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Invasibility of tree plantations by native and non-indigenous plant species in Hawaii

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Abstract

The Hawaiian archipelago, the most isolated on Earth, has proven to be especially vulnerable to invasions by non-indigenous species. Alien species now outnumber natives and the threat they pose is in part responsible for the fact that approximately 25% of Hawaii's native flora, 90% of which is endemic, has been listed as threatened or endangered. To assess the effect of stand characteristics on the colonization of the plantations by alien and native species, we measured basal area, leaf area index (LAI), litter depth and standing litter mass in 26- to 32-year-old plantations of *Eucalyptus saligna*, *Flindersia brayleyana* and *Fraxinus uhdei*. The plantations are surrounded by native Hawaiian rainforest which has been invaded by numerous non-indigenous species. The basal area of the planted *Flindersia* was 45.2 m^2/ha, three to four times that of the other two plantation species. Nevertheless, when colonizing species were included, total stand basal area and LAI did not differ significantly across the three plantation types. Litter depth ranged from 3.7 cm for *Flindersia* to 4.7 cm for *Eucalyptus*, and litter mass ranged from 7.4 Mg/ha for *Fraxinus* to 10.5 Mg/ha for *Eucalyptus*. Of 51 species identified in the plantation understories, 23 (45%) were common to all three plantation species. *Eucalyptus* plantations had 42 species, seven of which were uniquely found there, *Fraxinus* had 39 species, six of which were unique and *Flindersia* had 36 species, only one of which was unique. The most abundant understory species under *Fraxinus* were *Cibotium glaucum* and *Metrosideros polymorpha*, two dominant components of native Hawaiian rainforest. In contrast, the most abundant understory species in the *Eucalyptus* plantations was the alien tree, *Psidium cattleianum* and the understory of *Flindersia* was dominated by its own offspring. Average species richness (number of species per plot) of both native species and all species combined was significantly greater under *Fraxinus* than under the other two plantation species, but all plantations contained approximately equal numbers of non-indigenous species. Average density (number of individuals/m^2) was greatest under *Flindersia*, although the density of native species alone was greatest under *Fraxinus*. Species richness and plant density were not correlated with litter depth or mass, but total species richness and density of native species did decrease with increasing LAI. In general, abundance of native plants in the understory decreased with increasing abundance of non-indigenous species and increasing basal area of plantation species. © 1997 Elsevier Science B.V.

Keywords: Biodiversity; *Eucalyptus saligna*; *Flindersia brayleyana*; *Fraxinus uhdei*; Tree plantations; Understory vegetation

1. Introduction

Although plantations differ from natural forest ecosystems in a number of characteristics, there is increasing interest in the potential for plantations to serve as nurse crops for the establishment of native forest species on degraded lands. Tree plantations may facilitate forest succession through effects on soil fertility (Parrotta, 1992) and understory microcli-

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mate (Lugo et al., 1993; Parrotta, 1993; Guariguata et al., 1995; Fimbel and Fimbel, 1996), although the success of plantations in promoting native understory biodiversity depends partly on the tree species planted (Guariguata et al., 1995; Parrotta, 1995; Fimbel and Fimbel, 1996). Tree species differ in their canopy structure, which in turn affects light availability at the forest floor (Fimbel and Fimbel, 1996; Guariguata et al., 1995). Also, differences in rates of litter production and decomposition among plantation species could result in differences in standing litter depth and mass (Lugo et al., 1990; Lugo, 1992; Parrotta, 1995) which can affect species richness and seedling density in the understory (Parrotta, 1995). Nevertheless, competition from the many invasive non-indigenous plant species in Hawaii may reduce native biodiversity in plantation understories, despite the characteristics of the overstory species. Therefore, our objectives were (1) to relate understory species richness and plant density to stand and forest floor characteristics within exotic tree plantations, in order to assess which plantation characteristics most favor colonization by native species, and (2) to compare the relative abundance of native and non-indigenous species in the plantation understories.

Plantation species differ in canopy structure and leaf area, which may result in differences in the amount of light reaching the forest floor, and thus affect favorability of conditions for recruitment and survival of native Hawaiian forest species. In a pot experiment, Drake (1993) documented a light requirement for seed germination in *Metrosideros polymorpha*, the dominant native Hawaiian rainforest tree. In a natural forest, Burton and Mueller-Dombois (1984) observed greater recruitment and growth of *M. polymorpha* seedlings in cleared areas receiving 43% full sunlight than in control areas receiving only 10% full sunlight. Seedling density in native Hawaiian *Acacia koa* forests was positively correlated with light transmitted through the forest canopy (Harrington et al., 1997). Therefore, we hypothesized that understory plant density and species richness would be negatively correlated with stand LAI and canopy cover.

Plantation species also differ in the amount of standing litter (Lugo et al., 1990; Parrotta, 1995) which has implications for the establishment and survival of seedlings. A thick litter layer may impose a physical barrier and thus favor the establishment of plants with larger seeds which have larger reserves (Guzmán-Grajales and Walker, 1991; Parrotta, 1995). In Hawaii, germination of *M. polymorpha* seeds was inhibited by the presence of a dense litter layer in stands of the non-indigenous *Myrica faya* (Walker and Vitousek, 1991), and on abandoned montane pasture the native treefern *Cibotium glaucum* showed a stronger preference for establishment in mineral soil than in organic substrates (Scowcroft, 1992). Therefore, we hypothesized that understory plant density and species richness would decrease with increasing depth and mass of standing litter, both within and among plantation types.

Although plantation species play a role in promoting native understory biodiversity, the abundance of invasive non-indigenous plants in Hawaii may reduce native biodiversity in any restoration effort. The Hawaiian archipelago, the most isolated on earth, has proven to be especially vulnerable to invasions by non-indigenous species. Alien plant species now outnumber natives (Eldredge and Miller, 1996), and the threat they pose is in part responsible for the fact that 25% of Hawaii's native flora, 90% of which is endemic, has been listed as threatened or endangered. In Costa Rica (Guariguata et al., 1995) and Puerto Rico (Parrotta, 1993), competition from other understory species, especially grasses, greatly reduced recruitment of native woody species into plantations with fairly open canopies. Therefore, although high light conditions at the forest floor may favor recruitment of certain native Hawaiian forest species (Burton and Mueller-Dombois, 1984), such conditions may also favor invasion of non-indigenous species, which may reduce native biodiversity through competitive interactions. We hypothesized that native understory plant density and species richness would decrease with increasing abundance of alien plant species.

We tested the above hypotheses in replicate plantations of *Eucalyptus saligna*, *Flindersia brayleyana* and *Fraxinus uhdei* on the island of Hawaii. Plantations of alien tree species were established extensively in the 1950s and 1960s throughout the major Hawaiian islands for both watershed protection and timber production. Although these plantations were not originally established to foster regeneration of native forest species, they presented the opportunity to determine whether unmanaged plantations function as nurse crops and become repositories for native biodiversity, or merely harbor non-indigenous species. Our ability to relate recruitment of native and non-indigenous species to stand characteristics of different plantation species required a site where site preparation, planting and post-planting management were identical across plantation species, and where recruitment of both native and non-indigenous species was not limited by seed source. Our study site was once native rainforest and is now surrounded by native rainforest that has been invaded by a number of non-indigenous species. Therefore, most differences observed in patterns of colonization across plantation types can be attributed to the influence of the overstory species.

2. Methods

2.1. Site

The plantations surveyed in this study are part of the Waiakea Reforestation Plantings in the Upper Waiakea and Ola'a Forest Reserves on the island of Hawaii (latitude 19° 34–36′, longitude 155° 10–13′) (Fig. 1). Our study sites extend from 850 to 950 m elevation on the lower east slope of Mauna Loa, where mean annual rainfall is approximately 4800 mm (Giambelluca et al., 1986). Soils derived from basic-ash over pahoehoe or a'a lava flows are classified as isothermic Lithic Hydrudands and isothermic Typic Hydrudands, both with a Udic moisture regime (R. Gavenda, pers. commun.).

Site preparation consisted of bulldozing native forest that had been invaded by several introduced species. Before land clearing, the area was vegetated predominantly by the native tree *Metrosideros polymorpha* (ohi'a) and the native ferns *Cibotium spp.* and *Dicranopteris linearis*, but the non-indigenous shrubs and trees *Melastoma candidum*, *Psidium cattleianum* and *Melochia umbellata* were also present (Wick et al., 1971). Large *Acacia koa* and *Metrosideros polymorpha* trees were left standing at the time of clearing and the ground immediately surrounding them may not have been badly disturbed. Each plantation is 16 ha (approximately 400 × 400 m) and all species were planted at 3.1 × 3.1 m spacing. Planting was done from 1964 through 1970, and the plantations we surveyed have remained unmanaged. Today, the plantings are largely surrounded by rainforest dominated by native species but containing many introduced species.

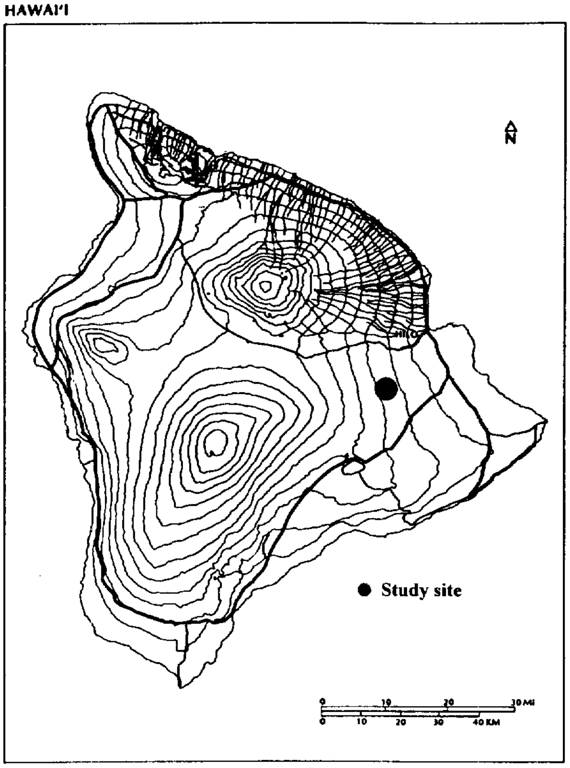

Fig. 1. Location of the study site on the island of Hawaii, HI.

2.2. Plantation species

The three plantation species included in this study were *Eucalyptus saligna* Sm. (Myrtaceae) (saligna eucalyptus), *Flindersia brayleyana* F. v. Muell. (Rutaceae) (Queensland maple) and *Fraxinus uhdei* (Wenzig) Lingelsh (Oleaceae) (tropical ash). Species were chosen based on hypothesized differences in canopy leaf area index (LAI) and standing litter depth and mass, which in turn can affect recruitment and survival of seedlings.

Eucalyptus saligna and *F. brayleyana* are evergreen trees native to Australia. *Eucalyptus saligna* trees have open, spreading crowns and stands tend to build up a thick litter layer. *Flindersia brayleyana* is extremely tolerant of shade, so we hypothesized that plantations of this species would have a much higher LAI that the other two plantation species. *Fraxinus uhdei* is native to Mexico, and although it is considered shade tolerant when young, this species is winter-deciduous in Hawaii and has a fairly open canopy the rest of the year. Although *F. uhdei* sheds all of its leaves every year, the resulting leaf litter decomposes in approximately 10 months (P. Scowcroft, pers. commun.), precluding a large build up of litter.

2.3. Plantation surveys

We surveyed three plantations of each species. Within each of the nine plantations five circular plots 10 m in diameter were randomly located. Within each plot, we noted the abundance (number of individuals) of all plant species present. We measured stem diameter at 1.3 m (D, to 0.1 cm) and height (H, to 0.1 m) of all woody species >2 m tall. When a tree forked below 1.3 m, D was measured on each stem.

Depth (to 1.0 cm) of the litter layer was measured at 10 points located randomly within each plot. Four other sample points were located systematically for sampling of litter and soil, one at 3 m from the plot center in each of the four compass directions. Standing litter mass was sampled using a 30 × 30 cm quadrant at each of the four sample points. Litter samples were returned to the lab where they were partitioned into fine (leaves plus wood <1 cm diameter) and coarse (wood >1 cm diameter) components, and then dried at 70°C. The four surface (0–5 cm) soil cores were composited within each plot for determination of soil pH.

Leaf area index (LAI) was estimated using a LiCor LAI-2000 plant canopy analyzer (LiCor, 1992). In previous tests, optical estimates agreed well with harvest and allometric estimates of LAI in plantations of several tropical tree species (Harrington and Fownes, 1995).

Differences in stand characteristics, species richness and plant density across the three plantation types were tested using ANOVA. Tukey's HSD multiple range test was used for comparison of means. Homogeneity of variance was achieved as needed through log transformations.

3. Results

3.1. Stand characteristics

The mean basal area of the *Flindersia* plantations was 45.2 m^2/ha, three to four times that of the other two plantation species (Table 1). Nevertheless, when colonizing species were included, total stand basal area and LAI did not differ significantly across the three plantation types.

The size of the planted trees differed significantly across the three plantation species (Table 1). Tree height and diameter of *Flindersia* were approximately three times that of *Fraxinus*, and *Eucalyptus* was intermediate in size. Litter depth ranged from 3.7

Table 1
Environment and structure of 26- to 32-year-old plantations

	Eucalyptus saligna	*Flindersia brayleyana*	*Fraxinus uhdei*
Soil pH	4.2 (0.11)^a	4.0 (0.07)^a	4.7 (0.09)^b
Litter depth (cm)	4.7 (0.35)^a	3.7 (0.28)^b	4.0 (0.36)^{ab}
Fine litter mass (Mg/ha)	9.6 (0.88)^a	6.6 (0.39)^b	7.2 (0.52)^{ab}
Coarse litter mass (Mg/ha)	0.89 (0.22)^a	3.2 (0.70)^b	0.19 (0.10)^a
Total litter mass (Mg/ha)	10.5 (0.93)^a	9.8 (0.77)^{ab}	7.4 (0.50)^b
Total basal area (m^2/ha)	33.1 (16.0)^a	48.4 (3.5)^a	18.0 (2.5)^a
Plantation basal area (m^2/ha)	12.5 (2.1)^a	45.2 (3.3)^b	14.4 (2.6)^a
Leaf area index	4.3 (0.38)^a	4.7 (0.24)^a	4.1 (0.20)^c
Tree height (m)	21.0 (1.2)^a	28.1 (1.3)^b	10.16 (0.42)^c
Tree diameter (cm)	23.6 (2.2)^a	34.1 (1.6)^b	13.7 (1.2)^c

Values represent the means of three plantations.
Standard errors are in parentheses.
Values within a row followed by the same letter do not differ significantly ($P = 0.05$).

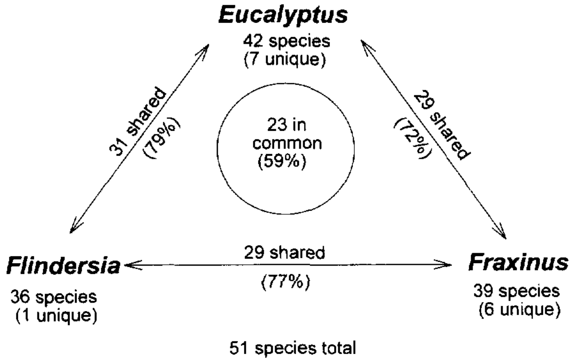

Fig. 2. The number of species found in each plantation type and the number of species shared between plantations. The Jaccard similarity index is shown in parentheses.

cm for *Flindersia* to 4.7 cm for *Eucalyptus*, and total litter mass ranged from 7.4 Mg/ha for *Fraxinus* to 10.5 Mg/ha for *Eucalyptus* (Table 1). Soil pH was significantly greater under *Fraxinus* than in the plantations of the other species (Table 1).

3.2. Understory vegetation

Of 51 species identified in the plantation understories, 23 (45%) were common to all three plantation species (Fig. 2, Table 2). Within plantation types, *Eucalyptus* had 42 species, seven of which were uniquely found there, *Fraxinus* had 39 species, six of which were unique and *Flindersia* had 36 species, with *Flindersia* seedlings being the only understory species unique to this plantation type (Fig. 2). Within all three plantation types, approximately 75% of the species observed were native, but the relative abundance of non-indigenous and native plants differed among the three plantation species. The most abundant understory species in the *Fraxinus* plantations were the treefern *Cibotium glaucum* and the canopy tree *Metrosideros polymorpha*, two dominant components of native Hawaiian rainforest. In contrast, the most abundant understory species in the *Eucalyptus* plantations was the alien tree, *Psidium cattleianum*, and the understory of *Flindersia* was dominated by its own offspring.

Average species richness (number of species per plot) of both native species and all species combined was significantly greater under *Fraxinus* than under the other two plantation species, but all plantations contained approximately equal numbers of non-indigenous species (Table 3). Average density (number of individuals/m^2) was greatest under *Flindersia*, although the density of native species was three times greater under *Fraxinus* than under the other two plantation species (Table 3).

Understory colonization was influenced by certain characteristics of the plantations. Density of native species decreased with increasing LAI, as hypothesized, in *Flindersia* and *Fraxinus* plantations, although density of native species was low throughout the range of LAI observed in *Eucalyptus* plantations (Fig. 3). Also, although native plant density varied greatly at the low plantation-tree basal area, density tended to decrease with an increasing basal area in *Flindersia* and *Fraxinus* plantations (Fig. 4). Density of native plants in the *Eucalyptus* plantations was consistently low and did not vary with the basal area of the planted trees. Contrary to our prediction, species richness and plant density were not correlated with litter depth or mass in any of the plantation types.

The abundance of native plants in the understory was inversely related to the density of non-indigenous plant species in our study plots (Fig. 5). Although the correlation was imperfect, high numbers of native plants were observed only at low densities of alien plants, and low numbers of natives were observed when the density of aliens was high. A similar decrease in the density of native plants was observed with increasing cover of the exotic palmgrass, *Setaria palmifolia* (not illustrated).

4. Discussion

4.1. Differences among plantation species

Our original choice of plantation species was based on hypothesized differences in canopy and forest floor characteristics that could affect seedling recruitment. Total stand LAI did not differ across the three plantation species. Although we did not partition total stand LAI between that contributed by the plantation overstory and that contributed by the subcanopy of colonizing trees, observations suggest that the LAI of the plantation overstory alone did differ across plantation species. For example, LAI measurements made in one of the *Fraxinus* plantations both before and after seasonal defoliation of the canopy indicate that 75% of

Table 2

Origin and life form of species identified in plantation understories

Species and authority	Family	Origin[a]	Life form[b]	Plantation species		
				E.s.	*F.b.*	*F.u.*
Acacia koa, A. Gray	Fabaceae	E	T	●		
Ageratina riparia (Regel), R. King and H. Robinson	Asteraceae	N	S			●
Alyyxia oliviformis Gaud.	Apocynaceae	E	V		●	●
Antidesma platyphyllum, H. Mann	Euphorbiaceae	E	T	●	●	
Arundina graminifolia (D. Don) Hochr.	Orchidaceae	N	H	●	●	●
Asclepias curassavica L.	Asclepiadaceae	N	H			●
Astellia menziesiana Sm.	Liliaceae	E	H		●	●
Asplenium nidus L.	Aspleniaceae	I	F	●		●
Broussaisia arguta Gaud.	Hydrangeaceae	E	S	●	●	●
Carex sp. L.	Cyperaceae	?	G	●	●	●
Cheirodendron trigynum (Gaud.), A. Heller	Araliaceae	E	T	●	●	●
Cibotium glaucum (Sm.) Hook. & Arnott	Dicksoniaceae	E	F	●	●	●
Cibotium menziesii Kaulf.	Dicksoniaceae	E	F	●	●	●
Clermontia sp.	Campanulaceae	E	S	●	●	
Coprosma sp.	Rubiaceae	E	S	●	●	●
Cyrtandra platyphylla, A. Gray	Gesneriaceae	E	S	●	●	●
Cyrtandra paludosa Gaud.	Gesneriaceae	E	S	●	●	●
Dioscorea bulbifera L.	Dioscoreaceae	P	H	●		●
Dicranopteris linearis (N.L. Burm.) Underw.	Gleicheniaceae	I	F	●	●	●
Diplopterygium pinnatum (Kunze) Nakai	Gleicheniaceae	I	F			●
Dianella sandwicensis Hook. & Arnott	Liliaceae	I	H	●	●	●
Dryopteris sp.	Asplidiaceae	?	F	●	●	●
Flindersia brayleyana F.v. Muello.	Rutaceae	N	T		●	
Freycinetia arborea Gaud.	Pandanaceae	I	V	●	●	●
Fraxinus uhdei (Wenzig) Lingelsh	Oleaceae	N	T			●
Grammitis tenella Kaulf.	Grammitaceae	E	F	●		
Hedyotis terminalis (Hook. & Arnott) W.L. Wagner and Herbst	Rubiaceae	E	T	●	●	●
Ilex anomala Hook. & Arnott	Aquifoliaceae	I	T	●	●	●
Labordia sp.	Loganiaceae	E	S	●	●	●
Lycopodium cernuum L.	Lycopodiaceae	I	F	●	●	●
Metrosideros polymorpha Gaud.	Myrtaceae	E	T	●	●	●
Myrcine sandwicensis A.DC	Myrcinaceae	E	T	●	●	●
Passiflora ligularis Juss.	Passifloraceae	N	V	●		
Peperomia membranacea Hook. & Arnott	Piperaceae	E	H	●	●	●
Perrottetia sandwicensis A. Gray	Celastraceae	E	T	●	●	●
Pipturus albidus (Hook. & Arnott) A. Gray	Urticaceae	E	T	●		
Psidium cattleianum Sabine	Myrtaceae	N	T	●	●	●
Psychotria hawaiiensis (A. Gray)Fosb.	Rubiaceae	E	T	●	●	
Setaria palmifolia (J. Kong)Stapf	Poaceae	N	G	●	●	
Sphenomeris chinensis (L.)Maxon	Lindsaeceae	I	F	●	●	●
Stenogyne calaminthoides A. Gray	Lamiaceae	E	V	●		●
Tibouchina urvilleana (DC)Cogn.	Melastomataceae	N	S	●		
Toona ciliata M.Roem.	Meliaceae	N	T	●		
Vaccinium reticulatum Sm.	Ericaceae	E	S		●	●
Verbena litoralis Kunth	Verbenaceae	N	H			●

● indicates the presence of the species in each of the plantation types. *Eucalyptus saligna* (*E.s.*), *Flindersia brayleyana* (*F.b.*) and *Fraxinus uhdei* (*F.u.*). This table does not include three unidentified species.

[a] E, endemic; I, indigenous; N, naturalized; P, Polynesian introduction.

[b] T, tree; S, shrub; H, herb; F, fern and fern allies; G, grass and sedge; V, vine.

Table 3

Species richness and plant density in plantations

	Eucalyptus saligna	*Flindersia brayleyana*	*Fraxinus uhdei*
Species richness (number species/plot)			
Native	8.7 (0.67)[a]	7.9 (1.3)[a]	12.7 (0.70)[b]
Non-indigenous	3.0 (0.49)[a]	3.2 (0.22)[a]	3.7 (0.47)[a]
Total	11.7 (0.77)[a]	11.1 (1.5)[a]	16.4 (0.77)[b]
Plant density (number plants/m²)			
Native	1.1 (0.13)[a]	1.1 (0.32)[a]	3.4 (0.39)[b]
Non-indigenous	1.9 (0.67)[a]	4.0 (0.80)[b]	0.33 (0.06)[a]
Total	3.0 (0.73)[a]	5.1 (0.69)[b]	3.7 (0.38)[ab]

Plot size is 78.5 m^2.
Standard errors are in parentheses.
Values within a row followed by the same letter do not differ significantly ($P = 0.05$).

the leaf area was contributed by the subcanopy, which was largely dominated by treefern (*Cibotium* sp.), and that the LAI of *Fraxinus* alone was only about 1.0 out of the total of 4.1. In contrast, the planted *Flindersia* trees made up 93% of the total basal area, and based on visual assessment the intact canopies of these planted trees made up the majority of the leaf area in the *Flindersia* plantations.

We observed significantly higher soil pH in *Fraxinus* plantations than in the other plantation types. The soil pH prior to planting is unknown, so we cannot assess whether the presence of *Fraxinus* increased soil pH or the other two species lowered it. The significantly higher pH observed in the *Fraxinus* plantations relative to the other plantation types may be a result of rapid cycling of cations through litterfall. This species (unlike the other two) is deciduous, and the resulting pulse of cation-rich litter decomposes in approximately 10 months (P. Scowcroft, pers. commun.). In a study of 50-year-old stands planted in an abandoned agricultural field in northeastern United States, Binkley and Valentine (1991) observed both higher soil pH and greater cation content of litter in stands of the congener, *Fraxinus pennsylvanica* (green ash), than in stands of *Pinus strobus* (white pine) and *Picea abies* (Norway spruce).

Other studies have also documented changes in soil pH following changes in vegetation. In southeast

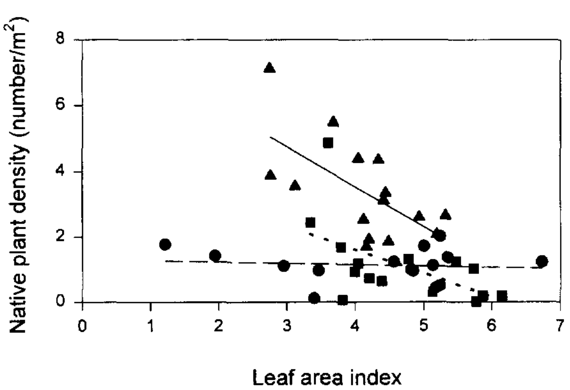

Fig. 3. Density of native species as a function of plantation leaf area index. The three plantation types are represented by ● (*Eucalyptus saligna*), ■ (*Flindersia brayleyana*) and ▲ (*Fraxinus uhdei*).

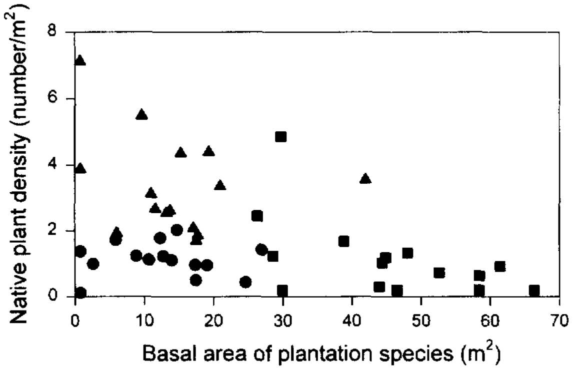

Fig. 4. Density of native species as a function of plantation basal area. The three plantation types are represented by ● (*Eucalyptus saligna*), ■ (*Flindersia brayleyana*) and ▲ (*Fraxinus uhdei*).

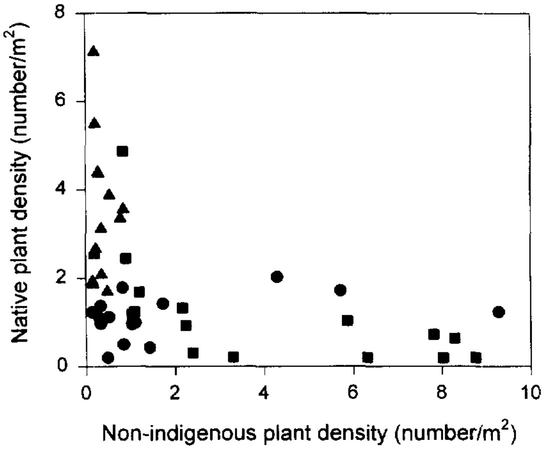

Fig. 5. Density of native species as a function of density of non-indigenous species. The three plantation types are represented by ● (*Eucalyptus saligna*), ■ (*Flindersia brayleyana*) and ▲ (*Fraxinus uhdei*).

Queensland, Australia, replacement of *Eucalyptus micrantha* forest with plantations of *Pinus elliottii* lowered soil pH from 5.4 to 4.9 (Jones and Richards, 1977). On abandoned sugar cane land in Hawaii, soil pH declined from 5.9 to 5.0 in 8 years in plantations of *Eucalyptus saligna* and from 5.9 to 4.6 in plantations of *Albizia falcataria* (Rhoades and Binkley, 1996). However, we do not know if the soil pH had been artificially raised by the previous agricultural practice, and Stone (1975) argues that species' effects on soil characteristics are small compared with effects of land-use history and management practices.

4.2. *Influence of plantation characteristics on understory colonization*

4.2.1. *Fraxinus uhdei*

Colonization of plantation understories by native Hawaiian species appeared to be limited by different factors in each of the three plantation types. The highest species richness and density of natives were observed in the *Fraxinus* plantations. The density of native plants decreased with increasing LAI across our study plots, suggesting increased recruitment of the two most abundant species, *Metrosideros polymorpha* and *Cibotium glaucum*, with increased light availability within the *Fraxinus* plantations. Although LAI did not differ across plantation types when the *Fraxinus* was in full leaf, this species is deciduous, losing all of its foliage for approximately 1 month in the winter. During this period, stand LAI dropped from approximately 4 to 3, resulting in increased light availability relative to the other two plantation types. Also, as discussed above, the LAI of the *Fraxinus* canopy itself is likely much lower than that of the other plantation canopies, which may have created the high light conditions that permitted the original recruitment of the now dominant understory.

In other studies, however, low stand LAI did not result in increased colonization of natives. In lowland Costa Rica, canopy cover varied across three plantation species, but showed no correlation with species richness or density of woody regeneration in the understory (Haggar et al., 1997). Low canopy cover could result in increased cover of alien species, especially grasses, which competitively exclude native species. Parrotta (1993) observed a decrease in seedling density of forest species with increasing light intensity in plantation understories, which corresponded to increased dominance of grasses. The success of *Pinus caribaea* plantations in fostering regeneration of native forest species in Uganda was attributed to the temporal pattern of canopy development of the plantation species (Fimbel and Fimbel, 1996); early canopy closure of the plantation shaded out competing understory grassland vegetation, but later in stand development the open crown structure characteristic of *P. caribaea* created a light regime favorable for the establishment of native woody species.

4.2.2. *Eucalyptus saligna*

The abundance and diversity of native species colonizing the *Eucalyptus* plantations were low across all plots and were not related to stand LAI or basal area. However, the understory of many plots in the *Eucalyptus* plantations was dominated by *Psidium cattleianum*, which may be the most abundant woody weed in Hawaii (Smith, 1989). This non-indigenous, thicket-forming tree may outcompete native species in the understory for light and soil resources. We also observed regeneration of *Psidium* when adult trees were present, suggesting that once it has invaded a plantation it will likely persist.

Recruitment and/or survival of native seedlings may have also been suppressed by the dense cover of the non-indigenous palmgrass, *Setaria palmifolia*, in plots where the *Eucalyptus* and *Psidium* canopies were open; we observed fewer native species in plots where the cover of palmgrass was high. A similar decrease in abundance of natives with increasing dominance of grasses was observed in *Albizia lebbek* plantations in Puerto Rico (Parrotta, 1993).

4.2.3. *Flindersia brayleyana*

The greatest understory plant density was observed in *Flindersia* plantations. However, the density of non-indigenous plants was almost four times that of native plants, and the understory was dominated by regeneration of *Flindersia* itself.

Flindersia is considered a shade tolerant, late secondary successional species (Osunkoya et al., 1992) with seeds that germinate independent of light (Claussen, 1996). Nevertheless, although seedlings can survive for long periods in the shade without growing, both survival (Claussen, 1996) and growth rate (Osunkoya et al., 1993) increase with increasing light availability. This agrees with our observations of the abundance of *Flindersia* seedlings in the dark plantation understory, as well as the abundance of *Flindersia* saplings in gaps.

4.3. Implications for restoration

Our results indicate that native forest species may successfully become established within exotic tree plantations in Hawaii, but their abundance is constrained by the presence of alien species. Although the total number of species colonizing each plantation type was fairly similar, and in each case approximately 75% of species were native, the abundance and distribution of native and non-indigenous plants varied greatly across plantation types. There may be the potential to restore native forest species on plantation sites, although success would likely vary with plantation type, and would require removal and subsequent control of invasive non-indigenous plants.

The selection of plantations with the best potential for future restoration requires a better understanding of the basic ecology of plantation species. For example, in this study, the understory in the *Fraxinus* plantations was dominated by regeneration of native forest species, and *Fraxinus* was not regenerating beneath its own canopy or in surrounding plantations. Our observations suggest that it is a successful nurse crop. Nevertheless, in other plantation settings in Hawaii, *Fraxinus* has spread into adjacent native *Acacia koa* forest where it has overtopped and suppressed the native *A. koa* canopy (P. Scowcroft, pers. commun.). Therefore, an understanding of the environmental factors controlling the regeneration and spread of *Fraxinus* would help assure that plantation establishment would facilitate, rather than hinder, native forest regeneration. Also, multiple species interactions may be important in determining success of native species regeneration. In our study site, *Psidium* colonizes and reproduces readily under *Eucalyptus*, and it may be the presence of the dense alien understory, rather than the presence of *Eucalyptus*, that is hindering regeneration of native species. Therefore, a better understanding of conditions favoring native and alien colonization in plantation settings would help assess which plantation species have the best potential for use in restoration. The fact that native species were present in all of our study plots suggests that restoration of these systems to native forest vegetation is a potential management alternative.

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