48.3% of untreated seeds. However, they stated that no inhibitory effects, other than that expected from deep shade, have been shown under canopies in the field. In South Africa, Richardson & Brink (1985) found no seedlings of *P. undulatum* or native species beneath established *P. undulatum* trees and thought that this was due to an allelopathic effect from *P. undulatum* foliage.
- 2. P. undulatum trees as a habitat. The greatest effect that P. undulatum may have as a different habitat to native trees is on animals, but the structure of its crown or nature of its bark may have an effect on epiphytic plants, independent from the density of its foliage. A large proportion of the non-woody plant species in the Blue Mountains are epiphytic (P.J. Bellingham, pers. comm., 1994), but the effect of P. undulatum on epiphytes was not specifically addressed in the study, mainly because of the great difficulty of seeing through dense canopies of P. undulatum trees. Our observations and data collected by Mitchell (1989) suggest that the numbers of epiphytes are much reduced both in the crowns of P. undulatum trees in comparison with native trees of similar size and on native species beneath dense P. undulatum canopies. This could be due to many factors such as reduced light levels and rain throughfall, the upright growth habit, different branch arrangement and bark characteristics of P. undulatum trees (hence less time for establishment).
- 3. Effects on animals. The most obvious example of the effect of *P. undulatum* on a native plant caused indirectly by the effect on an animal is the effect the alien may have on pollinators and seed dispersers of native plants. If *P. undulatum* is relatively successful in attracting pollinators and dispersers, and if those tree species that are less attractive are neglected as a consequence, these native species could find their regeneration threatened. These indirect effects could be very important, but they are hard to determine. Conversely, as native trees become isolated in heavily invaded forest, their predation by native, co-evolved pests and pathogens is likely to decline as they become harder to find.
- 4. Effects on susceptibility of native species to windthrow. Another possible mechanism by which *P. undulatum* could affect native trees is by changing their allometry through greater competition, thus changing their vulnerability to windthrow. Studies of the impact of Hurricane Gilbert show that hurricanes play a major role in the forest dynamics of the Blue Mountains. Also, *P. undulatum* trees do not get covered with lianes as frequently as native species (though this could be because most climber species seem to be restricted to primary and therefore less invaded forest), so would not pull down other trees when blown down, (though we have no evidence as to the importance of this phenomenon in the Blue Mountains).
- 5. Change in disturbance regime. As it is likely that *P. undulatum* trees are blown over at a smaller size than the average for native species (Healey & Goodland 1995), the advanced stage of invasion would see, after hurricanes, a high proportion of the area in gaps. Because of the sparse understorey beneath dense *P. undulatum* (few *P. undulatum* seedlings as well as few native seedlings) a few highly gap demanding native species, such as *Bocconia frutescens* and *Brunellia comocladiifolia*, (as well as alien weeds like *P. undulatum* and *Polygonum chinense*) may benefit.

Report structure

The report has two main chapters. The first examines the direct evidence for the effects of *P. undulatum*. The only way to do this is examine differences in the performance of native species with varying amounts of *P. undulatum*. We have tried three approaches:

- 1. Correlation between the dominance of *P. undulatum* and native vegetation in many plots at one point in time.
- 2. Correlation between the change in dominance of *P. undulatum* and native vegetation through time, in a smaller number of plots.
- 3. Experimental removal of *P. undulatum*.

We have not tried the fourth possibility, the experimental addition of *P. undulatum*, because of time, and ethical, constraints.

The second chapter considers the reasons for any competitive effects, though our understanding of causal mechanisms are not well advanced, and are partly conjecture. The project has not had the explicit objective of discovering the causes for any effects *P. undulatum* may be having. Despite this, data and observations collected from the Blue Mountains, together with information from other invasions, have been enough to provide strong indications on the underlying mechanisms.

We examine likely reasons for the competitive success and hence supression by *P. undulatum* of native species in three categories, in each case comparing *P. undulatum* with native species. These three categories are not true causes, in the sense that they themselves are the result of more underlying physiological or ecological mechanisms. We have discovered many facts about the biology of *P. undulatum* necessary to an understanding of its success without (mainly through time constraints) being able to find out similar information for native species - aspects such as age to reproductive maturity, seed production per individual. Full information on *P. undulatum* is given in Goodland & Healey (1996). In this report we focus on those important aspects of the invasion for which we have information on native species as well as *P. undulatum*. This list of questions and subsequent analyses are not intended to be comprehensive, but only to address the more important factors.

- 1. Growth rate of individuals. How fast do P. undulatum individuals grow?
- 2. Growth form of individuals. What is the growth form of *P. undulatum* individuals? How large do *P. undulatum* trees get?
- 3. **Population density**. What is the survival rate of *P. undulatum* juveniles? How dense can *P. undulatum* populations become?

The results from the two main chapters are discussed in the last chapter.

A full list of all woody species occurring in the Blue Mountains permanent sample plots, together with the 6-letter codes used in some figures, is given in an appendix.

2.

Direct evidence for the effect of Pittosporum undulatum

The most important direct evidence for the effects of *P. undulatum* on native plants come from two removal experiments established in forest near Cinchona (the place of introduction). More data and analyses are presently available from the first of these, Heavily Invaded Forest Experiment - its methods are described in detail in Healey *et al.* (1992), only briefly here. The second removal experiment, the Slightly Invaded Forest Experiment, is described fully, although the experiment is still at an early stage.

2.1 Methods

2.1.1 Heavily Invaded Forest Experiment

Pittosporum undulatum usually occurs on steep hillsides with thin and rocky soils and is typically associated with a sparse and depauperate understorey. To understand the effect *P. undulatum* is having on the native vegetation it is necessary to experimentally remove it. It is not sufficient to rely on simple correlations between *P. undulatum* dominance and the native vegetation alone, as *P. undulatum* might be largely restricted to unstable and often human disturbed forests, which may naturally have an understorey of low diversity. A removal experiment was established in forests with a range of degrees of invasion in the western end of the Blue Mountains during the latter half of 1991.

Specific questions

The questions concerned with the effect of *P. undulatum* that HIFE was designed to answer are:

- 1. How close is the apparent correlation between *P. undulatum* dominance and the recruitment, survival and growth of native vegetation?
- 2. Will there be a decline in the dominance of native species between the first and subsequent enumerations in the *Undisturbed control* treatment?
- 3. After *P. undulatum* removal, to what extent will the diversity and density of native species in the understorey increase?
- 4. What is the relative effect of *P. undulatum* trees and *P. undulatum* seedlings on native vegetation?

Methods

A randomised block design was used, with five blocks, five plots within each block and four treatments. Each block contained two replicates of the undisturbed control and one of the other three treatments. The design was partially orthogonal. Each plot was 12×12 metres, surrounded by a 9 m guard area (giving a 30×30 m treatment area). Twenty 1×1 m sub-plots were randomly selected within each plot. Woody plants over 3 m tall were enumerated within the 12×12 m plot, those less than 3m, in the twenty 1 m² sub-plots. Each individual was identified to species level wherever possible and labelled with an aluminium identification tag. There were four treatments:

- 1. Undisturbed Control (UC). No treatment.
- 2. *Remove P. undulatum Trees (RPT). P. undulatum* trees (plants >3m) were cut, the stumps were not treated with a herbicide, but the resprouts were removed three times after cutting in an attempt to kill them.
- 3. *Remove all P. undulatum (RAP).* All *P. undulatum* seedlings over 50 cm tall were killed (pulled up whenever possible) in the 30×30 m treatment area and all other *P. undulatum* seedlings were killed within the central 14×14 m area (ie. at least 2 m from the nearest sub-plots). All *P. undulatum* recruits in all the sub-plots have been removed on three occasions since the original treatment.
- 4. *Remove Equivalent Native Trees (RENT).* In this treatment native trees were removed until the same total GBH was removed as that of *P. undulatum* in the RPT treatment in that block.

Table 1. Enumeration activity, size class, treatment dates and months from the pre-treatment enumeration, in the Heavily Invaded Forest Experiment.

Activity	Size class	Date	Months
Pre-treatment enumeration (t0)	Trees and seedlings	July-August 1991	0
Imposition of treatments		SeptOct. 1991	2
First post-treatment enumeration (t1)	Seedlings	August 1992	12
Second post-treatment enumeration (t2)	Trees and seedlings	December 1993	28
Partial enumeration	Dead seedlings only	June 1995	46
Full enumeration of trees	Trees	July 1996	59

2.1.2 Slightly Invaded Forest Experiment

The Heavily Invaded Forest Experiment is providing valuable information on the effects of *P. undulatum* on native vegetation. However, HIFE has a major limitation in its ability to provide proof of the effects of *P. undulatum* in that, by necessity, it was carried out in highly disturbed secondary forest in which *P. undulatum* is abundant, (*P. undulatum* probably regenerates after near total clearance, cultivation and then abandonment) - the prime objective of the experiment had been to provide information on the management of *P. undulatum* in heavily invaded forest. Another characteristic of this secondary forest on the southern slopes of the mountain range is that it has a lower species diversity than primary and old secondary forest (T. Goodland, unpublished data). Therefore the capacity of native species to respond to the removal of *P. undulatum* is, as expected, limited. The primary factor is likely to be a lack of propagules, as there are no nearby potential seed parent trees of many species that would be expected to occur in primary forest on such sites. In addition, there may be characteristics of the soil in such secondary forest that limit the capacity of native species to colonize (Dalling (1992) studied the extreme case of landslides where all top soil had been lost from much of their surface). However, we have no evidence that the soil conditions in the HIFE plots do limit the establishment of native species that would occur in primary forest in these sites.

The only way to objectively determine the effect that *P. undulatum* has is to follow the whole invasion process in permanent plots, paired with plots in comparable forest from which *P. undulatum* is removed as a seedling or small tree. Therefore during June to September 1994 we established a second removal experiment. The experiment had the specific objective of investigating the effect of *P. undulatum* on native plants and so was set up in diverse primary forest only slightly invaded by *P. undulatum*. It is called the Slightly Invaded Forest Experiment (SIFE).

Objectives

The long-term objectives of SIFE are to investigate the following:

Population dynamics of the invasion

- Performance (recruitment, growth and survival) of *P. undulatum* and native species in gaps and understorey
- Relationship between *P. undulatum* seedling performance and distance to the nearest mature *P. undulatum* tree (for which an assessment of the fecundity, and position relative to the plot, of all *P. undulatum* trees in the treatment area or vicinity will be made)
- Micro-site distribution of *P. undulatum* and common native seedlings; to what extent is the distribution clumped, because of bird dispersal patterns or preferential establishment on certain substrates?

Effect of P. undulatum on the native community

• Performance of native tree seedlings, either by plot level correlations or by proximity to individual *P. undulatum* saplings and trees

- Growth form (eg. degree of branchiness, leaf area) of those native species able to grow in both treatments
- · Distribution of herbs, climbers, epiphytes, and non-vascular plants

Effect of P. undulatum on community level productivity

- Community productivity, in terms of basal area increment, biomass increment (perhaps by means of limited destructive harvesting in the treatment area or surrounding forest), and litterfall (quantity and quality)
- Soil chemistry and nutrient status
- Effect of *P. undulatum* on forest microclimate and hydrology, e.g. throughfall, stemflow, soil moisture
- · Light regimes, as characterised by hemispherical photographs, and/or PAR quantum sensors



Figure 3. Plan of a Slightly Invaded Forest Experiment plot

Differences between SIFE and HIFE

The similarities between the two experiments include, of course, the central interest in the effect that *P. undulatum* has on the forest, the identical height/girth thresholds used to define the different categories of plants, and the presence in SIFE of all the species present in HIFE. The most notable differences are:

• The forest in SIFE is generally much less invaded by *P. undulatum*, with only very occasional trees and a seedling density of around 0.1 to 0.5 m⁻². It seems unlikely that native plants in forest so little dominated by *P. undulatum* would have been appreciably affected yet. The forest in all SIFE plots appears either not to have ever been disturbed by man or to be very old secondary forest. All the forest in HIFE is certainly secondary (with the possible exception of about a third of one block), often relatively young (c. 40 rs old?) secondary forest.

- The plots in SIFE are much larger. This is to increase the chance that gaps will occur in each plot within the projected life of SIFE. The buffer zone is 20 m (10 m in HIFE); this is because we hope SIFE is going to be a longer term experiment than HIFE, and *P. undulatum* trees can attain heights greater than 20 m.
- The plots have been located on less steep slopes than HIFE. This is to minimise disturbance during enumerations and removals. Considerable time was spent on locating suitable sites, as most of the Blue Mountains are very steep, and if not too steep, usually sites were not suitable because of too little or too much *P. undulatum*; too much disturbance, mostly from Hurricane Gilbert; or the sites had Mor Ridge Forest which has a distinctively different species composition (Grubb & Tanner 1976) so would not have been comparable with other sites.

Methods

The experiment has a simple randomised block design, with six blocks and a single replicate of each treatment in each block, randomly assigned. Each 24×15 m plot is staked out in 3×3 m cells, with eight 3×15 m strata. In the centre of two cells in each strata a 1.2×1.2 m sub-plot has been established in which all tree seedlings were enumerated; all seedlings over 100 cm tall and all saplings (300 cm tall to 10 cm GBH) were enumerated in the remainder of the 3×3 m cell.

Enumeration

Trees (defined as those woody plants >3m tall). We identified and measured the GBH of all trees within the 30 x 21m plot. All individuals were tagged with aluminium tags (except plants >3m tall to 10 cm GBH within the 16 selected cells in each plot, which had their coordinates within the cell measured instead). Thirty-five individuals have not been identified yet, and a further 24 individuals have only tentatively been identified to specific level. Another 240 individuals belong to groups of closely related species either difficult to distinguish without fertile material or of doubtful status as separate species.

Large seedlings (defined as woody plants >1m tall). We identified and measured the height of all woody plant seedlings >1m tall in the sixteen 3×3 m cells. The spatial coordinate of each within the cell (to the nearest 5cm) was recorded.

Small seedlings (defined as woody plants <1m tall) occuring in the 1.2x1.2 m sub-plots were similarly measured, although the spatial coordinate of each was recorded to the nearest centimetre. Where a particular species occurred at a high density, seedlings were marked with aluminium tags.

There have been three enumerations so far, all carried out in the month of July:

1994 The full pre-treatment enumeration.

- 1995 We measured the height of *P. undulatum* seedlings only; we removed *P. undulatum* from half the plots as planned.
- 1996 We measured the height of all seedlings in 12 sub-plots, 6 beneath *P. undulatum* trees and 6 which had never been beneath *P. undulatum* trees. After an initial analysis it was decided that a full re-enumeration would be premature.

Results

2.2.1 Relationship at one time

The relationship between the basal area of *P. undulatum* and the density of native seedlings at the initial enumerations of the 37 HIFE and SIFE plots is shown in Figure 4.



Figure 4. Relationship between the basal area of P. undulatum (m^2 ha⁻¹) and the mean seedling density (m^2 , on the y-axis) of seven important native species, and all native species combined, in 37 plots (HIFE and SIFE). Each plot has been put into one of three classes of past human disturbance. Note the different scale in the bottom two graphs to the rest of the graphs.

There is a definite relationship between the basal area of *P. undulatum* and the density of all native seedlings combined. The relation is best described as linear if the very high values in some of the primary forest plots are excluded - these values are largely due to the shade-tolerant *Eugenia virgultosa*, (the species occurs at a much higher density (in primary forest) that any other native species in our permanent sample plots). The relationship indicates that the density of native seedlings falls to near zero in the most heavily invaded forest.

Two reasons for the fairly large amount of scatter in the relationship is firstly due to spatial variation in the density of *P. undulatum* trees in some plots, especially the large SIFE plots. Another reason may be the use of basal area and the way it increases so rapidly with DBH. For example, the basal area of the largest *P. undulatum* tree we have found is 3380 cm², 478 times that of a 3 cm DBH tree (the bottom of the tree size class). Given the usually dense crown of smaller *P. undulatum* trees and the often thinning crowns of larger trees it seems unlikely that there could be such a difference in the effect of trees of these different sizes.

Guarea glabra and *Cinnamomum montanum* are two shade-tolerant species common in primary forest, but rare as trees in secondary forest. Both species show signs of re-invading older secondary forest, however neither species appear to show an ability to grow into larger size classes beneath dense *P. undulatum. Maytenus jamaicensis* is a shade-tolerant species typically confined to primary forest (with only one secondary or intermediate plot with the species present in as a seedling) so making it very difficult to determine what effect *P. undulatum* has on the regeneration of the species. *Eugenia virgultosa* is the only species (for which we have sufficient data) that has significant numbers of seedlings reaching large seedling size in heavily invaded secondary forest. *Psychotria corymbosa* is a species (rarely exceeding 6 m in height) fairly common as a seedling in secondary as well as primary forest. However mortality of small (<20 cm) seedlings is high and there is very little recruitment of the species rare in forest with more than about 1 m² of *P. undulatum* per hectare; adult trees of both species are common in secondary forest so seed input is unlikely to be limiting.

2.2.2 Relationships through time

We have data on more than one seedling enumeration in HIFE, so allowing an examination of the relationship between the increase in dominance of *P. undulatum* (in every plot the total basal area of *P. undulatum* has increased between every enumeration - if *P. undulatum* trees are present at all) and change in native understorey vegetation. Only data from the ten *Undisturbed Control* plots in HIFE have been used for these through--time analyses. Three enumerations have been made of trees and seedlings in HIFE, however, the second and third tree enumerations did not coincide with the second and third seedling enumerations (the mean dates are given below). Therefore, the *P. undulatum* basal area at the time of the second seedling enumeration (t₁) was estimated from the growth of *P. undulatum* between t₀ and t₃.

Table 2. Mean dates of enumerations of seedlings and trees in the HIFE plots.

	to	t ₁	t ₂	t ₃
Seedlings	12/08/91	22/08/92	12/01/94	
Trees	12/08/91		24/12/93	08/07/96



Figure 5. The relationship between the basal area of P. undulatum and dominance of seedlings of native trees at three enumerations in the ten Undisturbed Control plots in HIFE., (a) absolute dominance values, (b) relative dominance values. Note that in all plots (except plot 15 where P. undulatum was not present) the basal area of P. undulatum increased between each enumeration

The relationship between the basal area of *P. undulatum* and <u>absolute</u> dominance of native seedlings at the three enumerations (Figure 5(a)) is not clear. Four plots experienced an increase in the dominance of the seedling layer in absolute terms, all plots where *P. undulatum* had not achieved great dominance, with the disturbance caused by Hurricane Gilbert in 1988 probably still having an effect.

The <u>relative</u> dominance of native seedlings shows a clearer relation with the dominance of *P. undulatum*. There is a general tendency for there to be a diminishing dominance of native seedlings with more *P. undulatum*. One notable aspect of this relationship is the presence of a clear boundary to the maximum dominance (or density or diversity) of native vegetation. This suggests that, though many factors (such as disturbance history, soil type and depth, and slope steepness) influence native vegetation, *P. undulatum* appears to be a clear limiting factor. It is not possible to say whether the species acts directly (by allelopathy for example) or indirectly (by depriving understorey plants of resources). Time does not appear to equate with space; if it did, one might expect the mean slope of the relationship for each plot through time to be about the same as that of the slope between plots at one point in time. Eight of the ten plots showed a decline in the relative dominance between t0 and t2 but the situation was complex - five plots showed a decline in both intervals, three plots showed a decline then increase, one plot showed an increase then decline and one an increase in both intervals.

Analyses of the effect of differing amounts of *P. undulatum* on the growth and survival of native species did not give clear results. There was a tendency for the growth rate and survivorship of *Eugenia virgultosa* and all native species combined to decrease with increasing *P. undulatum*, but there was much variation between plots. The problems of carrying out this investigation in forest with so few native seedlings was apparent.

In July 1996 we carried out a preliminary enumeration of SIFE, exactly one year after the removal of *P. undulatum*. It did not seem likely that there would be a major effect, as *P. undulatum* had not been dominant in any of the plots. The cover of native trees was sufficient to prevent a very marked increase in light levels

following *P. undulatum* removal. The table below shows the results from the enumeration. These results have been shown only to give an indication of the situation in 1996, they are not full statistically valid, because the data was collected from only two plots.

Table 3. Number of seedlings, mean absolute height increment (cm) and standard error of the mean (SEM), of Eugenia virgultosa, other native species and P. undulatum in SIFE. Results are shown from six sub-plots (in plot 1) beneath the crowns of at least one P. undulatum tree, and six sub-plots (in plot 2) that have never experienced shading from P. undulatum.

	Beneath P. undulatum			Not beneath P. undulatum			
	No.	MAI	SEM	No.	MAI	SEM	
Eugenia virgultosa	72	2.27	0.27	68	2.56	0.39	
Other native species	48	4.63	0.67	51	4.75	0.72	
P. undulatum	38	6.47	1.05	44	7.38	1.13	

The growth rate was not significantly different (at the 5% level) for any of the three species groups between the two treatments, though was significantly different for the three species groups.

2.2.3 Removal of P. undulatum

The density of *P. undulatum* and native species recruits is shown in Figure 6 with numbers of recruits for the two (post-treatment) enumerations combined.



Figure 6. Variation in the numbers of seedling recruits (log scale) between 1991 and 1993 of three species groups (P. undulatum, Shade-intolerant native species and Shade-tolerant native species) per plot, with basal area ($cm^2 m^2$) of P. undulatum. The results of three treatments are shown, each being the sum of the number of recruits at the two post-treatment enumerations. For the Undisturbed Control treatment (10 plots) the recruitment is plotted against the basal area of P. undulatum in 1991. For the Remove P. undulatum Trees and Remove all P. undulatum treatments (5 plots each) the recruitment is plotted against the basal area of P. undulatum removed in 1991.

Overall, the graph on the left (*Undisturbed Control*) shows that the number of recruits declined with increasing amounts of *P. undulatum*, whilst the two other graphs show that the number of recruits increased with increasing amounts of *P. undulatum* removed in 1991. Results are shown separately for the six commonest shade-tolerant species and the six commonest shade-intolerant species, commonest meaning as new recruits at the t₁ enumeration. The recruitment of shade-tolerant species was higher in the *Undisturbed Control* treatment though declined at about the same rate as the recruitment of shade-intolerant species declined with increasing *P. undulatum*. The recruitment of shade-intolerant species was on average greater following the removal of all *P. undulatum* compared with the removal of only *P. undulatum* tree, whereas there was no significant difference with shade-tolerant species.

There was no recruitment of *P. undulatum* in seven of the *Undisturbed Control* plots. In both the *Remove all P. undulatum* and *Remove P. undulatum* Trees treatments the recruitment of *P. undulatum* increased greatly with increasing amounts of *P. undulatum* removed, reaching 2144 recruits in plot 20 (107.2 seedlings m⁻²).

Analyses of the effect of *P. undulatum* removal on the growth and survival of those seedlings already present at the pre-treatment enumeration ("advance regeneration") show much less clear results. In brief, those few seedlings that were beneath dense *P. undulatum* were shade-tolerant species, mostly *Eugenia virgultosa*, and these showed little sign of increased growth; indeed in one plot (plot 20, south-eastern aspect, thin soils) from which all *P. undulatum* was removed (comprising 17.5% of the total basal area) most of the advance regeneration either died or died back. In less heavily invaded forest there was a greater diversity of advance regeneration but the removal of *P. undulatum* led to a lesser opening up of the canopy, so effects were slight.

3.

Mechanisms

This chapter examines the reasons for the effect of *P. undulatum*, Figure 7 showing our current understanding. We give a rather detailed account of our research into the comparative growth form of *P. undulatum* and native species as we think this may be one of the most important factors affecting the success of *P. undulatum*, and all the fieldwork and analysis on this subject was conducted during the Darwin Initiative project. The reference in Figure 7 to the distribution of *P. undulatum* indicates the importance of the spatial dimension to the invasion, but is a subject largely outside the scope of this report.



Figure 7. Factors determining the impact of P. undulatum

3.1 Methods

3.1.1 Growth rate

In this section we compare the growth rate of *P. undulatum* trees with those of native trees. We use trees in three plot series, those of E.V.J. Tanner, P.J. Bellingham and the Heavily Invaded Forest Experiment (*Undisturbed Control* plots only).

Table 4. Number of plots, total area (ha), and mean enumeration dates and intervals of the three series of plots

	number	area	tO	t1	years
E.V.J. Tanner plots ¹	40	0.400	14/03/91	08/08/94	3.405
P.J. Bellingham stratified plots	15	0.300	10/08/90	10/09/94	4.089
HIFE Undisturbed Control plots	10	0.144	14/08/91	09/07/96	4.905
¹ Col, Mull Ridge, Wet slope					

The tree threshold size is 3 cm DBH (7.0685 cm² BA). The relative basal area increment (RBAI) was calculated as follows:

 $RBAI = (InBA_{t1} - InBA_{t0}) / t_1 - t_0$

where BA is in m^2 , and t is time in years.

All results are given by size class. Five size classes were chosen to contain approximately the same number of individuals in each class, the size thresholds are:

Size class	BA (cm ²)
1	7.07-11.99
2	12.00-19.99
3	20.00-39.99
4	40.00-124.99
5	>125.00

As well as analysing data for individual species we grouped species into regeneration classes (mostly based on a number of independent field studies (Sugden *et al.* 1985, Healey 1990, Vernon 1991, Dalling 1992)):

GD gap-demanding - gaps or severe canopy disturbance essential for germination and recruitment

GB gap-benefitting - some disturbance necessary for germination and recruitment

SGP slow-growing pioneer - species with regeneration usually confined to habitats such as landslides

ST shade-tolerant - species relatively more successful as seedlings in undisturbed conditions than gaps

U unclassified - minor species for which we do not have sufficient information to confidently classify

3.1.2 Growth form

Above-ground growth form

During July 1995 we started two studies of the ability of common species to exploit and explore the aboveground environment. Both studies were carried out in forest that showed a range of disturbance from moderately disturbed (mostly by Hurricane Gilbert seven years previously) to very undisturbed. It is important to note that areas of severe or recent disturbance (or well-defined gaps) were not included. Some bias is likely, as those more gap-benefitting species were more likely to be growing in areas that experienced higher light levels in the past, even if the light levels were fairly uniform throughout the plots in 1995.

The first study was directed at looking at the effect of *P. undulatum* trees on the above-ground growth form of large seedlings (between 1 and 3 metres tall) of common native species and *P. undulatum* itself. The species were chosen for commoness and from three "regeneration groups" - *Gap demanding, Gap benefitting* and *Shade tolerant.* The seedlings were sampled in the *Undisturbed Control* and *Remove all P. undulatum* treatments of SIFE, all beneath the crowns of *P. undulatum* saplings (which were subsequently removed of course in the latter treatment). The seedlings were not confined to the plot itself but were often in the treatment area, and were tagged and flagged for later relocation. The parameters measured were:

- Distance and compass bearing from the P. undulatum sapling
- Length of stem (to leaf tip)
- Length to first living leaf
- Maximum distance in each of four quadrants (see Figure 8)
- Angle of stem from the horizontal
- Number of leaves; on *Eugenia virgultosa* and on larger individuals of *E. monticola* the number was estimated by counting the number on randomly selected branches

In 1996 between 10-20 leaves per species (depending on the within-species variability) were collected from large seedlings of each species just outside the plots in similar forest. The area of the fresh leaves was estimated by measuring the mean length and breadth of each leaf. Although the aspect of the slope on which each individual occurred was measured, this factor is unlikely to have been significant, as the slopes in the SIFE plots are gentle, between 0-10°.



Figure 8. Method of measuring branch extension. The maximum distance that any living part of any branch reaches to the NE, SE, SW and NW from the stem was measured, such as distance **a** in the NE quadrant.

In the second study we investigated the same aspects of the growth of a slightly wider range of species, this was possible because of the much larger area within the SIFE plots not beneath the crowns of *P. undulatum*. The differences were that:

- the seedlings were not beneath the crowns of *P. undulatum* saplings or trees
- they were all within the marked subplots (therefore their heights were measured in 1994 and will be in future enumerations)
- as the x-y coordinates were recorded, the seedling density, i.e. the extent of interference from neighbours, can be calculated.

The coefficient of variation (CV) of branch extension was calculated, using a correction for bias (Sokal & Rohlf 1981):

$$CV = \left(\frac{s100}{x}\right)\left(1 + \frac{1}{4n}\right)$$

Data were collected from a total of 18 species in the two studies, but in the figures, results are just shown for 15 of these, the five commonest gap-demanding, gap-benefitting and shade-tolerant species.

Maximum DBH of each species

The maximum DBH of any individual stem in any plot at any enumeration for each of 119 species (those present in at least one of the 144 permanent sample plots) was calculated. The heights of trees have not been recorded in most of the plots in the Blue Mountains and even when they have been the measurements have often not been accurate (P.J. Bellingham, pers. comm., 1993), so we do not provide an analysis of maximum heights here.

Population density

Seedling survival. The seedling survival of different species in the ten *Undisturbed Control* plots in the Heavily Invaded Forest Experiment was calculated. Mortality per year was calculated in the form:

$$m = 1 - (N_1/N_0)^{1/t}$$

where N_0 and N_1 are population counts at the beginning and end of the measurement interval, and t is in years (Sheil *et al.* 1995).

Maximum population density. The maximum seedling density (m⁻²) per sub-plot in the 25 HIFE plots and 12 SIFE plots (692 sub-plots altogether) reached by each of the 119 species occurring in at least one of the 144 permanent sample plots; and the maximum tree density (m⁻²) reached by the same species in any one of the 144 plots at any enumeration, was calculated.

Species dominance. The summed heights of all seedlings in a plot or sub-plot is a useful measure of dominance (Healey 1990). The heights of all seedlings in the 692 sub-plots in the 37 HIFE and SIFE plots at the pre-treatment enumeration was summed, and expressed as a density per square metre. The maximum value for all 89 species occuring as a seedling in either HIFE or SIFE was calculated.

3.2 Results

3.2.1 Growth rate

The relative basal area increment (RBAI) between 1991 and 1994 of the five regeneration classes in the Tanner (Col, Mull Ridge and North slope) plots, Bellingham stratified plots and HIFE *Undisturbed Control* plots is shown in Figure 9.



Figure 9. Mean (and standard error of mean) relative basal area increment of five size classes of different regeneration classes between 1991 and 1994 in the Tanner Col, Mull ridge and Wet slope plots, Bellingham stratified plots and the Undisturbed Control plots of HIFE.

The RBAI declines with increasing size as would be expected, with an increase from Size class 2 to 3 for the Slow growing pioneer class, largely due to the RBAI of *Cyrilla racemiflora*, shown in Figure 10). The similarity in RBAI between the gap-benefitting, shade-tolerant and slow growing pioneers trees is interesting, given the very different growth rates of seedlings of these classes. There are few small stems of gap-demanding species, mostly because of the lack of disturbance of these forests between Hurricane Hazel in 1951 and H. Gilbert in 1988. No individuals of gap-demanding species recruited as a result of H. Gilbert had reached tree size by 1991.

The RBAI between 1991 and 1994 of *P. undulatum* and the nine commonest native species (all species with >100 stems) in the same Tanner (Col, Mull Ridge and North slope) plots, Bellingham stratified plots and HIFE *Undisturbed Control* plots is shown in Figure 10.



(a) Gap demanding or benefitting species

0.00



2

3 4

5

2

5

5

5 1

2 3

The most striking result is the high RBAI of some gap demanding or benefitting species compared with the dominant tree species *Clethra occidentalis, Podocarpus urbanii, Eugenia virgultosa,* and *Vaccinium meridionale. Hedyosmum arborescens* was the only species of these nine to have a growth pattern similar to that of *P. undulatum,* although the growth rate of *P. undulatum* was higher than *H. arborescens* for all size classes, particularly the middle size classes. *H. arborescens* is a relatively short-lived, though medium sized, tree. A higher proportion of *H. arborescens* trees were killed by Hurricane Gilbert than any other of the 47 commonest tree species (Bellingham *et al.* 1995).

The high variability of growth of small stems of *Alchornea latifolia* and *Cyrilla racemiflora* is partly due to the common occurrence of large sprouts from the trunk of large trees of these species. These sprouts can sometimes grow very fast, significantly faster than individual small trees of the same species and size in the same environment. But this is not so for all species which produce many sprouts. For example *llex macfadyenii* produces a higher number of sprouts (that reach 3 cm DBH) than any other species, but sprouts as well as main stems grow slowly.

The results of an analysis of *P. undulatum* and native seedling growth (not presented here) show a similar pattern, with *P. undulatum* consistently having a faster mean growth than almost all native species. In four experimentally created gaps however a small number of native species (particularly *Brunellia comocladiifolia* and *Miconia dodecandra*) grew faster as juveniles and small trees than *P. undulatum*. Both of these species can be described as pioneer trees typical of lowland tropical rain forest. *B. comocladiifolia* can become a large tree (>50 cm DBH) but its regeneration is confined to areas of high disturbance and is uncommon in forest (occurring at a mean density of only 1.59 stems per hectare in our permanent sample plots). *M. dodecandra* is a small, even less common tree, and is similarly confined to disturbed areas.

3.2.2 Growth form

Mean crown extension of large seedlings

The relationship between the height and the mean crown extension of the large seedlings is shown in Figure 11 overleaf.



Figure 11. Relationship between the height (cm, on the x-axis) and the mean branch extension (cm, on the yaxis) of large (100-300 cm) seedlings of 15 species. Blue diamonds represent individuals not growing directly beneath the crown of P. undulatum trees, whereas red crosses represent individuals beneath P. undulatum trees. The top five species are gap demanding, the middle five are gap benefitting and the bottom five are shade tolerant. Mean branch extension on the y-axis, height on the x-axis, both in cm.

It is evident that the steepness of the regression relationship between height and mean crown extension is greater for *P. undulatum* than for any native species and that the relationship is a relatively close one (the data has not yet been statistically analysed). *Urbananthus critoniforme* (a small short-lived near-pioneer tree) is the only one of these native species to show a similar increase in branch extension with increasing size, though unfortunately it was not possible to find more individuals in the SIFE plots to make the relationship clearer. Overall there is no obvious difference between gap-demanding, gap-benefitting and shade-tolerant species. Note that the gap-benefitting class includes species with a wide degree of response to gap formation, from species clearly greatly favoured by disturbance (for example *Hedyosmum arborescens*) to species apparently little affected (for example *Ilex harrisii*). Of the shade-tolerant species three of the commonest (*Eugenia virgultosa, E. monticola* and *Guarea glabra*) show a noticeably similar relationship. *Cinnamomum montanum* has a particularly extensive crown.

Myrsine coriacea shows a much greater degree of variability in mean branch extension for a given height than *P. undulatum* or native species such as *Hedyosmum arborescens* or *Alchornea latifolia*. *M. coriacea* is a species that has branches that fail to grow if the light intensity from the side, or if inter-plant competition, is intense (leafless dying-back branches are common). In these situations *M. coriacea* seedlings appear (above-ground) to put all their resources into height growth.

Table 5. Mean crown area (m^2) ; maximum branch extension as a percentage of the individual's height for any individual; mean of the coefficient of variation (CV) of branch extension for each individual; mean of the height:crown diameter ratio for each individual; mean Leaf Area Index (LAI); and mean crown volume (m^3) for the 18 species

Species	Mean crown area (m ²)	Max. branch extension as % of height	Mean CV of branch extension	Mean height/ crown diam. ratio	Mean LAI	Mean crown volume (m³)
Alchornea latifolia	0.09	28.3	25	4.28	3.15	0.02
Cinnamomum montanum	0.29	55.2	26	2.26	1.07	0.09
Clethra occidentalis	0.23	41.7	38	2.60	1.11	0.04
Dendropanax pen/nut	0.11	37.9	31	4.18	1.84	0.02
Eugenia monticola	0.18	31.6	29	3.38	2.48	0.09
Eugenia virgultosa	0.13	44.9	40	3.48	0.89	0.04
Guarea glabra	0.16	54.5	37	3.04	1.45	0.04
Hedyosmum arborescens	0.18	37.0	34	2.93	1.71	0.06
llex harrisii	0.09	46.8	46	4.73	3.88	0.02
Maytenus jamaicensis	0.20	58.5	37	2.82	2.06	0.06
Mecranium purpurascens	0.10	39.0	41	3.89	0.99	0.03
Myrsine coriacea	0.20	47.4	42	4.46	0.94	0.06
Palicourea alpina	0.14	47.1	47	3.85	1.41	0.04
Pittosporum undulatum	0.41	69.3	43	2.29	1.39	0.17
Psychotria corymbosa	0.13	40.1	47	3.65	1.06	0.04
Sapium harrisii	0.17	27.7	18	3.62	1.51	0.06
Sideroxylon montanum	0.31	49.7	25	2.52	1.84	0.11
Urbananthus critoniformis	0.30	29.0	28	2.62	1.67	0.08
Native species	0.17	58.5	36	3.52	1.72	0.05

The mean branch extension of *P. undulatum* was 4 cm greater than the mean branch extension of any native species, and 14.6 cm (54.3%) greater than the mean for all native species. The maximum branch extension of *P. undulatum* was 25 cm longer than that of any branch of any native species, or when extensions are expressed as a percentage of seedling height (column 3), over 10% greater than that of any native species. The height:crown diameter ratio (column 5) of *P. undulatum* was 2.29, just above *Cinnamomum montanum*, i.e. both these species have a very broad crown for a given height. The mean L.A.I. of *P. undulatum* was near the average for all species, the high leaf area per individual (Fig. 13) being distributed over a larger crown area than native species (column 2). The high crown area of *P. undulatum* combined with its deep crown (Fig. 12) to give a mean crown volume over three times the mean for native species combined.

Variability of branch extension

The ability to efficiently exploit above-ground resources depends on the degree to which plants can increase their lateral growth towards areas of higher resource availability. The light environment in many areas of the Blue Mountains has been highly spatially variable since Hurricane Gilbert, with many gaps created by the fall of large branches or trees, or the later death of standing damaged trees (though most of these gaps have now "filled in"). As the distance of branching was measured in four directions for each seedling we have been able to calculate the coefficient of variation of branch length for each individual plant and derive the mean for each species, shown in Table 5 (column 4).

P. undulatum had the third highest value, lower than the two gap demanding or benefitting species *Palicourea alpina* and *Psychotria corymbosa*. The mean branch extension of both these native species is only about 60% that of *P. undulatum* and their high degree of variability in branch extension is partly due to a failure of some seedlings to produce branches in some directions. Whether this was a failure to produce a branch, mechanical damage to a developing branch (*P. corymbosa* is very weak stemmed) or a "tactical" exploitation of resources by the plant (effected by a diversion of resources into those branches produced on the side of the plant experiencing higher light levels) we cannot say. Such a tactical explanation seems more likely with *P. alpina* than with *P. corymbosa*, and very likely with *P. undulatum*.

Crown depth of large seedlings

The crown depth of the seedlings is shown in Figure 12 on the next page. It would be expected that, for individuals with equal leaf area, those with deep crowns would collect less light from vertically above and more sidelight, hence deep crowns would be more prevalent in shade-tolerant species. For these 15 species the relationships are not at all clear, though there appears to be some evidence to support this hypothesis. Shade-tolerant *Eugenia monticola* had a consistently deep crown, whereas the gap-demanding *Alchornea latifolia* had a consistently shallow crown. The deep crowns of *Sapium harrisii* and *Palicourea alpina* are rather deceptive, as both species can retain leaves produced on the main stem early in growth, and whether the crown can really be said to extend this low is questionable. *Hedyosmum arborescens* had a very similar regression relationship to *P. undulatum*, both having a rather consistently deep crown. Both *Eugenia virgultosa* (probably the most shade-tolerant of these species) and *Myrsine coriacea* (one of the least shade-tolerant species) had very variable crown depths.



Figure 12. The relationship between seedling height (cm, on the x-axis) and the crown depth (cm, on the y-axis), for each large seedling of the 15 species. Crown depth was calculated as total height minus height to the lowest living leaf. Leaf area of large seedlings



The relationship between the height of the saplings and the total leaf area is shown in Figure 13.

Figure 13. The relationship between the height (cm, on the x-axis) and the total leaf area (m^2 , on the y-axis) of large seedlings of 15 species. Blue diamonds represent individuals not growing directly beneath the crown of P. undulatum trees, whereas red crosses represent individuals growing beneath P. undulatum trees. The top five species are gap demanding, the middle five are gap benefitting and the bottom five are shade tolerant.

In general the mean leaf area per species increased in the order gap-demanding < gap-benefitting < shadetolerant, with much variation between species within class. The leaf area of *P. undulatum* was strikingly higher than any native species (again with the possible exception of *Urbananthus critoniforme*). The shade-tolerant *Maytenus jamaicensis* had a noticeably high leaf area. Although the slopes of the regression relationship of *Alchornea latifolia* and *Sapium harrisii* are similar to *Palicourea alpina*, *Psychotria corymbosa* and *Myrsine coriacea* the leaves of both species are significantly larger, partly explaining why their slopes intercept the yaxis at a higher level than the other three gap favoured species. The difference between the congenerics *Eugenia monticola* and *E. virgultosa* is very noticeable. The two species had almost identical mean branch extensions, whereas *E. monticola* had a consistently deeper crown than *E. virgultosa*, but the most noteworthy difference between them is the different leaf sizes (a mean of 0.0004 m² for *E. virgultosa* and 0.0018 m² for *E. monticola*).

Maximum DBH of each species

The maximum DBH of any tree for each of the 116 species occurring as a tree in at least one of the 144 plots permanent sample plots in the Blue Mountains is shown in Table 6. The small size of the trees compared with lowland tropical rain forest is obvious but is typical of montane forests (Grubb & Tanner 1976). Larger trees occur outside plots of course, the largest typically-shaped native tree (a *Sapium harrisii*) so far encountered having a DBH of 97 cm. The largest *P. undulatum* had a DBH of 41.8 cm, the 21st in rank, and the DBH of the largest measured *P. undulatum* outside plots was 65.6 cm. Judged by the size of crowns we think that a few significantly larger *P. undulatum* trees occur on a remote hillside which we have never been able to visit.

Table 6. The maximum DBH (cm) of any tree for each of the 116 species occurring as a tree in at least one of the 144 plots permanent sample plots in the Blue Mountains.

Species	DBH	Species	DBH	Species	DBH	Species	DBH
Jun luc	75.0	Eug mon	30.5	Cya woo	14.1	Cli ter	6.4
Alc lat	71.9	Rha sph	29.2	Den pen	13.9	Bid shr	6.3
Sid mon	71.3	Den nut	28.3	Psy cor	13.8	Con mon	5.7
Tur occ	68.1	Clu hav	28.1	Cal rig	13.7	Tou gla	5.5
Hae inc	61.0	Sym oct	27.8	Lyo jam	13.0	Sch inv	5.5
Pod urb	58.2	Cle the	27.5	Psy slo	12.5	Mal arb	5.3
Vac mer	57.1	lle mac	27.1	Cle oxa	12.2	Boc fru	5.1
Gor hae	55.8	Myr cor	26.7	Xyl nit	12.0	Oss asp	5.1
Cyr rac	55.4	Hed arb	26.6	Tre flo	11.8	Pip arb	5.0
Gua gla	52.8	Vib spp	26.5	Ges alp	11.4	Ure ela	4.7
Sol pun	52.7	B1 mel	25.4	Vib vil	11.3	Bla tri	4.6
Cle occ	52.5	lle har	25.2	Per alp	11.0	Aca vir	4.3
Sap har	52.3	lle obc	24.2	Mar bro	10.8	Lob ass	3.8
Myr cer	51.1	Den p/n	24.0	Cri par	10.4	Wei pin	3.7
Bru com	50.1	lle vac	23.8	Mec pur	10.4	Wal faw	3.6
Den arb	47.7	Eug har	23.8	Mer leu	10.2	Dur ere	3.4
Cha glo	44.7	Cin pub	23.7	Cya con	9.9	Bes lut	3.4
Cin mon	44.6	Gar fad	23.1	Bru jam	9.8	Sal sca	3.1
May jam	44.1	Eug mar	23.0	Ces hir	9.4	Lob mar	3.0
Lyo oct	43.0	Sch sci	21.4	Mic rig	9.1	Pip fad	3.0
Pit und	41.8	Eug vir	20.4	Phy arb	8.8	Mic dod	2.5
Cle ale	38.5	Mer pur	20.1	Boe cau	8.3	Ver plu	1.9
Cit cau	37.2	Wal cal	19.7	Pic ant	7.9	Phe hir	1.1
lle nit	36.6	Eug bra	18.9	Urb cri	7.7	Koa har	1.0
Myr acr	34.4	Cin off	17.8	Wal cra	7.6	Met spp	0.9
Vib alp	33.6	Mic the	17.4	Cas vim	7.5	Smi bal	0.8
Myr fra	33.6	Cya fur	17.2	Pit vir	7.1	Mik max	0.7
Oco pat	33.3	Mic qua	17.1	Odo fad	6.6	Com cli	0.6
Cya pub	31.8	Pru occ	16.7	Cal fer	6.5	Pas pen	0.5

Population density

Seedling survival

The mortality of *P. undulatum* and native species classified into regeneration groups is shown in Figure 14 and is shown for all native species with over ten individuals in Table 7.

Table 7. Annual mortality rate of five size classes of P. undulatum, all individual native species with over ten individuals and four regeneration groups of native species (in bold) in the ten Undisturbed Control plots in HIFE between 1991 and 94; results are in the sequence of decreasing overall mortality. RG = regeneration group. The five size classes are, in cm: **1** < 10, **2** 10-19, **3** 20-49, **4** 50-99, **5** > 100 cm.

Number of seedlings in 1991 Annual mortality rate													
Species/class	RG	1	2	3	4	5	all	1	2	3	4	5	all
Turpinia occidentalis	GB	6	15	5	0	0	26	0.365	0.421	0.191			0.356
Alchornea latifolia	GD	14	19	5	0	0	38	0.472	0.233	0.088			0.283
Gap demanding		27	29	11	2	0	69	0.337	0.198	0.080	0.000		0.219
Podocarpus urbanii	GB	3	1	1	2	3	10	0.365	0.000	1.000	0.250	0.000	0.191
Psychotria corymbosa	GB	169	85	24	17	24	319	0.266	0.094	0.035	0.051	0.035	0.166
Clethra occidentalis	GB	9	5	0	2	1	17	0.285	0.088		0.000	0.000	0.165
Gap benefitting		249	142	57	36	46	530	0.229	0.107	0.053	0.048	0.028	0.142
Palicourea alpina	GD	7	7	3	1	0	18	0.130	0.130	0.155	0.000		0.126
Myrsine coriacea	GB	28	9	7	1	4	49	0.148	0.099	0.130	0.000	0.000	0.120
Citharexylum caudatum	U	10	2	3	1	1	17	0.088	1.000	0.000	0.000	0.000	0.105
llex harrisii	GB	6	1	0	3	3	13	0.250	0.000		0.000	0.000	0.103
Smilax balbisiana	U	10	6	7	2	4	29	0.191	0.073	0.062	0.000	0.000	0.092
Prunus occidentalis	ST	0	3	9	1	8	21		0.000	0.155	1.000	0.000	0.084
Eugenia virgultosa	ST	206	133	87	49	26	501	0.130	0.072	0.044	0.009	0.016	0.081
Xylosma nitida	U	3	3	9	3	4	22	0.365	0.155	0.048	0.000	0.000	0.080
Pittosporum undulatum	GB	414	435	369	269	307	1794	0.175	0.094	0.039	0.005	0.005	0.070
Myrcianthes fragrans	U	135	10	13	9	2	169	0.085	0.000	0.033	0.000	0.000	0.070
Shade tolerant		383	244	153	96	72	948	0.116	0.055	0.042	0.017	0.006	0.069
Cinnamomum montanum	ST	5	6	10	11	4	36	0.088	0.073	0.088	0.039	0.000	0.060
Unclassified		277	76	96	60	73	582	0.084	0.051	0.040	0.007	0.000	0.053
Psychotria sloanei	U	89	11	5	0	4	109	0.058	0.039	0.000		0.000	0.051
Guarea glabra	ST	2	11	10	4	3	30	0.250	0.080	0.000	0.000	0.000	0.043
Cassia viminea	GB	21	17	17	5	1	61	0.084	0.051	0.000	0.000	0.000	0.042
Ocotea patens	ST	5	4	22	11	10	52	0.000	0.000	0.039	0.000	0.000	0.016
Maytenus jamaicensis	ST	13	10	1	2	2	28	0.033	0.000	0.000	0.000	0.000	0.015
Eugenia monticola	ST	43	51	33	25	26	178	0.010	0.016	0.000	0.000	0.000	0.007
Eugenia harrisii	U	4	12	8	14	31	69	0.000	0.035	0.000	0.000	0.000	0.006
Vernonia pluvialis	U	1	6	10	9	7	33	0.000	0.000	0.000	0.000	0.000	0.000
Eugenia marchiana	ST	10	7	1	1	0	19	0.000	0.000	0.000	0.000		0.000
Malvaviscus arboreus	GB	4	7	3	1	0	15	0.000	0.000	0.000	0.000		0.000
Picramnia antidesma	U	3	9	0	1	0	13	0.000	0.000		0.000		0.000



Figure 14. Annual mortality rate between 1991-93 of seedlings of P. undulatum, and those of native species classified into four regeneration 10 Undisturbed groups. in Control plots in HIFE; see text for an explanation of how annual mortality was calculated.

The mortality rate for smaller seedlings was greater than that for larger seedlings for P. undulatum and all regeneration groups. Shade-tolerant species generally had lower mortality, though two climber/scramblers classified as gap benefitting (Cassia viminea and Malvaviscus arboreus) had a lower overall mortality than the mean for all shade-tolerant species. The mortality rate of Eugenia monticola was only about one-tenth that of E. virgultosa. There was a low density of gap-demanding species (many of those that were present were recruited by Hurricane Gilbert); there were seedlings of the gapno demanding class in the largest size class.

The mortality rate for all size classes of P. undulatum was very similar to gap-benefitting native species, the group which P. undulatum would be placed into, based on growth rate criteria. For the largest three size classes the mortality of P. undulatum was less than that of the mean for shade-tolerant species. Of the 24 native tree species with >10 individuals, all those classified as gap demanding or gap benefitting (and some classified as shadetolerant) had a higher overall mortality than *P. undulatum*.

Maximum population density

The maximum seedling density (m^{-2}) per sub-plot in the 37 HIFE and SIFE plots reached by each of the 119 species occurring in at least one of the 144 permanent sample plots; and the maximum tree density (m^{-2}) reached by the same species in any one of the 144 plots at any enumeration is shown in Table 8.

Table 8. The maximum seedling density (m^{-2}) per sub-plot in the 37 HIFE and SIFE plots reached by each of the 119 species occurring in at least one of the 144 permanent sample plots in the western Blue Mountains; and the maximum tree density (m^{-2}) reached by the same species in any one of the 144 plots at any enumeration. The species are arranged in order of decreasing seedling density within each column.

Species	Sdlgs	Trees	Species	Sdlgs	Trees	Species	Sdlgs	Trees
Eugenia virgultosa	215.97	0.347	Wallenia calyptrata	3.00	0.050	Cionosicys pomiformis	0.69	0.000
Pittosporum undulatum	197.00	0.306	Malvaviscus arboreus	3.00	0.030	Gonolobus jamaicensis	0.69	0.000
Maytenus jamaicensis	47.22	0.076	Miconia theaezans	3.00	0.008	Gonolobus stapelioides	0.69	0.000
Myrcianthes fragrans	43.00	0.042	Passiflora penduliflora	2.78	0.000	llex vaccinoides	0.69	0.030
Clethra occidentalis	40.28	0.175	llex obcordata	2.78	0.080	Marcgravia brownei	0.69	0.024
Psychotria corymbosa	29.00	0.095	Symplocos octopetala	2.78	0.020	Conostegia montana	0.69	0.020
Eugenia monticola	26.00	0.192	Acalypha virgata	2.78	0.017	Persea alpigena	0.69	0.020
Alchornea latifolia	22.92	0.110	Wallenia fawcettii	2.78	0.010	Odontocline fadyenii	0.69	0.011
Guarea glabra	18.75	0.165	Sideroxylon montanum	2.08	0.050	Brunellia comocladiifolia	0.69	0.008
Psychotria sloanei	16.00	0.125	llex harrisii	2.08	0.049	Duranta erecta	0.69	0.007
Palicourea alpina	15.28	0.165	Tournefortia glabra	2.08	0.003	Lyonia octandra	0.00	0.370
Eugenia marchiana	15.28	0.049	Calyptranthes rigida	2.00	0.060	Cyathea pubescens	0.00	0.173
Mecranium purpurascens	11.11	0.080	Miconia quadrangularis	2.00	0.050	Clethra alexandra	0.00	0.130
Cassia viminea	9.72	0.020	Urbananthus critoniformis	2.00	0.050	Dendropanax pendulus	0.00	0.120
Myrsine coriacea	9.00	0.069	Dendropanax arboreus	2.00	0.040	Cyrilla racemiflora	0.00	0.117
Koanophyllon hardwarense	7.64	0.000	Bidens shrevei	2.00	0.021	Cyathea furfuracea	0.00	0.110
Hedyosmum arborescens	7.64	0.150	Callicarpa ferruginea	2.00	0.020	Juniperus lucayana	0.00	0.100
Sapium harrisii	7.64	0.010	Rhamnus sphaerospermus	2.00	0.015	Boehmeria caudata	0.00	0.083
Turpinia occidentalis	6.94	0.083	Wallenia crassifolia	2.00	0.015	Miconia rigida	0.00	0.070
Mannetia lygistum	6.25	0.000	Dendropanax pen/nut	1.39	0.000	Cleyera theaoides	0.00	0.045
Phyllanthus arbuscula	6.25	0.051	Phenax hirtus	1.39	0.000	Myrica cerifera	0.00	0.042
Cinnamomum montanum	6.25	0.021	Vaccinium meridionale	1.39	0.326	Bocconia frutescens	0.00	0.033
Meriania purpurea	5.56	0.085	Solanum punctulatum	1.39	0.050	Mecranium virgatum	0.00	0.033
Piper arboreum	5.56	0.020	Haenianthus incrassatus	1.39	0.030	Eugenia alpina	0.00	0.030
Salmea scandens	4.17	0.000	Gordonia haematoxylum	1.39	0.021	Schradera involucrata	0.00	0.025
Eugenia brachythrix	4.17	0.017	Cestrum hirtum	1.39	0.017	Cinchona pubescens	0.00	0.021
Lobelia assurgens	4.17	0.005	Besleria lutea	1.00	0.000	Cyathea woodwardioides	0.00	0.020
Smilax balbisiana	4.00	0.000	Cissampelos pareira	1.00	0.000	Lyonia jamaicensis	0.00	0.017
Podocarpus urbanii	4.00	0.180	Daphnopsis americana	1.00	0.000	Gesneria alpina	0.00	0.015
Eugenia harrisii	4.00	0.132	Cinchona officinalis	1.00	0.195	Urera elata	0.00	0.015
Citharexylum caudatum	4.00	0.058	llex macfadyenii	1.00	0.192	Clibadium terebinthinaceum	0.00	0.014
Brunfelsia jamaicensis	4.00	0.044	Chaetocarpus globosus	1.00	0.150	Cyathea concinna	0.00	0.010
Myrsine acrantha	4.00	0.035	Clusia havetiodes	1.00	0.120	Lobelia martagon	0.00	0.010
Ocotea patens	4.00	0.035	Schefflera sciadophyllum	1.00	0.083	Viburnum villosum	0.00	0.010
Prunus occidentalis	4.00	0.021	Garrya fadyenii	1.00	0.076	Weinmannia pinnata	0.00	0.010
Vernonia pluvialis	3.47	0.000	Viburnum alpinum	1.00	0.063	llex sideroxyloides	0.00	0.007
Picramnia antidesma	3.47	0.028	Critonia parviflora	1.00	0.060	Pittosporum viridiflorum	0.00	0.007
Piper fadyenii	3.47	0.005	Meriania leucantha	1.00	0.040	Ossaea asperifolia	0.00	0.005
Xylosma nitida	3.00	0.066	llex nitida	1.00	0.020	Dendropanax nutans	0.00	0.002
			Blakea trinerva	1.00	0.010	Trema floridanum	0.00	0.002

Eugenia virgultosa was the only native species to occur at a similar high density to *P. undulatum*. Of the other common species, *Maytenus jamaicensis* is another shade-tolerant species common in primary forest; and *Myrcianthes fragrans* is a species with an unusually clumped distribution - the mean density in one plot was 8.05 seedlings m⁻² compared with a mean density in the other HIFE and SIFE plots of 0.21 seedlings m⁻². Recruitment of *Clethra occidentalis* is almost confined to the lower stems of *Cyathea* tree ferns (Newton & Healey 1989), where it can be dense. All the sub-plots in which seedlings were enumerated occured in forest that was relatively undisturbed, and densities of several species were much higher in gaps (Healey 1990). *P. undulatum* was one of only four species to have a maximum tree density of over 200 stems per hectares; *Eugenia virgultosa* is the commonest tree in the Blue Mountains, whilst *Vaccinium meridionale* and especially *Lyonia octandra* are abundant in the localised Mor Ridge forest, where both occur typically as multi-stemmed individuals. Twelve of the 14 species occurring as seedlings but not as trees were climbers that never reach 3 cm DBH. The maximum density of saplings (stems >3 m high but <3 cm DBH) of *P. undulatum* was 0.605 m⁻², nearly twice that of *Eugenia virgultosa*, the densest native species - this data is not presented in full as saplings were enumerated in only 59 of the 144 plots.

3.2.4 Species dominance

The maximum seedling dominance for all 89 species occuring as a seedling is shown in Table 9.

Table 9. The maximum seedling dominance (M.D.) per sub-plot (in terms of summed heights (m m⁻²)) of all 89 species occuring as seedlings in at least one of the 692 sub-plots in HIFE or SIFE. The species are arranged in order of decreasing seedling dominance within each column.

Species	M.D.	Species	M.D.	Species	M.D.
Pittosporum undulatum	52.04	llex harrisii	3.02	Eugenia brachythrix	1.82
Alchornea latifolia	20.47	Dendropanax arboreus	2.97	Brunfelsia jamaicensis	1.81
Koanophyllon hardwarense	16.88	Citharexylum caudatum	2.95	Turpinia occidentalis	1.76
Eugenia virgultosa	15.35	Tournefortia glabra	2.93	Daphnopsis americana	1.60
Mecranium purpurascens	14.97	Mannetia lygistum	2.84	Passiflora penduliflora	1.60
Eugenia monticola	8.01	Myrsine coriacea	2.80	Persea alpigena	1.59
Piper arboreum	7.95	Psychotria sloanei	2.80	llex macfadyenii	1.54
Psychotria corymbosa	7.95	Chaetocarpus globosus	2.75	llex obcordata	1.54
Guarea glabra	7.63	Clusia havetiodes	2.70	Phyllanthus arbuscula	1.53
Maytenus jamaicensis	6.88	Malvaviscus arboreus	2.70	Viburnum alpinum	1.48
Acalypha virgata	6.79	Urbananthus critoniformis	2.70	Conostegia montana	1.24
Hedyosmum arborescens	6.60	Meriania purpurea	2.64	Odontocline fadyenii	1.19
Palicourea alpina	5.78	Cinnamomum montanum	2.62	Haenianthus incrassatus	1.11
Smilax balbisiana	5.30	Eugenia marchiana	2.51	llex nitida	1.05
Clethra occidentalis	5.12	Wallenia calyptrata	2.50	Cestrum hirtum	1.02
Ocotea patens	4.87	Picramnia antidesma	2.33	Cionosicys pomiformis	0.67
Cassia viminea	4.84	Miconia quadrangularis	2.30	Bidens shrevei	0.60
Eugenia harrisii	4.76	Myrsine acrantha	2.23	Gonolobus jamaicensis	0.60
Prunus occidentalis	4.66	Critonia parviflora	2.22	Solanum punctulatum	0.56
Wallenia fawcettii	4.58	Podocarpus urbanii	2.22	Besleria lutea	0.54
Salmea scandens	4.44	Sideroxylon montanum	2.17	Cissampelos pareira	0.51
Wallenia crassifolia	4.31	Xylosma nitida	2.16	Blakea trinerva	0.48
Piper fadyenii	4.11	Gordonia haematoxylum	2.16	Lobelia assurgens	0.45
Sapium harrisii	3.86	Schefflera sciadophyllum	2.15	Vaccinium meridionale	0.39
Phenax hirtus	3.75	Brunellia comocladiifolia	1.99	Marcgravia brownei	0.26
Symplocos octopetala	3.49	Miconia theaezans	1.95	Garrya fadyenii	0.25
Calyptranthes rigida	3.44	Callicarpa ferruginea	1.92	llex vaccinoides	0.18
Vernonia pluvialis	3.30	Cinchona officinalis	1.90	Gonolobus stapelioides	0.13
Myrcianthes fragrans	3.15	Rhamnus sphaerospermus	1.90	Meriania leucantha	0.11
				Duranta erecta	0.03

The maximum dominance of *P. undulatum* as a seedling can be very great, 52 m m⁻², 2.5 times the dominance of the highest native species, *Alchornea latifolia*. *A. latifolia* is a species whose germination and recruitment is greatly enhanced by disturbance and after Hurricane Gilbert achieved dominance, over large areas in the more disturbed areas, to a much greater degree than any native species. *Koanophyllon hardwarense* is a climber that forms clumps, one clump dominating a single sub-plot in SIFE, giving the species such a high value. *Eugenia virgultosa* is the commonest understorey species and can achieve dominance of the seedling layer except under the densest shade. *Mecranium purpurascens* is a species that produces suckers, and can achieve high local dominance by that means.

Dominance of trees as expressed by basal area is less illuminating, as *P. undulatum* is present in most plots only as a small tree, because of the early stage of the invasion. In one plot *P. undulatum* comprised 68% of the total plot basal area, though in most plots in heavily invaded forest, larger native trees, possibly left when the original forest was cleared, dominate in terms of basal area.

4.

Discussion

4.1 Relationship between the dominance of *P. undulatum* and native species

There is a clear, approximately linear, negative relationship between the basal area of *P. undulatum* and the density of the native seedling layer. A similar result is obtained when the dominance of *P. undulatum* is expressed in relative terms (i.e. as a proportion of plot basal area) and when dominance (absolute or relative) is regressed against the dominance (summed heights) of native seedlings. The density of native seedlings can be very low in primary forest (though only one sub-plot in SIFE had no seedlings in it at all), but the SIFE plots are large enough (21x15 m) for every plot to have some sub-plots with the much higher seedling densities associated with disturbance, therefore averaging-out plot means.

An interesting question that we have not addressed in this study is where in the Blue Mountains species diversity is highest. A preliminary inspection of the data suggests it may not always be in primary forest, as sometimes old secondary forest (little invaded by *P. undulatum*) can have a high diversity. It is possible that the density and diversity of the understorey in secondary forest would decline (perhaps in the short-term only) even without *P. undulatum*, as the native shade-tolerant species that are dominant in primary forest invade. Some of them (for example *Guarea glabra* and *Dendropanax arboreus*) can have crowns that are about as dense as those of *P. undulatum* trees (T. Goodland, unpublished data). But we do not have sufficient data from old secondary forest, where this re-invasion appears to be happening, to draw firm conclusions.

In the study of the growth form of *P. undulatum* and native species (section 3.2.2) a visual examination of the data shows that for some species (such as *Eugenia virgultosa*, *Guarea glabra*) there seems to be a significant effect of *P. undulatum* on leaf area, and for one species (*E. virgultosa*) *P. undulatum* appears to be affecting mean branch extension, though we have not yet carried out any statistical analyses. There seems to be little effect of *P. undulatum* adults on crown depth, so overall it is clear that the small *P. undulatum* trees in the SIFE plots are not yet having a major impact on native regeneration.

There does not appear to be any relationship between the number of *P. undulatum* and native trees (results not given here). This is probably because when the forest started to regrow following clearance, *P. undulatum* was not dominant as a species, but the scattered trees that did establish have now lead to dense regeneration of the species, which now seems to be suppressing the growth of smaller native plants.

All the correlations presented here suffer from confounding, and this is particularly true when interpreting the results for individual species. Several species occur commonly as seedlings in primary forest but are rare or absent from secondary forest. We cannot say whether this is due to the effects of *P. undulatum* or the fact that adult trees of most of the species were eliminated when the original forests were cut down, (21 (84%) of the HIFE plots are in forest that is definitely secondary). The recruitment and growth of *P. undulatum* has been markedly increased by the past human disturbance in these forests. Also the disturbance created by Hurricane Gilbert has complicated the results of HIFE as the density of advance regeneration at the initial enumeration was probably significantly higher in some plots than would have been the case without the hurricane. Another complication is that all the HIFE plots are on the southern slopes of the Blue Mountains, whilst four out of the 12 SIFE plots were either on the north slopes or Grand Ridge, areas which tend to have a different forest composition, perhaps because of higher rainfall.

Ideally an experimental approach is needed if the objective is to find out what is limiting the re-invasion of these secondary forests by primary forest species, planting seedlings of those common primary forest species absent or rare in secondary forest, beneath dense stands of *P. undulatum* and beneath stands of native trees in univaded secondary forest. The majority of native species in the Blue Mountains either require disturbance for their recruitment or benefit from it. Of the 27 most studied species the recruitment of 22 was increased by disturbance (Sugden *et al.* 1988, Healey 1990, Vernon 1991, Dalling 1992). Therefore the effect of *P. undulatum* on recruitment following disturbance is probably crucial to a majority of species.

Competitive success of *P. undulatum*

4.2.1 Performance of individuals

Many analyses of the growth of species in our permanent sample plots (including several not presented here) show that *P. undulatum* is one of the fastest growing species in a wide range of degrees of disturbance, from its seedling stage through to the tree stage. Our analysis of the above-ground growth form of large seedlings shows that *P. undulatum*, compared with the 17 native species, has:

- a high mean branch extension, therefore low height:crown diameter ratio and high crown area
- an exploratative branching pattern, able to exploit higher light levels arriving from a particular direction
- a consistently deep crown
- a high leaf area per individual

It will be possible with further enumerations of SIFE to accurately age these seedlings, so allowing an examination of how these parameters vary with age, not just size. Our information on the growth form and architecture of trees of these species is much less complete. The native species with the closest growth form to *P. undulatum* is *Hedyosmum arborescens*, (though *P. undulatum* had a greater mean branch extension and crown depth and significantly larger leaf area), and interestingly *H. arborescens* had a closer similarity in the RBAI of its trees to *P. undulatum* than any other native species. Overall there was no close comparison between *P. undulatum* and native species.

One way in which species may differ in their response to a low light environment is their ability to position their whole axis towards higher light levels. In very low light levels (usually beneath dense stands of *P. undulatum* trees) *P. undulatum* seedlings are often leaning or prostrate. This is probably a sign of stress (indeed where this occurs in the most heavily invaded HIFE plots a number of these seedlings have died-back, and even died) but they do tend to be oriented towards higher light levels. This is occasionally seen in native species, though not so often (T. Goodland, pers. obs.).

We have some intriguing evidence that the below-ground competitive ability of *P. undulatum* is very high, but further research would be needed to provide a clearer picture. The evidence that we do have comes from measurements of the root system of six seedlings of *P. undulatum* and eight native species (Goodland & Healey, unpublished data). In summary, the root system of *P. undulatum* was comparatively extensive, usually shallow, and with individual roots sometimes longer than the height of the stem. In Australia the root system of *P. undulatum* seedlings was highly variable, depending on soil type (Gleadow & Ashton 1981).

4.2.2 Populations

The high population density that *P. undulatum* can reach is one of the most striking aspects of the invasion when seen in the forest, a characteristic of invasive plants (Huenneke & Vitousek 1990). The high seed production of *P. undulatum* (Goodland & Healey 1996) is clearly important, but we have no information on the seed production of native species.

In HIFE following the removal of all existing *P. undulatum* the recruitment of *P. undulatum* could be very high. In plot 20 at t_0 (before treatment, but after the effects of Hurricane Gilbert) the density of *P. undulatum* seedlings had been 105.6 m⁻² whilst the density of *P. undulatum* recruits was 155.3 m⁻² at t_1 and 161.9 m⁻² at t_2 , a combined recruitment density of 317.2 m⁻². The t1 *P. undulatum* recruitment density of 155.3 m⁻² compares with a total recruitment of native species of only 6.9 seedlings m⁻² in that plot. We do not have data from HIFE or SIFE on seedling recruitment in primary forest so cannot make a quantitative comparison between secondary and primary forest, but the density of recruitment of some species (for example *Eugenia virgultosa, Guarea glabra* and *Prunus occidentalis*) can be high (>50 seedlings m⁻²) in primary forest (T. Goodland, personal observations).

The survivorship of *P. undulatum* is also surprisingly high for a species whose recruitment is so affected by degree of disturbance, although mortality of small seedlings can be very high. For example, in one sub-plot in

HIFE that had experienced quite severe disturbance by Hurricane Gilbert, then heavy shading by *P. undulatum* saplings, of 115 *P. undulatum* seedlings \leq 20 cm high in 1991, 109 had died by 1995, a mortality of 94%.

4.3 Persistence of *P. undulatum*

The persistence of *P. undulatum* (or any species, introduced or native), in the Blue Mountains can be considered in three different categories:

- The longevity of individual trees; in the case of *P. undulatum* or any invasive species, the longevity of the "founding" individuals.
- The rate of recruitment of new individuals
- Changes in the physical environment, and biotic relations of the species

These are shown in Figure 15, and discussed in greater detail below.



Figure 15. Factors determining the persistence of P. undulatum

4.3.1 Longevity of individuals

It is difficult to say how old the largest *P. undulatum* trees close to Cinchona are, as the species does not have distinct growth rings (Meir 1991). We have found a few (less than 10) dying trees in the lower Clydesdale valley (within a kilometre of Cinchona), presumably "dying back" either as a result of senescence, disease or adverse environmental conditions. But there are other trees nearby of a similar size that seem perfectly healthy, so *P. undulatum* is not a short-lived species. These trees are about 20 m tall but in Australia *P. undulatum* can reach 30 m, indicating a much greater age for the Australian trees.

As the invasion progresses, the reaction of *P. undulatum* trees to future hurricanes will become more important. Useful data is now available on the effects of H. Gilbert on *P. undulatum* and native trees in mostly primary forest (Bellingham 1993). The effect of H. Gilbert was assessed in 91 plots totalling 1.10 ha between February 1989 and August 1990, i.e. 5-23 months after the hurricane; namely the E.V.J. Tanner (Tanner 1977); J.R. Healey plots (Healey 1990); 26 non-bounded plots along a transect in the Mabess River valley and the 16 systematically placed plots of P.J. Bellingham (Bellingham 1993). A total of 5242 native and 53 *P. undulatum* trees were sampled.

Data on the 47 commonest species were analysed. *P. undulatum* was one of nine species that had no stems killed by the hurricane. *P. undulatum* was also one of only five species which had no stems that were completely defoliated and no stems broken. However 11.4% of *P. undulatum* were uprooted (the ninth highest species percentage, the mean for all species was 0.49%). Bellingham (1993) classified all the species into five categories of resistance to the hurricane according to levels of non-fatal damage and mortality. *P. undulatum* was placed into the most resistant category, though the relatively small number of stems (53) makes the classification tentative. In contrast to all the other species in the resistant category, *P. undulatum* is readily recruited into hurricane caused gaps. Because of this, Bellingham (1993) considered the species to have no ecological analogue in the native tree flora.

P. undulatum should also be considered a resilient species, in the sense that if damaged (for example, blown down or snapped) it shows a great ability to survive. Trees that have been blown down often put up many vertical ("epitrophic") sprouts along the fallen trunk. These sprouts can become very large (>25 cm DBH) and would indicate a prolonged life perhaps similar to that of the long-lived native tree *Cyrilla racemiflora*. Cut stems of *P. undulatum* produced a much greater biomass of resprouts than all native species except *llex macfadyenii*. After 27 months *P. undulatum* produced about ten times the mean biomass of all native species combined (Healey *et al.*).

4.3.2 Recruitment of new individuals

The ability of a species to build up a soil seed bank can be an important means of persisting in an area, so we investigated the soil seed bank of *P. undulatum* and native species in the *Remove P. undulatum Trees* and *Undisturbed Control* treatments in HIFE in 1993. The maximum mean *P. undulatum* soil seed bank density for any plot (based on the number of emergents from 10 soil samples) was 17,540 seeds m⁻², (with a maximum of 65,000 seeds m⁻² for a single sample), 8.6 times as dense as the next densest species (*Clethra occidentalis*). It is unusual for a species commonly with a "seedling bank" (i.e. seedlings existing beneath the canopy) to build up such a large soil seed bank. In this respect *P. undulatum* is quite unlike any native species in the Blue Mountains.

P. undulatum is rather poor at recruiting beneath dense canopies of *P. undulatum* trees. But, given the high seed production and soil seed bank, and the requirement for only slight disturbance for germination and recruitment, there usually are some *P. undulatum* seedlings of a range of size classes beneath all but the densest *P. undulatum* stands. It is likely that these have been recruited after sporadic, usually hurricane-caused, disturbance events.

There are native species able to grow in less disturbed conditions that *P. undulatum*, species that may have a higher chance of growing up beneath mature *P. undulatum* trees than *P. undulatum* itself. As the crowns of large *P. undulatum* trees rise above ground level, the light levels on the forest floor seems to increase (and the crown itself sometimes appears to thin). It is possible that light levels would be significantly raised beneath a stand of uniformly large and tall *P. undulatum*, but we know of no such stands at present, large *P. undulatum* trees are still scattered either in otherwise lightly invaded forest or amongst smaller *P. undulatum* regeneration. From what we know it seems highly unlikely that any native shade-tolerant species could start to replace *P. undulatum*, though the most shade-tolerant species such as *Eugenia virgultosa* or *Guarea glabra* may be able to survive in a Blue Mountains completely invaded by *P. undulatum*.

4.3.3 Changes in the biological and physical environment of the Blue Mountains

Global climate change is likely to lead to an increase in the strength of hurricanes. This would more likely favour *P. undulatum* than most native species, though it is clearly possible that some gap-demanding native species would also benefit. There is the possibility that non-tree plants may become much more dominant constituents of the forest, especially introduced species such as *Polygonum chinense*, *Hedychium gardneranum* or *Shuteria vestita*. If the Blue Mountains were to become drier, and suffer longer periods of very low rainfall (continuing a trend that many local people say has been evident for the last several years), fire could start to affect forest undisturbed by humans in a much more serious way, excluding trees altogether and favouring introduced grasses such as *Melinis minutiflora*.

The future biotic relations of *P. undulatum* could be very important, and are very unpredictable. For example in the British Isles sycamore (*Acer pseudoplatanus*) is a common invader of ash woodlands but once it has achieved dominance it fails to regenerate beneath its own canopy, whilst ash does (P. Savill, pers. comm., 1994). A possible explanation for this is that the litter layer builds up beneath a sycamore canopy providing shelter for slugs from frost during the winter; sycamore seedlings are vulnerable to slug damage whilst ash seedlings are not (P. Binggeli, pers. comm.). It is this type of unexpected interaction with native organisms that could provide an effective limit on the density, if not distribution, of *P. undulatum*. *P. undulatum* does suffer some herbivory in the Blue Mountains. So far we have identified seven different patterns of damage that we suspect are caused by seven distinct agents (Goodland & Healey 1996). Three of the types of damage were very localised (several square metres) in which all *P. undulatum* individuals were damaged, suggesting the possibility of future spread. All the responsible pest and pathogen species are most likely to be local "generalist" species and none have lead to such extensive defoliation that death seems likely. It is much too early to say what the ultimate population density of *P. undulatum* might be, when in equilibrium with native plants, pests and pathogens.

Weedy species usually have a depauperate genetic structure (Burdon & Marshall 1981) and this can be particularly pronounced when introduced to a new location in small numbers because of a "bottleneck effect" (Harper 1977). We think that *P. undulatum* was introduced to Jamaica in very small numbers, so presumably the population is likely to have a narrow genetic range. We do not know to what extent *P. undulatum* will change genetically now that it has been introduced to the Blue Mountains.

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Appendix. Woody plant species occurring in permanent sample plots in the western Blue Mountains.

Status: BME - Endemic to the BMts; JE - Jamaican endemic; N - Native to Jamaica; I - Introduced.

Code	Full species name	Family	Local name	Statu
Aca vir	Acalypha virgata L.	Euphorbiaceae		JE
Alc lat	Alchornea latifolia Sw.	Euphorbiaceae	Womanwood	Ν
Bes lut	Besleria lutea L.	Gesneriaceae		Ν
Bid shr	Bidens shrevei Britton	Asteraceae		JE
Bla tri	Blakea trinerva L.	Melastomataceae		Ν
Boc fru	Bocconia frutescens L.	Papaveraceae	John Crow bush	Ν
Boe cau	Boehmeria caudata Sw.	Urticaceae		Ν
Bru com	Brunellia comocladiifolia Humb. & Bonpl.	Brunelliaceae	Sumach	Ν
Bru jam	Brunfelsia jamaicensis (Benth.) Griseb.	Solanaceae		BME
Cal fer	Callicarpa ferruginea Sw.	Verbenaceae		Ν
Cal rig	Calyptranthes rigida Sw.	Myrtaceae		Ν
Cas vim	Cassia viminea L.	Caesalpiniaceae	Treeribs; fourvine	JE
Ces hir	Cestrum hirtum Sw.	Solanaceae		Ν
Cha glo	Chaetocarpus globosus (Sw.) Fawcett & Rendle	Euphorbiaceae		Ν
Cin mon	Cinnamomum montanum (Sw.) Bercht.& Presl.	Lauraceae	Wild cinnamon	Ν
Cin off	Cinchona officinalis L.	Rubiaceae		I
Cin pub	Cinchona pubescens Vahl.	Rubiaceae		I
Cio pom	Cionosicys pomiformis Griseb.	Cucurbitaceae	Duppy apple	JE
Cis par	Cissampelos pareira L.	Menispermaceae		Ν
Cit cau	Citharexylum caudatum L.	Verbenaceae	Fiddlewood	Ν
Cle ale	Clethra alexandra Griseb.	Clethraceae		BME
Cle occ	Clethra occidentalis (L.) Kuntze	Clethraceae	Soapwood	Ν
Cle the	Cleyera theaoides (Sw.) Choisy	Theaceae		Ν
Cli ter	Clibadium terebinthinaceum (Sw.) DC.	Asteraceae		Ν
Clu hav	Clusia havetiodes (Griseb.) Planch. & Triana	Guttiferae	Fan fan; wild mango	JE
Con mon	Conostegia montana (Sw.) DC.	Melastomataceae		BME
Cri par	Critonia parviflora DC.	Asteraceae		JE
Cya con	Cyathea concinna (Baker ex Jenman) Jenman	Cyatheaceae		BME
Cya fur	Cyathea furfuracea Baker	Cyatheaceae		Ν
Cya pub	Cyathea pubescens Mettenius ex Kuhn	Cyatheaceae		BME
Cya woo	Cyathea woodwardioides Kaulf.	Cyatheaceae		Ν
Cyr rac	Cyrilla racemiflora L.	Cyrillaceae	Beetwood	Ν
Dap ame	Daphnopsis americana (Mill.) J.R.Johnston	Thymelaeaceae		Ν
Den arb	Dendropanax arboreus (L.) Decne & Planch.	Araliaceae	Manjack	Ν
Den nut	Dendropanax nutans (Sw.) Decne & Planch.	Araliaceae	Manjack	BME
Den p/n	Dendropanax pen/nut	Araliaceae		
Den pen	Dendropanax pendulus (Sw.) Decne & Planch.	Araliaceae	Manjack	JE
Dur ere	Duranta erecta L.	Verbenaceae		Ν
Eug alp	<i>Eugenia alpina</i> (Sw.) Willd.	Myrtaceae		BME
Eug bra	Eugenia brachythrix Urban	Myrtaceae		BME
Eug har	Eugenia harrisii Krug & Urban	Myrtaceae	Rodwood	JE
Eug mar	Eugenia marchiana Griseb.	Myrtaceae		JE
Eug mon	Eugenia monticola (Sw.) DC	Myrtaceae	Rodwood	Ν

Eug vir	Eugenia virgultosa (Sw.) DC	Myrtaceae	Rodwood	JE
Gar fad	Garrya fadyenii Hook.	Garryaceae		Ν
Ges alp	Gesneria alpina (Urb.) Urb	Gesneriaceae		BME
Gon jam	Gonolobus jamaicensis Rendle	Asclepiadaceae		BME
Gon sta	Gonolobus stapelioides Desv.	Asclepiadaceae		JE
Gor hae	Gordonia haematoxylum Swartz	Theaceae	Bloodwood	JE
Gua gla	Guarea glabra Vahl	Meliaceae	Broadleaf: alligator wood	JE
Hae inc	Haenianthus incrassatus (Sw.) Griseb	Oleaceae		BME
Hed arb	Hedyosmum arborescens Sw.	Chloranthaceae	Headache bush	Ν
Hed nut	Hedyosmum nutans Sw.	Chloranthaceae	Headache bush	Ν
Het umb	Heterotrichum umbellatum (Mill) Urb.	Melastomataceae		Ν
lle har	llex harrisii Loes.	Aquilfoliaceae		JE
lle mac	<i>llex macfadyenii</i> (Walp.) Rehder	Aquilfoliaceae	Black tea	Ν
lle nit	<i>llex nitida</i> (Vahl) Maxim	Aquilfoliaceae		Ν
lle obc	llex obcordata Sw.	Aquilfoliaceae		BME
lle sid	llex sideroxyloides (Sw.) Griseb.	Aquilfoliaceae		Ν
lle vac	llex vaccinoides Loes.	Aquilfoliaceae		BME
Jun luc	Juniperus lucayana Britton	Cuppressaceae	Juniper	Ν
Koa har	Koanophyllon hardwarense (Proctor ex C.Adams) R.King & H.Robinson	Asteraceae		BME
Lob ass	Lobelia assurgens L.	Campanulaceae	Fat & borrow; milkbush	Ν
Lob mar	Lobelia martagon (Griseb.) Hitchc.	Campanulaceae		BME
Lyo jam	Lyonia jamaicensis (Sw.) D.Don	Ericaceae		Ν
Lyo oct	Lyonia octandra (Sw.) Griseb.	Ericaceae		JE
Mal arb	Malvaviscus arboreus Cav.	Malvaceae		Ν
Man lyg	Mannetia lygistum (L.) Sw.	Rubiaceae		BME
Mar bro	Marcgravia brownei (Triana & Planch.) Krug & Urban	Marcgraviaceae		JE
May jam	Maytenus jamaicensis Krug & Urban	Celastraceae	Sweetwood	Ν
Mec pur	Mecranium purpurascens (Sw.) Triana	Melastomataceae		JE
Mel Bl1	Unidentified Melastome species in block 1 of HIFE	Melastomataceae		
Mer leu	Meriania leucantha (Sw.) Sw.	Melastomataceae		JE
Mer pur	Meriania purpurea (Sw.) Sw.	Melastomataceae		Ν
Met atr	Metastelma atrorubens Schltr.	Asclepiadaceae		Ν
Met har	Metastelma harrisii Schltr.	Asclepiadaceae		BME
Mic dod	<i>Miconia dodecandra</i> (Desr.) Cogn.	Melastomataceae		Ν
Mic qua	Miconia quadrangularis (Sw.) Naud.	Melastomataceae		Ν
Mic rig	<i>Miconia rigida</i> (Sw.) Triana	Melastomataceae		Ν
Mic the	Miconia theaezans (Bonpl.) Cogn.	Melastomataceae		Ν
Mik max	Mikania maxonii Proctor	Asteraceae		BME
Myr acr	Myrsine acrantha Krug & Urban	Myrsinaceae		Ν
Myr cer	Myrica cerifera L.	Myricaceae	Waxwood	Ν
Myr cor	Myrsine coriacea (Sw.) R.Br. ex Roem.& Schult.	Myrsinaceae		Ν
Myr fra	Myrcianthes fragrans (Sw.) McVaugh	Myrtaceae		Ν
Oco pat	Ocotea patens (Sw.) Nees	Lauraceae	Sweetwood	Ν
Odo fad	Odontocline fadyenii (Griseb.) B.Nord.	Asteraceae		JE
Oss asp	Ossaea asperifolia (Naud.) Triana	Melastomataceae		Ν
Pal alp	Palicourea alpina (Sw.) DC.	Rubiaceae		Ν
Pas pen	Passiflora penduliflora Bert. ex DC.	Passifloraceae		Ν
Per alp	Persea alpigena (Sw.) Spreng.	Lauraceae	Wild Pear	JE

Phe hir	Phenax hirtus (Sw.) Wedd.	Urticaceae		Ν
Phy arb	Phyllanthus arbuscula (Sw.) J.F. Gmelin	Euphorbiaceae		Ν
Pic ant	Picramnia antidesma Sw.	Simaroubaceae		Ν
Pip arb	Piper arboreum Aublet	Piperaceae		Ν
Pip fad	Piper fadyenii C.DC.	Piperaceae		JE
Pit und	Pittosporum undulatum Vent.	Pittosporaceae	Wild coffee; mock orange	I .
Pit vir	Pittosporum viridiflorum Sims vel.aff.	Pittosporaceae	Wild coffee; mock orange	I
Pod urb	Podocarpus urbanii Pilger	Podocarpaceae	Fineleaf; yucca	Ν
Pru occ	Prunus occidentalis Sw.	Rosaceae		Ν
Psy cor	Psychotria corymbosa Sw.	Rubiaceae		JE
Psy slo	Psychotria sloanei Urban	Rubiaceae		BME
Rha sph	Rhamnus sphaerospermus Sw.	Rhamnaceae	Buckthorn	Ν
Sal sca	Salmea scandens (L.) DC.	Asteraceae		Ν
Sap har	Sapium harrisii Urban ex Pax	Euphorbiaceae	Milkwood	JE
Sch inv	Schradera involucrata (Sw.) K.Schum.	Rubiaceae		JE
Sch sci	Schefflera sciadophyllum (Sw.) Harms	Araliaceae	Old name=woman wood	JE
Sid mon	Sideroxylon montanum (Swartz) Pennington	Sapotaceae	Bulletwood	JE
Smi bal	Smilax balbisiana Kunth	Smilacaceae	Chainy root	Ν
Smi dom	Smilax domingensis Willd.	Smilacaceae		Ν
Sol pun	Solanum punctulatum Dunal	Solanaceae		BME
Sym oct	Symplocos octopetala Sw.	Symplocaceae		JE
Tou gla	Tournefortia glabra L.	Boraginaceae		Ν
Tre flo	Trema floridanum Britton	Ulmaceae		Ν
Tur occ	Turpinia occidentalis (Sw.) G.Don	Staphyleaceae	Candlewood	Ν
Urb cri	Urbananthus critoniformis (Urban) R.King	Asteraceae		BME
Ure ela	Urera elata (Sw.) Griseb.	Urticaceae		JE
Vac mer	Vaccinium meridionale Sw.	Ericaceae	Bilberry	Ν
Ver plu	Vernonia pluvialis Gleason	Asteraceae		BME
Vib alp	Viburnum alpinum Macf. ex Britton	Caprifoliaceae	Blackwattle	Ν
Vib vil	Viburnum villosum Sw.	Caprifoliaceae		Ν
Wal cal	Wallenia calyptrata Urban	Myrsinaceae		BME
Wal cra	Wallenia crassifolia Mez	Myrsinaceae		BME
Wal faw	Wallenia fawcettii Mez	Myrsinaceae		BME
Wei pin	Weinmannia pinnata L.	Cunoniaceae		Ν
Xyl nit	<i>Xylosma nitida</i> (Hellenius) I.Gray ex Griseb.	Flacourtiaceae		JE