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Seedling Mortality in Hawaiian Rain Forest: The Role of Small-Scale Physical Disturbance[1]

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ABSTRACT

Most montane rain forests on the island of Hawaii consist of a closed canopy formed by *Cibotium* spp. tree ferns beneath an open canopy of emergent *Metrosideros polymorpha* trees. We used artificial seedlings to assess the extent to which physical disturbance caused by the senescing fronds of tree ferns and the activities of feral pigs might limit tree regeneration. Artificial seedlings were established terrestrially (N = 300) or epiphytically (N = 300) on tree fern stems. Half of the seedlings on each substrate were in an exclosure lacking feral pigs and half were in forest with pigs present. After one year, the percentage of seedlings damaged was significantly greater among terrestrial seedlings (25.7%) than epiphytic seedlings (11.3%). Significantly more terrestrial seedlings were damaged in the presence of pigs (31.3%) than in the absence of pigs (20.0%). Senescing fronds of tree ferns were responsible for 60.3 percent of the damaged seedlings. Physical disturbance is potentially a major cause of seedling mortality and may reduce the expected half-life of a seedling cohort to less than two years.

Key words: artificial seedlings; Cibotium; *disturbance; Hawaii;* Metrosideros polymorpha; *montane rain forest; seedling; tree ferns.*

THE EFFECTS OF DISTURBANCE on tropical plant populations and communities are well-known at scales ranging from treefalls (Denslow 1987) to hurricanes (Walker *et al.* 1996). At smaller scales, tropical forest understory plants are subject to disturbances such as limbfalls and litterfall (Vandermeer 1977; Aide 1987; Clark & Clark 1987, 1991; Alvarez-Buylla & Martinez-Ramos 1992), trampling and digging by animals (Salick *et al.* 1983, Clark & Clark 1989), and substrate instability (Alvarez-Buylla & Martinez-Ramos 1992, Mack 1998). If species differ in their ability to tolerate physical disturbance, the cumulative effects of these small-scale, high-frequency disturbances could influence community dynamics and composition through differential attrition in seedling populations (Clark 1990).

Tree seedling densities are very low in the understory of montane rain forest on the island of Hawaii (Burton & Mueller-Dombois 1984, Drake & Mueller-Dombois 1993). This forest is composed of a dense, closed canopy of tree ferns (*Cibotium glaucum, C. chamissoi,* and *C. hawaiense*) with stems *ca* 4 m tall beneath an open layer of emergent trees up to 25 m tall, dominated almost exclusively by *Metrosideros polymorpha* (Burton & Mueller-Dombois 1984, Drake & Mueller-Dombois 1993, Kitayama *et al.* 1995). Low seedling densities of *M. polymorpha* have been attributed to the effects of above- and belowground competition with tree ferns (Burton & Mueller-Dombois 1984): however, *M. polymorpha* seedlings maintain a net positive carbon balance for at least four months after germination at an irradiance of 13 μmol/m^2/sec (12-hour photoperiod, white light; Friend 1981), suggesting that its seedlings are at least somewhat shade tolerant.

We tested the hypothesis that physical disturbance caused by senescing fronds of tree ferns has the potential to damage significant numbers of tree seedlings in the understory of Hawaiian montane rain forest, and is thus a factor limiting their regeneration. We used artificial seedlings to test our hypothesis because they offer distinct advantages over natural seedlings (Clark & Clark 1989, McCarthy & Facelli 1990, Mack 1998). For example, artificial seedlings are insensitive to environmental stresses such as shading, drought, and temperature extremes, and they are not susceptible to negative effects of many biotic agents such as competitors, predators, pathogens, or parasites. The use of ar-

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tificial seedlings therefore allows assessment of the specific contribution of physical damage to seedlings in the absence of potential confounding influences such as climate and biotic interactions.

MATERIALS AND METHODS

The study took place at an elevation of 1150 m in the *Metrosideros*/*Cibotium* montane rain forest of ‘Ola‘a Tract, Hawaii Volcanoes National Park (19°27′N, 155°14′W), on the east flank of Mauna Loa on the island of Hawaii (described in Burton & Mueller-Dombois 1984). Climate at this windward site is cool and humid all year. Mean annual rainfall is 2000–4000 mm and shows no distinct seasonality (Giambelluca *et al.* 1986). Ground slope was less than 5°.

Artificial seedlings were constructed from a 13 cm long, 3 mm diameter wire root stapled inside a 19.5 cm long, 0.7 cm diameter stem made from a plastic drinking straw. A second straw of equal size was stapled at right angles to the stem to represent leaves or branches. The top 5 cm of the stem was folded down and the tip stapled to the intersection of the stem and the branch straw. The finished seedling was shaped like a cross and consisted of a 10 cm long root, a 14.5 cm long stem, and two branches (each 9.75 cm long) attached 4 cm from the top of the stem (Fig. 1 in Clark & Clark 1989).

Three hundred terrestrial seedlings were inserted in the ground at intervals of exactly 2 m, regardless of microhabitat, along six parallel 120 m long transects spaced 10 m apart. When points coincided with tree stems, seedlings were placed adjacent to the stems. Because tree seedlings often establish epiphytically on tree fern stems in Hawaiian rain forest (Drake & Mueller-Dombois 1993), an additional 300 epiphytic seedlings were rooted upright at a height of 1 ± 0.25 m on the upright stems of 300 tree ferns found along, and within 1 m of, the transects containing terrestrial seedlings. Epiphytic seedlings were established by inserting the wire root vertically into the interwoven rootlets that comprise the tree fern stems. The transects were bisected by a fence such that half of the seedlings (both epiphytic and terrestrial) were in a fenced exclosure lacking feral pigs (*Sus scrofa*) and the other half were in topographically and structurally similar forest outside in which pigs were present. No seedlings were placed within 10 m of the fence. Pig density was estimated at 5.3 animals/km^2 when the 174 ha exclosure was established in 1986 (Anderson & Stone 1994). The area outside the exclosure received no direct pig control during the study but was open to public hunting. No estimates of pig density for the unprotected forest are available for the period of the study, but density estimates ranged from 3.4 to 7.3 pigs/km^2 along a nearby transect monitored in 1997 and 1998 (USGS, unpublished data). The availability of just one pig-free forest patch prevented true replication of sites with and without pigs.

Seedlings were established in February 1991. At ten intervals of 5 or 6 weeks for 52 weeks, seedlings were examined and classified as damaged or undamaged using the criteria of Clark and Clark (1989). Terrestrial seedlings were considered damaged if they had bent so that the stem was horizontal or the branch was touching the ground. Epiphytic seedlings were considered damaged if they had been bent from upright to horizontal (*i.e.,* at a ≥90° angle to the tree fern stem). Uprooted and missing seedlings were also considered damaged. For all damaged seedlings, the type(s) of litter and/or disturbance were identified whenever possible. A cause of damage was assigned only if the disturbing agent (*e.g.,* litter) was still in contact with the seedling or identifiable animal signs were associated with the damaged seedling. When a seedling was beneath litter from two different species, each species was assigned half of the disturbance.

A *G*-test (Zar 1984) was used to test for differences in numbers of damaged seedlings among the treatments (terrestrial/epiphytic and with/without pigs). Because pigs were unlikely to affect epiphytic seedlings, tests for effects of pig presence/absence were done only for terrestrial seedlings.

RESULTS

During the year, seedling losses to disturbance ranged from 11.3 percent in the two epiphytic treatments to 31.3 percent in the terrestrial treatment in the presence of pigs (Fig. 1).

Terrestrial seedlings were two to three times more likely to be damaged as epiphytic seedlings (Table 1; $G = 22.8$, df = 1, $P < 0.001$). Terrestrial seedlings were more likely to be damaged in the presence than in the absence of pigs ($G = 4.56$, df = 1, $P < 0.05$). The most common agent of disturbance was *Cibotium* tree fern leaves, which were responsible for 60.3 percent (67/111) of damaged seedlings overall and 85 percent (67/79) of those damaged by litter. All 24 terrestrial seedlings damaged by causes not identified as litter were in the presence of pigs. All uprooted seedlings occurred in patches of ground dug by pigs. Although tree

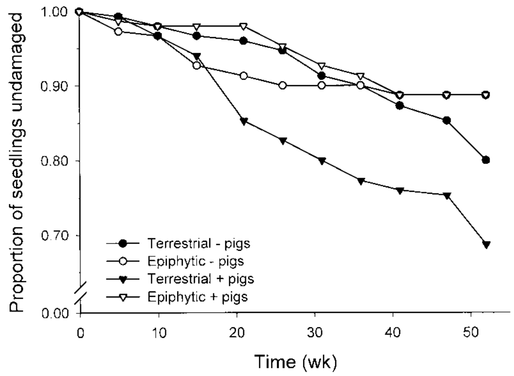

FIGURE 1. Proportion of artificial seedlings not damaged by physical disturbance during one year in a Hawaiian rain forest. Seedlings were established terrestrially or epiphytically in the presence or absence of pigs (N = 150 in each of four conditions).

ferns regularly fall (sometimes due to predation by pigs) and resprout, no tree ferns that supported epiphytic seedlings fell during the study.

Of the undamaged seedlings remaining at the end of the study, 22.4 percent (50/223) of the terrestrial and 14.7 percent (39/266) of the epiphytic seedlings were encumbered by litter loads (93.5% *Cibotium*) heavy enough to bend them from their upright position (although not severely enough to categorize them as damaged).

DISCUSSION

Tree seedlings in Hawaiian montane rain forest experienced potential mortality rates of 11.3 to 31.3 percent/yr through the effects of physical disturbance. The rate of damage to artificial seedlings in Hawaii (Table 1) was slightly lower than in Papua New Guinea (Mack 1998) and much lower than in Costa Rica (Clark & Clark 1989). Fallen litter damaged similar percentages of terrestrial seedlings in all three forests. In contrast, the proportion of seedlings damaged by animals or unidentified causes was highest in Costa Rica, probably reflecting its relatively rich fauna of ground-dwelling vertebrates. Where present in Hawaii, introduced pigs accounted for relatively few of the disturbances for which causes could be identified; however, the fact that most of the disturbances attributed to unidentified causes occurred among terrestrial seedlings in the presence of pigs may mean that damage attributed to pigs was underestimated.

The chief cause of damage to artificial seedlings in Hawaii was fallen litter. The senescing fronds of *Cibotium* spp. tree ferns may damage 14–15 percent of terrestrial tree seedlings each year. If tree fern litter caused mortality among seedlings at a rate of 15 percent/yr for just four years, half of a cohort of seedlings would be lost from this cause alone. Other large leaves, such as palm leaves, cause seedling mortality in other tropical forests (Vandermeer 1977, Clark 1990, Clark & Clark 1991).

Several factors combine to make leaves of *Cibotium* spp. tree ferns particularly hazardous for *M. polymorpha* seedlings. Tree ferns occur at densities of up to 2500/ha in Hawaiian montane rain forests (Drake & Mueller-Dombois 1993). Each tree fern sheds 3–5 leaves/yr and each leaf is 3–4 m long (Wick & Hashimoto 1971, Walker & Aplet 1994). This results in an annual leaf fall of *ca* 1 leaf/m^2/yr. Senescing leaves buckle at the point of attachment and fall to the ground intact, maximizing their impact. In contrast, *M. polymorpha* seeds are *ca* 2 mm wide and 5 mm long with a mean fresh mass of 57 μg (Drake 1992), and seedlings grow

TABLE 1. *Percentages of artificial seedlings that suffered damage from various agents of disturbance during one year in rain forests of Hawaii, Costa Rica, and Papua New Guinea (*N *= 150, 500, and 846/column, respectively).*

Cause of disturbance	Hawaii				Costa Rica[1]	P.N.G.[2]
	Terrestrial		Epiphytic		Terrestrial	Terrestrial
	− pigs	+ pigs	− pigs	+ pigs		
Litter	20.0	15.3	6.7	9.0	19.2	13.8
Uprooted	0.0	4.7	0.0	1.7	21.0	7.0
Unknown	0.0	11.3	4.7	0.7	42.2	11.0
Water wash	—	—	—	—	—	2.9
Total damaged	20.0	31.3	11.3	11.3	82.4	34.7
Undamaged	80.0	68.7	88.7	88.7	17.6	65.3

[1] Data from Clark and Clark (1989).
[2] Data from Mack (1998). If criteria used for counting seedlings as damaged in the Costa Rican and Hawaiian studies were applied to Papua New Guinea, 58 percent of the seedlings remained undamaged in Papua New Guinea.

≤10 cm/yr (Burton & Mueller-Dombois 1984). It is therefore likely that for the first few years after germination, understory seedlings would remain small enough to be prone to damage from falling fronds, and that our relatively large artificial seedlings underestimated potential mortality. Other common tree species of Hawaiian montane rain forest, such as *Cheirodendron trigynum, Myrsine lessertiana, Ilex anomala,* and *Coprosma ochracea,* also have seeds <1 cm diameter (D. Drake, pers. obs.). Seedlings from small seeds are especially vulnerable to effects of physical damage (Armstrong & Westoby 1993), perhaps because of the lack of nutrient reserves to replace or repair damaged parts.

Metrosideros polymorpha populations may overcome the hazards posed by tree ferns through sheer reproductive volume. Seed rain of viable seeds is *ca* 5000/m^2/yr (Drake 1998). The seeds are widely dispersed by wind (Drake 1992) and germinate rapidly under a wide range of environmental conditions (Drake 1993). Because the tree fern canopy is typically only 5–7 m high, trees that reach sapling size penetrate the tree fern layer and escape the effects of litterfall and shading (Drake & Mueller-Dombois 1993).

Mature individuals of many tropical woody species regenerate vegetatively following physical damage; even severed branches can root and survive (Gartner 1989, Kinsman 1990, Greig 1993). The ability of saplings of the invasive alien tree *Psidium cattleianum* to resprout after being damaged by tree fern fronds may help account for its success as an invader of Hawaiian forests (Huenneke & Vitousek 1990); however, little is known about the ability of seedlings to recover from physical damage.

A further threat to seedlings is that they may be slowly buried by litter rather than damaged by its initial impact. Many undamaged artificial seedlings remained upright or only slightly bent but were invisible beneath a framework of tree fern litter.

Ironically, the artificial seedlings least prone to damage by tree fern fronds were those established epiphytically on tree fern stems. Many seedlings in Hawaiian montane rain forest establish epiphytically on tree ferns and on emergent *M. polymorpha* trees (Burton & Mueller-Dombois 1984, Drake & Mueller-Dombois 1993). Although epiphytic seedlings grow more slowly than terrestrial seedlings (Burton & Mueller-Dombois 1984), they face reduced threats from litter and pigs and probably reduced shading as well. Epiphytically established tree seedlings may reestablish terrestrially and claim gaps when their host trees or branches fall, as in Costa Rican rain forest (Lawton & Putz 1988).

Our results demonstrate the value of using standardized methodology as a means to generate genuinely comparable data among tropical forests (Clark & Clark 1989). Our results also highlight the need for long-term studies to measure the relative roles of terrestrial and epiphytic seedlings in the natural recruitment of Hawaiian rain forest trees.

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