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Population ecology of *Metrosideros polymorpha* and some associated plants of Hawaiian volcanoes

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University of Hawaii, 1993

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POPULATION ECOLOGY OF METROSIDEROS POLYMORPHA AND
SOME ASSOCIATED PLANTS OF HAWAIIAN VOLCANOES

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE
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BOTANICAL SCIENCES (BOTANY)

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ABSTRACT

Metrosideros polymorpha is the dominant tree of Hawaiian rain forests and lava flows. Research was undertaken to explain: the pattern of Metrosideros forest development on lava flows; the role seed ecology plays in maintaining Metrosideros populations; and the relationships between Metrosideros and associated species.

Long-term rain forest development was inferred from measurements of population structure for Metrosideros, other trees, and tree ferns on a chronosequence of five lava flows (aged 47-3000 yr; Mauna Loa). Metrosideros comprised $\geq 70\%$ of the tree basal area at each site. Although Metrosideros basal area increased with flow age, population densities peaked on the 137 yr flow, then declined, apparently through self-thinning. On the older flows, a dense tree fern canopy may have inhibited regeneration of Metrosideros. Dominance shifted from pubescent to glabrous varieties of Metrosideros as flow age increased.

Seed dispersal data, collected on a lava flow downwind of Metrosideros forest, indicated that seed density decreased from $5580 \text{ m}^{-2}\text{yr}^{-1}$ at the forest edge, to $20 \text{ m}^{-2}\text{yr}^{-1}$ 250 m away. However, seedling density did not

decrease across the flow, suggesting that recruitment is not limited by seed rain.

In the laboratory, Metrosideros seeds germinated over a wide range of temperatures and light qualities. Germination in the dark and emergence after burial were poor. The light requirement was not overcome by a fluctuating thermoperiod. Seeds from glabrous and pubescent plants differed in their germination characteristics.

In a Kilauea forest, abundances were quantified for seed plants in the vegetation, seed rain, and seed bank. The seed rain and vegetation were more similar to each other than either was to the seed bank. Metrosideros dominated the vegetation and seed rain, but formed only a pseudo-persistent seed bank. Native species dominated the vegetation and seed rain, but alien species dominated the seed bank, suggesting that aliens may replace many of the natives if the forest is disturbed.

Metrosideros seeds are produced in great numbers, are widely dispersed, and can germinate under diverse environmental conditions. These attributes contribute to the success of Metrosideros as an early colonizer of new substrates and should also promote regeneration in established forests.

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CHAPTER 1: LITERATURE REVIEW AND PROPOSED RESEARCH

Literature Review

Introduction:

The study of plant succession involves the synthesis of information obtained from a wide range of more narrowly defined ecological fields. Therefore, following a brief discussion of certain concepts concerning succession theory in general, and a review of the relevant results of published studies of succession on volcanic substrates in Hawai'i, the overall process of succession will be divided into relatively discrete subtopics. These subtopics will correspond to some basic divisions in the "ecological life cycle" of a plant (Fig. 1.1), including dispersal, germination, seedling establishment, and population development. Each subtopic will be examined in relation to the process of succession in general, and with respect to the ecology of the pioneer tree Metrosideros polymorpha (Myrtaceae), and other selected pioneer plant species that participate in volcanic successions in Hawai'i.

Throughout, the emphasis will be placed on illustrating how the process of succession relates to the development of the three major pools of species that comprise a plant community, i.e. the seed rain, the seed bank, and the standing vegetation (Fig. 1.1). For topics on which there

are no data describing Hawaiian plants, only general ecological trends observed elsewhere will be discussed.

Succession as a general concept:

Plant succession has been defined in different ways by different ecologists (McIntosh, 1985). Finegan (1984) gives a clear definition of the term "succession" as it is commonly used today: "the directional change with time of the species composition and vegetation physiognomy of a single site where climate remains effectively constant." Forest succession results in the production of a forest. Most forest successions can be classified as either primary or secondary. Primary successions occur on newly exposed, previously unvegetated areas such as lava flows or glacial moraines, while secondary successions occur on sites where the previous vegetation cover has been disrupted, such as burned or logged areas (Miles, 1979). The development of vegetation from the first pioneers to the final mature phase is called a sere (Clements, 1916).

Clements (1916) produced the first comprehensive attempt to explain the process of plant succession. According to Clements, succession can be divided into six subprocesses:

- 1) nudation - the exposure of the site;
- 2) migration - the arrival of plant propagules;
- 3) ecesis - germination and establishment;

- 4) competition - leading to dominance and subordination;
- 5) reaction - site modification resulting from occupancy by plants;
- 6) stabilization - the production of a self-maintaining, climatic climax.

Clements considered succession to be a unidirectional, deterministic process, driven by reaction, and culminating in a stable, climax vegetation type determined by the prevailing regional climate. While the existence of stable, climax vegetation is questionable (Gleason, 1926, 1927, 1939; Miles, 1979; White, 1979; Sousa, 1984), and the importance of reaction as a driving force has been challenged (Miles, 1979; Finegan, 1984), Clements' first five subprocesses still serve as useful divisions of the overall process of succession (Miles, 1979).

Clements' concept of succession was in sharp contrast with that of Gleason (1926, 1927, 1939), who believed that the process of succession and the resulting composition of the plant community are probabilistic, rather than deterministic. Gleason proposed that the direction and outcome of succession depend on the interaction between environmental fluctuations and the plant propagules arriving at a site. Furthermore, Gleason (1927) did not believe that succession results in the eventual production of a stable, climax community, but rather that succession

is "continuous and universal, and the rate of change alone remains the fundamental successional difference between associations." Clements' (1916) and Gleason's (1926, 1927, 1939) views on succession have come to represent opposite poles of the spectrum of successional theories, and the intervening space has become filled with dozens of additional theories, each at odds with most of the others (McIntosh, 1985; Miles, 1987).

For the past decade, perhaps the most popular theory has been that of Connell and Slatyer (1977), who developed a reinterpretation of the models of successional pathways produced by previous authors (Miles, 1987), most notably Clements (1916) and Egler (1954). Connell and Slatyer proposed that any given succession was driven by one of three processes: facilitation, tolerance, or inhibition. According to the facilitation model (corresponding to the primary succession scheme of Clements and the relay floristics model of Egler) the first pioneers modify the microenvironment so that it comes to favor the next (or future) species in the successional sequence more than it favors the first pioneers themselves, which are then replaced. Thus, the pioneers facilitate the establishment of the later successional species, and the successional communities, or dominant species, are relatively distinct and do not overlap in time. In the tolerance model (corresponding to Clements' secondary succession model and

Egler's initial floristic composition model), propagules of species of many, if not all, seral stages are present at the outset of the succession, residing in seed banks. Different species dominate the sere at different times due to differences in growth rate and longevity. The slow-growing, long-lived species that come to be dominant during late successional stages are able to tolerate the presence of the fast-growing, short-lived species dominant during the early stages, and establish and grow up through them. Finally, according to the inhibition model (Clements' subclimax), the first pioneers to establish are able to hold the site indefinitely, preventing the establishment of later successional species. When the pioneers senesce and die, the resulting gap is open to colonization by other pioneers or later successional species. As in the tolerance model, the directional or progressive nature of the successional sequence is derived, in part, from differences in longevity among the species of the different stages; the long-lived, slow-growing species eventually capture all of the open space, and the pioneers disappear from the community.

While Connell and Slatyer (1977) originally proposed facilitation, inhibition, and tolerance as independent, mutually exclusive mechanisms, they are now generally considered to be complementary, operating both simultaneously and sequentially during any given

succession (Miles, 1987). This is because these mechanisms describe interspecific interactions, the nature of which will be determined by the ecological characteristics of the species involved, with each pair of species having its own unique relationship. Similar lines of thought have led many authors to advocate studying any particular succession by understanding and then linking together the population ecologies of all significant species that participate in that succession (Drury and Nisbet, 1973; Horn, 1974; Noble and Slatyer, 1980; Peet and Christensen, 1980; Finegan, 1984; Grubb, 1986; Mortimer, 1987). As a consequence, several recent reviews of vegetation dynamics in general (c.f. van der Maarel, 1988), and succession in particular (Finegan, 1984; Miles, 1987), suggest that the search for a single general model, applicable to all successions, is being abandoned as unrealistic.

General aspects of volcanic succession in Hawai'i:

During the past several hundred years, the two most active Hawaiian volcanoes have been Mauna Loa and Kilauea, both of which are located on the island of Hawai'i (Macdonald et al., 1986). The plant communities found on the recent substrates produced by these two volcanoes have been the subject of numerous studies.

Environmental factors, such as rainfall, substrate type, temperature, and nutrient availability have been identified as important variables controlling the rate of succession on volcanic substrates; the most critical are those determining the amount of moisture available to the pioneer plants. The rate of succession is generally most rapid where moisture availability is greatest (Forbes, 1912; MacCaughey, 1917; Skottsberg, 1941; Fosberg, 1967; Atkinson, 1969, 1970; Egger, 1971; Jackson, 1971; Smathers and Mueller-Dombois, 1974). Moisture availability is determined by the interaction between precipitation, which is influenced by elevation and aspect (Carlquist, 1980), and the water-holding characteristics of the substrate ('a'ā or pāhoehoe lava, spatter, ash, etc.; Atkinson, 1969; Smathers and Mueller-Dombois, 1974).

High substrate temperatures, due to residual heat in the core of a lava flow, can increase the moisture supply in the rooting zone by refluxing percolated rainwater back to the surface as steam which then condenses, permitting colonization by plants (Doty, 1967). Alternatively, high surface temperatures attributable to subterranean volcanic activity may surpass the tolerance limits of potential pioneers, thus retarding colonization (Smathers and Mueller-Dombois, 1974). At the other extreme, the combination of low temperatures and low rainfall combine to slow the rate of succession at high elevations

(Mueller-Dombois and Krajina, 1968; Mueller-Dombois et al., 1981)

Young, volcanic substrates in Hawai'i are known to contain little or no nitrogen, and this is believed to be another important factor limiting the rate of succession on these surfaces (Balakrishnan and Mueller-Dombois, 1983; Vitousek et al., 1983; Vitousek and Walker, 1987). Several species of nitrogen-fixing lichens and free-living cyanophytes commonly colonize the new surfaces (Doty, 1967; Jackson and Keller, 1970; Jackson, 1971; Smathers and Mueller-Dombois, 1974), and are presumably responsible for contributing the majority of the nitrogen accumulated in the developing soils. Atmospheric deposition also contributes small amounts of nitrogen to these substrates (Smathers and Mueller-Dombois, 1974).

Another important, though often overlooked, factor influencing the rate of succession is the availability of diaspores of pioneer species in the vicinity of the newly deposited surface. Several authors (MacCaughey, 1917; Smathers and Mueller-Dombois, 1974; Mueller-Dombois, 1987a) suggest that the lack of reproductively mature representatives of pioneer species in the vicinity of a new surface may slow the rate of colonization of that surface.

A main objective of previous studies of volcanic succession in Hawai'i has been to document the presence of

species on recent volcanic surfaces. Studies have been carried out on a variety of substrates encompassing a wide range of ages as well as elevations and aspects (and therefore climates). Because these studies were not designed in such a way that they bear any systematic relationship to each other, generalizations are difficult to extract. Nevertheless, a few taxa deserve mention because they have been so successful in colonizing young (< 100 yr old) lava flows in so many situations.

Investigators seeking blue-green algae on recent lava have found them (Stigonema spp. and Scytonema spp.) to be among the very first colonizers, appearing within the first year after the surface hardened (Doty, 1967; Smathers and Mueller-Dombois, 1974). Other cryptogams commonly found among the earliest colonizers include the lichens Stereocaulon vulcani and Cladonia spp. and the mosses Campylopus spp., Rhacomitrium lanuginosum, and Grimmia trichophylla (Miller, 1960; Doty, 1967; Egglar, 1971; Jackson, 1971; Smathers and Mueller-Dombois, 1974).

Several species of pteridophytes are also able to colonize lava within the first several years after formation, including Psilotum nudum, Lycopodium cernuum, Nephrolepis spp., Polypodium spp., Pityrogramma calomelanos, Sphenomeris chinensis, Dicranopteris linearis, and Sadleria cyatheoides (Forbes, 1912;

MacCaughey, 1917; Skottsberg, 1941; Atkinson, 1969, 1970; Egger, 1971; Smathers and Mueller-Dombois, 1974).

Among the angiosperms, the following taxa are some of those most frequently recorded from a wide range of climatic and elevational situations on relatively recent (historic) flows: Andropogon virginicus (alien, Gramineae), Machaerina angustifolia (indigenous, Cyperaceae), Arundina graminifolia (alien, Orchidaceae), Dubautia scabra and D. ciliolata (endemic, Compositae), Hedyotis centranthoides and Coprosma ernodeoides (endemic, Rubiaceae), Vaccinium calycinum and V. reticulatum (endemic, Ericaceae), Buddleia asiatica (alien, Buddleiaceae), Styphelia tameiameiae (indigenous, Epacridaceae), and Metrosideros polymorpha (endemic, Myrtaceae) (Forbes, 1912; MacCaughey, 1917; Skottsberg, 1941; Atkinson, 1969, 1970; Egger, 1971; Smathers and Mueller-Dombois, 1974; Carlquist, 1980). Other taxa may be abundant in particular situations, depending on local environmental conditions.

Plant dispersal, the seed rain, and succession:

The sum of all seeds arriving on a particular site is referred to as the seed rain. The seeds comprising the seed rain on a site are derived through dispersal of diaspores produced by distant (off-site) plants and from dispersal of diaspores produced by local (on-site) plants

(Fig. 1.1). The composition of the seed rain falling on a site is determined by the proximity of reproductive plants, the reproductive output of those plants, and the availability of dispersal vectors (Harper, 1977).

Primary succession, by definition (Miles, 1979), takes place on a site lacking plants or plant propagules. All potential colonizers (i.e. the seed rain) must therefore arrive on-site via dispersal of propagules from individuals established elsewhere. Only after the first colonists have begun to reproduce will the seed rain also include seeds produced by, and dispersed from, the pioneers themselves. Thus, MacCaughey (1917) and Smathers and Mueller-Dombois (1974) noted that an important factor in the colonization of volcanic surfaces is the availability of plant propagules supplied by the surrounding vegetation. The critical nature of accessibility has been stressed in the literature on succession theory (Gleason, 1926, 1927; Kellman, 1970; Harper, 1977; Johnstone, 1986), but has often been underappreciated, if not completely ignored, in most field studies, even though its importance has been clearly demonstrated by those ecologists who have chosen to investigate it (Mcquilkin, 1940; Spring et al., 1974; Purata, 1986; Olsson, 1987).

While most species of seed plants are dispersed by animals (Gentry, 1982; Howe and Smallwood, 1982; van der

Pijl, 1982; Fenner, 1985), pioneer species are primarily wind-dispersed (Howe and Smallwood, 1982; van der Pijl, 1982; Fenner, 1985, 1987). One explanation for the paucity of animal-dispersed diaspores among pioneer species may be that animals do not frequent barren sites until some vegetation development has taken place, and therefore animal-dispersed species are unlikely to be included in the very first wave of pioneers on a site. For example, in studies of old-field succession it was demonstrated that bird-dispersed diaspores were concentrated under perch sites, such as living, dead, or artificial trees, and were very rarely found in the intervening spaces or in treeless fields (Debussche et al., 1982, 1985; McDonnell and Stiles, 1983; Willson and Crome, 1989). Some animals may require the presence of plants that provide cover or forage before they will visit an early successional site (Fenner, 1985, 1987). Such situations, where the first pioneers provide a mechanism for the arrival of later species, are examples of facilitation (sensu Connell and Slatyer, 1977).

The pioneer plants common on Hawaiian lava flows in the montane rain forest zone appear to produce diaspores corresponding to one of two dispersal syndromes. Many of the pioneers produce diaspores that seem likely to be wind-dispersed; most of the rest produce diaspores possessing morphological features that suggest ingestion

and subsequent dispersal by birds. Few, if any, of the pioneer species of the montane rain forest zone produce diaspores that appear to be adapted for dispersal by mammals. The lack of mammal-dispersed species is consistent with the lack of frugivorous mammals in the native fauna (Carlquist, 1974). These conclusions are based on morphology, since no hard data concerning the dispersal of these species have been published. It is important to bear in mind, however, that the presence of morphological features that appear to correspond to dispersal by any one particular vector does not ensure dispersal by that vector, nor does the absence of particular morphological features preclude the possibility of dispersal by a given vector (van der Pijl, 1982).

The spores of the ferns and fern allies found on Hawaiian lava flows, like spores of most isosporous pteridophytes elsewhere, are almost certainly dispersed by wind, and the colonizing abilities of these plants are unlikely to be limited by problems of dispersal (Carlquist, 1974; van der Pijl, 1982).

Empirical studies of wind-dispersed diaspores have demonstrated that patterns of seed deposition following wind-dispersal tend to be leptokurtic, with the greatest concentration of diaspores travelling downwind, and most of them falling quite close to the parent plant (Pinus taeda, McQuilkin, 1940; Eucalyptus spp., Cremer, 1965;

Melaleuca quinquinervia, Woodall, 1982; Nothofagus menziesii, Allen, 1987a; Protea spp., Bond, 1988). Nevertheless, significant numbers of seeds are dispersed to distances of at least several hundred meters away from the source. The most important factors determining dispersal distance are: wind velocity, air turbulence, terminal velocity of the diaspore, and height of diaspore release (Cremer, 1977; van der Pijl, 1982; Burrows, 1986). Calculated dispersal distances, based on these factors, conform well to observed dispersal distances (Cremer, 1977; Woodall, 1982; Augspurger, 1986).

Metrosideros polymorpha is among the first pioneers to appear on Hawaiian lava flows, and is almost invariably the first tree species to appear on flows in the montane rain forest zone (Atkinson, 1969; Smathers and Mueller-Dombois, 1974). Metrosideros produces capsules containing numerous small seeds (mean fresh wt. of embryo-containing seeds \approx 0.07mg) that are believed to be wind dispersed (Carlquist, 1974; Corn, 1979), although the possibility that they could be carried by birds has also been suggested (Guppy, 1906). While no data describing the dispersal of M. polymorpha exist, it is likely that wind-blown seeds commonly travel over distances of at least several hundred meters, as other Myrtaceous tree species that have similar-sized seeds, such as Metrosideros umbellata (Wardle, 1971) and Melaleuca quinquinervia

(Woodall, 1982), are known to attain such distances. Fruit dehiscence and seed dispersal of Metrosideros polymorpha tend to be concentrated in the fall and winter (Porter, 1972).

Among the other angiosperms common on recent Hawaiian lava flows, several produce diaspores with morphologies suggesting adaptation for wind-dispersal (although again, no empirical data have been collected for any of the species). Arundina graminifolia produces the minute, dust-like seeds typical of the Orchidaceae, a family for which wind is presumed to be the principal dispersal vector (van der Pijl, 1982). The caryopses of Andropogon virginicus and the achenes of Dubautia scabra are small and light and possess parachute-like appendages (awns and pappus, respectively) which are typically considered to be indicators of adaptation for wind-dispersal (van der Pijl, 1982). The achenes of Machaerina angustifolia and the seeds of Buddleia asiatica are small and winged, likewise suggesting dispersal by wind (van der Pijl, 1982).

The following are some of the features that characterize diaspores that are dispersed by being ingested and later ejected by birds (adapted from van der Pijl, 1982):

1. attractive, edible tissue (fruit, aril, etc.);

2. protection against premature consumption (green, acid, etc.);
3. protection of seed (indigestible endocarp or testa);
4. colors signaling maturity (red, yellow, black, blue);
5. weak odor;
6. permanent attachment (not abscised when mature).

Several of the common pioneer taxa produce fruits that exhibit some or all of these characteristics; examples include Vaccinium reticulatum and Vaccinium calycinum, both of which produce red berries, Coprosma ernodeoides, which has shiny black drupes, and Styphelia tameiameia, which has red or white drupes. Fleshy fruits suggestive of bird-dispersal are also produced by many of the tree species that appear during the middle stages of forest development on lava flows, including Coprosma spp., Cheirodendron trigynum, Myrsine lessertiana, and Ilex anomala.

Development of the seed bank:

As the seed rain falls onto and within a plant community, most of the seeds find their way down to the level of the soil. The viable seeds found in the soil comprise the soil seed bank (Fig. 1.1).

Seed banks in lowland tropical rain forests have, on average, between 300 and 800 germinable seeds/m², representing between 20 and 50 species, with one species usually contributing more than half the individuals present (Guevara and Gómez-Pompa, 1972; Cheke, et al., 1979; Hall and Swaine, 1980; Hopkins and Graham, 1983; Uhl and Clark, 1983; Garwood, 1989). Although fewer studies have been done in upland tropical rain forests (Cheke, et al., 1979; Hall and Swaine, 1980; Lawton and Putz, 1988), seed banks there seem to contain both fewer seeds and fewer species than are found in the lowlands (table 1.1); as in lowland forests, seed banks of upland forests are dominated by one or a few species.

The potential composition of the seed bank is determined by the composition of the seed rain, which is its sole source of seed gains (Harper, 1977). These seeds may represent elements of the present and former on-site species as well as off-site species which have dispersed seeds onto the site (Fig. 1.1; Harper, 1977; Uhl and Clark, 1983; Saulei and Swaine, 1988). Losses occur through predation, decay/senescence, and germination (Harper, 1977; Hopkins and Graham, 1984, 1987; Fenner, 1985; Silvertown, 1987; Willson, 1988; Baker, 1989; Garwood, 1989). The composition of the seed bank at any one time, as well as the abundance of any particular species in the seed bank, is therefore the result of these

gains and losses. Differences in behavior among species are determined by the different rates at which the four processes involved in seed gain and loss occur, and these rates are, in turn, related to the particular reproductive and seed characteristics of the species (Baker, 1989; Garwood, 1989).

The length of time that a seed can survive in the soil depends on characteristics of the soil environment as well as inherent characteristics of the seeds. Species differ not only in their ability to escape or resist predation, but also in their ability to remain viable in the absence of predation (Hopkins and Graham, 1987; Willson, 1988). Seeds of some species die within a few weeks if they are prevented from germinating, while seeds of others retain viability for at least several years (Ng, 1980; Garwood, 1983, 1989; Vázquez-Yanes and Orozco-Segovia, 1984).

Because species differ in seed longevity, it is not surprising that, in those situations in which it has been investigated, there has been little correspondence between the composition of the vegetation and the composition of the seed bank (Guevara and Gómez-Pompa, 1972; Hall and Swaine, 1980; Saulei and Swaine, 1988), or between the annual seed rain and the seed bank (Uhl and Clark, 1983; Saulei and Swaine, 1988).

One important factor affecting seed longevity is the capacity for seeds to remain dormant in the soil. The seeds in the seed bank may be active, and thus capable of germinating soon after arrival, or dormant, requiring stimuli to trigger germination (Harper, 1977). Ecologists recognize three main classes of dormancy: innate, enforced, and induced (Harper, 1977).

An innately dormant seed is one that is incapable of germination at the time of release from the parent, even if it is exposed to conditions suitable for seedling growth. These seeds may require scarification, a period of embryo maturation, or the removal of an inhibitor from the seed coat before they are able to germinate (Harper, 1977).

Enforced dormancy refers to a condition in which a seed is not innately dormant, but is instead simply deprived of some basic requirement for germination, such as water or oxygen; such seeds are considered by some to not be dormant at all (Garwood, 1989), or to be merely quiescent (Fenner, 1985), since the "stimuli" required for germination are simply the requirements for metabolism in general. Therefore, those seeds considered here (Fig. 1.1) to be active at the time of release, would be considered by some others to be quiescent or dormant.

Some seeds that are not dormant at the time of release, but do not immediately experience conditions

suitable for germination may acquire an induced dormancy (Harper, 1977). For example, seeds that are initially able to germinate either in darkness or full sunlight may acquire dormancy if they are exposed to light which has passed through a canopy of leaves; after exposure to such light, which has a low red/far-red (R/FR) ratio, the seeds will germinate only when exposed to full sunlight (Silvertown, 1980). Such a response is indicative of dormancy mediated by the photoreversible pigment phytochrome, in which the R/FR ratio of the incident light determines the germination response (Vázquez-Yanes and Smith, 1982).

Most forms of dormancy are regarded by ecologists as being mechanisms for avoiding germination under conditions which are likely to be unfavorable for seedling emergence, growth, or survival (Harper, 1977; Vázquez-Yanes and Orozco-Segovia, 1982, 1984; Vázquez-Yanes and Smith, 1982; Fenner, 1985; Silvertown, 1987). In many cases the stimuli required to break dormancy in seeds of tropical rain forest species are phenomena associated with disruption of an overlying plant canopy. Perhaps the most common stimulus involves a shift from light with a low R/FR ratio to light with a high R/FR ratio (indicating removal of an overlying plant canopy; Vázquez-Yanes and Smith, 1982; Vázquez-Yanes and Orozco-Segovia, 1984, 1987). Other common stimuli involved in breaking dormancy

in tropical plants include: a shift from dark to light (indicating removal of overlying soil; Koller, 1972), an increase in the amplitude of diurnal temperature fluctuations (indicating increased insolation at ground-level, and therefore canopy removal; Vázquez-Yanes, 1981; Vázquez-Yanes and Orozco-Segovia, 1982), and brief exposure to a relatively high temperature (indicating removal of the overlying canopy by fire; Vázquez-Yanes, 1981). Since no plant cover exists on fresh lava flows, conditions associated with plant canopies would not impose dormancy on the seeds found there. However, as succession proceeds, the development of a plant canopy could have an increasing influence on the developing seed bank, by inducing dormancy in shaded seeds of late-successional species (an example of inhibition, sensu Connell and Slatyer, 1977).

Species can be classified according to the behavior of their seeds in the soil, and the type of seed bank they are capable of forming. Garwood (1989) described five major "tropical soil seed bank strategies" (or syndromes) and several variations, based on germination behavior and phenology of seed dispersal. These seed bank strategies or types include:

1. transient: composed of seeds that are short-lived ($< \frac{1}{2}$ yr) and lack dormancy (i.e. are quiescent or

- exhibit enforced dormancy), and are dispersed for brief periods during the year;
2. seasonal-transient: composed of seeds that have intermediate longevity (<1 yr) and that seasonally acquire an induced dormancy, usually during the dry season;
 3. delayed-transient: composed of seeds that have intermediate or long (≥ 1 yr) lifespans and innate dormancy;
 4. persistent: composed of seeds that are long-lived and exhibit some form of dormancy;
 5. pseudo-persistent: composed of seeds that are short-lived, lack dormancy, and are dispersed throughout the year.

Some species exhibit behaviors that conform to none of these categories, or overlap categories. According to Garwood (1989) "at least two of the following criteria must be known to identify seed bank syndromes: seasonal changes in the seed bank, seasonal timing of dispersal, or the presence of ... dormancy."

The seed bank determines the potential vegetation of a site, in that the standing vegetation must comprise some subset of those species (and individuals) present in the seed bank. At the outset of a primary succession, by definition (Fenner, 1987), no seed bank exists. It, and therefore the vegetation, develops as a consequence of

seed rain originating from off-site (Harper, 1977). In contrast, when regeneration occurs following a disturbance on a site which already contains a seed bank, the in situ seeds can play an important role in the regeneration process (Harper, 1977), regardless of whether the disturbance is small-scale, such as a treefall gap (Lawton and Putz, 1988), or a large-scale, secondary succession occurring on cleared land (Ewel et al., 1981; Uhl et al., 1981, 1982; Uhl and Clark, 1983; Fenner, 1987). In montane tropical rain forests, those seeds (or seedlings) which are already in place at the time of such a disturbance often have a great advantage in claiming space compared to those which are not already present, and which must therefore arrive via dispersal (Lawton and Putz, 1988; Garwood, 1989). Because persistence in the seed bank can allow a species that was formerly present on a site to reclaim that site when a gap forms, maintenance of a seed bank is often considered to represent dispersal in time, a strategy that is complementary to dispersal in space (Grubb, 1986).

Not all seeds in the seed rain reach the soil. Some remain lodged in epiphytic plants, forks in trees, patches of moss on fallen logs, or any other small crevices capable of trapping a seed (Ogden, 1971; June and Ogden, 1975; Burton and Mueller-Dombois, 1984; Allen, 1987b; Lawton and Putz, 1988). Seeds trapped above the ground

are, for no obvious reason, usually not included in discussions of seed banks, even though data exist which seem to indicate that seedlings drawn from this pool may survive and contribute to the standing vegetation (Burton and Mueller-Dombois, 1984; Lawton and Putz, 1988). Given the importance, in montane tropical forests, of establishment both on live trees and on "nurse logs" (Burton and Mueller-Dombois, 1984; Lawton and Putz, 1988), it is surprising that more attention has not been devoted to "above-ground" seed banks.

There are no published data concerning either the seed banks of Hawaiian forests, or the dormancy characteristics of Hawaiian rain forest species.

Seed germination and seedling emergence:

The terminology applied to stages in the transition from seed to seedling is rather arbitrary and inconsistently applied. In the discussion below, the terms will be defined in the following consistent, though arbitrary, manner. A "germinant" is a germinated seed which still derives at least some nutrition from its cotyledon(s), endosperm, or other seed storage products, regardless of whether or not it has produced any true leaves. An "established seedling" is a seedling that no longer receives nutrition from cotyledons or endosperm, and is presumably somewhat able to withstand a mild shock,

such as a brief dry spell or removal of some of its foliage. The term "seedling" will be used in a general sense to refer to both germinants and established seedlings.

The period between germination and seedling establishment is one of great vulnerability for a germinant (Harper, 1977). Classic experiments (Harper et al. 1965; Harper and Obeid, 1967) clearly demonstrated the importance of viewing the environment on a scale appropriate for a seed when they found that subtle differences both in micro-topography, such as scratches on the surface of the soil, and in depth of seed burial, could have profound effects on seed germination and seedling emergence. Such studies of seed germination and seedling emergence led to the development of the "safe site" concept. The term describes a place in the environment (or a set of environmental conditions) in which seeds germinate and the germinants emerge; it is a micro-site in which all the requirements for germination are met, and which is free from hazards such as pathogens, predators, and competitors (Harper, 1977).

One of the most commonly reported safe sites for seeds of tree species is a fallen log, usually with a well-developed cover of bryophytes (Nothofagus fusca, June and Ogden, 1971; Metrosideros umbellata, Stewart and Veblen, 1982; Metrosideros polymorpha, Burton and Mueller-

Dombois, 1984; Nothofagus menziesii, Allen, 1987b; eight species of trees, Lawton and Putz, 1988). It is not clear whether the bryophytes themselves provide a favorable microenvironment for germination and establishment, or whether both the mosses and seedlings are responding independently to some set of conditions associated with the logs (e.g. elevation above the soil surface), and therefore have correlated distribution patterns. On 'a'ā lava flows in the montane rain forest zone of Hawai'i, the remains of logs are quite rare, while bryophyte cover is often extensive (Atkinson, 1969). It is not known whether mats of bryophytes on these lava flows influence germination or establishment of pioneer vascular plants.

The only published data (Burton, 1982) on the germination characteristics of M. polymorpha indicate that, as in other species of Metrosideros (Dawson, 1970; Wardle, 1971), less than 15% of the seeds actually contain embryos. Furthermore, Burton (1982) reported that only 30% of the seeds that have embryos were viable. Unfortunately, because all of Burton's (1982) seeds were collected from a single tree, and they were not sorted to ensure that only seeds containing embryos were used in germination experiments, his results must be interpreted with caution. Data from several germination experiments suggest that the optimum temperatures for germination occur between 22-32°C (Burton, 1982). Optimum germination

occurred at relatively low light intensities (15% and 12% germination at 133 and 211 $\mu\text{Em}^{-2}\text{s}^{-1}$, respectively), though some germination occurred across the entire spectrum of treatments, which ranged from full sunlight (2000 $\mu\text{Em}^{-2}\text{s}^{-1}$) to complete darkness (Burton, 1982). In contrast, Corn (1979) claimed that M. polymorpha requires light for germination, and Wardle (1971) claimed the same for M. umbellata in New Zealand, though neither reported any data.

There are no published studies describing germination of Metrosideros on lava flows, but Burton and Mueller-Dombois (1984) reported some data on observations of the germination (actually emergence) of Metrosideros in the montane Metrosideros/Cibotium rain forest on Hawai'i. At least twice as many germinants appeared in experimental plots, in which the overlying leaf canopy was thinned or removed, as appeared in control plots, in which the canopy was left intact. This may be due to the increased temperatures recorded in the sunnier plots (Burton and Mueller-Dombois, 1984), although such a response would also be consistent with a phytochrome-mediated dormancy (Vázquez-Yanes and Orozco-Segovia, 1987). Germination (emergence) took place throughout the year but exhibited a pronounced seasonality, with peak germination occurring in July and August. It is unclear whether this peak was due to summer weather that favored germination of accumulated

seeds or to a phenological flush of available seeds, imposed by an earlier phenological concentration of flowering and fruit maturation (Burton and Mueller-Dombois, 1984).

According to Burton and Mueller-Dombois (1984), germinants of Metrosideros in the Metrosideros/Cibotium forest "were restricted almost exclusively to the mats of mosses and liverworts that cover fallen logs and tree fern trunks (both fallen and upright)." Of the 1052 Metrosideros seedlings found in the plots, only 1.8% were found on the soil, while 98.2% were found on logs or upright plant stems. Because there was no significant difference in mortality between those seedlings found on soil and those perched above-ground, it would seem that the distribution pattern of seedlings may reflect the distribution of safe-sites for germination rather than differential survival following uniform germination.

Seedling establishment:

There are no quantitative studies describing establishment of Metrosideros seedlings on lava flows. However, it is known that established seedlings found on pyroclastic substrates and smooth, pāhoehoe lava are associated with relatively sheltered micro-sites, such as tree snags and lava cracks, rather than with bare, exposed volcanic surfaces (Smathers and Mueller-Dombois, 1974;

Wright and Mueller-Dombois, 1988). No clear pattern is discernable for the more heterogeneous surfaces of 'a'a flows (Atkinson, 1969).

It has frequently been reported that Metrosideros seedlings, and especially saplings, are rare in the understory of closed-canopy forest (Atkinson, 1969; Mueller-Dombois et al., 1980). These findings have been interpreted as an indication that Metrosideros is relatively shade-intolerant. Nevertheless, the results of two studies indicate that seedlings of Metrosideros are able to tolerate at least some shade (Friend, 1980; Burton and Mueller-Dombois, 1984).

Friend (1980) determined that newly germinated Metrosideros seedlings were able to maintain a net positive carbon balance when grown for 126 days under white light with a photosynthetic photon flux density (PPFD) of between 8 and 13 $\mu\text{Em}^{-2}\text{s}^{-1}$ ($\approx 0.6\%$ full sunlight), and a daylength of 12 h. Net primary production increased as PPFD increased from 8 to 235 $\mu\text{Em}^{-2}\text{s}^{-1}$, the highest light intensity used. It is not clear whether Metrosideros can grow under such low PPFDs when the light they receive has been filtered through a plant canopy, because filtered light would have a lower R/FR ratio than white light has (Friend, 1980), and it would also be depleted in the red and blue wavelengths which are most important for photosynthesis. Furthermore, because

all seedlings were derived from seeds collected from a single tree growing in Kilauea forest, it is not clear how representative the results are. Nevertheless, Friend's (1980) data do indicate that Metrosideros seedlings do not require full sunlight, but can instead grow at very low PPFDs, such as might be found deep in the lava cracks where it is known to establish (Forbes, 1912; Skottsberg, 1941; Atkinson, 1969; Smathers and Mueller-Dombois, 1974).

Burton and Mueller-Dombois (1984) presented additional evidence of the ability of Metrosideros seedlings to tolerate moderate shade. They followed survival and growth of Metrosideros seedlings in forest plots in which the tree fern canopy was either left intact (control plots) or thinned to 75%, 50%, 25%, or 0% of its original frond density. While many of the results were quite variable, several trends were noted. Those seedlings that had established prior to the beginning of the experiment ("shade-born" seedlings) suffered low mortality at intermediate light intensities, and higher mortality in the control plots and in full sunlight. Average annual height increments for the shade-born seedlings were greatest (2-10.5 cm/yr) at intermediate light intensities. However, a few seedlings grew very well (up to 53 cm/yr) at high light intensities, and these seedlings may be sufficient in number to maintain the forest population (Burton and Mueller-Dombois, 1984).

Only a longer-term experiment would determine whether most population regeneration comes from seedlings growing in sun or shade, and from the seed bank ("sun-born" seedlings) or the "seedling bank" (shade-born seedlings). The significance of this is that it is evidence against continuous regeneration by Metrosideros under closed canopies. This supports earlier observations (Atkinson, 1969, Mueller-Dombois et al., 1980;) and reinforces the idea that regeneration usually occurs as a result of a disturbance that opens the plant canopy (Mueller-Dombois et al., 1980; Jacobi, 1983; Jacobi et al., 1983, 1988; Mueller-Dombois, 1983, 1986, 1987b).

Population development and decline:

Plant populations are often described on the basis of size frequency distributions, and plant sizes are often measured in terms of biomass. Tree sizes are most often reported in terms of stem diameter, basal area, or tree volume. The latter two measurements are usually linearly related to biomass, while the former is not (Mohler et al., 1978). Figure 1.2A depicts a tree population with a normal diameter distribution. Such a population will have a lognormal (inverse-J shaped) basal area (or biomass) size distribution (Fig. 1.2B; Mohler et al., 1978). Lognormal biomass distributions can be found in growing or invading populations that are increasing in density

(Spring, et al., 1974; Wright and Mueller-Dombois, 1988), or stable populations that are continuously regenerating (Ahmed and Ogden, 1987; Ogden, 1985), or populations that are decreasing in density because they are self-thinning (Ford, 1975; Cannell, et al., 1983; White, 1980; Weiner, 1985; Drake and Ungar, 1989). The importance of this is that instantaneous size distributions alone are not sufficient to describe population dynamics; they must be combined with other information about the ecology of a species. When possible, a single population should be followed through time, or populations of different ages, but with similar histories, should be compared (Silvertown, 1987).

Populations of shade-intolerant plants that establish evenly and densely often experience intraspecific competition and suffer density-dependent mortality, usually through self-thinning (Harper, 1977). The $-3/2$ self-thinning rule (Fig. 1.3) predicts that when a dense cohort of relatively shade-intolerant plants develops, and the plants reach a size at which they begin to interfere with each other, plant growth beyond that point is accompanied by mortality within the stand, resulting in a decrease in density (Harper, 1977). Numerous studies suggest that mortality during self-thinning is concentrated among the smallest individuals in the stand, preventing continuous regeneration and recruitment into

the canopy (McQuilkin, 1940; Ford, 1975; Mohler, et al., 1978; Cannell et al., 1984; Weiner, 1985; Ogden, 1985; Westoby and Howell, 1986; Peet and Christensen, 1987). Mortality is presumed to be a direct or indirect result of competition for some limiting resource (Harper, 1977), usually light (Weiner, 1985; Weiner and Thomas, 1986).

Self-thinning has usually been described for cohorts of individuals growing in even-aged stands. These cohorts may be found in artificial situations such as forestry plantations in which trees are planted simultaneously (White, 1980; Weiner and Thomas, 1986). Self-thinning is also believed to occur in the relatively even-aged stands (less well-defined cohorts) that are often found in natural situations in which a relatively mono-dominant forest stand develops as a result of rapid colonization of a disturbed area (Atkinson, 1969; Stewart and Veblen, 1982; Norton, 1983; Ogden, 1985; Mueller-Dombois, 1987b; Ogden et al., 1987). In this context, "relatively even aged refers to the situation where a site is 'fully stocked' with seedlings over a time period which is considerably less than the normally attainable age" (Ogden, 1985). Self-thinning has been shown to operate in populations that are not uniform in age (Westoby and Howell, 1986). In such populations, suppression of late recruits by larger, already-established plants may possibly reinforce the relatively even age structure as

self-thinning proceeds (Black and Wilkinson, 1963; Westoby, 1984; Peet and Christensen, 1987). The importance of self-thinning in stands of mixed species is not known (Peet and Christensen, 1987).

Many of the montane rain forests on Hawai'i have been observed to go into a condition of dieback, in which most or all of the Metrosideros trees that form the upper canopy die during a period of just several years (Mueller-Dombois et al., 1980; Mueller-Dombois, 1983, 1986; Jacobi, 1983; Jacobi et al., 1983, 1988). To explain stand-level dieback in Hawai'i, Mueller-Dombois (1983) has proposed a theory of "cohort senescence" which, while continuously evolving, can be summarized as follows:

1. A catastrophic disturbance (e.g. volcanic eruption) opens up a site, and a relatively even-aged cohort of Metrosideros becomes established during primary succession.
2. During population development, the cohort comes to consist of "individuals of similar age and physiological constitution, particularly when growing on uniform habitats".
3. Eventually, the trees reach a "senescing life stage" roughly simultaneously, in which they are in a state of relatively low vigor.
4. While the cohort is in the low vigor, senescing life stage, an "environmental stress factor" can trigger

the onset of stand level dieback. An example of an environmental stress factor is a drought of a severity which would not be threatening to trees in full vigor, but which may surpass the tolerance limits of over-mature or senescing plants.

5. As the canopy begins to break up, additional abiotic and biotic stress factors may hasten and further synchronize tree death.

Thus there are two components to dieback, an intrinsic component relating to stand demography, and an extrinsic component relating to environmental stress. It should be noted that synchronous dieback, as explained by the cohort senescence theory, is not deterministic; it is believed to take place only when all of the above-mentioned factors occur in sequence. If one or more of these factors is not present, synchronous dieback may not take place. For example, steps 1 and 2 involve a cohort of Metrosideros individuals becoming established after a disturbance, and then developing into a population that is relatively homogeneous in size, age, or life-stage. While such a scenario seems quite reasonable (Pinus taeda, McQuilkin, 1940; Metrosideros polymorpha, Atkinson, 1969), this is one of the least investigated aspects of the cohort senescence theory. If a population is for some reason prevented from developing as a cohort, it would presumably

be much less likely to be prone to cohort senescence and synchronous dieback.

A number of different types of dieback have been described, based primarily on the age and type of underlying substrate, and the extent and nature of regeneration that occurs following loss of the canopy trees (Mueller-Dombois et al. 1980; Mueller-Dombois, 1983). The type of dieback most likely to be encountered on the young, 'a'ā flows in the montane rain forest zone is "dryland dieback", which is described as "a salt-and-pepper dieback or patchy dieback on shallow lava rock outcrop soils" (Mueller-Dombois, 1983). Dryland dieback is usually followed by regeneration of a forest dominated by Metrosideros (Mueller-Dombois et al., 1980; Jacobi, 1983; Jacobi et al., 1983, 1988).

Vegetation on recent lava flows:

The preceding sections have discussed the ways the vegetation interacts with the seed rain and seed bank. The purpose of this section is to briefly describe what is known about the vegetation on recent 'a'ā lava flows in the montane rain forest zone on Mauna Loa.

Jacobi (1989) has produced maps of generalized plant associations for the montane rain forest zone on Mauna Loa (based on aerial photos taken between 1972 and 1977; map scale = 1:24,000). The vegetation on the lava flows to be

investigated in the proposed study (flows aged 47, 137, \approx 300, \approx 400, and \approx 3000 yr, excluding the 1984 flow) changes along the age sequence, from an open, mesic, pioneer community dominated by native shrubs (57 yr flow), to tall (> 10 m), open-canopied, Metrosideros forest with a subcanopy of native trees and an understory of native shrubs and tree ferns (310 and 2500 yr flows). This supports Atkinson's (1969) estimate that 300-400 years would be required for forest development on these lava flows.

Ecological differences among varieties of M. polymorpha:

The main focus of this study does not involve seeking to determine the extent of ecological differentiation among the varieties of M. polymorpha. However, since significant variation, correlated with habitat differences, has been reported within this species (Porter, 1972; Corn and Hiesey, 1973; Stemmermann, 1983; Dawson and Stemmermann, 1990), such variation must be taken into consideration in any ecological study. Stemmermann (1983) found that relatively drought-tolerant, pubescent varieties of M. polymorpha (M. p. var. polymorpha and M. p. var. incana) were associated with young lava flows, while less drought-tolerant, glabrous varieties (M. p. var. macrophylla and M. p. var. glaberrima) were associated with wetter, later

successional habitats. She also demonstrated experimentally that seedlings of the pubescent varieties grow faster than seedlings of the glabrous varieties. These results have been interpreted as indicating that the varieties were diverging into different ecological roles.

Proposed Research

Objectives:

This study has three major objectives: 1) to describe the processes by which pioneer, Metrosideros polymorpha forests develop on lava flows in the montane rain forest zone on the island of Hawai'i; 2) to determine what role seed ecology plays in maintaining the abundance of M. polymorpha in the Hawaiian environment; and 3) to generate baseline data concerning seed rain and seed banks of plant species found in the Metrosideros forest.

Significance:

The proposed research will fill several gaps in the present knowledge of tropical (and Hawaiian) forest ecology. It will be the first study to describe the quantitative relationships among the vegetation, seed rain, and seed bank of a tropical forest community. It will provide the first community-wide data concerning the abilities of native and alien species in Hawai'i to

disperse their seeds into intact native forests, as well as the first such data concerning the abilities of these species to maintain viable soil seed banks. It will define the dispersal and germination characteristics of M. polymorpha, the dominant tree of most Hawaiian forests. In addition, this study will test an underlying assumption of the theory proposed to explain dieback of Metrosideros forest stands, namely, that these stands are pre-disposed to synchronous senescence and dieback because they are composed of populations that establish and develop as cohorts (Mueller-Dombois, 1986). Finally, further insight will be gained into the possible ecological divergence of M. polymorpha varieties.

Research questions and preliminary hypotheses:

Q1. Are changes in the population structure of M. polymorpha along the chronosequence consistent with density-dependent mortality through self-thinning?

H1. Population basal area of M. polymorpha increases with lava flow age.

H2. Population density of M. polymorpha peaks early in succession, then declines as regeneration beneath the closed-canopied, older stands decreases.

Q2. Is colonization of the 1972 Kilauea lava flow limited by seed dispersal or seedling establishment?

H1. The density of seed rain of M. polymorpha on the

1972 flow decreases with increasing distance from the edge of the flow.

H2. The density of established M. polymorpha seedlings on the 1972 flow decreases with increasing distance from the edge of the flow, paralleling the density of M. polymorpha seed in the seed rain.

Q3. What are the germination requirements of M. polymorpha seeds?

H1. Seeds require light for germination.

H2. Seeds can germinate over a broad range of temperatures.

Q4. How distinct are the ecological differences among the hypothetical "successionally differentiated" varieties of M. polymorpha?

H1. The varieties of M. polymorpha differ with respect to characteristics of population distribution and structure.

H2. The varieties of M. polymorpha differ with respect to germination characteristics.

Q5. What types of seed bank syndromes are represented among species found in a native Hawaiian forest?

H1. The qualitative and quantitative composition of the seed rain and the seed bank vary seasonally.

Q6. What are the relationships among the seed rain, seed bank, and vegetation in a native Hawaiian forest?

H1. A given species currently represented in the

vegetation, seed rain, or seed bank may not be equally abundant in all three pools of species.

Methods and analysis:

Field sites will be established on a chronosequence of 5 'a'ā lava flows (aged 47, 137, \approx 300, \approx 400, and \approx 3000 yr), each at the same elevation in the montane rain forest zone on the eastern slope of Mauna Loa (1235 m), and each receiving equal rainfall (\approx 4000 mm). Because the substrate and climate variables are similar at all sites, age is assumed to be the most significant variable distinguishing the sites, and thus differences between them will be attributable to the different lengths of time that ecological processes have been operating at the different sites.

Characteristics of the populations found along the chronosequence will be compared to infer how a single population might develop in several hundred years on a single flow. Tree diameters will be measured in belt transects running across each flow, along the 1235 m contour. Population densities of seedlings, saplings, and trees of M. polymorpha, other common forest tree species, and tree ferns, will be measured in these transects.

Seed dispersal of M. polymorpha will be measured by placing seed traps along transects on a recent (1972 Kilauea) lava flow, and in the adjacent M. polymorpha

forest, then periodically collecting and identifying the seeds that fall into the traps, for one year. Seed rain on the 1972 flow (which lacks reproductively mature M. polymorpha) must come entirely from the adjacent forest. Thus, seed rain falling at various distances onto the flow can be compared to seed rain in a stand representing a potential seed source. Seedling establishment on the same flow will be estimated by counting the net numbers of seedlings established at various distances onto the flow, after 20 yr of colonization.

The germination ecology of Metrosideros seeds will be assessed in the greenhouse and laboratory. Controlled laboratory experiments will be performed in order to determine what influence light (including red, far-red, natural light, and darkness) has on germination. Other experiments will be performed in order to determine the optimum temperature for germination, and to determine what effect fluctuating temperatures have on germination. The ability of buried seeds to germinate and emerge will be assessed. In all germination experiments, seeds will be sorted to ensure that only those with embryos are used.

The hypothetical, "successionally differentiated" varieties of M. polymorpha will be compared with respect to their germination characteristics, spatial distributions, and population structures in order to

determine whether they differ in any systematic way with respect to their colonizing abilities.

The seed rain in an intact M. polymorpha forest will be measured by placing seed traps along transects in the forest, and then periodically collecting and identifying seeds collected throughout the year. The diaspores collected will be assumed to have originated both from plants growing in the study forest and from plants found in adjacent forests.

The development of soil seed banks will be analyzed by periodically collecting numerous samples of soil from along the seed trap transects, spreading these soils out in trays in the greenhouse at University of Hawai'i Agricultural Experimental Farm in Volcano Village, watering them regularly, and identifying and counting all seedlings that emerge from these samples (Simpson et al., 1989). Data on the seasonal abundance of species in the seed bank, combined with data on seasonal abundance of species in the seed rain, will allow identification of seed bank syndromes (Garwood, 1989).

These same transects will be divided into segments in which the abundance of each vascular plant species in the standing vegetation will be assessed using the point-intercept method (Mueller-Dombois and Ellenberg, 1974).

The absolute and relative abundance of each species within each of the three pools of species (seed rain, seed

bank, vegetation) will be determined. For each species, seasonal abundance in the seed rain and seed bank will allow seed bank syndromes to be identified.

Proposed schedule:

Measurements of stand structure will be conducted on the island of Hawai'i from 6/89 to 8/89. Germination experiments in the laboratory will be done in Honolulu from 8/89 to 5/90 and in Hawai'i Volcanoes National Park from 6/90 to 8/91. All other field work will be conducted while living on the island of Hawai'i from 6/90 to 8/91. The data will be analyzed and the results prepared for publication by summer 1992.

Table 1.1. Characteristics of seed banks from montane tropical rain forests.

LOCATION (REF.)	ELEVATION (m)	VIABLE SEEDS/m ²	AREA SAMPLED (cm ²)	# OF SPECIES
THAILAND(1)	1,000	161	7,500	22
	1,350	243	7,500	27
GHANA(2)	780	45	20,000	17
COSTA RICA(3)	1,500	406	5,000	-

References: 1) Cheke *et al.*, 1979; 2) Hall and Swaine, 1980; 3) Lawton and Putz, 1988.

Figure 1.1. A generalized model representing an "ecological life cycle" of a plant. The model depicts the three pools of individuals/species comprising a plant population/community (standing vegetation, seed rain, and seed bank), and the processes by which individuals cycle among the pools (Based on models in Kellman [1970] and Harper, [1977]). Gains and losses to the community come from immigration of seeds from and emigration of seeds to other communities. Death can occur at any point in the cycle. In general, the risk of mortality for: seeds > seedlings > saplings > mature individuals < senescing individuals.

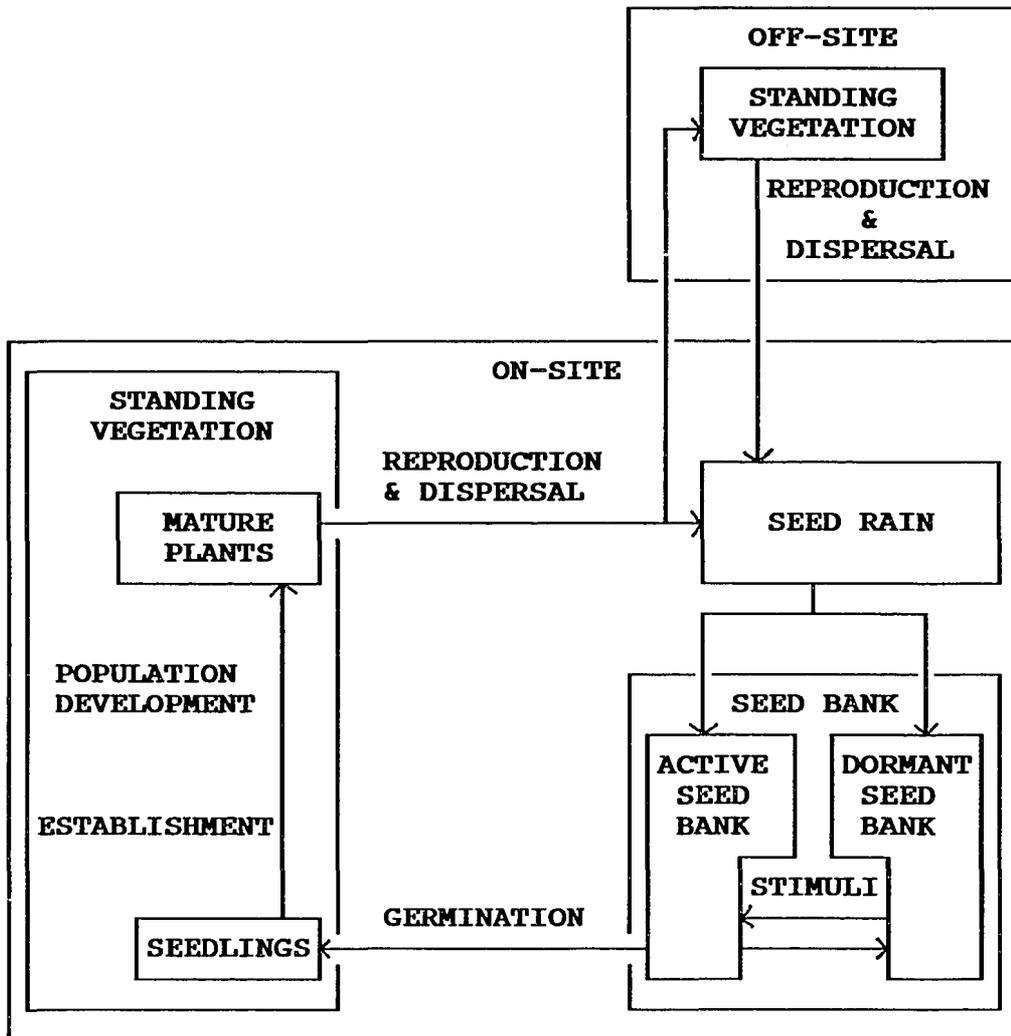


Figure 1.2. Idealized representations of typical size distributions found in plant populations. A) Normal distribution; B) Lognormal distribution.

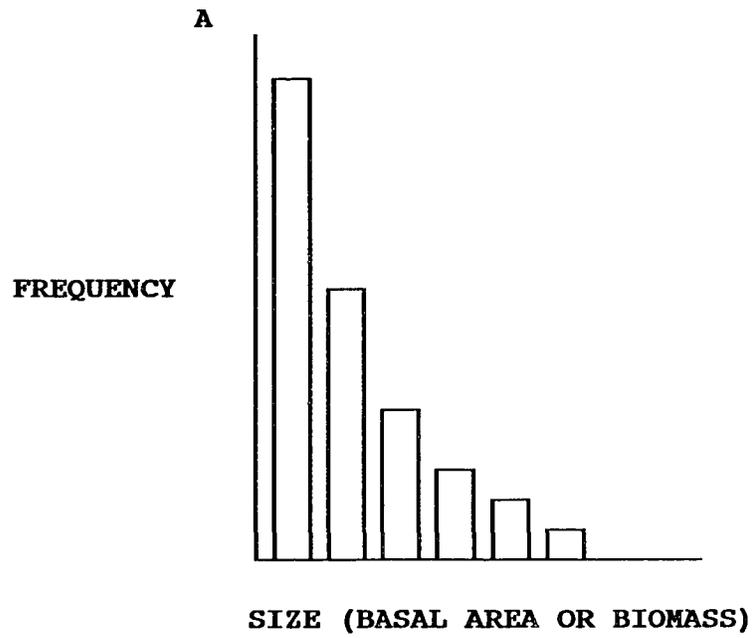
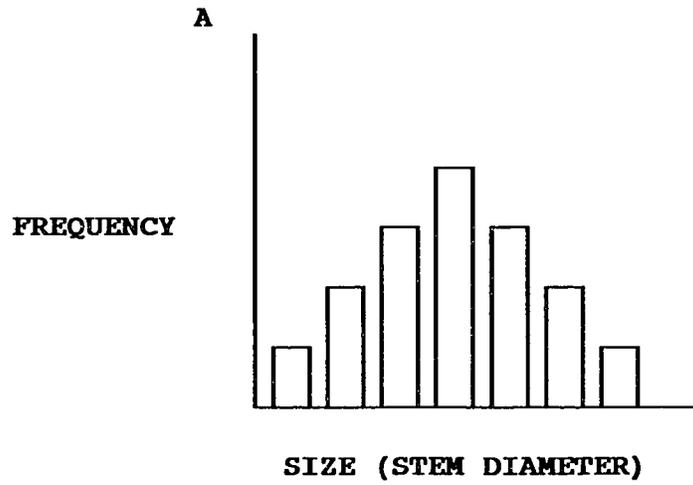
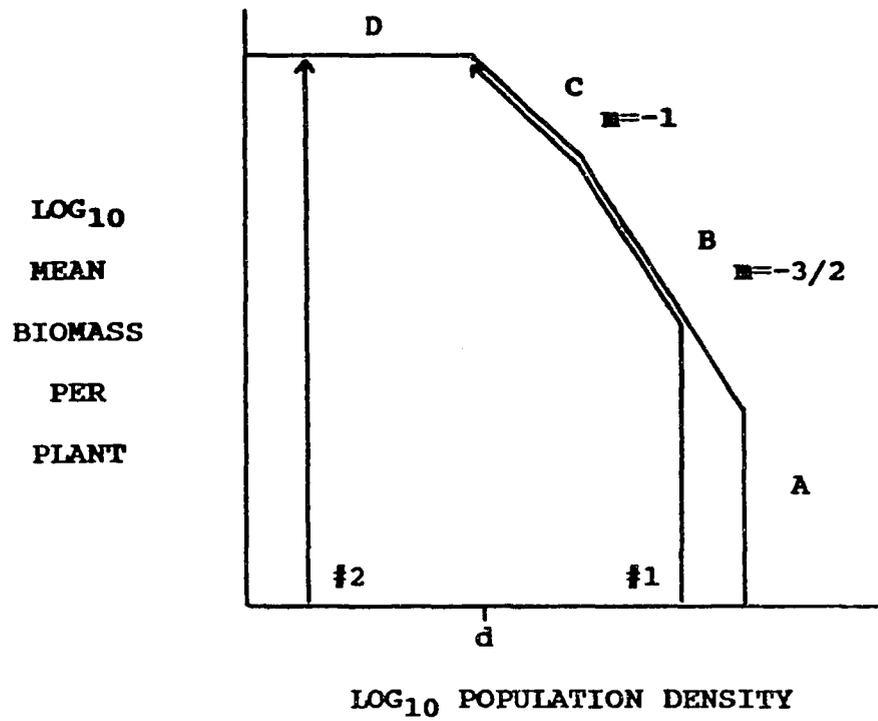


Figure 1.3. Trajectories followed by plant populations with different initial densities (after White [1980]).

Population #1 (high density, undergoes self-thinning): A) When plants are too small to interfere with each other, growth is not density-dependent. B) When plants reach a certain critical size they begin to interfere with each other, yet mean plant biomass continues to increase faster than mortality causes density to decrease; therefore, population biomass continues to increase. C) When the carrying capacity (for population biomass) of the habitat has been reached, increases in population biomass are exactly balanced by decreases in density (mortality).

Population #2 (low density, does not undergo self-thinning): D) In a population with density $\leq d$ plants do not interfere with each other and the population will develop without density-dependent mortality.



CHAPTER 2: POPULATION DEVELOPMENT OF RAIN FOREST TREES
ON A CHRONOSEQUENCE OF HAWAIIAN LAVA FLOWS

Abstract

The purpose of this study was to compare forest structure on a series of geologically similar lava flows that differed in age, but not in climate or in accessibility to pioneer plants. The data were then used to infer the pattern of forest development over 3000 yr on a single flow. Stand structure was measured for populations of Metrosideros polymorpha, other canopy trees, and tree ferns on a chronosequence of lava flows aged 47, 137, \approx 300, \approx 400, and \approx 3000 yr, in the montane rain forest zone on Mauna Loa, Hawai'i. The upper stratum of vegetation at all sites was dominated by M. polymorpha; populations of other trees were relatively sparse throughout the study area. For M. polymorpha populations, basal area/ha increased, at an ever-decreasing rate, as flow age increased; population densities of seedlings, saplings, and trees peaked on the 137 yr flow, then declined, apparently through self-thinning and wind-throw, with further increases in flow age. The decrease in M. polymorpha population density on older flows was accompanied by an increase in the density of tree ferns, which formed a closed sub-canopy on the 3000 yr flow, and may have inhibited regeneration of M.

polymorpha. Among M. polymorpha trees, there was a successional transition from pubescent varieties on the three youngest flows, to glabrous varieties on the oldest flow. A comparison between plant populations on the chronosequence and on one other flow, aged \approx 1400 yr, but containing some volcanic ash, indicated that ash may alter some aspects of forest development.

Introduction

The ecosystems on the slopes of the active Hawaiian volcanoes (Mauna Loa and Kilauea) have provided the basis for numerous studies of primary succession. Most studies have documented the presence of species on young lava flows (Forbes, 1912; MacCaughey, 1917) or monitored colonization over just a few years on new flows (Skottsberg, 1941; Doty, 1967; Smathers and Mueller-Dombois, 1974). Attempts to compare scattered flows of different ages (Atkinson, 1970; Egger, 1971; Uhe, 1988) have generally been unsatisfying because the effects of the steep climatic gradients that occur in Hawai'i were not controlled for systematically. Therefore, there are presently no published data documenting long-term rain forest development on Hawai'i's volcanic substrates.

One generalization resulting from the study of primary succession in Hawai'i is that the tree Metrosideros polymorpha (Myrtaceae) dominates many

volcanic seres, from the earliest pioneer stages to rain forests on substrates millions of years old (Atkinson, 1969; Egger, 1971; Jacobi, 1989; Gagné and Cuddihy, 1990; Kitayama and Mueller-Dombois, 1992). As its name implies, M. polymorpha is extremely variable in morphology, and this variability appears to reflect significant intraspecific ecological differentiation (Corn and Hiesey, 1973; Mueller-Dombois et al., 1980; Stemmermann, 1983; Kitayama and Mueller-Dombois, 1992). Four taxonomic varieties, differentiated by a suite of morphological characters, occur on Mauna Loa (Dawson and Stemmermann, 1990). The most consistent ecological difference among these varieties is that the pubescent ones (M. p. var. incana, M. p. var. polymorpha, and apparent hybrids) tend to be associated with relatively dry sites, while the glabrous ones (M. p. var. macrophylla, M. p. var. glaberrima, and apparent hybrids) are most abundant in wetter sites (Mueller-Dombois et al., 1980; Stemmermann, 1983).

Long-term forest succession can be investigated by comparing sites which differ in age, but are climatically and geologically similar, and which have been equally accessible to successional plant species (Drury and Nisbet, 1973; Miles, 1979). However, because substitution of space for time (i.e. a chronosequence) provides only an indirect assessment of succession, such studies can yield

only tentative conclusions. In addition, replicate sites of a given age are often unavailable, making statistical analysis difficult. Nevertheless, the method has been widely applied because chronosequences provide opportunities to study successions over longer periods of time than can be studied by direct methods (Drury and Nisbet, 1973; Miles, 1979). The purpose of this study was to compare forest structure on a series of geologically similar lava flows that differed in age, but not in climate or in accessibility to pioneer plants. The data were used infer how forest might develop in 3000 yr on a single flow. Attention was focussed on population attributes of M. polymorpha and other abundant large tree species, many of which are little studied. Several species are facultative hemiepiphytes. These can establish terrestrially, but sometimes establish epiphytically on emergent M. polymorpha and later send roots to the ground.

Methods

Study area:

The study was conducted in the montane rain forest zone (500-2700 m asl; Gagné and Cuddihy, 1990) on the eastern slope of Mauna Loa (Fig. 2.1). Because moisture availability affects succession rates (MacCaughey, 1917; Atkinson, 1970; Egglar, 1971; Uhe, 1988) and rainfall

changes rapidly with elevation (Giambelluca et al., 1986), all sites were located at 1235 ± 15 m asl, where rainfall is 4000 mm/yr (Giambelluca et al., 1986) and mean monthly temperature ranges from 15.5° C in January to 18.3° C in August (State of Hawai'i, 1970).

Hawaiian lavas are chemically uniform, but structurally variable (Macdonald et al., 1986). Relatively fluid magma cools to form smooth, solid, pāhoehoe lava. Relatively viscous magma forms rough, rubbly, 'a'ā lava. Because lava texture affects succession rates (Forbes, 1912; Skottsberg, 1941; Atkinson, 1969), all study sites were located on 'a'ā lava. Ages of recent (<200 yr) Hawaiian lava flows are known from historic records. Older flows (>200 yr) have been dated from ^{14}C analysis of charcoal buried at flow margins (cf. Lockwood and Lipman, 1980; Macdonald et al., 1986). Five sites were located on a chronosequence of 'a'ā flows aged 47, 137, ≈ 300 , ≈ 400 , and ≈ 3000 yr at the time of the study in 1989 (Fig. 2.1; United States Geological Survey, 1986; Lockwood et al., 1988; J. P. Lockwood, USGS, personal communication). The only local 'a'ā flow aged between 400 and 3000 yr (≈ 1400 yr) had a shallow layer of soil derived from volcanic ash (probably < 10 cm of eutrophic ash; cf. Balakrishnan and Mueller-Dombois, 1983), and so was studied for comparative purposes only. At the time of their formation, each of

the study flows passed through older terrain which presumably supported montane rain forest vegetation. All but the 3000 yr flow are still bounded (on at least one side) by older flows that contain populations of the pioneer species selected for study (Jacobi, 1989). In the montane rain forest zone on Mauna Loa, young (<150 yr) substrates are dominated by shrubs and Metrosideros polymorpha saplings (Jacobi, 1989). Older substrates support M. polymorpha forest with a subcanopy of other pioneer trees and an understory of tree ferns and shrubs. Invasive alien species are rare in the study area (Jacobi, 1989).

Population assessment:

The four most abundant pioneer tree species were studied: Metrosideros polymorpha; Cheirodendron trigynum, Araliaceae; Ilex anomala, Aquifoliaceae; and Myrsine lessertiana, Myrsinaceae. Life stages were defined as: seedlings = ht \geq 0.1 m and < 1.0 m; saplings = ht \geq 1.0 m and basal diameter < 5 cm; and trees = basal diameter \geq 5 cm. Five cm was chosen as a uniform lower limit for trees since individuals of these species can flower at this size when growing in the open on young lava or as epiphytes upon trees on older flows. Most populations were sampled in a 10 m wide belt transect placed perpendicular to the long axis of each flow. On flows where the density of a

given life stage of a species was high, that life stage of that species was sampled in a 5 m wide transect.

Transects started \approx 100 m from the boundary with the oldest adjacent flow and proceeded away from the boundary. Within each transect, all saplings and trees of the four tree species were counted (count-plot method; Mueller-Dombois and Ellenberg, 1974) and stem diameter at the lowest point above basal swelling (usually 10-50 cm height), was measured to the nearest cm with a diameter tape. Minimum and maximum transect lengths were 120 m and 200 m respectively. Transects were extended beyond 120 m until a sample size of 80 M. polymorpha trees or a sampled area of 0.2 ha was reached (range = 64-130 M. polymorpha trees). Seedlings were counted in every third 10x10 m segment of each transect. Within each transect, total numbers of mature (stem length \geq 1 m) tree ferns (Cibotium glaucum, C. chamissoi, and C. hawaiiense, Dicksoniaceae) were also recorded.

Saplings and trees of M. polymorpha were classified as pubescent (var. incana, var. polymorpha, and intermediates) or glabrous (var. macrophylla, var. glaberrima, and intermediates). Seedlings were not so classified, because pubescence and other adult characters are often not expressed until plants are 50 cm tall (R. L. Stemmermann, personal communication). Chi-squared analysis of contingency tables was used to determine the

statistical significance of within-flow differences in the numbers of pubescent and glabrous plants sampled.

Results

The chronosequence:

For populations of Metrosideros polymorpha trees, basal area/ha increased, at an ever-decreasing rate, with increasing flow age (Fig. 2.2). The combined basal area of the other three tree species remained fairly constant on the three oldest flows.

For M. polymorpha, population densities of seedlings, saplings, and trees peaked on the 137 yr flow, then declined as flow age increased (Fig. 2.3). Although M. polymorpha dominated the upper stratum of forest at all sites (other species rarely exceeded 20 cm basal diameter), it did not form a closed canopy at any site. Mature Cibotium spp. tree ferns first appeared on the 300 yr flow (Fig. 2.3), and reached maximum density on the 3000 yr flow, where they formed a closed canopy beneath the scattered, emergent M. polymorpha. At all sites, the density of Cibotium glaucum > C. chamissoi > C. hawaiiense. Beneath the tree ferns on the 400 and 3000 yr flows, the densities of M. polymorpha seedlings and saplings (Fig. 2.3) were lower than on the three youngest flows.

On the three youngest flows, pubescent M. polymorpha generally outnumbered glabrous M. polymorpha saplings

(Table 2.1) and trees (Fig. 2.4A-C; on the 47, 137, and 300 yr flows, $\chi^2 = 3.9, 54.2, 29.7$, and $P < 0.05, 0.001, 0.001$ respectively, $df = 1$). Pubescent trees also dominated the larger size classes. The 400 yr flow lacked pubescent saplings, and densities of pubescent and glabrous M. polymorpha trees were not significantly different (Fig 2.4D; $\chi^2 = 0.5, P > 0.05, df = 1$). However, the mean diameter of the pubescent trees was greater than that of the glabrous trees (Fig. 2.4D; a posteriori Fisher-Behrens test, $\theta=42.8, v_1=44, v_2=35$, observed $d = 3.26, P < 0.01$; Campbell 1989). The 3000 yr flow had deeper soil than the four younger flows, and lacked pubescent M. polymorpha (Table 2.1; Fig. 2.4E).

Cheirodendron trigynum was the second canopy tree to colonize the lava, and scattered individuals occurred on the 137 yr flow (Table 2.2). On the 300 yr flow, populations of all life stages of Cheirodendron trigynum, Ilex anomala, and Myrsine lessertiana were relatively dense, and trees exhibited the positively skewed diameter distributions typical of invading populations (Table 2.2). Beyond 300 yr, the density of Cheirodendron trigynum trees established epiphytically on live M. polymorpha increased (8/ha on 300 yr, 108/ha on 400 yr, 200/ha on 3000 yr). Ilex anomala and Myrsine lessertiana at 400 and 3000 yr were represented (at least in the larger size classes) by

only moderate numbers of trees, and few trees were epiphytic ($\leq 8/\text{ha}$).

Effects of ash:

Basal area of M. polymorpha trees on the 1400 yr + ash flow ($36.4 \text{ m}^2/\text{ha}$) was slightly higher than on the 400 and 3000 yr flows, though lack of replication precludes a test for statistical significance (Fig. 2.2). Basal area of the other three tree species on the 1400 yr + ash flow ($7.22 \text{ m}^2/\text{ha}$) was similar to that on the 400 and 3000 yr flows.

On the 1400 yr + ash flow, population densities of seedlings, saplings, and trees of M. polymorpha, and saplings and trees of other canopy species, were not intermediate to densities on the 400 and 3000 yr flows (Fig. 2.3). Densities of pubescent and glabrous M. polymorpha trees on the 1400 yr + ash flow were not significantly different (Fig. 2.4F; $\chi^2 = 0.1$, $P > 0.05$, $df = 1$). However, the mean diameter of the pubescent trees was greater than that of the glabrous trees (Fig. 2.4F; a posteriori Fisher-Behrens test, $\theta=72.7$, $v_1=33$, $v_2=29$, observed $d = 4.10$, $P < 0.01$; Campbell 1989). On this flow, the only pubescent M. polymorpha trees $< 10 \text{ cm}$ diameter were epiphytic on larger M. polymorpha trees, above the tree fern canopy, and the few saplings were glabrous.

The density of Cheirodendron trigynum trees on the 1400 yr + ash flow was lower than on the 300, 400, and 3000 yr flows (Table 2.2). Most (88%) of the Cheirodendron trigynum trees on the 1400 yr + ash flow were relatively small epiphytes. Ilex anomala trees were rare. Myrsine lessertiana was represented by moderate numbers of relatively large trees (Table 2.2).

Discussion

The rate of primary succession is influenced by climate, the moisture-holding and nutrient status of the substrate, the accessibility of the site to pioneer plants, and interactions among pioneers on the site (Miles, 1979). The time required for pioneer forest development during primary succession ranges from ≤ 150 yr on rock exposed by glaciers (Crocker and Major, 1955; Wardle, 1980), to 1500 yr on lava in California (Heath, 1967), or longer. Forest dominated by Metrosideros polymorpha develops within 400 yr on new lava in the montane rain forest zone in Hawai'i, as predicted by Atkinson (1969). Seeds of M. polymorpha are widely dispersed by wind, and dense seedling populations can establish on new lava in < 20 yr. Based on an extrapolation of the regression line in Fig. 2.2, a new 'a'ā flow should support M. polymorpha trees 27 yrs after

formation. The warm, moist, aseasonal climate apparently allows M. polymorpha to colonize new surfaces rapidly.

Low levels of soil nitrogen may limit plant growth during primary succession (Vitousek and Walker, 1987). Volcanic ash weathers, releases nutrients, and accumulates nitrogen faster than lava does (Balakrishnan and Mueller-Dombois, 1983; Vitousek et al., 1983). Ash-derived soil has apparently altered succession on the 1400 yr + ash flow, making populations of M. polymorpha relatively advanced in terms of density, basal area, and size distribution.

Dense populations of shade-intolerant trees typically self-thin following canopy closure (Harper, 1977; Mohler, et al., 1978; Peet and Christensen, 1980; Ogden, 1985). During self-thinning, increases in stand biomass are accompanied by death of the smaller individuals. The canopy remains closed (through lateral ingrowth of survivors) and recruitment from below ceases. Between 137 and 300 yr, M. polymorpha basal area/ha increased (Fig. 2.2); this implies that biomass also increased. In the same interval, M. polymorpha tree density decreased (Fig. 2.3). This pattern supports Atkinson's (1969) view that M. polymorpha populations self-thin during primary succession; it also implies that closed-canopy forest should occur at some point between 137 and 300 yr. However, the 300 yr flow did not support the closed-canopy

forest which self-thinning should produce. Instead, the canopy was broken by treefall gaps in which there were many seedlings, saplings, and small trees. The treefalls apparently resulted from wind-thrown trees whose roots were inadequately supported by the physically unstable, young 'a'ā lava. This disturbance probably prevented development of a uniform cohort stand. The failure of populations on young 'a'ā to develop as cohorts may explain why such populations rarely undergo the stand-level dieback seen on pāhoehoe flows (cf. Mueller-Dombois, 1986). Populations of M. polymorpha on solid pāhoehoe are apparently less prone to wind-throw, and their development as cohorts predisposes them to synchronous senescence and dieback (Mueller-Dombois et al., 1980; Jacobi et al., 1983, 1988; Mueller-Dombois, 1986). Unfortunately, M. polymorpha does not form annual growth rings, so the true age structure of the hypothetical cohorts cannot be determined.

The typically shade-intolerant species of pioneer vegetation tend to be replaced by shade-tolerant trees as succession proceeds (Crocker and Major, 1955; Olson, 1958; Heath, 1967; Wardle, 1980; Mark et al., 1989). Shade-tolerant (Becker, 1976) Cibotium spp. tree ferns outnumbered the trees and formed a closed canopy on the two oldest flows. However, large M. polymorpha trees were common above the tree fern canopy. Shade cast by tree

ferns may limit seedling regeneration by M. polymorpha (Burton and Mueller-Dombois, 1984). In addition, studies of artificial seedlings suggest that the senescing fronds of tree ferns crush tree seedlings (7-15% of seedlings damaged/yr; Appendix A). Litterfall has also been implicated in seedling mortality in a neotropical forest (Clark and Clark, 1989). Any M. polymorpha trees that do penetrate the short (5-7 m) tree fern layer receive full sunlight because trees are widely spaced in the overstory. Penetration of the tree fern canopy may be facilitated by seedling establishment directly on tree fern stems (Burton and Mueller-Dombois, 1984).

While tree regeneration from seed is limited, the importance of vegetative reproduction in Hawaiian forests is unknown. Several M. polymorpha trees were noted which had fallen, re-rooted at several points, and sent branches upward from the prostrate stem. Such layering has also been reported for M. polymorpha in Hawaiian wetlands (Takeuchi, 1991), and Metrosideros umbellata in New Zealand forests (Stewart and Veblen, 1982).

Cheirodendron trigynum can establish on young lava or in the crowns of large trees. Where emergent M. polymorpha trees are available, epiphytic establishment may allow some Cheirodendron trigynum to avoid shade and physical disturbance. In New Zealand, several pioneer species occur terrestrially on boulders, but as epiphytes

or hemiepiphytes in forests (Wardle, 1980, 1991; Stewart and Veblen, 1982). As sites for establishment, tree crowns and bare rock are similar in that both are drought-prone (Benzing, 1990; Wardle, 1991).

Moisture availability increases as soil develops during succession on lava (Balakrishnan and Mueller-Dombois, 1983). The transition from pubescent to glabrous varieties of M. polymorpha with increasing flow age is probably a response to increasing moisture availability. This trend is consistent with the hypothesis that these varieties are adapted to different moisture regimes (Mueller-Dombois et al., 1980; Stemmermann, 1983). Earlier colonization or faster growth rates may make pubescent plants larger than glabrous plants on the same flow. On volcanic ash, pubescent seedlings grow faster than glabrous ones (Stemmermann, 1983).

After 3000 yr of primary succession, the Hawaiian montane rain forest consists of an open, upper stratum of M. polymorpha, an open, middle stratum of other pioneer trees, and a closed, lower stratum of Cibotium spp. tree ferns. Other species participate in succession, but generally contribute little to forest structure, and do not displace Metrosideros-Cibotium forest on well-drained, moist sites (Jacobi, 1989; Gagné and Cuddihy, 1990; Kitayama and Mueller-Dombois, 1992). Forest development in which the initial pioneer remains the dominant species

in the vegetation has been termed direct succession (Whittaker and Levin, 1977) or auto-succession (Mueller-Dombois, 1992). Such successions occur in harsh environments (Miles, 1987) such as desert (Shreve, 1942), tundra (Muller, 1952; Babb and Bliss, 1974), and a volcanically active island in New Zealand, on which Metrosideros excelsa is the only tree (Clarkson, 1990). In Hawai'i, M. polymorpha undergoes direct succession in a more benign environment. Due to isolation, Hawai'i has a relatively depauperate and disharmonic flora (Carlquist, 1974). Hawaiian montane rain forests apparently lack the late-successional species that displace pioneers in species-rich, continental forests (Mueller-Dombois, 1987). Some taxa have responded to Hawai'i's species-poor environment by undergoing extensive adaptive radiation and speciation (Carlquist, 1974; Simon, 1987). In contrast, M. polymorpha has responded by simply expanding its ecological range through increased intraspecific variation (Corn and Hiesey, 1973; Carlquist, 1974; Stemmermann, 1983; Mueller-Dombois, 1987; Simon, 1987).

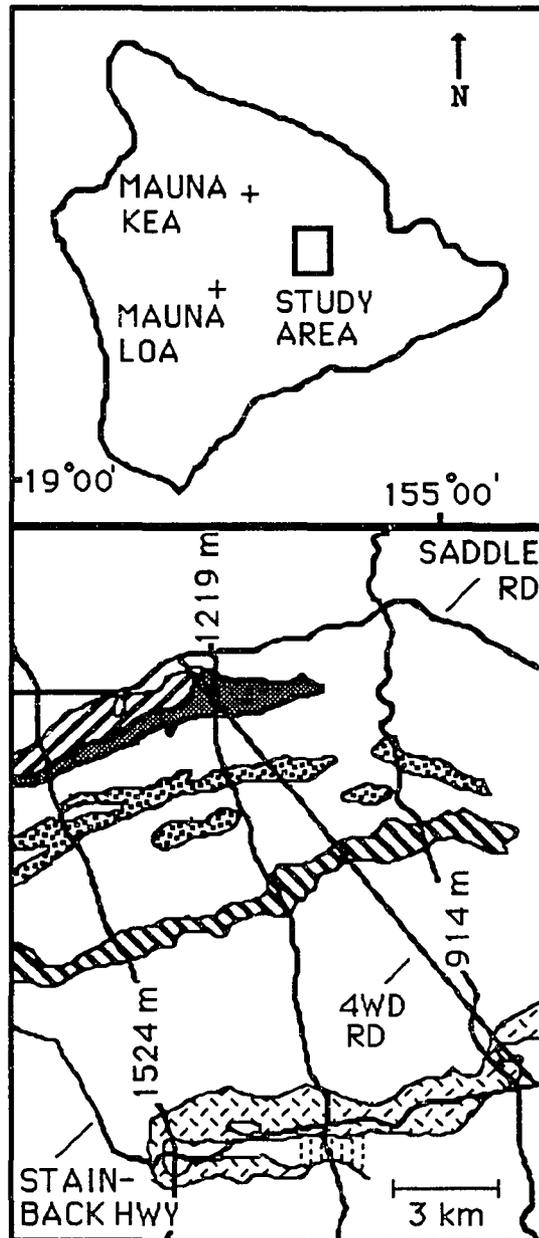
Table 2.1. Numbers of glabrous and pubescent Metrosideros polymorpha saplings (ht \geq 1 m and basal diameter < 5 cm) sampled on five lava flows of different ages, and one lava flow with volcanic ash. Significant chi-squared indicates proportion of glabrous : pubescent \neq 1:1 (df = 1).

FLOW AGE (yr)	NO. OF INDIVIDUALS		CHI-SQUARED	P<
	GLABROUS	PUBESCENT		
47	70	46	2.5	NS
137	66	499	194.5	0.001
300	59	245	62.8	0.001
400	16	0	10.7	0.01
3000	10	0	6.5	0.05
1400 + ash	3	0	-----	-----

Table 2.2. Densities (no./ha) of Cheirodendron trigynum, Ilex anomala, and Myrsine lessertiana on five lava flows of different ages, and one lava flow with volcanic ash. Tree basal diameter classes represent the lower limit of 5 cm intervals (except 35, which represents 35-44 cm). Seedlings = ht \geq 0.1 m and $<$ 1.0 m, saplings = ht \geq 1 m and basal diameter $<$ 5 cm, and trees = basal diameter \geq 5 cm.

FLOW AGE (yr)	SEED-LINGS	SAP-LINGS	TREES - BASAL DIAMETER (cm)						
			5	10	15	20	25	30	35
<u>C. trigynum</u>									
47	0	0	0	0	0	0	0	0	0
137	300	100	33	8	0	0	0	0	0
300	12800	225	200	100	50	0	0	0	0
400	1200	285	192	85	8	0	0	0	0
3000	660	331	423	131	15	0	0	0	0
1400 + ash	1401	140	45	25	5	5	0	0	0
<u>I. anomala</u>									
47	0	0	0	0	0	0	0	0	0
137	0	0	0	0	0	0	0	0	0
300	4700	642	167	42	8	17	0	0	0
400	12300	400	85	0	8	0	0	0	0
3000	800	354	46	15	8	0	0	8	0
1400 + ash	1433	155	0	0	10	5	5	5	0
<u>M. lessertiana</u>									
47	0	0	0	0	0	0	0	0	0
137	100	0	0	0	0	0	0	0	0
300	450	300	283	158	8	0	0	0	0
400	275	200	15	23	31	8	15	0	0
3000	320	231	15	38	0	8	0	0	0
1400 + ash	200	45	5	10	5	20	25	10	15

Figure 2.1. Map of the five 'a'ā lava flows of different ages (and one 'a'ā flow with volcanic ash) selected for study. Other lava flows, and pāhoehoe segments of the six study flows, are omitted for clarity. The 1400 yr + ash flow is unbounded because the extent of the 'a'ā portion is unknown.



- | | |
|--------|---------------|
| 47 yr | 400 yr |
| 137 yr | 3000 yr |
| 300 yr | 1400 yr + ASH |

Figure 2.2. Basal area of populations of Metrosideros polymorpha saplings (triangles), M. polymorpha trees (Xs), and other trees (squares) (Cheirodendron trigynum, Ilex anomala, and Myrsine lessertiana) vs. \log_{10} lava flow age. For M. polymorpha trees, $y = 17.11x - 24.47$, $r = .910$, $P < .05$. Saplings = $ht \geq 1$ m and basal diameter < 5 cm, and trees = basal diameter ≥ 5 cm.

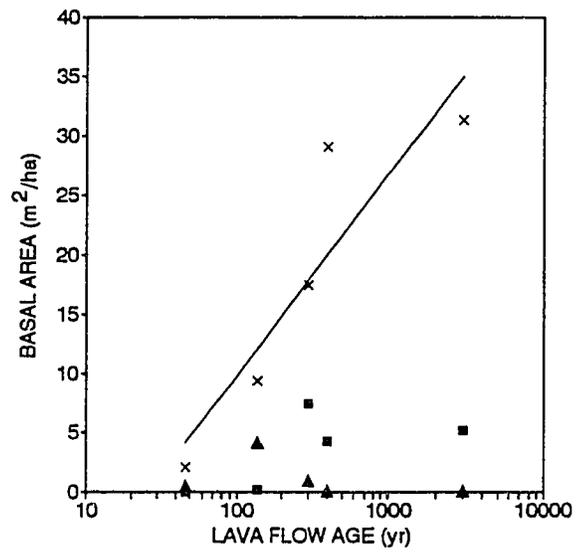
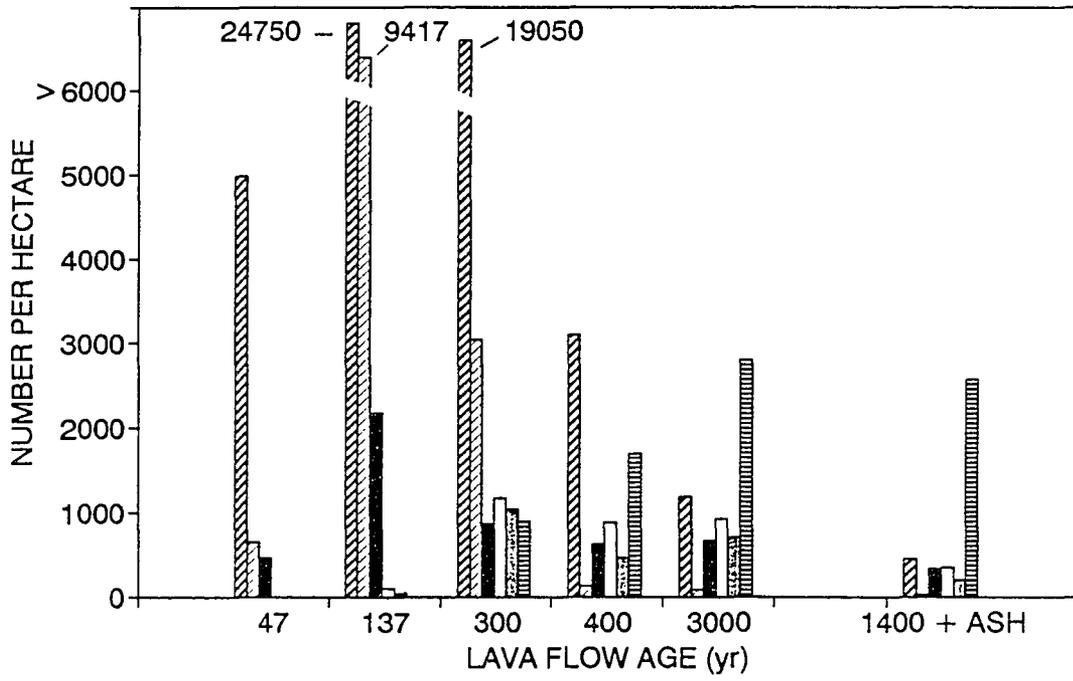
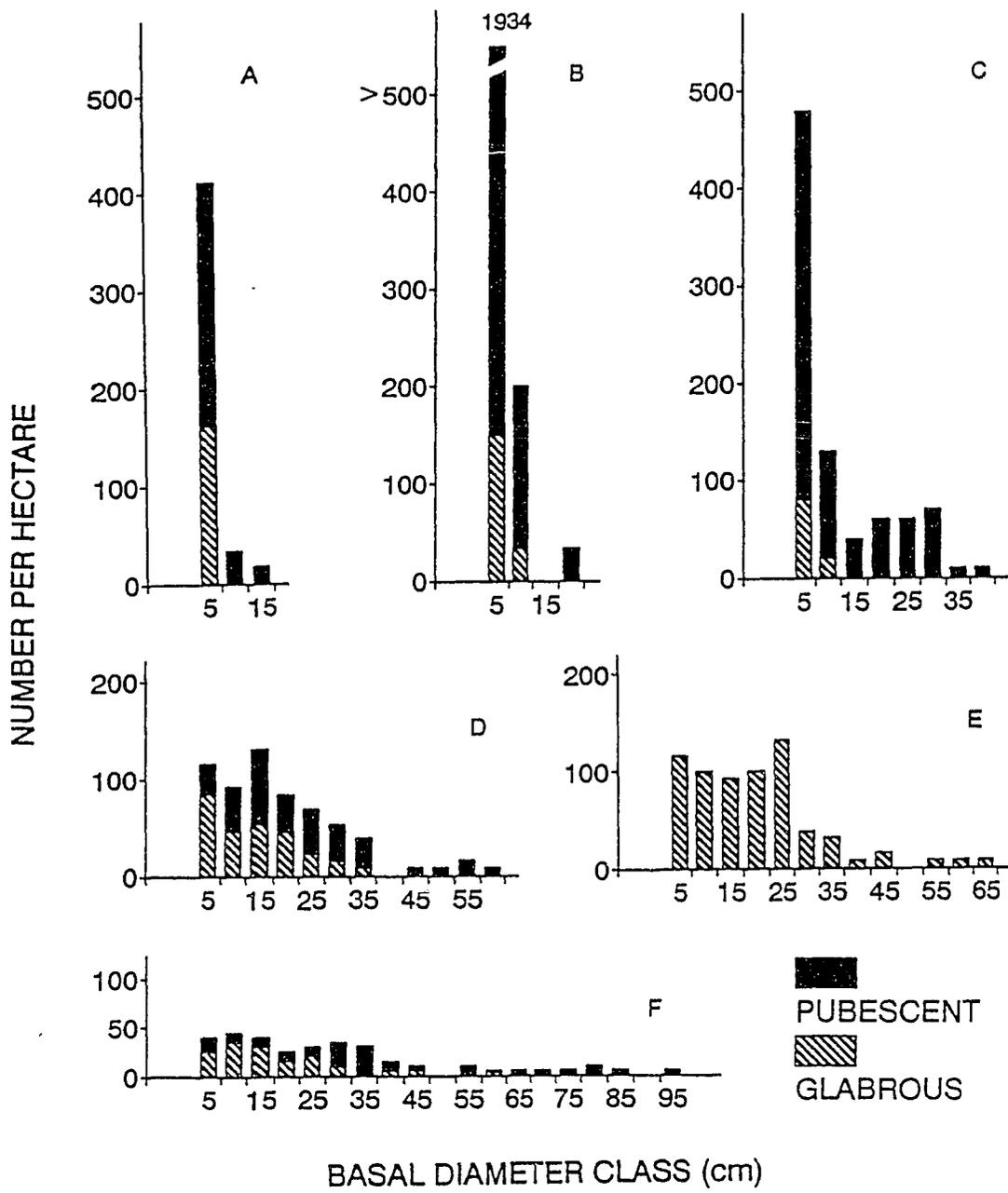


Figure 2.3. Population densities of Metrosideros polymorpha seedlings, saplings, and trees, other saplings and trees (Cheirodendron trigynum, Ilex anomala, and Myrsine lessertiana), and mature tree ferns (Cibotium spp.) on five lava flows of different ages, and one lava flow with volcanic ash. Seedlings = ht \geq 0.1 m and $<$ 1.0 m, saplings = ht \geq 1 m and basal diameter $<$ 5 cm, and trees = basal diameter \geq 5 cm.



MET. SEEDLINGS MET. SAPLINGS MET. TREES
 OTHER SAPLINGS OTHER TREES TREE FERNS

Figure 2.4. Diameter distributions of Metrosideros polymorpha trees (≥ 5 cm basal diam) on five lava flows of different ages, and one lava flow with volcanic ash: (A) 47 yr, n = 83, area sampled = 0.18 ha; (B) 137 yr, n = 130, area sampled = 0.06 ha; (C) 300 yr, n = 86, area sampled = 0.10 ha; (D) 400 yr, n = 81, area sampled = 0.13 ha; (E) 3000 yr, n = 85, area sampled = 0.13 ha; (F) 1400 yr + ash, n = 64, area sampled = 0.20 ha. Basal diameter classes represent the lower limit of 5 cm intervals.



CHAPTER 3: SEED DISPERSAL OF METROSIDEROS POLYMORPHA
(MYRTACEAE), A PIONEER TREE OF HAWAIIAN LAVA FLOWS

Abstract

Wind dispersal of seeds of Metrosideros polymorpha, the dominant tree of rain forests and the main pioneer of volcanic substrates in Hawai'i, was measured on a 20-yr-old lava flow downwind of a M. polymorpha forest. Seed rain was concentrated in December and January, when 74.5% of the annual total was dispersed. Annual seed rain at the forest edge was 63,893 seeds/m², of which 5,580 (8.7%) contained embryos and were potentially viable. Beyond the forest edge, the density of embryo-containing seed decreased to 363, 137, 37, 25, and 20/m² at distances of 25, 50, 100, 150, and 250 m, respectively. In contrast, the density of established M. polymorpha seedlings remained relatively constant beyond 25 m, a fact suggesting that the density of safe sites for germination and establishment was also constant over the same distance. It was concluded that colonization of the lava flow was limited by the density of safe sites, i.e. conditions for establishment, rather than by seed rain, i.e. dispersal, which was more than sufficient to saturate the available safe sites.

Introduction

During primary succession on lava, all pioneer plants must be recruited from the seed rain, since no seed bank exists in the sterile new substrate. Wind is regarded as the main vector responsible for dispersing pioneer species of primary succession (van der Pijl, 1982; Fenner, 1987). In Hawai'i, the endemic tree Metrosideros polymorpha (Myrtaceae) is the dominant pioneer in most volcanic successions (Atkinson, 1970; Egglar, 1971; Smathers and Mueller-Dombois, 1974) and often remains the dominant species in mature rain forests (Mueller-Dombois et al., 1981; Gagné and Cuddihy, 1990). Its ancestor is one of only four species of seed plants believed to have successfully colonized Hawai'i via wind dispersal (Carlquist, 1974), though it has also been suggested that birds might have acted as its dispersal vector (Guppy, 1906). Experiments have demonstrated that the tiny seeds of M. polymorpha (median fresh mass 70 μg) can be kept aloft by winds of 5.6-18.5 km/hr (Corn, 1972). Because it produces small, light seeds that are borne in the upper canopy of the forest and are directly exposed to the wind, and because it is a highly successful colonist of fresh volcanic substrates, M. polymorpha is commonly believed to be both well adapted to wind dispersal and effectively dispersed by wind (Skottsberg, 1941; Corn, 1972; Carlquist, 1974).

Mueller-Dombois and co-workers (Mueller-Dombois et al., 1980; Jacobi et al., 1983, 1988; Mueller-Dombois, 1986) have proposed a model of Hawaiian rain forest dynamics in which relatively synchronous and uniform colonization of disturbed areas by M. polymorpha is one factor that predisposes its populations to eventual synchronous breakdown. Long-distance dispersal is believed to play a key role in the initial establishment of these uniform, cohort populations.

In spite of the importance of M. polymorpha in Hawaiian plant communities, actual dispersal of its seeds has never been measured in the field. The purposes of this study were 1) to estimate the dispersal potential for M. polymorpha by measuring seed rain on a recent lava flow downwind of a forest and 2) to compare seed rain and seedling population density on the lava flow to determine whether colonization of the flow was limited by dispersal or by conditions for seedling establishment.

Methods

Field site:

The study took place at the boundary between the forest and a recent lava flow, at an elevation of 700 m asl in the Kealakomo section of Hawai'i Volcanoes National Park on the island of Hawai'i. The upper canopy of the forest was dominated by Metrosideros polymorpha (53.5%

absolute cover), which reached a stem diameter of 65 cm and a height of 15-20 m. The forest was bounded by a lava flow of the smooth, rolling, pāhoehoe type, formed in 1972. The flow supported few plants other than scattered seedlings and saplings of M. polymorpha. The boundary between forest and lava was sharp and oriented at 160-340° (true).

During the study (11/9/90 to 11/7/91), the prevailing winds measured at Hilo were the tradewinds, which blew consistently from the NE (monthly wind vector resultants ranged from 10-90° true) during the months of March to September, but were less predictable during the rest of the year (National Oceanic and Atmospheric Administration, 1990, 1991). Although Hilo is at sea level, 45 km east of the study site, the smooth topography of this part of the island probably does not significantly affect wind patterns between the two points. Thus for most of the year the prevailing winds blew from the forest to the lava flow at a nearly perpendicular angle. Mean monthly wind speed changed little over the course of the year (range 9.2-13.5 km hr⁻¹; National Oceanic and Atmospheric Administration, 1990, 1991).

Seed characteristics:

Seeds of M. polymorpha are 1.5-3 mm long and 0.2-0.4 mm wide (Corn, 1972). Although the seeds are slightly

flattened in cross section, they are not winged, and possess no appendages that might facilitate dispersal by wind. Microscopic examination can be used to distinguish between filled (embryo-containing) and unfilled (embryo-lacking) M. polymorpha seeds (Burton, 1982). Germination experiments indicate that $\geq 90\%$ of filled seeds are viable, compared with $< 1\%$ of unfilled seeds (Chapter 4). Mean fresh mass of filled and of unfilled seeds is $57 \mu\text{g}$ and $47 \mu\text{g}$, respectively (based on 18 random samples of 25 seeds each, taken from pooled seeds of 40 trees; D. Drake, unpublished data).

Seed rain:

On the lava flow, six 33 m transects were established. Transects were parallel to the forest edge and located 0, 25, 50, 100, 150, and 250 m from it. One seed trap was placed at a random point in each 3 m segment of each transect (total = 11 traps/transect). A trap consisted of a cylindrical plastic pot (diam = 15.4 cm; depth = 19.0 cm) with the bottom replaced by a piece of cotton cloth secured by a rubber band. The weave of the cloth retained all seeds, yet allowed water to drain freely. Traps were held in place by stakes and rocks. To reduce the possibility of capturing seeds originating on the flow rather than in the forest, one or two infructescences were removed from each of two small ($< 2 \text{ m}$

tall) saplings located near the seed traps on the flow. Every 3 weeks the cloths were changed, all material from each trap was examined under a dissecting microscope, and M. polymorpha seeds were counted and classified as filled or unfilled. A reference specimen (D. Drake #66) bearing seeds was collected from a M. polymorpha tree growing in the forest adjacent to the lava flow and was deposited in the herbarium at Hawai'i Volcanoes National Park.

Established seedlings:

For assessment of population densities of plants established on the lava flow, five of the seed trap transects (those at 25, 50, 100, 150, and 250 m) were extended to 120 m length, and an additional 120 m transect was placed 200 m from the forest. On each transect, seedlings and saplings were counted in five 200 m² circular plots. Plots were centered at stratified random points (20-30 m apart) on each transect. Live M. polymorpha plants between 0.1 m and 1.0 m tall were counted as seedlings, and those \geq 1.0 m tall were counted as saplings. Because seedlings cultivated in a greenhouse require at least 1 yr to reach a height of 0.1 m (Walker and Vitousek, 1991), all plants sampled were assumed to be well established.

Results

Metrosideros polymorpha seed rain decreased sharply with distance from the forest edge, though the rate of decrease lessened with distance (Fig. 3.1). Of the 13,944 seeds caught in the traps, 1,240 (8.9%) were filled and thus potentially viable. The percentage of filled seeds was slightly greater among those seeds dispersed onto the flow than among those falling at the forest edge (10.8% vs 8.7%, respectively; chi-squared = 4.35; df = 1; $P < 0.05$). Nevertheless, the curves for filled and for unfilled seeds were roughly parallel, indicating that the unfilled seeds, although biologically insignificant, are still useful as model diaspores and can serve to validate the dispersal pattern measured for filled seeds.

In contrast to the trend in seed rain, the combined density of seedlings plus saplings did not decrease with distance from the forest edge (Fig. 3.2), though the density of plants established at 25 m was significantly higher than the densities at most other distances (Duncan's multiple range test, df = 24, MSE = 92.62, $P < 0.05$; SAS Institute, Inc., 1985). Greater than 94% of the M. polymorpha plants encountered were seedlings < 1.0 m tall, and all were ≥ 0.1 m tall and therefore did not represent merely an ephemeral flush of recent germinants. All plants were restricted to cracks in the lava. No dead plants were encountered.

Both seed rain and plant density data were used to estimate the probability of establishment for seeds dispersed onto the lava flow (Table 3.1). First, seed rain was multiplied by 20 yr to estimate total seed rain since the flow stopped. This value was divided by the density of established plants surviving on the flow after 20 yr. The quotient represents the number of seeds dispersed from the forest per net individual established on the flow after 20 yr. This value decreased with distance from the forest edge ($y = -0.0043x + 4.81$, $y = \log_{10}[\text{seeds dispersed per plant established}]$, $x = \text{distance from forest in m}$, $n = 5$, $r = -0.93$, $P < 0.05$).

Seed rain was distinctly seasonal, with 52.2% of the annual total of filled seed falling during the 3 week period from 11/30/90-12/20/90, and 74.5% during the 9 week period from 11/30/90-1/31/91 (Fig. 3.3). In contrast, lowest totals were recorded during the 3 week period of 6/27/91-7/18/91 and during the 12 week period of 5/16/91-8/8/91, when 0.1% and 2.0% of the annual total fell, respectively. Seeds were dispersed onto the flow throughout the year.

Discussion

Metrosideros polymorpha seed rain decreased continuously with distance from the seed source. This produced a pattern of seed distribution roughly similar to

that of other small-seeded, wind-dispersed tropical trees such as Eucalyptus regnans (Cremer, 1965) and Toona australis (Willson and Crome, 1989) which were dispersed from forest edges, and Melaleuca quinquinervia (Woodall, 1982) and Nuytsia floribunda (Lamont, 1985) which were dispersed from isolated trees.

In contrast, seedling density changed little with distance. If seedling density can be regarded as a measure of the density of safe sites available for germination and establishment, then, except for a slight edge effect, safe sites were present at a constant, low density across the first 250 m of the lava flow. This is not surprising, since M. polymorpha seedlings on pāhoehoe flows are restricted to cracks (Forbes, 1912; MacCaughey, 1917; Skottsberg, 1941; Atkinson, 1970; Egger, 1971; Smathers and Mueller-Dombois, 1974), and crack density is unlikely to change across the flow. The density of safe sites was greater at 25 m than elsewhere probably because the physical environment near the flow edge was influenced by the nearby forest. Because the site was on the western (leeward) side of the forest, it not only was shaded during the morning and somewhat sheltered from the wind, but also received leaf litter from the forest. All three of these effects should increase moisture availability in the cracks, raising the density of safe sites and favoring establishment. None of these effects were noticeable much

beyond 25 m from the forest edge. Water availability is generally considered the most important physical factor limiting colonization of Hawaiian lava flows by vascular plants (Forbes, 1912; MacCaughey, 1917; Skottsberg, 1941; Atkinson, 1970; Egglar, 1971; Smathers and Mueller-Dombois, 1974).

Wind speed and direction during the peak fruiting season of December and January determine dispersal patterns for most of the annual seed crop of M. polymorpha at Kealakomo, yet this is the season when wind speed and direction are least consistent (National Oceanic and Atmospheric Administration, 1990, 1991). On the other hand, rainfall at Kealakomo during the same period is often heavy and prolonged (mean = approximately 350 mm/mo; Giambelluca et al., 1986). On exposed sites such as recent lava flows, where moisture is the limiting environmental factor, heavy rains should favor both germination and establishment.

Wood and del Moral (1987, 1988) noted a tradeoff between seed dispersibility and establishment success for pioneers of volcanic debris on Mount St. Helens. Large-seeded species were assumed to be poorly dispersed, but their seeds possessed enough resources for seedlings to establish when seeds were sown artificially. Small-seeded species were assumed to be well dispersed, but their seeds lacked the resources necessary for seedlings to establish

on the harsh substrate. The minute seeds of M. polymorpha possess meager resources, so seedlings on lava may be susceptible to environmental stresses, such as drought, and the probability of establishment for any individual seedling is small. However, the seed rain is apparently heavy enough to compensate for the low probability of survival.

Data for both seed rain and established plants generally support Harper's (1977, p. 460) model of seed dispersal and plant establishment (Fig. 3.4). Taken together, the fact that plant density remained constant as seed rain decreased implies that the probability of establishment, i.e., the likelihood that a seed will produce a seedling, increased with distance. In other words, the number of seeds dispersed from the forest per net individual established on the flow decreased with distance. From distance 0 to B, seed rain was sufficient to saturate the safe sites, as indicated by the fact that seedling density remained relatively constant as seed rain decreased. Because seed rain decreased with distance, the density of "wasted" seeds, i.e. the surplus above the density required to establish in all available safe sites, also decreased with distance; thus, the probability of establishment increased. Beyond distance B (unmeasured, but > 250 m in this study) the seed rain should be too sparse to fill all the available safe sites. Here, the

probability of establishment should continue to increase because the density of unexploited safe sites increases, but the overall density of established plants should decrease, being limited by seed rain. Of course the ratio of seeds dispersed to seedlings established will never reach 1 : 1 because many seeds and seedlings will die due to density-independent causes that are presumed to change little with distance (Harper, 1977).

Because of the orientations of wind, forest, and lava flow, and because of the height of the M. polymorpha canopy, this study represents an estimate of the dispersal potential of M. polymorpha seeds under nearly ideal dispersal conditions. Under such conditions, seed rain is adequate for the rapid establishment of large populations over broad areas, as suggested by Mueller-Dombois (1987a), though the uniformity of the populations is apparently due to establishment conditions rather than to uniform seed rain. Studies of other wind-dispersed species suggest that seed rain may become limiting much closer to the edge of the open area if the diaspores are more poorly adapted to wind dispersal (Augspurger, 1986, 1988), if the seed-producing trees are shorter or less abundant (Cremer, 1965, 1977; Lamont, 1985), if the open area is less directly downwind of the source or is simply wider (Woodall, 1982), and in secondary succession, where the open area possesses a higher density of safe sites

suitable for both germination and establishment
(McQuilkin, 1940).

Table 3.1. Metrosideros polymorpha seed rain (extrapolated over 20 yr), present density of established plants, and the ratio of seeds to plants, measured on a 20-yr-old lava flow, at various distances from the boundary between forest and lava. The ratio of seeds to plants represents the number of seeds dispersed from the forest per net individual established on the lava flow after 20 yr.

	DISTANCE FROM FOREST EDGE (m)					
	25	50	100	150	200	250
SEEDS $m^{-2}20yr^{-1}$	7,260	2,740	740	500	-	400
PLANTS m^{-2}	0.124	0.057	0.058	0.029	0.047	0.069
SEEDS:PLANTS	58,548	48,070	12,759	17,241	-	5,797

Figure 3.1. Annual seed rain of filled (embryo-containing) and unfilled (embryo-lacking) Metrosideros polymorpha seeds on a 20-yr-old lava flow, measured at various distances from the boundary between forest and lava.

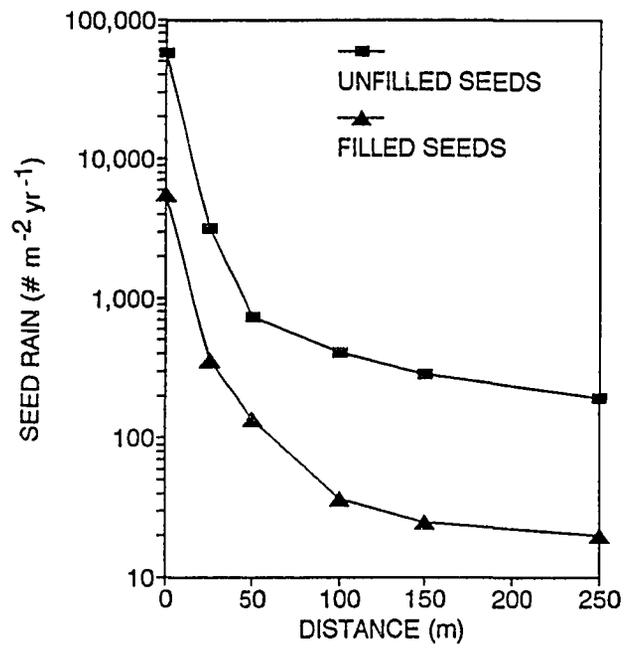


Figure 3.2. Density of established Metrosideros polymorpha seedlings (≥ 10 cm and \leq cm tall) and saplings (≥ 100 cm tall) on a 20-yr-old lava flow at various distances from the boundary between forest and lava (Standard error bars apply to combined densities of seedlings and saplings). Mean values beneath the same letter are not significantly different at $P < 0.05$ (Duncan's multiple range test; SAS Institute, Inc., 1985).

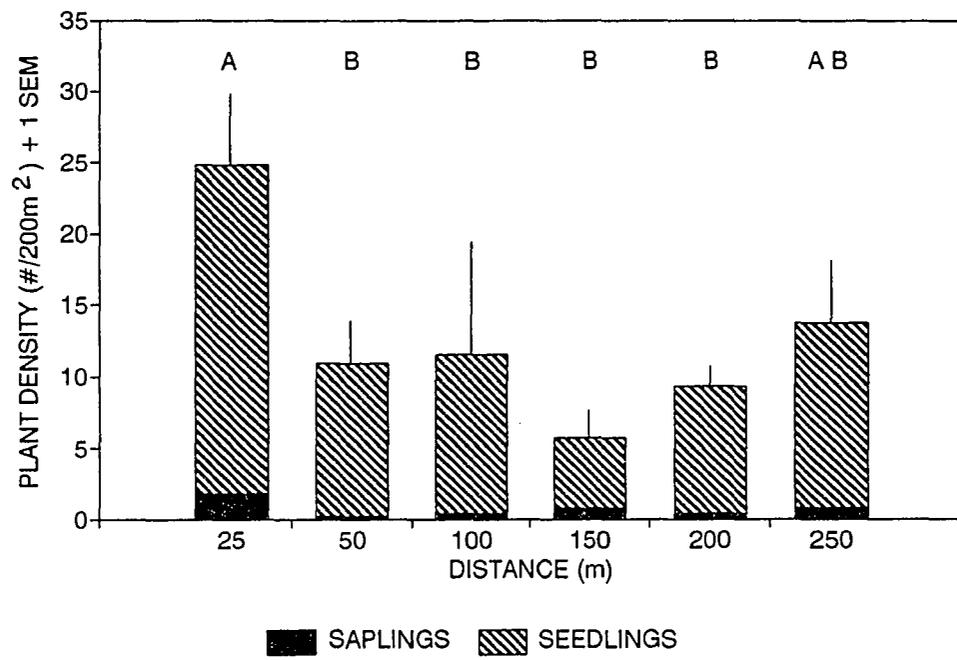


Figure 3.3. Phenology of seed rain of filled (embryo-containing) seeds of Metrosideros polymorpha at the edge of a M. polymorpha forest (0 m) and on a 20-yr-old lava flow downwind of the forest. Data for the lava flow represent the mean of values from five distances (range = 25-250 m). Data are for 3 week intervals ending on the dates shown, except for the interval ending on 11/7, which was 4 weeks.

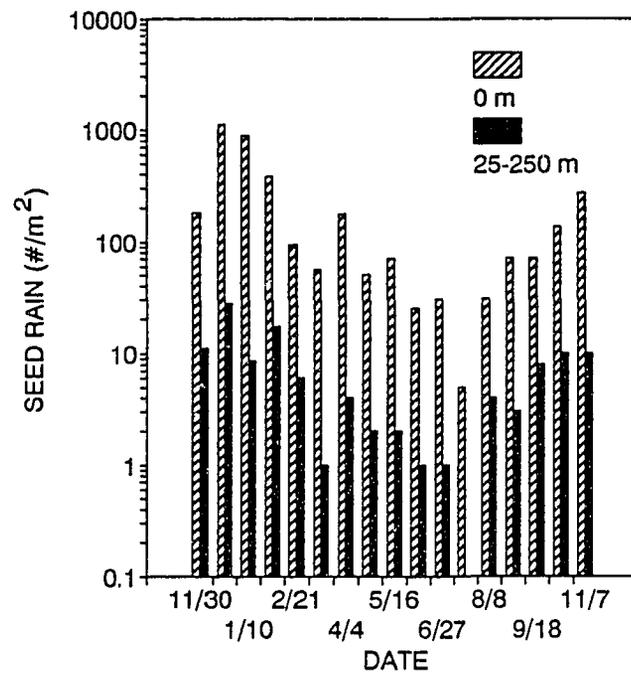
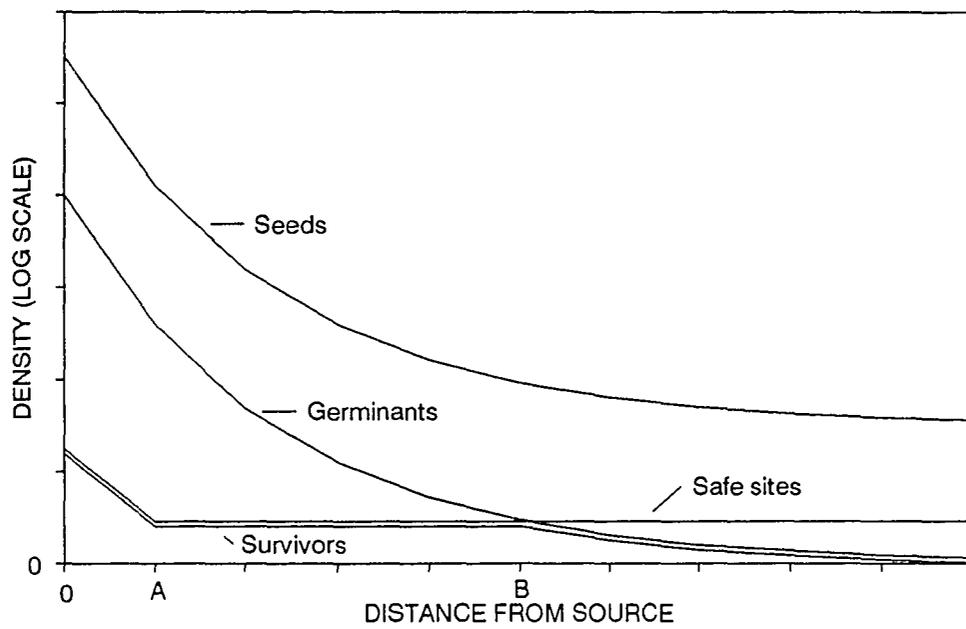


Figure 3.4. Model of the idealized relationships among distance from seed source, and densities of dispersed seed, germinants, safe sites for germination and establishment, and surviving plants, (modified from Harper, 1977, p. 460). From 0-A, density of safe sites is relatively high due to the ameliorating influence of the nearby forest. From 0-B, colonization is limited by the density of safe sites for germination and establishment; beyond B, colonization is limited by seed rain. The density of survivors would be expected to change during succession as plants alter the physical environment, grow, and interfere with each other.



CHAPTER 4: GERMINATION REQUIREMENTS OF METROSIDEROS
POLYMORPHA, THE DOMINANT TREE OF HAWAIIAN LAVA FLOWS AND
RAIN FORESTS

Abstract

Experiments were performed to determine the effects of burial, light quality, and temperature on seed germination of Metrosideros polymorpha, the dominant tree of Hawaiian lava flows and rain forests. Fewer than 1% of seeds buried under 5 mm of sand were able to germinate and emerge, compared to 90% for seeds sown on the sand surface. Germination was greater under white, red, or far-red light (all $\geq 62\%$) than in the dark ($\leq 10\%$). The light requirement was not overcome by a fluctuating thermoperiod (of $5^{\circ}/15^{\circ}$ C or $15^{\circ}/25^{\circ}$ C). Seeds germinated in all constant-temperature treatments (10° to 34° C). Germination percent and rate (pace) were highest at 22° C and lowest at 34° C. There were intraspecific differences between seeds from pubescent and glabrous parents, with seeds from pubescent plants germinating in slightly higher numbers at high temperatures, and slightly faster in many treatments. The results suggest that M. polymorpha seeds are capable of germinating rapidly under a wide variety of environmental conditions.

Introduction

The endemic tree Metrosideros polymorpha (Myrtaceae) dominates many native plant communities in Hawai'i, from pioneer vegetation on recent volcanic substrates (Atkinson, 1970; Egler, 1971; Smathers and Mueller-Dombois, 1974) to mature rain forest on older substrates (Mueller-Dombois et al., 1981; Gagné and Cuddihy, 1990). Metrosideros forest occurs from near sea level to 2,900 m (Gagné and Cuddihy, 1990).

Metrosideros polymorpha displays a broad range of morphological variation, which appears to reflect significant intraspecific ecological differentiation (Rock, 1913; Porter, 1972; Corn and Hiesey, 1973; Mueller-Dombois et al., 1980; Stemmermann, 1983; Dawson and Stemmermann, 1990). In general, the pubescent varieties (M. p. var. polymorpha and M. p. var. incana) tend to occupy relatively dry sites, while the glabrous ones (M. p. var. macrophylla and M. p. var. glaberrima) are most common in wetter sites (Mueller-Dombois et al., 1980; Mueller-Dombois, 1983; Stemmermann, 1983).

The seeds of M. polymorpha share at least two features with those of Metrosideros species from the South Pacific (Dawson, 1970; Wardle, 1971); the seeds are minute (mean fresh mass $\approx 57 \mu\text{g}$; D. R. Drake, unpublished data) and few (usually $< 20\%$) contain embryos (Corn, 1972; Burton, 1982). Burton (1982) reported that maximum

germination of M. polymorpha occurred at moderate temperatures (13% germination at 20° C) and relatively low photosynthetic photon flux densities (15% germination at 133 $\mu\text{mole m}^{-2} \text{s}^{-1}$), though seeds germinated in conditions ranging from complete darkness to full sunlight. However, Burton's (1982) seeds were collected from a single tree, and, in most experiments, were not sorted to ensure that only seeds containing embryos were used. Furthermore, even when seeds were sorted, only 30% of the embryo-containing seeds germinated. Therefore, it is unclear how representative Burton's (1982) results are. Seeds of M. polymorpha retain viability following freezing or immersion in seawater (Corn, 1972). Corn (1979) claimed that M. polymorpha requires light for germination, and Wardle (1971) claimed the same for M. umbellata in New Zealand, though neither reported any data.

The purpose of this study was to determine the germination requirements of M. polymorpha by examining the effects of burial, temperature, and light quality on seed germination. In addition, comparisons were made between seeds of pubescent and glabrous plants to determine whether the germination characteristics of the seeds parallel the differences in the ecological distributions of their parents.

Methods

During three separate years, seeds were collected from a population of Metrosideros polymorpha growing in the montane rain forest zone on Mauna Loa, at an elevation of 1130 m above sea level, on the lava flow of 1852. The forest was composed of approximately equal numbers of pubescent and glabrous individuals 2-5 m tall. After each collection, seeds were stored in open, wax paper bags, on a window ledge exposed to indirect sunlight, at 22° C, for less than two weeks before sowing. In each experiment, seeds were taken from equal numbers (12-20) of both parental types (pubescent and glabrous; seeds from each will hereafter be referred to as P seeds and G seeds, respectively). Seeds were sorted under a dissecting microscope and classified as filled (containing an embryo, and potentially viable) or unfilled (lacking an embryo, non-viable). Following an initial experiment that tested this classification procedure, all subsequent experiments used filled seeds only. Within each experiment, equal numbers of filled seeds were taken from each plant and then pooled within parental type.

As a test of the seed sorting and classification procedure, filled and unfilled seeds were sown separately at a density of 50 seeds/50 cm² pot, on the surface of fine (< 2 mm diam), black basalt sand from a 5 yr old lava flow (n = 200 filled and 200 unfilled seeds per parental

type). Pots were placed in a neutrally-shaded (whitewashed) greenhouse where they received 6 sec of tap water mist every 3 min. Temperatures ranged from 23° to 32° C during the day and 16° to 20° C at night. Germination (protrusion of the radicle ≥ 2 mm) and emergence (raising of cotyledons above the substrate) were counted daily for four weeks.

Together with the surface-sown seeds in the sorting experiment (above), additional seeds were sown at a density of 50 seeds/50 cm² pot, beneath either 2 or 5 mm of fine (< 2 mm diameter), black basalt sand (n = 200 seeds per parental type x two depth treatments). Germination and emergence were counted daily for four weeks.

As a test of the effects of light quality on germination, seeds were sown on filter paper at a density of 50 seeds/57 cm² Petri plate, and exposed to indirect sunlight (25-35 $\mu\text{mole m}^{-2} \text{ s}^{-1}$, 12 hr day-night cycle), continuous red light (fluorescent bulb, Carolina Biological Supply red 650 nm filter, 3 $\mu\text{mole m}^{-2} \text{ s}^{-1}$), continuous far-red light (incandescent bulb, Carolina Biological Supply far-red 750 nm filter, 3 $\mu\text{mole m}^{-2} \text{ s}^{-1}$), or continuous darkness (n = 200 seeds per parental type x four light treatments). All treatments were kept at 22° C except the far-red, which was at 28° C (the higher temperature being caused by the incandescent bulb). Seeds

were moistened daily with deionized water. Germination in the light was counted daily for four weeks; germination in the dark was counted only at the end of the four week dark period. After four weeks, all plates were placed in indirect sunlight, where germination was monitored for an additional week.

As a test of the effects of temperature on germination, seeds were sown on filter paper at a density of 25 seeds/24 cm² Petri plate, and exposed to constant temperatures of 10°, 16°, 22°, 28°, or 34° C (n = 100 seeds per parental type x five temperature treatments). All treatments received continuous white light (14 μmole m⁻² s⁻¹). Plates were sealed with paraffin film, and watered weekly with deionized water. Germination was counted weekly for four weeks.

As a test of the combined effects of light and fluctuating temperatures on germination, seeds were sown on filter paper at a density of 25 seeds/24 cm² Petri plate, and exposed to fluctuating thermoperiods of 12 hr/5° C night and 12 hr/15° C day, or 12 hr/15° C night and 12 hr/25° C day. Half of the plates in each thermoperiod treatment were kept in continuous darkness, and half received 12 hr of white light (27 μmole m⁻² s⁻¹) during the warm part of the day (n = 100 seeds per parental type x two thermoperiod x two photoperiod treatments). Plates were sealed with paraffin film, and

watered weekly with deionized water. Germination was counted weekly for four weeks, except in the dark treatments, where germination was counted only after four weeks.

One-, two-, or three-way ANOVAs of arcsine-transformed germination percentages were performed assess the effects of treatments on germination (Little and Hills, 1978). In cases where the initial ANOVA indicated no significant effect for parental type, data from P and G seeds were combined and a new ANOVA was performed. Following one-way ANOVAs, Tukey's test was used to assess differences among treatment means within each parental type (Zar, 1984). To allow comparison of germination rates, time (d) required for seeds to reach 50% of the final germination total (GT₅₀; c.f. Walker, 1990) was calculated for all treatments except those having few germinants or those in which germination was assessed only at the end of the experiment (dark treatments). In the following sections, germination percentages and GT₅₀s are presented as mean \pm one standard deviation, based on four replicates of 25 or 50 seeds per treatment.

Results

Overall, 90% of the seeds classified as filled germinated in the greenhouse, compared to 0.25% of those classified as unfilled, indicating that filled (viable)

seeds can be identified visually. There was no significant difference in the number of germinants based on parental type. Of the 360 filled seeds that germinated, only 3 failed to emerge (i.e. died before raising their cotyledons above the substrate).

Burial under sand significantly reduced seedling emergence, and there was no significant difference in percent emergence of P and G seeds (Fig. 4.1; one-way ANOVA, depth $F_{2,23} = 222.0$, $P < 0.001$). Seeds of both parental types emerged simultaneously, but required 4-5 days longer to emerge from under 2 mm of sand than from the surface.

Data from the light quality experiment were analyzed both with and without the inclusion of data from the far-red treatment because temperature was a possible confounding factor in that treatment. Seeds from both parental types germinated well under indirect sunlight and red light, but poorly in the dark (Table 4.1; two-way ANOVA excluding the far-red treatment, light $F_{2,18} = 223.2$, $P < 0.001$, parental type $F_{1,18} = 6.8$, $P < 0.02$, interaction $F_{2,18} = 1.0$, $P > 0.05$). Relative to other light treatments, germination of G seeds was reduced under far-red light, but germination of P seeds was not (Table 4.1; two-way ANOVA including the far-red treatment, light $F_{3,24} = 178.3$, $P < 0.001$, parental type $F_{1,24} = 28.2$, $P < 0.001$, interaction $F_{3,24} = 4.8$, $P < 0.01$). Germination of

P and G seeds from the far-red and dark treatments all rose to $\geq 87.5\%$ within one week after seeds were transferred to indirect sunlight.

In all three light treatments, P seeds consistently germinated faster than G seeds (Table 4.1). During much of the early course of germination (e.g., from days 5 to 10), the number of P germinants was often nearly twice that of G germinants (Fig. 4.2).

Seeds germinated in all constant temperature treatments, with peak germination occurring between 16° and 22° C (Fig. 4.3; two-way ANOVA, temperature $F_{4,30} = 53.9$, $p < 0.001$, parental type $F_{1,30} = 26.8$, $P < 0.001$, interaction $F_{4,30} = 6.4$, $P < 0.005$). High temperatures apparently reduced germination of G seeds more than that of P seeds. Overall, germination was twice as rapid at intermediate temperatures as at the extremes, and P seeds germinated slightly faster than G seeds; the mean difference between GT_{50} s of P and G seeds was 1.7 d (all treatments combined).

In the light vs. fluctuating temperature experiment, there was no significant difference between germination of P and G seeds, and germination was poor in all but the warm, light treatment (Table 4.2; two-way ANOVA, temperature $F_{1,28} = 198.2$, $P < 0.001$, light $F_{1,28} = 180.5$, $P < 0.001$, interaction $F_{1,28} = 125.9$, $P < 0.001$).

Germination rates were similar for both parental types (compared only at 15°/25° C in the light).

Discussion

Light is an important stimulus for seed germination of many small-seeded, woody, tropical species (Ng, 1980; Uhl and Clark, 1983; Vázquez-Yanes and Orozco-Segovia, 1984; Garwood, 1989; Hopkins *et al.*, 1990). Where the mechanism controlling the response of these species to light has been investigated, phytochrome has been identified as the pigment involved (Vázquez-Yanes and Orozco-Segovia, 1982, 1990a; Vázquez-Yanes and Smith, 1982; Orozco-Segovia and Vázquez-Yanes, 1989). In a typical phytochrome-mediated response, germination is promoted by light with a high red/far-red ratio and inhibited by light with a low red/far-red ratio, such as that beneath a plant canopy (Frankland and Taylorson, 1983).

Although a few *Metrosideros polymorpha* seeds germinated in the dark, exposure to light greatly enhanced germination; this supports earlier assertions of the importance of light for germination of *Metrosideros* spp. (Wardle, 1971; Corn, 1979; Burton, 1982). Interestingly, *M. polymorpha* seeds even germinated well under far-red light. Reduced germination of G seeds under far-red was probably a temperature effect; in separate experiments at

28° C, 62% and 63% of G seeds germinated under far-red (Table 4.1) and white light (Fig. 4.3), respectively. It is uncommon for species to germinate well under both red and far-red light, but poorly in the dark. This germination syndrome has been described for two African grasses (Fenner, 1980) and two small-seeded, woody, Mexican species: Buddleja cordata, a pioneer tree of lava flows (Vázquez-Yanes and Orozco-Segovia, 1990b), and Piper hispidum, a shrub of the forest understory and treefall gaps (Orozco-Segovia and Vázquez-Yanes, 1989).

In some tropical species, a fluctuating thermoperiod can substitute for light as a stimulus for germination (Vázquez-Yanes, 1981; Vázquez-Yanes and Orozco-Segovia, 1982). Stimulation by a fluctuating thermoperiod is interpreted as a mechanism whereby seeds can detect shallow burial under soils that experience relatively large diurnal temperature changes caused by sunlight in exposed sites such as canopy gaps. It is not surprising that a fluctuating thermoperiod failed to stimulate germination of M. polymorpha, since the seeds apparently contain such meager reserves that even those few that may be able to germinate while buried (i.e., in the dark) are unable to emerge through even 5 mm of soil (this study; Walker and Vitousek, 1991). Thus there would probably be selection against any mechanism stimulating germination underground.

The fact that seeds collected from a single population (at a single elevation) were able to germinate over a wide range of temperatures is consistent with the broad ecological amplitude of M. polymorpha. Although germination was reduced at extreme temperatures (Fig. 4.3), it was still much greater than previously reported (0% and 7% germination of filled seeds at 12° and 35° C respectively, assuming 14% of the seeds were filled; calculated from Burton, 1982). However, the surface temperatures reached by fresh volcanic substrates exposed to the sun (> 45° C; Walker, 1990) may often exceed the tolerance range of the seeds (Walker and Vitousek, 1991). Less than 1% of the filled M. polymorpha seeds sown on exposed cinder on Kilauea Volcano produced seedlings (Walker and Vitousek, 1991), though some seeds may have percolated to a depth from which they could not emerge.

There were slight, but statistically significant, differences between the germination characteristics of P and G seeds. This is surprising in light of the fact that the seeds were collected from populations that were growing sympatrically, overlapped in reproductive phenology, and thus lacked any obvious barriers to gene flow. Apparently P seeds are better able to tolerate high temperatures, such as those likely to be encountered in exposed sites, than are G seeds. Furthermore, P seeds frequently germinated slightly faster than G seeds. Rapid

germination should be favored in exposed sites where the moist conditions required for germination and establishment are unlikely to be as prolonged as in the wetter forest habitats, where, presumably, the G seeds have their greatest success. Both of these differences are consistent with the interpretation that pubescent plants are pioneers (Mueller-Dombois et al., 1980; Mueller-Dombois, 1983; Stemmermann 1983), though further studies would be required to predict whether the observed differences are great enough to be of adaptive significance in nature.

The results of the present study indicate that M. polymorpha seeds: 1) require no after-ripening (as evidenced by the fact that they can germinate immediately after being harvested); 2) germinate rapidly; 3) can germinate under low levels of light, including far-red; and 4) can germinate over a broad range of temperatures. In addition, the seeds lose viability after just a few months of storage at room temperature (Corn, 1972; Burton, 1982). Given these seed characteristics, and the fact that temperature and moisture levels in Hawaiian rain forest habitats should be favorable for germination throughout the year (Giambelluca et al., 1986), it is likely that most seeds either germinate soon after dispersal or die, and do not become incorporated into a persistent, soil seed bank.

Table 4.1. Percent germination (\pm one standard deviation) and time (days \pm 1 standard deviation) required for seeds to reach 50% of the final germination total (GT₅₀), of Metrosideros polymorpha seeds exposed to various light treatments (N = 4 plates of 50 seeds per parental type per treatment; all treatments were at 22 C except far-red, which was at 28 C; in rows, the numbers of germinants in treatments designated by the same letter are not significantly different at a family α of 0.05, Tukey's test; ND = no data).

PARENTAL TYPE	LIGHT TREATMENT			
	INDIRECT SUNLIGHT	CONTINUOUS RED	CONTINUOUS FAR-RED	CONTINUOUS DARKNESS
PUBESCENT				
%	94.5 \pm 5.2 A	96.0 \pm 4.3 A	90.0 \pm 4.0 A	10.0 \pm 5.9 B
GT ₅₀ (d)	7.9 \pm 0.2	6.5 \pm 0.2	9.7 \pm 0.8	ND
GLABROUS				
%	90.5 \pm 1.0 A	90.0 \pm 2.8 A	62.0 \pm 4.6 B	6.0 \pm 5.7 C
GT ₅₀ (d)	9.3 \pm 0.5	8.1 \pm 0.3	14.8 \pm 3.1	ND

Table 4.2. Percent germination (\pm one standard deviation) of Metrosideros polymorpha seeds exposed to various light and temperature treatments (n = 4 plates of 25 seeds per parental type per treatment).

PARENTAL TYPE	<u>CONTINUOUS DARKNESS</u>		<u>12 hr DARK/12 hr LIGHT</u>	
	<u>5°/15° C</u>	<u>15°/25° C</u>	<u>5°/15° C</u>	<u>15°/25° C</u>
PUBESCENT	2 \pm 2.3	16 \pm 6.5	10 \pm 7.7	74 \pm 12.4
GLABROUS	0 \pm 0.0	4 \pm 5.7	6 \pm 4.0	79 \pm 6.8

Figure 4.1. Percent emergence (+ one standard deviation) of Metrosideros polymorpha seeds buried under various depths of basalt sand (seeds collected from pubescent or glabrous parents; n = four pots of 50 seeds per parental type per treatment). Within a parental type, means designated by the same letter are not significantly different at a family α of 0.05 (Tukey's test, following one-way ANOVAs within each parental type).

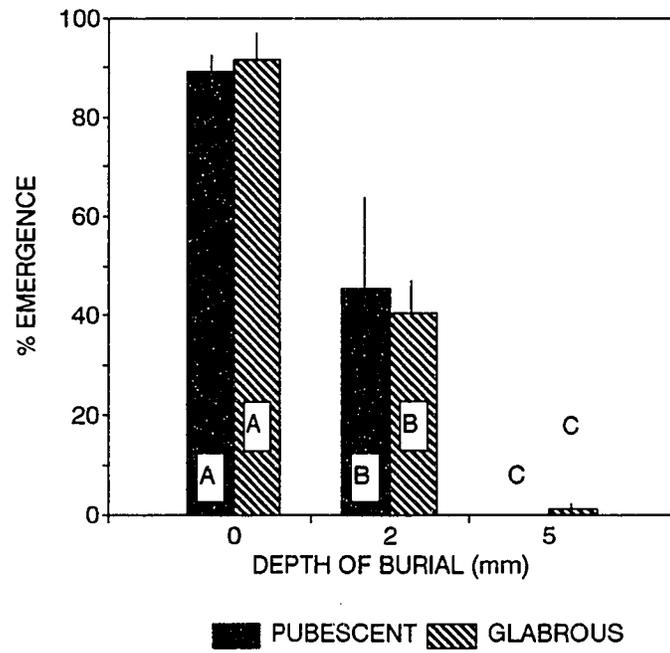


Figure 4.2. Cumulative percent germination of Metrosideros polymorpha seeds (exposed to red light) vs time (seeds collected from pubescent or glabrous parents; n = four plates of 50 seeds per parental type).

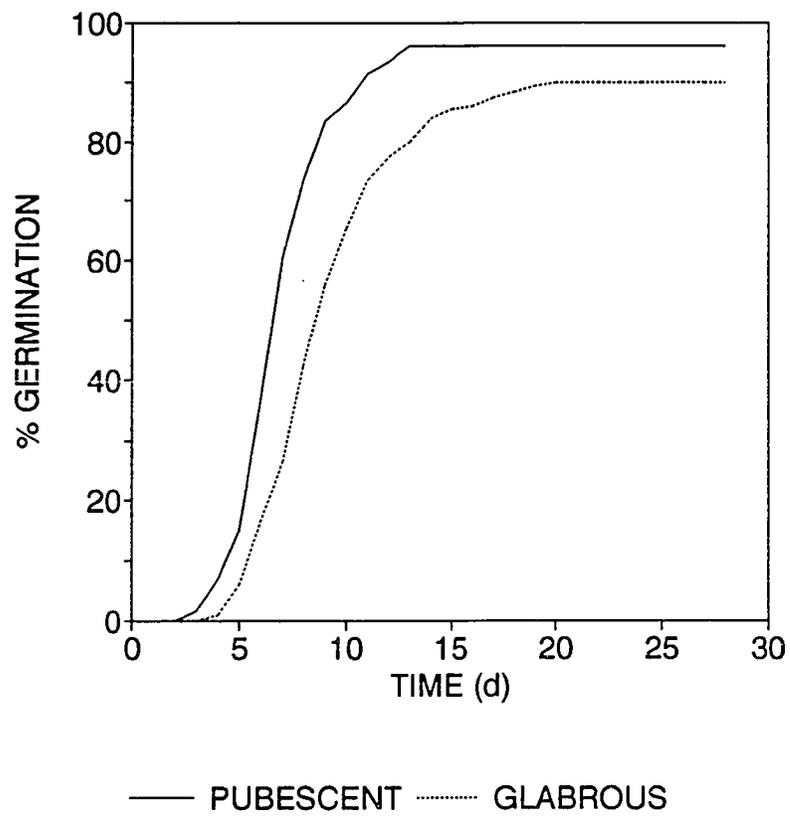
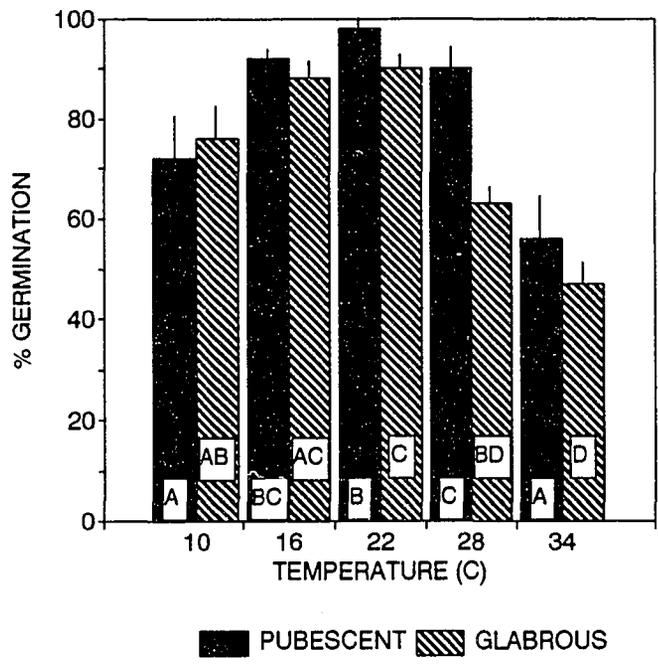


Figure 4.3. Percent germination (+ one standard deviation) of filled Metrosideros polymorpha seeds exposed to various temperatures (seeds collected from pubescent or glabrous parents; n = 4 plates of 25 seeds per parental type per treatment). Within a parental type, means designated by the same letter are not significantly different at a family α of 0.05 (Tukey's test, following one-way ANOVAs within each parental type).



CHAPTER 5: THE VEGETATION, SEED RAIN, AND SOIL SEED BANK
OF A HAWAIIAN FOREST

Abstract

The composition of the vegetation, seed rain, and soil seed bank of a Hawaiian forest was described and compared; the data were used to identify species' seed bank syndromes and to predict which species would be favored in the regeneration if the forest is disturbed. Abundances were quantified for seed plant species in the vegetation (% cover; 200 points), seed rain (87 seed traps = 5 m²; 17 samples/yr), and seed bank (87 soil cores = 1 m²; 4 samples/yr, spread for germination). It was possible to identify all plants in the vegetation (21 spp. = 125.5% total cover), 99% of the seeds in the seed rain (23 spp. = 5713.4 seeds m⁻²yr⁻¹), and 95% of the seedlings from the seed bank (29 spp. = 1023.75 seedlings m⁻² [quarterly mean]). The seed rain and vegetation were more similar to each other than either was to the seed bank. The native tree Metrosideros polymorpha dominated the vegetation (53.5% cover) and seed rain (5461 seeds m⁻²yr⁻¹), but formed only a pseudo-persistent seed bank. Among the remaining 15 species common in the seed rain and/or seed bank, 12 formed persistent seed banks and 3 formed transient seed banks. Excluding M. polymorpha, native species dominated the vegetation (91% relative

cover) and seed rain (68% relative density), but alien species dominated the seed bank (82% relative density), and two of these may replace many of the natives if the forest is disturbed.

Introduction

Most communities of seed plants are composed of three pools of species: the vegetation, the seed rain, and the soil seed bank. The latter two are inconspicuous, but are important determinants of the present and future vegetation on a site. The vegetation on a site is a subset of those species (and individuals) present in the seed bank. The seed bank, in turn, is a subset of those species and individuals deposited on the soil by the seed rain. Seeds therefore play a critical role in the dynamics of vegetation. Little is known about the seed ecology of native or alien plants in Hawai'i.

Invasion of native ecosystems by alien plants is an issue of serious concern on tropical islands throughout the world (Darwin, 1959; Wallace, 1911; Carlquist, 1974; Bramwell, 1979; Vitousek, 1988; Loope and Mueller-Dombois, 1989), particularly in areas managed for conservation, such as Hawai'i's National Parks (Smith, 1985; Mooney and Drake, 1986; Vitousek, 1988; Mueller-Dombois and Loope, 1990; Wester, 1992). Invasion implies movement or dispersal of propagules; although few data are available

(Vitousek and Walker, 1989), the most troublesome alien species in Hawaii are assumed to be dispersed as seeds (Smith, 1985).

Hawaiian ecosystems are exposed to disturbances ranging from the effects of feral animals, to fire, to hurricanes. Disturbance facilitates invasion by alien plants in Hawaii (Mueller-Dombois et al., 1981; Hughes et al., 1991) and elsewhere (Hobbs, 1989; Rejmánek, 1989). In general, species that colonize disturbed sites have propagules that are widely-dispersed, form long-lived soil seed banks, or both (Thompson, 1992). Furthermore, the nature of the disturbance may determine not only which seeds in the seed bank remain viable, but also whether or not those seeds are exposed to conditions favorable for germination and establishment (Grubb, 1977; Uhl, 1982; Hodgkinson and Oxley, 1990).

Thompson and Grime (1979) classified temperate plants according to the behavior of their seeds in the soil, and the types of seed banks they form. Garwood (1989) modified the classification scheme and described five major "tropical soil seed bank strategies" (or syndromes) and several variations, based on germination behavior and seed dispersal phenology. These seed bank syndromes include:

1. transient: seeds are short-lived (< 1/2 yr), lack dormancy (i.e., are quiescent or exhibit enforced

dormancy), and are dispersed for brief periods during the year;

2. seasonal-transient: seeds have intermediate longevity (< 1 yr) and seasonally acquire an induced dormancy, usually during the dry season;

3. delayed-transient: seeds have intermediate or long (≥ 1 yr) lifespans and innate dormancy;

4. persistent: seeds are long-lived (usually $\gg 1$ yr) and exhibit some form of dormancy;

5. pseudo-persistent: seeds have short or intermediate lifespans, lack dormancy, and are dispersed throughout the year.

According to Garwood (1989) "at least two of the following criteria must be known to identify seed bank syndromes: seasonal changes in the seed bank, seasonal timing of dispersal, or the presence of ... dormancy."

The purpose of this study was to describe the composition of, and relationships among, the vegetation, seed rain, and seed bank, of a Hawaiian forest dominated by native vegetation. The data were used to identify the seed bank syndromes of the common species and to make predictions concerning the composition of the vegetation expected to regenerate from seed following disturbance of the forest.

Methods

Site description:

The study was conducted in a forest located at ≈ 700 m above sea level in the Kealakomo section of Hawaii Volcanoes National Park (HAVO). Median annual rainfall is ≈ 2000 mm, with most falling in the winter months (Giambelluca et al. 1986). The substrate consists of 'a'ā lava covered with litter (depth range = 0-19 cm) and a shallow (depth = 6.3 ± 0.7 cm [$\bar{x} \pm$ s.e.m.], range = 0-36 cm, $n = 89$ random points along vegetation sampling transects) soil composed of sandy basalt mixed with organic matter. The site was selected because of the dominance of native species and lack of noticeable activity by pigs (a dispersal vector unaccounted for by the seed traps used to sample seed rain).

The site supports an open-canopied forest consisting mainly of native species and dominated by the tree Metrosideros polymorpha (dbh ≤ 65 cm, ht ≤ 20 m). In some places this forest is bounded by patches of pāhoehoe lava that support vegetation that appeared to have burned in the early 1970s when an active lava flow passed nearby. The relatively treeless vegetation on the pāhoehoe is dominated by Nephrolepis spp. ferns, mixed with the alien grass Setaria gracilis and native shrubs. No evidence of fire was noted in the forest vegetation on 'a'ā.

Characterization of the seed rain:

A 64 m baseline transect was established within the Metrosideros forest on 'a'ā lava. In each 8 m segment of the baseline transect, a random point was chosen as a starting point for a sampling transect. Eight parallel sampling transects (7-12 m apart and 40-120 m long) were established. Transects were terminated when they reached 120 m or approached within 5 m of the non-forest vegetation on pāhoehoe lava. A seed trap was placed at a random point in each 8 m segment of each sampling transect (total = 87 traps).

Traps were plastic pots from which the bottoms had been removed and replaced with cotton cloth secured by rubber bands (trap diam = 27 cm; depth = 19 cm; total area sampled by 87 traps = 5.0 m²). The weave of the cloth was fine enough to retain all seeds, yet allow water to drain freely. Traps were placed directly on the ground. Wire screens were placed over the tops of the traps to prevent rats from consuming seeds. Seeds placed in the traps (as a test of screen effectiveness) were not removed by rats. Screen apertures (minimum x maximum aperture = 2.4 x 3.8 cm) were at least three times wider than the largest diaspores in the forest.

Every 3 weeks (from November 1990 to November 1991) the cloths were changed and all material from each trap was examined under a dissecting microscope. Diaspores

were identified by comparison with reference specimens collected from mature plants. All seeds, including those inside multi-seeded pyrenes, were counted and classified as sound (whole and apparently undamaged) or unsound (damaged or lacking embryos). Unless stated otherwise, all data presented will refer to sound seeds. For large-seeded, fleshy-fruited species, whole diaspores/pyrenes that lacked flesh but contained an undamaged seed were counted as sound seeds that had passed through a bird. Pairs of split halves of pyrenes that bore the tooth marks of rats and lacked seeds were counted as unsound seeds that had been eaten by rats. The translucent seeds of M. polymorpha were examined microscopically and classified as containing or lacking an embryo (sound or unsound, respectively). Because seed rain of M. polymorpha was so dense, it was counted from 15 randomly selected traps in each 3 week interval.

Characterization of the seed bank:

The seed bank was sampled following weeks 12, 24, 36, and 48 of the seed rain sampling. The area around each of the 87 seed rain traps was divided into four quadrants, and every 12 weeks a soil core was taken from a different quadrant. Each core was taken from a point one meter away from the seed trap (core diam = 12.1 cm; depth = 5.0 cm

plus overlying litter; total area sampled by 87 cores = 1.0 m²).

Within 24 hr, the soil and litter were pressed through a sieve (aperture = 4.7 mm; greater than the diameter of the largest diaspores in the forest), and large pieces of rock, roots, and litter were discarded. After being passed through the sieve, each sample was spread to a depth of ≤ 1.8 cm on a 1 cm layer of peat moss in a tray (diam = 20.3 cm). Trays were placed in a screened, neutrally-shaded greenhouse at the University of Hawaii Agriculture Experimental Farm at Volcano (elevation = 1220 m above sea level), and watered daily. To monitor for contamination from seeds dispersed within the greenhouse, five control trays containing only peat moss were randomly distributed among the samples. One unidentified species of grass germinated in the control trays and emerged from the peat layer in the sample trays, and so was eliminated from the analysis; no other species germinated in the control trays. Seedlings that emerged during the ensuing 12 weeks were identified, counted, and removed from the trays. Individuals too small to identify at the end of 12 weeks were transplanted and grown to a larger size.

Characterization of the vegetation:

Plant cover was sampled at 200 points (two random points every 5 m) using the point intercept method (Mueller-Dombois and Ellenberg 1974). Sampling points were taken along seven transects placed midway between, and parallel to, the seed sampling transects. For each species, absolute percent cover was determined by counting the number of points at which a vertically-projected line intercepted parts of living plants, and dividing this value by the total number of points sampled. It was possible for more than one species to be counted at any given point, but each species was counted no more than once per point. Any species not encountered at a sampling point, but present within 100 m of the area bounded by the transects, was noted.

Limitations to the methodologies:

There are certain limitations to the methodologies used to assess species abundance in each of the three pools. The importance of annual variation in the seed rain at Kealakomo is unknown. Seed densities and species numbers in the seed rain were overestimated if not all apparently sound seeds were viable. Seed densities and species numbers in the seed bank were underestimated if not all seeds, or not all species, had their germination requirements met; this could occur because of suboptimal

light, moisture, or temperature conditions, insufficient time for germination, or the inability of small seeds to emerge from deep burial. The seed bank of M. polymorpha was probably underestimated due to the inability of buried seedlings to emerge. However, failure to emerge from depth should be consistent year-round (across seasons) and not affect patterns of seasonal variation in abundance.

Plant identification:

Taxonomy follows Wagner et al. (1990). For most species, voucher and reference specimens of fruiting plants and their seeds, plants cultivated from the seed bank, and other species from the vegetation (e.g. ferns) were deposited in the herbarium at HAVO. Two pairs of congeneric species produced seeds that could not be identified to species (Myrsine spp. and Wikstroemia spp.); in the data analysis, each of these two genera was treated as a single species in the seed rain, seed bank, and vegetation. Appendix B contains a complete list of seed plant species sampled in the seed rain, seed bank, or vegetation, or present in the vegetation within 100 m of the area bounded by the sampling transects at Kealakomo.

Data analysis:

Data analyses used only those 42 species that were sampled in the vegetation, seed rain, or seed bank, and were identifiable or able to be sampled (where present) in all three pools (Appendix B). Species that grew on the site, but were too short to deposit seeds in the seed traps (e.g., small sedges) were excluded from the analysis. Short species that did not grow on the site were included in the analysis because, during the study, their seeds (where present) could only have arrived via long-distance dispersal and were probably not discriminated against by the seed traps.

Motyka's Index (Mueller-Dombois and Ellenberg 1974) was used to make pairwise comparisons between the composition of the vegetation, seed rain, and seed bank. The index was based on comparisons of species' relative density in the annual seed rain, relative density in the mean quarterly seed bank, and relative cover in the vegetation.

Friedman's Test (adjusted for ties; Zar 1984) was used to assess temporal/seasonal variation in the abundance of seeds in the quarterly samples of the seed rain and the seed bank; the four seasons were the treatments and the 87 sampling sites (trap or core locations) were the blocks. Because seed rain data for M. polymorpha were collected from subsamples consisting of

randomly-selected traps, the data were analyzed using the Kruskal-Wallis test (adjusted for ties; Zar 1984). Each of these tests was applied only to species present at a density of ≥ 5 seeds/m² in the annual seed rain or a quarterly mean of ≥ 5 seed/m² in the seed bank.

Results

The vegetation was dominated by M. polymorpha, which formed an open, upper canopy (Table 5.1). An open, middle stratum was dominated by native trees and shrubs, and a denser lower stratum was dominated by Nephrolepis spp. ferns (53.0% cover) mixed with lesser amounts of alien grasses, native shrubs, and forbs. Total plant cover was 125.5 % (187.5%, including pteridophytes).

Total annual seed rain was 5713.4 seeds/m², of which Metrosideros polymorpha comprised 95.6% (Table 5.1). Total annual seed rain of M. polymorpha was 56,755 seeds/m², but only 5461 (9.6%) contained embryos. A significant number of the captured seeds of two species (Coprosma menziesii and Myrsine spp.) had been destroyed by rats prior to being captured (Fig. 5.1). Nearly one quarter of the fruits/seeds of these two species fell whole from the tree. Birds dispersed relatively few Myrsine seeds, but nearly one quarter of C. menziesii seeds. Other species showed little evidence of having been handled by animals. Excluding M. polymorpha, native

shrubs and alien grasses were the main contributors to the seed rain, and native seeds were twice as abundant as alien seeds.

The seed bank was dominated by alien species (Table 5.1). After the January quarter, during which M. polymorpha dominated the seed bank, aliens were three times as abundant as natives in the seed bank. The major plant groups in the seed bank were alien shrubs, alien graminoids, alien forbs, native shrubs, and, in some seasons, M. polymorpha.

Because M. polymorpha was so overwhelmingly abundant in the seed rain, comparisons between the vegetation, seed rain, and seed bank were made both with and without M. polymorpha. Either way, the seed rain and the vegetation were more similar to each other than either was to the seed bank (Table 5.2).

It is estimated that M. polymorpha occurred in all 87 seed traps during the course of the year (Table 5.3); this estimate is based on 100% occurrence in 135 randomly selected seed traps (15 sampled in every 3 week period) between 16 September and 11 March, and $\geq 60\%$ occurrence in each 3 week period during the rest of the year. The only other species to occur in $\geq 1/3$ of the 87 seed traps was Andropogon virginicus. Most species occurred in fewer than 6 traps (Fig. 5.2). The number of species captured

per trap was 3.38 ± 0.14 ($\bar{x} \pm \text{s.e.m.}$; range for 87 traps = 1 - 7; Fig. 5.3).

In contrast, six species occurred in $\geq 30\%$ of the soil cores in all seasons (Table 5.3). However, as in the seed rain traps, most species occurred in relatively few soil cores (Fig. 5.4). The number of species germinated per core ranged from 4.81 ± 0.20 ($\bar{x} \pm \text{s.e.m.}$) in January to 3.52 ± 0.18 in July (range for 348 cores = 0 - 9; Fig. 5.5). Only three soil cores produced no identifiable germinants, and only one produced no germinants at all.

The sixteen species that were present at a density of ≥ 5 seeds/m² in the annual seed rain or mean quarterly seed bank were classified according to seed bank syndrome (c.f. Garwood, 1989). For 12 species, seed density in the seed bank was generally \geq seed density in the annual seed rain, indicating that seed longevity in the soil was ≥ 1 yr; the species that formed these persistent seed banks were forbs (Fig. 5.6), graminoids (Fig. 5.7), and shrubs (Fig. 5.8). Only three native species formed persistent seed banks: Machaerina mariscoides, Dodonaea viscosa, and Pipturus albidus. Four species had seed densities in the seed bank that were consistently \leq seed densities in the seed rain for the corresponding quarter, and \ll seed densities in the annual seed rain (Fig. 5.9). These four native shrubs and trees had short-lived seeds and formed

pseudo-persistent (Metrosideros polymorpha) or transient seed banks.

For most species that were common in the seed rain there was significant seasonal variation in seed abundance in the seed rain (Table 5.4, Figs. 5.6-5.9). In contrast, species common in the seed bank were generally less variable in their seasonal abundance (Table 5.4, Figs. 5.6-5.9).

Discussion

Seed banks in tropical forests have, on average, between 300 and 800 germinable seeds/m², representing between 20 and 50 species, with one species usually contributing more than half of the individuals present (Guevara and Gómez-Pompa, 1972; Cheke et al., 1979; Hall and Swaine, 1980; Hopkins and Graham, 1983; Uhl and Clark, 1983; Garwood, 1989). Seed density in the Kealakomo forest seed bank is comparatively high, perhaps because of seed input from the (former and present) vegetation on the surrounding pāhoehoe lava. Seed density and species richness in the seed bank are higher beneath forests that receive seed rain from nearby disturbed areas (de Foresta and Prevost, 1986; Young et al., 1987; Saulei and Swaine, 1988).

In tropical forests, there is often little correspondence between the composition of the vegetation

and the seed bank (Guevara and Gómez-Pompa, 1972; Hall and Swaine, 1980; Saulei and Swaine, 1988), or between the annual seed rain and the seed bank (Uhl and Clark, 1983; Saulei and Swaine, 1988). At Kealakomo, the vegetation and seed rain were moderately similar to each other, and the seed bank was not very similar to the seed rain or vegetation. The seed rain is probably dominated by local species because most seeds of most plants fall very near the parent plant (Harper, 1977). The relatively unique composition of the seed bank is due to the fact that some species in the local vegetation produce non-dormant seeds and some seeds in the seed bank are relicts of species no longer present in the vegetation or dispersed to the site from afar.

Several species, such as Rubus rosifolius, Pipturus albidus, and Gnaphalium purpureum, were poorly represented in the vegetation on and around the study site, and were at least 100x as abundant in their maximum quarterly seed bank as in total annual seed rain. It is not clear whether these species: 1) are, in some years, more abundant in the seed rain that arrives via long-distance dispersal; 2) have extremely long-lived seeds that slowly accumulate in the seed bank over many years; 3) were formerly abundant in, and dispersed from, the early-successional, post-fire vegetation on the pāhoehoe lava adjacent to the study site; 4) were common in, and

dispersed from, the vegetation destroyed by the 1970 lava flows that passed within 100 m of the study site; or 5) were formerly present in the vegetation on the site, and left relictual seed banks.

The mean number of species per soil core was \geq the mean number of species per seed trap, even though the area of each trap was five times that of each core. This may be because the seed traps capture only a short-term sample of seeds/species falling on an area, whereas the soil cores (seed bank) contain not only a sample of recently-dispersed seeds, but also a subset of species/seeds from the past seed rain.

In the competition to establish on a disturbed site, those species whose propagules are already present in the seed bank or are dispersed to the site shortly after the disturbance have a great advantage over later arrivals (Harper, 1977; Thompson, 1992). However, numerical dominance in the seed rain or seed bank does not necessarily guarantee dominance among the regenerants on a disturbed site (Uhl et al., 1981; Putz, 1983; Swaine and Hall, 1983; Lawton and Putz, 1988). A single seedling of a fast-growing tree such as Myrica faya is likely to overtop and shade out large numbers of tiny, slow-growing Metrosideros polymorpha seedlings (Vitousek and Walker, 1989). In addition, the potential for vegetative regeneration (not assessed in this study) is another

factor that must be accounted for; depending on the nature of the disturbance, vegetative regrowth may account for much of the regeneration (e.g., for Nephrolepis spp. ferns). Nevertheless, the composition of the vegetation that regenerates on disturbed sites is typically similar to the composition of the site's seed bank (Uhl et al., 1981; Putz, 1983; Swaine and Hall, 1983; Lawton and Putz, 1988). Thus, knowledge of the composition of the seed rain and seed bank at Kealakomo allows some tentative predictions to be made about the potential composition of the regeneration that would follow disturbance of the forest.

At Kealakomo, the seed bank was dominated by alien species, most of which were abundant in the seed bank year-round. Many of the alien species in the seed bank at Kealakomo were relatively small, shade-intolerant herbs and weakly-woody shrubs (e.g., Gnaphalium purpureum, Stachytarpheta urticifolia, and Rubus rosifolius). These species, by virtue of their density in the seed bank, might dominate the early phases of post-disturbance secondary succession, but would probably be successionaly displaced on a site capable of supporting forest. However, two alien species in the seed bank (Andropogon virginicus and Myrica faya) have the potential, once established, to completely alter the ecosystem at Kealakomo. Elsewhere in HAVO, A. virginicus dominates

grasslands that are both prone to, and perpetuated by, fire (Mueller-Dombois, 1981; Smith, 1985; Smith and Tunison, 1992). The native vegetation is poorly adapted to fire, and is usually displaced once a frequent fire-disturbance regime is established (Mueller-Dombois, 1981; Hughes et al. 1991). In much of HAVO, the fast-growing, nitrogen-fixing tree Myrica faya has rapidly invaded disturbed areas, formed monospecific stands, and altered soil properties (Vitousek et al., 1987; Vitousek and Walker, 1989). Though presently rare in the vegetation and seed bank at Kealakomo (Appendix B), M. faya is capable of explosive population growth, and so poses a serious threat.

Few native species were common in the seed bank. One of these, Dodonaea viscosa, regenerates from the seed bank following fire in Australia (Hodgkinson and Oxley, 1990). Another, Pipturus albidus, is likely to respond to disturbance by regenerating rapidly from the seed bank, as P. argenteus does in the South Pacific (Enright, 1985; Saulei and Swaine, 1988).

Seeds of Metrosideros polymorpha apparently do not survive long in the seed bank and are present in the soil for only a short time following dispersal. Although seed production fluctuates seasonally, seeds are produced year-round, are widely dispersed, and can germinate under a wide range of environmental conditions. Thus, large

numbers of M. polymorpha seedlings would be likely to appear after disturbance (their number and origin depending on the season), but slow growth may mean relatively few would establish among more vigorous competitors.

At least 50% of the relatively large seeds of Myrsine spp. and Coprosma menziesii were eaten by rats directly on the tree; If rats also consume seeds that have dropped beneath the parent tree, the rate of predation is even higher. Such severe predation could be one factor explaining the relative scarcity of these species in the seed bank. Alternatively, any seeds cached by rats may be favorably placed for germination and establishment, as occurs with other species eaten/dispersed by rats (Price and Jenkins, 1986).

Several other, mainly woody, native species produced few seeds or produced them mainly during the winter. For these species, the degree of regeneration would be strongly affected by the seasonal timing of the disturbance.

In summary, alien species, by virtue of their abundance in the seed bank, would be likely to regenerate more strongly than natives following a major disturbance at Kealakomo. However, the seasonal timing of disturbance would likely play critical role in determining the composition of the regenerating vegetation. For example,

many natives are rare in the seed bank, and abundant in the seed rain during the fall and winter only. In contrast, most alien species are more or less equally abundant (especially in the seed bank) at all seasons. Overall, however, the resulting vegetation would probably include a higher proportion of aliens than the present vegetation does. If these aliens restock the seed bank with even greater densities of seeds, the aliens would be likely to become a persistent (perhaps dominant) component of the vegetation dynamics at Kealakomo. On the other hand, if the area is managed so that a disturbance that is likely to stimulate regeneration from the seed bank is prevented, natives may be more likely to persist.

Table 5.1. Summary of the composition of the annual seed rain, quarterly soil seed bank, and vegetation (absolute % cover) in a Metrosideros polymorpha forest at Kealakomo.

TAXA (# OF SPECIES) ¹	DENSITY (SEEDS/m ²)				COVER (%)	
	SEED RAIN	SEED BANK			VEGE-TATION	
		JAN	APR	JUN	OCT	
NATIVE SPECIES						
<u>M. polymorpha</u> (1)	5461.0	568	60	28	62	53.5
OTHER TREES (4)	27.4	1	0	0	1	16.0
SHRUBS (9)	139.2	223	103	97	111	40.0
LIANAS (2)	1.2	1	0	0	0	5.5
GRAMINOIDS (2)	2.6	3	16	30	29	2.5
FORBS (2)	0.0	2	2	3	0	1.5
TOTAL NATIVES						
- <u>M. poly.</u> (19)	170.4	230	121	130	141	65.5
+ <u>M. poly.</u> (20)	5631.4	798	181	158	203	119.0
ALIEN SPECIES						
TREES (2)	0.6	6	4	0	3	1.5
SHRUBS (3)	6.6	301	390	276	277	0.0
LIANAS (0)	0.0	0	0	0	0	0.0
GRAMINOIDS (8)	73.0	223	188	242	195	5.0
FORBS (9)	1.8	158	214	142	136	0.0
TOTAL ALIENS (22)	82.0	688	796	660	611	6.5
TOTAL IDENTIFIABLE SPECIES						
- <u>M. poly.</u> (41)	252.4	918	917	790	752	72.0
+ <u>M. poly.</u> (42)	5713.4	1486	977	818	814	125.5
UNIDENTIFIABLE TAXA ²	5.2	120	75	19	46	8.0

¹Pairs of Wikstroemia spp. (native shrubs) and Myrsine spp. (native trees) are each counted as one species because seeds of individual species are indistinguishable within each genus.

²Includes all individuals of all taxa not identifiable or not possible to sample in one or more of the three species pools (see text) and all seedlings that died before growing large enough to be identified in the seed bank.

Table 5.2. Index of similarity (Motyka's Index) between the seed rain, seed bank, and vegetation in a Metrosideros polymorpha forest at Kealakomo. The index is based on comparisons of species' relative density in annual seed rain, relative density in mean quarterly seed bank, and relative cover in the vegetation.

	INDEX OF SIMILARITY	
	+ <u>M. polymorpha</u>	- <u>M. polymorpha</u>
SEED RAIN x VEGETATION	46.3	50.2
SEED RAIN x SEED BANK	20.0	31.8
SEED BANK x VEGETATION	25.9	12.9

Table 5.3. Relative frequency of occurrence of the most common species in the seed rain, seed bank, and vegetation at Kealakomo (values represent the percent occurrence of each species at seed traps [n = 87], soil cores [n = 87], or vegetaton sampling points [n = 200], respectively).

SPECIES	SEED	SEED BANK				VEGE- TATION
	RAIN	JAN	APR	JUN	OCT	
NATIVE SPECIES:						
TREES						
<u>Metrosideros polymorpha</u> ¹	100	100	45	30	41	53.5
<u>Myrsine</u> spp.	24	1	0	0	1	13.5
SHRUBS						
<u>Coprosma menziesii</u>	6	1	0	0	0	1.5
<u>Dodonaea viscosa</u>	29	15	9	8	15	14.5
<u>Pipturus albidus</u>	6	53	34	37	39	0.0
<u>Styphelia tameiameia</u>	33	1	3	1	5	13.0
GRAMINOIDS						
<u>Machaerina mariscoides</u>	1	3	9	11	8	1.5
ALIEN SPECIES:						
SHRUBS						
<u>Rubus rosifolius</u>	7	46	48	41	45	0.0
<u>Stachytarpheta urticifolia</u>	14	49	51	43	56	0.0
<u>Pluchea symphytifolia</u>	1	32	21	9	10	0.0
GRAMINOIDS						
<u>Andropogon virginicus</u>	55	64	53	57	52	4.0
<u>Paspalum conjugatum</u>	16	14	14	9	9	0.5
<u>Paspalum scrobiculatum</u>	8	3	6	2	8	0.5
FORBS						
<u>Erechtites valerianifolia</u>	8	10	8	10	6	0.0
<u>Gnaphalium purpureum</u>	0	69	78	67	64	0.0
<u>Youngia japonica</u>	0	8	11	7	10	0.0

¹Estimated value, based on 100% occurrence in 135 randomly selected seed traps (15 sampled in every 3 week period) between 16 September and 11 March, and $\geq 60\%$ occurrence in each 3 week period during the rest of the year.

Table 5.4. Results of Friedman's test. A significant P value indicates significant seasonal variation in the abundance of a species in the seed rain or seed bank at Kealakomo; df = 3; results are corrected for ties (Zar, 1984).

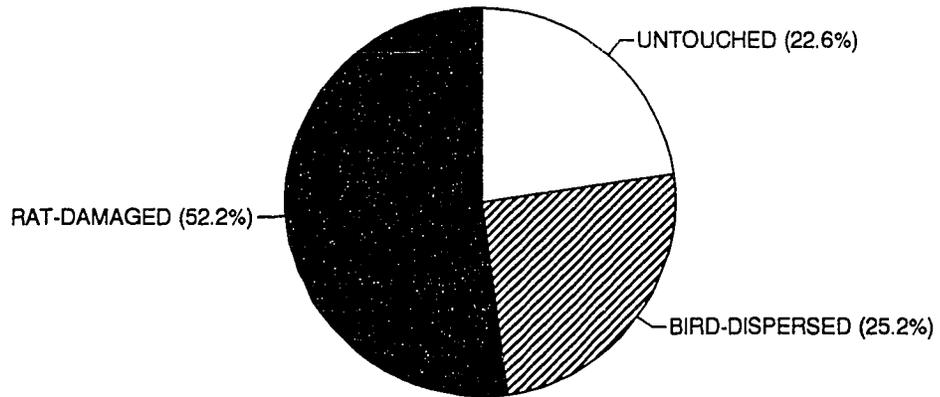
SPECIES	SEED RAIN ¹		SEED BANK	
	S	P ≤	S	P ≤
<u>Andropogon virginicus</u>	12.8	0.005	7.8	0.051
<u>Coprosma menziesii</u>	13.6	0.004	3.0	0.392
<u>Dodonaea viscosa</u>	16.7	0.001	6.4	0.095
<u>Erechtites valerianifolia</u>	9.8	0.021	1.7	0.639
<u>Gnaphalium purpureum</u>	ND	-----	14.0	0.003
<u>Machaerina mariscoides</u>	3.0	0.392	7.2	0.066
<u>Metrosideros polymorpha</u> ²	116.2	0.001	176.6	0.001
<u>Myrsine spp.</u>	12.2	0.007	2.0	0.573
<u>Paspalum conjugatum</u>	4.3	0.230	1.3	0.742
<u>Paspalum scrobiculatum</u>	0.6	0.893	0.9	0.816
<u>Pipturus albidus</u>	4.4	0.224	12.7	0.005
<u>Pluchea symphytifolia</u>	6.0	0.112	26.5	0.001
<u>Rubus rosifolius</u>	11.3	0.010	6.3	0.100
<u>Stachytarpheta urticifolia</u>	15.5	0.002	1.0	0.809
<u>Styphelia tameiameiae</u>	13.1	0.005	4.4	0.222
<u>Youngia japonica</u>	ND	-----	4.5	0.217

¹ND = no data (species not represented in the seed rain).

²Because seed rain data for M. polymorpha were collected from subsamples consisting of randomly-selected traps, the data were analyzed using the Kruskal-Wallis test, and the value in the first column represents H rather than S.

Figure 5.1. Condition of propagules of Coprosma menziesii (n = 115) and Myrsine spp. (M. lessertiana and M. sandwicensis; n = 535) captured in seed traps. Untouched = whole fruits that bear no marks of being handled by animals; Bird-dispersed = whole pyrenes that lacked flesh but contained an undamaged seed; Rat-damaged = pairs of split halves of pyrenes that bore the tooth marks of rats and lacked seeds.

Coprosma menziesii



Myrsine spp.

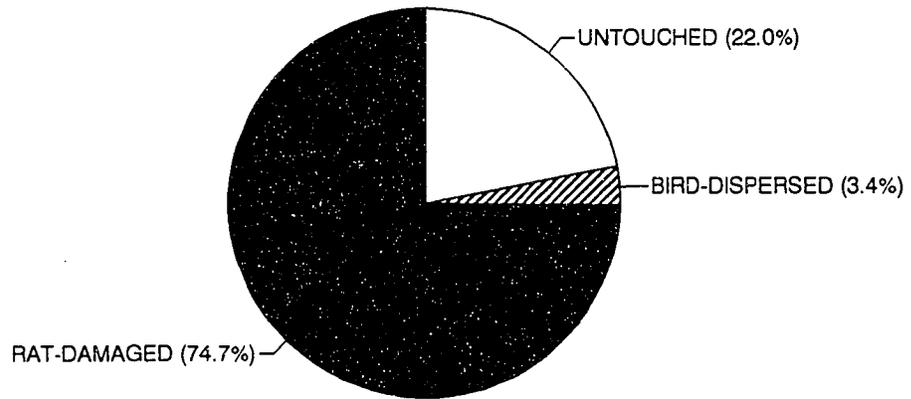


Figure 5.2. Numbers of seed traps (out of 87 possible) in which individual species were captured in the annual seed rain at Kealakomo. Although Metrosideros polymorpha was counted in only a subsample of traps, it has been included as present in all 87 traps in the graphed data (based on 100% occurrence in 135 randomly selected seed traps [15 sampled in every 3 week period] between 16 September and 11 March, and $\geq 60\%$ occurrence in each 3 week period during the rest of the year).

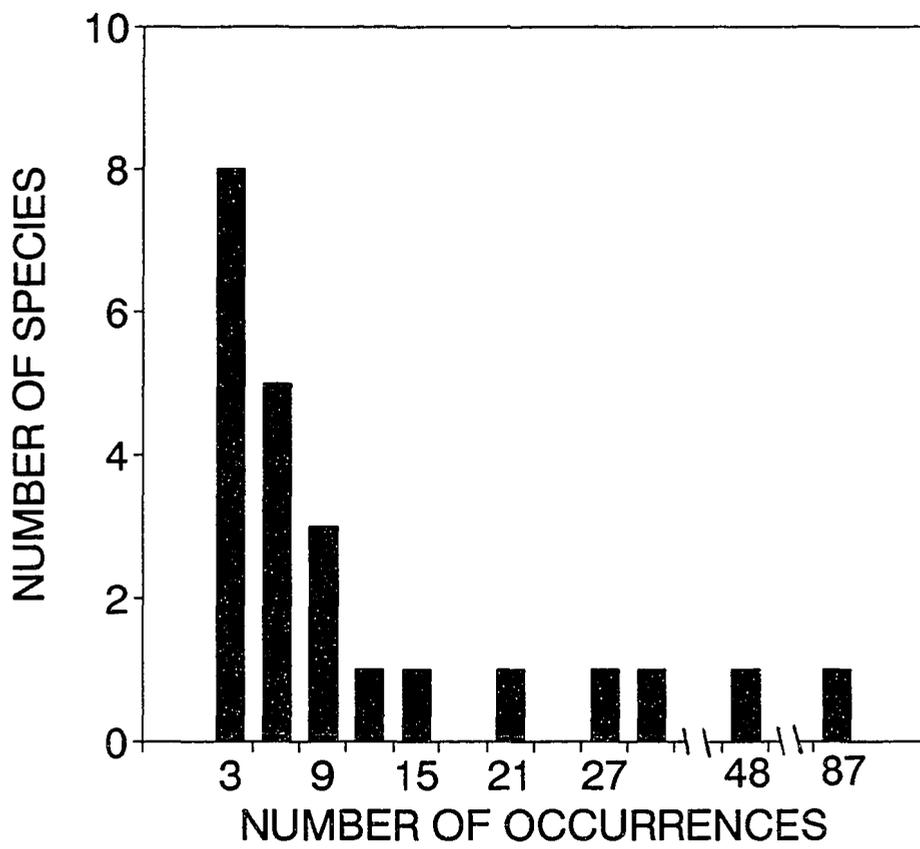


Figure 5.3. Numbers of species captured per seed trap, in the annual seed rain at Kealakomo. Although Metrosideros polymorpha was counted in only a subsample of traps, it has been included as present in all 87 traps in the graphed data (based on 100% occurrence in 135 randomly selected seed traps [15 sampled in every 3 week period] between 16 September and 11 March, and $\geq 60\%$ occurrence in each 3 week period during the rest of the year).

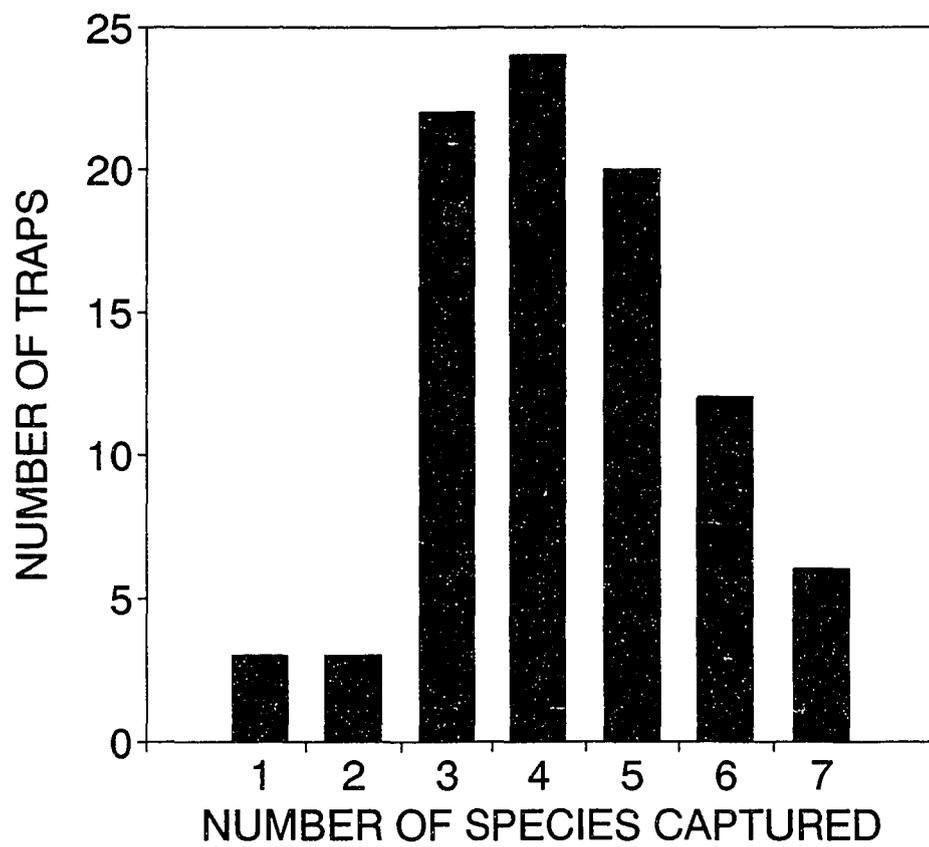


Figure 5.4. Numbers of soil cores in which individual species germinated, from four, quarterly sets of 87 soil cores collected at Kealakomo.

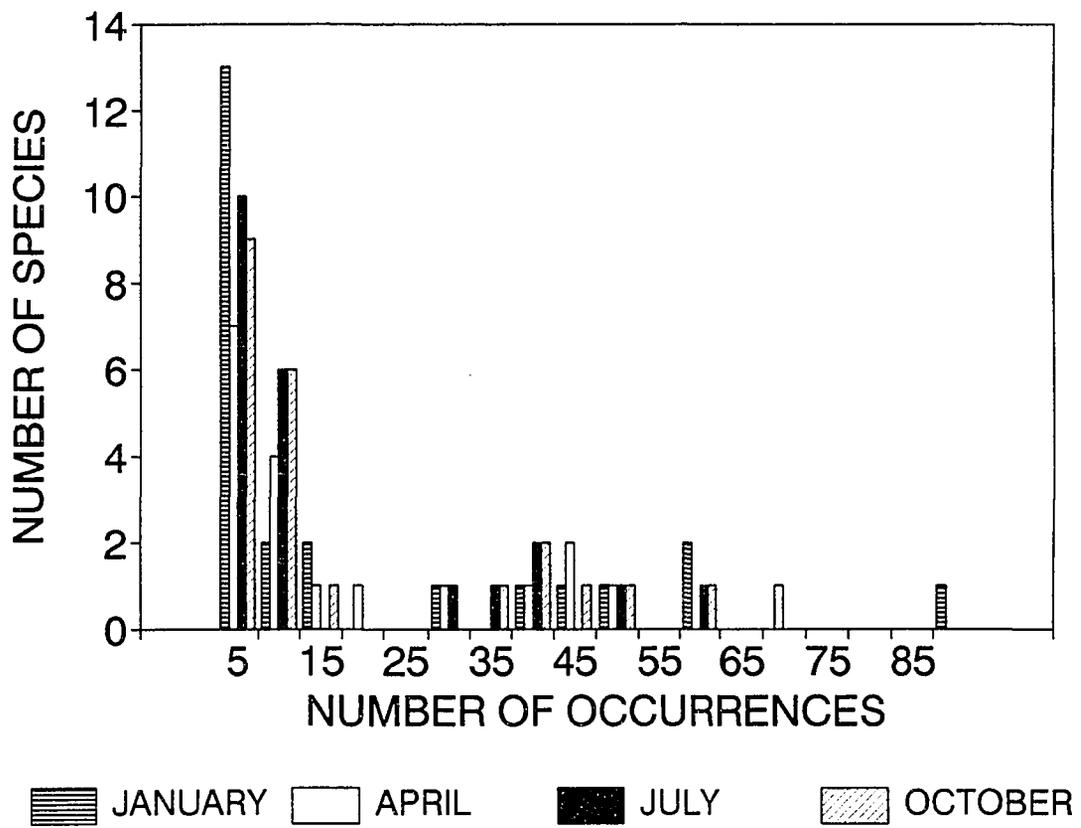


Figure 5.5. Numbers of species germinated per soil core,
from four, quarterly sets of 87 soil cores from Kealakomo.

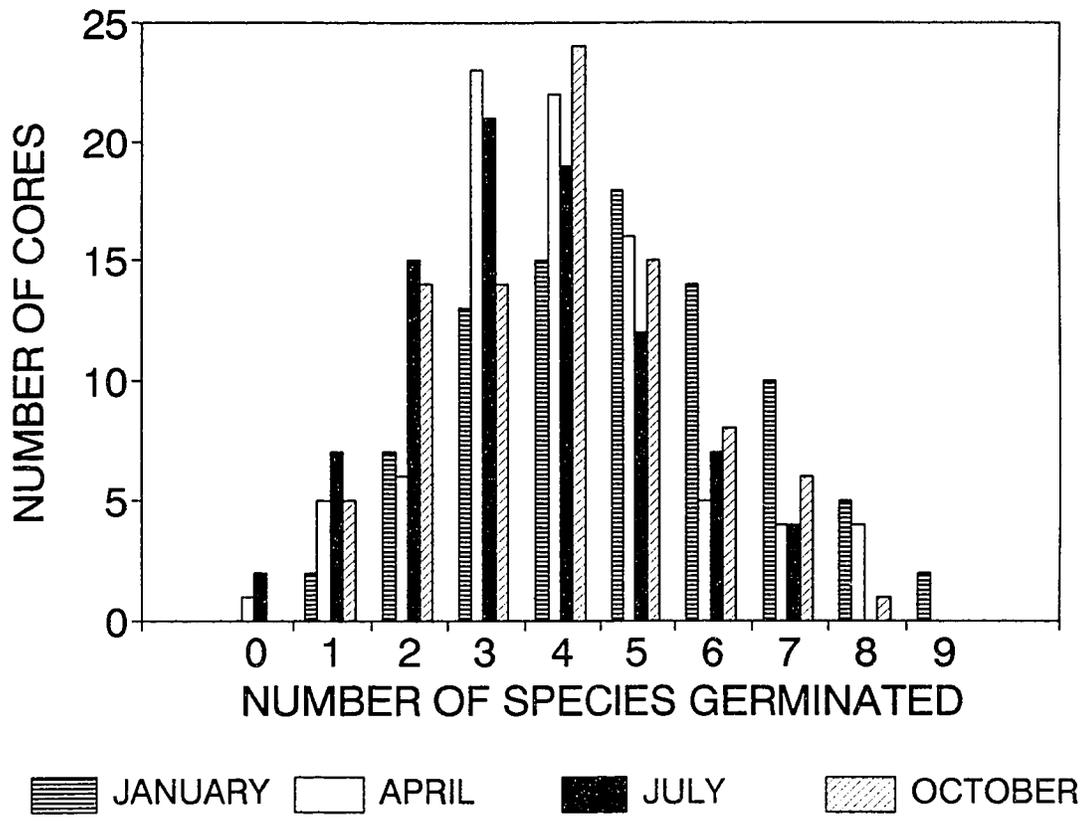
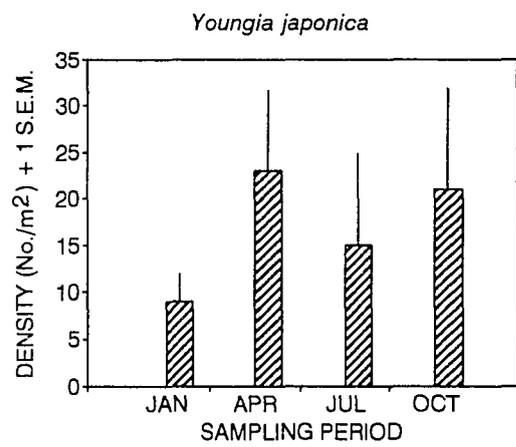
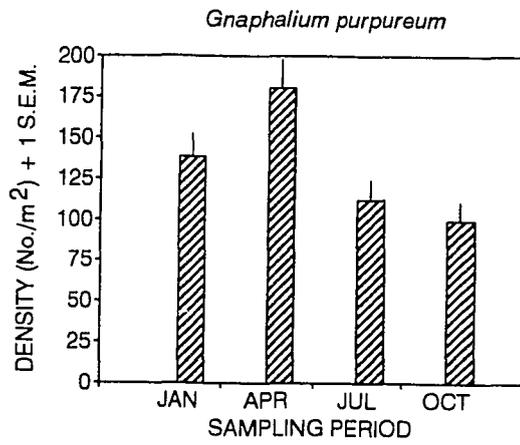
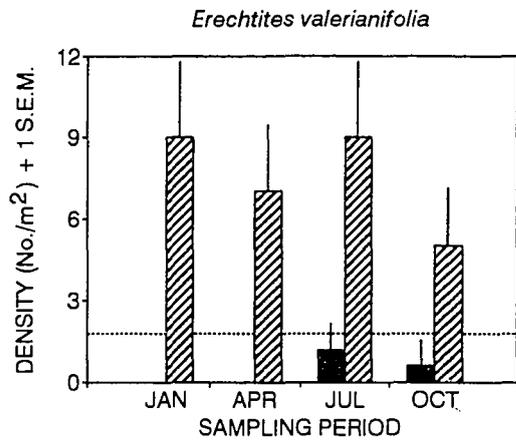
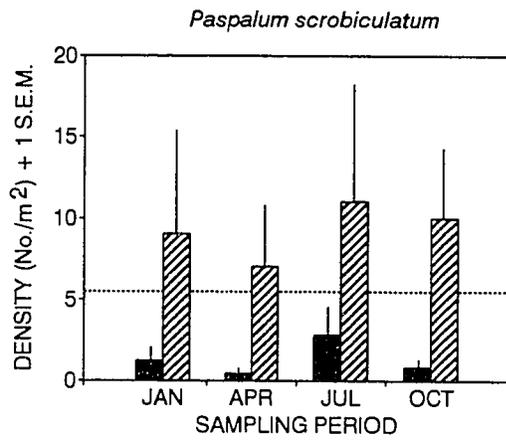
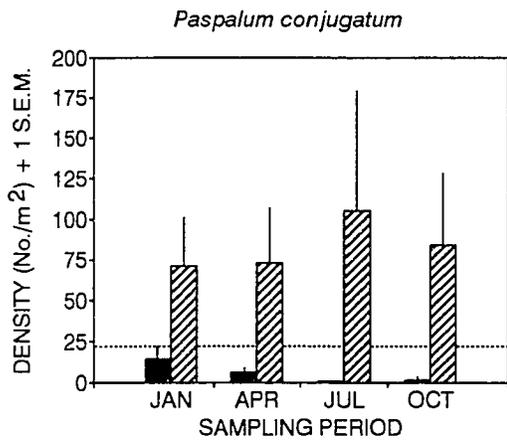
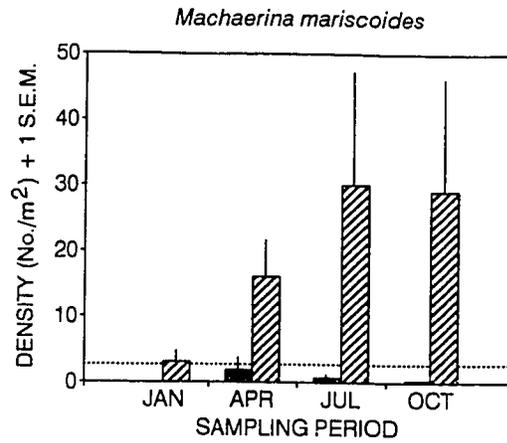
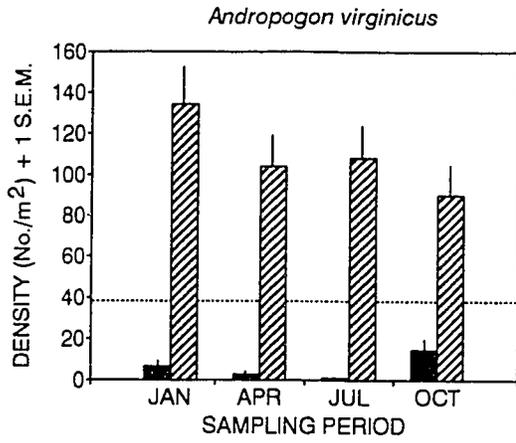


Figure 5.6. Seed population profiles for three forbs that form persistent seed banks at Kealakomo. Values for seed rain represent seed rain total for a 12 week period ending in the month labelled on the abscissa. Values for seed bank represent the number of germinants emerging from soil samples collected at the end of the corresponding seed rain interval. The horizontal line represents total annual seed rain (from the four 12 week intervals plus one additional 4 week interval).



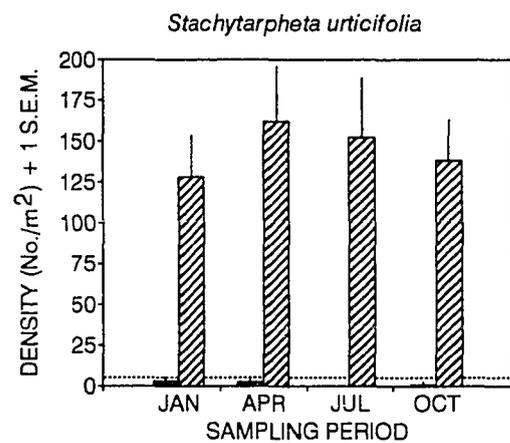
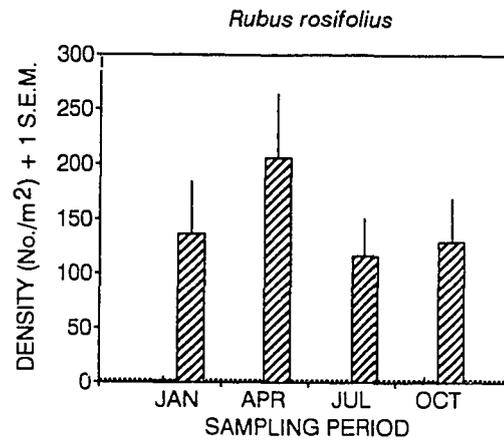
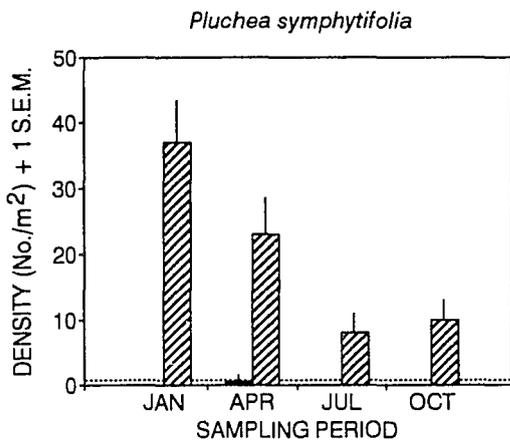
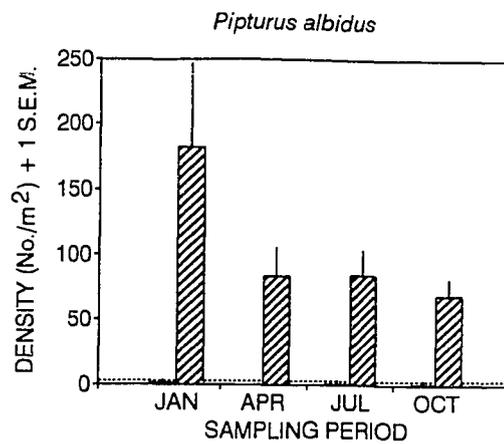
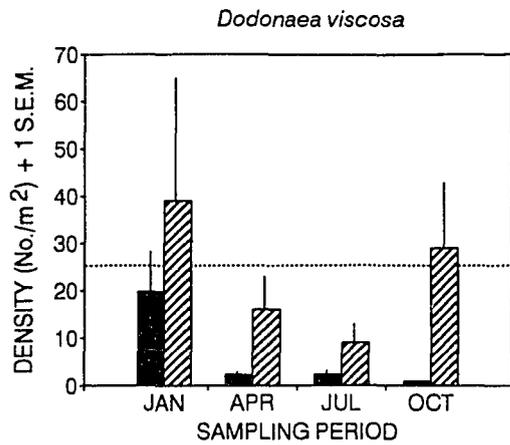
 SEED RAIN
 SEED BANK

Figure 5.7. Seed population profiles for four grasses and sedges that form persistent seed banks at Kealakomo. Values for seed rain represent seed rain total for a 12 week period ending in the month labelled on the abscissa. Values for seed bank represent the number of germinants emerging from soil samples collected at the end of the corresponding seed rain interval. The horizontal line represents total annual seed rain (from the four 12 week intervals plus one additional 4 week interval).



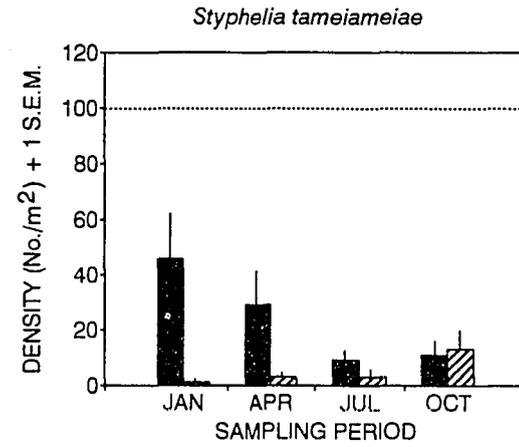
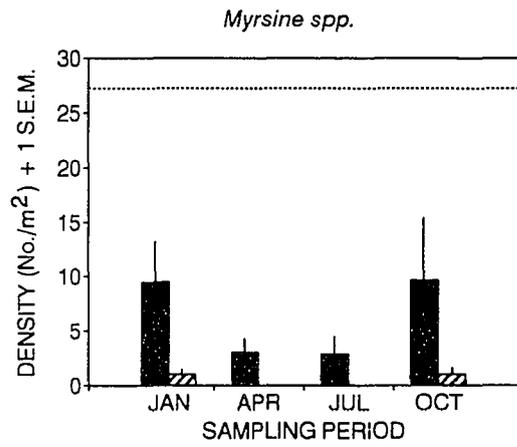
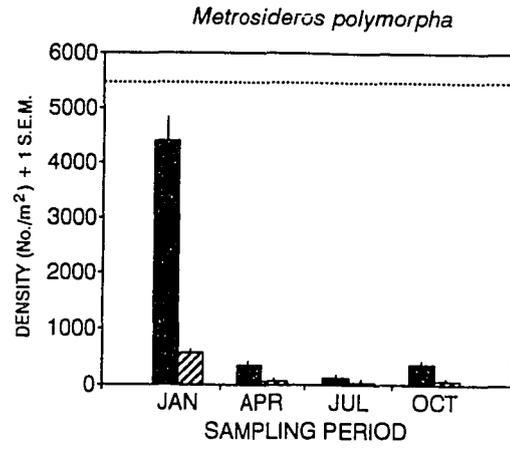
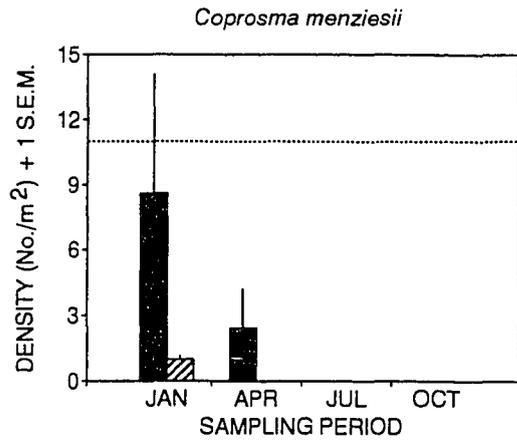
SEED RAIN
 SEED BANK

Figure 5.8. Seed population profiles for five shrubs that form persistent seed banks at Kealakomo. Values for seed rain represent seed rain total for a 12 week period ending in the month labelled on the abscissa. Values for seed bank represent the number of germinants emerging from soil samples collected at the end of the corresponding seed rain interval. The horizontal line represents total annual seed rain (from the four 12 week intervals plus one additional 4 week interval).



 SEED RAIN
 SEED BANK

Figure 5.9. Seed population profiles for four shrubs and trees that form pseudo-persistent (*M. polymorpha*) or transient seed banks at Kealakomo. Values for seed rain represent seed rain total for a 12 week period ending in the month labelled on the abscissa. Values for seed bank represent the number of germinants emerging from soil samples collected at the end of the corresponding seed rain interval. The horizontal line represents total annual seed rain (from the four 12 week intervals plus one additional 4 week interval).



SEED RAIN
 SEED BANK

CHAPTER 6: SYNTHESIS

In this section, the specific questions and hypotheses posed in the research proposal will be addressed briefly. Afterwards, brief summaries will discuss how the study meets the three major objectives posed in the research proposal.

Research questions and hypotheses

Q1. Are changes in the population structure of M. polymorpha along the chronosequence consistent with density-dependent mortality through self-thinning?

H1. Population basal area of M. polymorpha increases with lava flow age.

H2. Population density of M. polymorpha peaks early in succession, then declines as regeneration beneath the closed-canopied, older stands decreases.

Basal area of M. polymorpha tree populations increased with lava flow age. Population density of M. polymorpha trees peaked at 137 yr then declined. This combination of patterns is consistent with density-dependent mortality caused by self-thinning. The overall pattern of forest development is, however, more complex. Apparently, density-independent mortality through wind throw may open up the M. polymorpha canopy, allow

regeneration from seed, and disrupt formation of strict cohorts. Tree ferns may ultimately be the life form that closes the canopy and limits regeneration beneath a relatively broadly-aged overstory cohort, at least on lava flows \leq 300 years old.

Q2. Is colonization of the 1972 Kilauea lava flow limited by seed dispersal or seedling establishment?

H1. The density of seed rain of M. polymorpha on the 1972 flow decreases with increasing distance from the edge of the flow.

H2. The density of established M. polymorpha seedlings on the 1972 flow decreases with increasing distance from the edge of the flow, paralleling the density of M. polymorpha seed in the seed rain.

Seed rain decreased with distance from the edge of the flow, though the length of the tail of the dispersal curve suggests that moderate numbers of seeds ($\leq 20 \text{ m}^{-2} \text{ yr}^{-1}$) are dispersed for relatively long distances. Although seedling density was high near the margin of the flow, perhaps due to environmental edge effects, seedling density did not decrease in parallel with seed rain density across the flow. Therefore, at least across the first 250 m of the 1972 Kealakomo flow, colonization appeared to be limited by conditions for seedling

establishment rather than by availability of seeds in the seed rain. Uniform establishment of seedlings could be a first step leading toward cohort development in a M. polymorpha population.

Q3. What are the germination requirements of M. polymorpha seeds?

H1. Seeds require light for germination.

H2. Seeds can germinate over a broad range of temperatures.

Seeds of M. polymorpha germinate poorly in the dark, but relatively well under red, white, and far-red light. Seeds germinate well over a relatively broad range of temperatures. Overall, results of the germination experiments suggest that M. polymorpha seeds are able to germinate rapidly, immediately after dispersal, and under a wide range of environmental conditions.

Q4. How distinct are the ecological differences among the hypothetical "successionally differentiated" varieties of M. polymorpha?

H1. The varieties of M. polymorpha differ with respect to characteristics of population distribution and structure.

H2. The varieties of M. polymorpha differ with respect to germination characteristics.

There is a shift in dominance from pubescent to glabrous varieties of M. polymorpha as lava flow age increases. Seeds of the pubescent varieties of M. polymorpha germinate in higher numbers at high temperatures, and slightly faster under most conditions than do seeds of the glabrous varieties. These trends are consistent with the interpretation that the pubescent varieties are relatively better adapted to the relatively dry conditions associated with pioneer environments.

Q5. What types of seed bank syndromes are represented among species found in a native Hawaiian forest?

H1. The qualitative and quantitative composition of the seed rain and the seed bank vary seasonally.

The seed rain and seed bank both vary seasonally. The amount of seasonal variation in the seed rain and seed bank depends on the species in question. Seasonal variation in the seed rain is more common than variation in the seed bank. Alien species most commonly form persistent seed banks. Native species form persistent, pseudo-persistent, and transient seed banks.

Q6. What are the relationships among the seed rain, seed bank, and vegetation in a native Hawaiian forest?

H1. A given species currently represented in the seed rain, seed bank, or extant vegetation on a site may not be equally abundant in all three of these species pools.

Few species, if any, are equally abundant in all three species pools; most species are abundant in no more than one pool. The vegetation and seed rain are moderately similar to each other. There is relatively little similarity between the seed bank and either the seed rain or the vegetation.

Major objectives of the research

Objective 1. to describe the processes by which pioneer, Metrosideros polymorpha forests develop on lava flows in the montane rain forest zone on the island of Hawai'i.

The pattern of forest development along the chronosequence may be summarized as follows. Pubescent M. polymorpha colonizes first; as its population increases in density and biomass and begins to self-thin and suffer wind-throw, populations of other pioneer tree species, and then tree ferns, colonize and begin to develop. After 3000 yr, each of these groups is still present, and the

forest consists of an open, upper stratum dominated by glabrous M. polymorpha (which have replaced the pubescent individuals), an open, middle stratum consisting of Cheirodendron trigynum, Ilex anomala, and Myrsine lessertiana, and a dense, closed, lower stratum of Cibotium spp. tree ferns.

Objective 2. to determine what role seed ecology plays in maintaining the abundance of M. polymorpha in the Hawaiian environment.

Seed ecology very likely plays a major role in maintaining the abundance of M. polymorpha as in the Hawaiian environment. In summary, M. polymorpha seeds are: 1) produced in massive numbers; 2) produced year-round (though most are shed in the relatively cool, moist winter months, when conditions should be most favorable for germination and establishment); 3) dispersed over relatively long distances; 4) capable of germinating rapidly, immediately after dispersal; 5) capable of germinating under a wide range of temperature and light conditions (given sufficient moisture and oxygen). Thus, even though M. polymorpha does not form a persistent seed bank, its seeds are apparently everywhere, all the time, and always ready to germinate. Given that the chances of establishment for any individual seedling are very small,

and that seedlings and saplings are slow-growing and shade-intolerant, the opportunistic nature of the seeds may of great importance because it ensures that the environment is perpetually saturated with seeds/germinants.

Objective 3. to generate baseline data concerning seed rain and seed banks of plant species found in the Metrosideros forest.

At Kealakomo, many alien species formed relatively large, persistent seed banks. These included included many relatively small, shade-intolerant herbs and weakly-woody shrubs (e.g., Gnaphalium purpureum, Stachytarpheta urticifolia, and Rubus rosifolius). Two aliens in the seed bank (Andropogon virginicus and Myrica faya [the latter present at only low density]) have the potential to dominate and alter the ecosystem at Kealakomo.

A Few native species formed persistent seed banks (Dodonaea viscosa, Machaerina mariscoides, and Pipturus albidus); most others formed transient seed banks. Metrosideros polymorpha forms only a pseudo-persistent seed bank; its seeds apparently are present in the soil for only a short time following dispersal. In summary, alien species, by virtue of their abundance in the seed bank, would be likely to regenerate more strongly than

natives after a major disturbance at Kealakomo. Thus, the resulting vegetation would probably include a higher proportion of aliens than the present vegetation does.

APPENDIX A: EFFECTS OF PHYSICAL DISTURBANCE ON ARTIFICIAL
SEEDLINGS IN THE RAIN FOREST UNDERSTORY

An experiment was designed to determine the potential for physical disturbances to damage tree seedlings in the understory of Metrosideros/Cibotium montane rain forest on Mauna Loa. Methods were adopted from Clark and Clark (1989). Artificial seedlings were constructed from a 13-cm-long, 19 gauge, wire root stapled inside a 19.5-cm-long, 0.7 cm diam, stem made from a plastic, drinking straw. The top 5 cm of the stem was folded down and the tip stapled to a lower portion of the stem and the middle of another straw which represented branches. The final 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 (illustrated in Clark and Clark, 1989, p. 226).

Three hundred seedlings were inserted in the ground, in an upright position, at intervals of 2 m, along six transects in the Metrosideros/Cibotium rain forest in Ola'a Tract, in Hawaii Volcanoes National Park. An additional 300 seedlings were rooted on the upright stems of tree ferns found along, and within 1 m of, the transects containing the terrestrial seedlings. The transects were bisected by a fence such that half of the seedlings (both epiphytic and terrestrial) were placed in

a fenced enclosure lacking pigs, and the other half were placed on the opposite side of the fence, where low numbers of pigs were present (L. W. Cuddihy, personal communication). No seedlings were placed within 10 m of the fence. At ten, 5-6 week intervals (total = 52 weeks), each seedling was examined and classified into one of three categories: 1) undisturbed = undamaged and lacking a litter load large enough to bend the seedling; 2) touching litter = being burdened by plant litter to the extent that the seedling was bent; or 3) disturbed = having been bent so that the stem or branch was touching the ground, having been uprooted, or having disappeared. Seedlings classified as "disturbed" were considered to have been disturbed to a degree that probably would have caused significant damage to, or killed, a true plant seedling. For all seedlings that were touching litter or disturbed, the type(s) of litter and/or disturbance were identified wherever possible. Where the cause of the disturbance was not identifiable, the cause was classified as unknown.

Data were analyzed using chi-square analysis of contingency tables based on the number of seedlings disturbed by a particular agent vs. the number of seedlings not disturbed by that agent (including both undisturbed seedlings and seedlings disturbed by other agents). For the purpose of this analysis, seedlings classified as "touching litter" were lumped with

"undisturbed" seedlings. More seedlings were disturbed by Cibotium litter than by all other causes combined ($P < 0.05$; Table A1.1). Terrestrial seedlings were more likely than epiphytic seedlings to be disturbed by Cibotium litter ($P < 0.05$), all forms of litter combined ($P < 0.05$), or all causes combined ($P < 0.05$). Terrestrially-established seedlings were more likely to be disturbed in the presence of pigs than in the absence of pigs ($P < 0.05$). The numbers of seedlings (terrestrial, epiphytic, and combined) damaged by litter (Cibotium, other, and combined) were not significantly different in the presence vs. absence of pigs ($P > 0.05$).

The results of the study indicate that, annually, the senescing fronds of Cibotium spp. tree ferns may damage 14-15% of the tree seedlings established on the ground beneath their canopies, at least in forests where tree fern density is high. Surprisingly, pigs and plant litter from species other than tree ferns accounted for relatively few of the disturbances for which causes could be identified. However, the fact that most of the disturbances classified as unknown occurred among seedlings established terrestrially on the side with pigs present may mean that the number of disturbances attributed to pigs was underestimated.

Seedlings of Metrosideros polymorpha are very slow-growing, and require one year to reach a height of 10 cm

when grown under greenhouse conditions (Walker and Vitousek 1991). It is therefore likely that, for the first several years after germination, seedlings in the forest understory would remain small enough to be prone to damage from the 5-7 m long fronds of the Cibotium tree ferns. In fact, it is not unusual to see 2-m-tall saplings M. polymorpha pinned to the ground by the senescent fronds of the tree ferns. If tree fern litter caused mortality among M. polymorpha seedlings to occur at a rate of 15%/yr for just four years, half of a cohort of seedlings would be lost from this cause alone. If, as in the case of terrestrial seedlings in the presence of pigs, mortality from all causes occurs at a rate of 31.3%/yr, half of a seedling cohort would be lost in just two years. Results of this study indicate that physical disturbance, both by senescent fronds of tree ferns and by other agents, is a potentially significant source of mortality for tree seedlings growing in the understory of the Metrosideros/Cibotium rain forest. Thus, physical disturbance, along with shading (c.f. Burton and Mueller-Dombois, 1984) may both be involved in the displacement of M. polymorpha by Cibotium spp. in some situations (c.f. "displacement dieback" in Mueller-Dombois et al. 1980).

Table A.1. Numbers of artificial seedlings disturbed by various physical agents in Metrosideros/Cibotium rain forest. Treatments = terrestrial/epiphytic establishment x pigs absent/present; n = 150 seedlings/treatment; causes of disturbance: CL = Cibotium litter; OL = other litter; U = uprooted; M = missing; H = human; ? = unknown.

WEEK	TERRESTRIAL SEEDLINGS								EPIPHYTIC SEEDLINGS				
	- PIGS		+ PIGS						- PIGS		+ PIGS		
	CL	OL	CL	OL	U	M	H	?	CL	?	CL	OL	?
5	1	0	1	0	0	0	0	0	2	2	1	1	0
10	2	0	3	0	0	0	0	1	1	0	1	0	0
15	2	0	1	0	3	0	0	0	3	3	0	0	0
21	0	1	4	0	1	0	6	2	1	1	0	0	0
26	1	1	3	0	0	0	0	1	1	1	2	1	1
31	3	2	1	0	1	0	0	2	0	0	4	0	0
36	2	0	1	1	1	0	0	1	0	0	2	0	0
41	4	0	1	0	1	0	0	0	2	0	3.5	0.5	0
47	3	0	0	1	0	0	0	0	0	0	0	0	0
52	5	3	5.5	0.5	0	2	0	2	0	0	0	0	0
SUB-TOTAL	23	7	20.5	2.5	7	2	6	9	10	7	13.5	2.5	1
TOTAL	30		47						17		17		

APPENDIX B: LIST OF SEED PLANT SPECIES AT KEALAKOMO

Table B.1. Seed plant species in the seed rain, seed bank, or vegetation, or in the vegetation within 100 m of the area bounded by the sampling transects, at Kealakomo.

Asterisks mark the 42 species that were sampled in the vegetation, seed rain, or seed bank, and were identifiable or able to be sampled (where present) in all three pools; these 42 species were used in the data analyses. Taxonomy follows Wagner et al. (1990).

TAXON	STATUS ¹	LIFE FORM	ABUNDANCE		IN:
			SEED RAIN ²	SEED BANK ³	VEGETATION ⁴
DICOTS					
APOCYNACEAE					
<u>Alyxia oliviformis</u> *	E	LIANA	1.2	0.0	3.5
AQUIFOLIACEAE					
<u>Ilex anomala</u> *	I	TREE	0.2	0.0	P
ASTERACEAE					
<u>Conyza bonariensis</u> *	A	FORB	0.0	0.3	0.0
<u>Dubautia scabra</u> *	E	SHRUB	0.2	0.0	N
<u>Erechtites</u>					
<u>valerianifolia</u> *	A	FORB	1.8	7.5	0.0
<u>Gnaphalium purpureum</u> *	A	FORB	0.0	132.3	0.0
<u>Pluchea symphytifolia</u> *	A	SHRUB	0.4	19.5	N
<u>Sonchus oleraceus</u> *	A	FORB	0.0	0.3	0.0
<u>Youngia japonica</u> *	A	FORB	0.0	17.0	0.0
BRASSICACEAE					
<u>Cardamine flexuosa</u> *	A	FORB	0.0	0.5	0.0
BUDDLEIACEAE					
<u>Buddleia asiatica</u>	A	SHRUB	0.0	0.0	N

Table B.1. (Continued) Seed plants sampled at Kealakomo.

TAXON	STATUS ¹	LIFE FORM	ABUNDANCE		IN:
			SEED RAIN ²	SEED BANK ³	VEGETATION ⁴
CONVOLVULACEAE					
<u>Ipomoea indica</u>	I	LIANA	0.0	0.0	N
EBENACEAE					
<u>Diospyros sandwicensis</u> *	E	TREE	0.0	0.0	1.0
EPACRIDACEAE					
<u>Styphelia tameiameia</u> *	I	SHRUB	100.2	5.0	13.0
ERICACEAE					
<u>Vaccinium reticulatum</u>	E	SHRUB	0.0	0.0	N
FABACEAE					
<u>Chamaecrista nictitans</u>	A	FORB	0.0	0.0	N
<u>Indigofera suffruticosa</u>	A	SHRUB	0.0	0.0	N
MALVACEAE					
<u>Sida fallax</u>	I	SHRUB	0.0	0.0	N
MENISPERMACEAE					
<u>Cocculus trilobus</u> *	I	LIANA	0.0	0.3	2.0
MYRICACEAE					
<u>Myrica faya</u> *	A	TREE	0.0	3.3	0.5
MYRSINACEAE					
<u>Myrsine</u>					
<u>lessertiana</u>					
<u>sandwicensis</u>	}*	E	27.2	0.5	13.5
MYRTACEAE					
<u>Metrosideros polymorpha</u> *	E	TREE	5461.0	179.5	53.5
<u>Psidium cattleianum</u> *	A	TREE	0.6	0.0	1.0
<u>Psidium guajava</u>	A	TREE	0.0	0.0	N
OXALIDACEAE					
<u>Oxalis corniculata</u> *	A	FORB	0.0	3.0	0.0
PITTOSPORACEAE					
<u>Pittosporum</u>					
<u>confertiflorum</u> *	E	TREE	0.0	0.0	1.5

Table B.1. (Continued) Seed plants sampled at Kealakomo.

TAXON	STATUS ¹	LIFE FORM	ABUNDANCE		IN:
			SEED RAIN ²	SEED BANK ³	VEGE- TATION ⁴
POLYGONACEAE					
<u>Rumex skottsbergii</u>	E	SHRUB	0.0	0.0	N
ROSACEAE					
<u>Fragaria vesca</u> *	A	FORB	0.0	1.5	0.0
<u>Osteomeles</u>					
<u>anthyllidifolia</u> *	I	SHRUB	0.0	0.0	3.5
<u>Rubus rosifolius</u> *	A	SHRUB	1.2	146.5	0.0
RUBIACEAE					
<u>Canthium odoratum</u>	I	TREE	0.0	0.0	P
<u>Coprosma menziesii</u> *	E	SHRUB	11.0	0.3	1.5
RUTACEAE					
<u>Pelea radiata</u> *	E	SHRUB	0.2	0.0	2.5
SANTALACEAE					
<u>Santalum paniculatum</u> *	E	SHRUB	0.0	0.0	0.5
SAPINDACEAE					
<u>Dodonaea viscosa</u> *	I	SHRUB	25.2	23.3	14.5
SOLANACEAE					
<u>Physalis peruviana</u> *	A	FORB	0.0	0.3	0.0
<u>Solanum americanum</u> *	I	FORB	0.0	1.8	0.0
THYMELAEACEAE					
<u>Wikstroemia</u>					
<u>phillyreifolia</u>					
<u>sandwicensis</u>	}*	SHRUB	1.2	0.0	4.5
URTICACEAE					
<u>Pipturus albidus</u> *	E	SHRUB	1.2	105.0	P
VERBENACEAE					
<u>Lantana camara</u>	A	SHRUB	0.0	0.0	N
<u>Stachytarpheta</u>					
<u>urticifolia</u> *	A	SHRUB	5.0	145.0	P

Table B.1. (Continued) Seed plants sampled at Kealakomo.

TAXON	STATUS ¹	LIFE FORM	ABUNDANCE IN:		
			SEED RAIN ²	SEED BANK ³	VEGETATION ⁴
MONOCOTS					
AGAVACEAE					
<u>Cordyline fruticosa</u>	A	SHRUB	0.0	0.0	P
CYPERACEAE					
<u>Bulbostylis capillaris</u> *	A	SEDGE	0.0	4.3	0.0
<u>Machaerina mariscoides</u> *	E	SEDGE	2.6	19.5	1.5
LILLIACEAE					
<u>Dianella sandwicensis</u> *	I	FORB	0.0	0.0	1.5
ORCHIDACEAE					
<u>Arundina graminifolia</u>	A	FORB	ND	0.0	P
<u>Phaius tankarvilleae</u>	A	FORB	ND	0.0	P
<u>Spathoglottis plicata</u>	A	FORB	ND	0.0	P
POACEAE					
<u>Andropogon virginicus</u> *	A	GRASS	39.2	109.0	4.0
<u>Ehrharta stipoides</u> *	A	GRASS	1.2	0.0	0.0
<u>Isachne distichophylla</u> *	E	GRASS	0.0	0.0	1.0
<u>Oplismenus hirtellus</u>	A	GRASS	ND	24.5	4.5
<u>Paspalum conjugatum</u> *	A	GRASS	22.6	83.3	0.5
<u>Paspalum scrobiculatum</u> *	A	GRASS	5.2	9.3	0.5
<u>Schizachyrium condensatum</u> *	A	GRASS	0.2	0.3	P
<u>Setaria gracilis</u> *	A	GRASS	4.6	4.8	P
<u>Sporobolus africanus</u> *	A	GRASS	0.0	1.3	0.0
UNKNOWN					
unidentified sedges	?	SEDGE	ND	41.0	3.5
all others	?	?	5.2	15.5	0.0

¹A = alien, E = endemic, I = indigenous, ? = unknown.

²Numbers represent annual seed rain (seeds/m²); ND = no data, for cases where a species grew within the site, but was not tall enough to drop seeds in the seed traps, and for orchids, whose seeds were too small to identify.

³Numbers represent mean density of seedlings in the seed bank (seedlings/m²), based on four quarterly seed bank samples.

⁴Numbers represent absolute cover (as a percent of points sampled); N = a species present in the in the vegetation outside, but within 100 m of, the area bounded by the sampling transects. P = a species present in the vegetation on the site, but not sampled in the seed rain, seed bank, or vegetation.

LITERATURE CITED

- Ahmed, M., and J. Ogden. 1987. Population dynamics of the emergent conifer Agathis australis (D. Don.) Lindl. (kauri) in New Zealand I: population structures and tree growth rates in mature stands. *New Zealand Journal of Botany* 25: 217-229.
- Allen, R. B. 1987a. Ecology of Nothofagus menziesii in the Catlins Ecological Region, southeast Otago, New Zealand: (I) seed production, viability, and dispersal. *New Zealand Journal of Botany* 25: 5-10.
- . 1987b. Ecology of Nothofagus menziesii in the Catlins Ecological Region, southeast Otago, New Zealand: (II) Seedling establishment. *New Zealand Journal of Botany* 25: 11-16.
- Atkinson, I. A. E. 1969. Rates of ecosystem development on some Hawaiian lava flows. Ph.D. Dissertation, University of Hawaii, Honolulu.
- . 1970. Successional trends in the coastal and lowland forest of Mauna Loa and Kilauea volcanoes, Hawaii. *Pacific Science* 24: 387-400.
- Augspurger, C. K. 1986. Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. *American Journal of Botany* 73: 353-363.
- . 1988. Mass allocation, moisture content, and dispersal capacity of wind-dispersed tropical diaspores. *New Phytologist* 108: 357-368.
- Babb, T. A., and L. C. Bliss. 1974. Effects of disturbance on Arctic vegetation in the Queen Elizabeth Islands. *Journal of Applied Ecology* 11: 549-562.
- Baker, H. G. 1989. Some aspects of the natural history of seed banks. pp. 9-21 In: M. A. Leck, V. T. Parker, and R. L. Simpson [eds.], *Ecology of soil seed banks*. Academic Press, Inc., New York.
- Balakrishnan, N., and D. Mueller-Dombois. 1983. Nutrient studies in relation to habitat types and canopy dieback in the montane rain forest ecosystem, island of Hawaii. *Pacific Science* 37: 339-359.

- Becker, R. E. 1976. The phytosociological position of tree ferns (Cibotium spp.) in the montane rain forests on the island of Hawaii. Ph.D. Dissertation, University of Hawaii, Honolulu.
- Benzing, D. H. 1990. Vascular Epiphytes. Cambridge University Press, New York.
- Black, J. N., and G. N. Wilkinson. 1963. The role of time of emergence in determining the growth of individual plants in swards of subterranean clover (Trifolium subterraneum L.) Australian Journal of Agricultural Research 14: 628-638.
- Bond, W. J. 1988. Proteas as 'tumbleseeds': wind dispersal through air and over soil. S. Afr. J. Bot. 54:455-460.
- Bramwell, D. 1979. Plants and Islands. Academic Press, Inc., London, England.
- Burton, P. J. 1982. The effect of temperature and light on Metrosideros polymorpha seed germination. Pacific Science 36: 229-240.
- _____, and D. Mueller-Dombois. 1984. Response of Metrosideros polymorpha seedlings to experimental canopy opening. Ecology 65: 779-791.
- Burrows, F. M. 1986. The aerial motion of seeds, fruits, spores and pollen. pp. 1-47. In: D. R. Murray [ed.], Seed Dispersal. Academic Press, Inc., Orlando.
- Campbell, R. C. 1989. Statistics for biologists. Cambridge University Press, Cambridge, England.
- Cannell, M. G. R., P. Rothery, and E. D. Ford. 1984. Competition within stands of Picea sitchensis and Pinus contorta. Journal of Ecology 53: 349-362.
- Carlquist, S. 1974. Island Biology. Columbia University Press, New York.
- _____. 1980. Hawaii: a natural history. Pacific Tropical Botanical Garden, Lawai.
- Cheke, A. S., W. Nanakorn, and C. Yankoses. 1979. Dormancy and dispersal of secondary forest species under the canopy of a primary tropical rain forest in Northern Thailand. Biotropica 11: 88-95.

- Clark, D. B., and D. A. Clark. 1989. The role of physical damage in the mortality regime of a neotropical rain forest. *Oikos* 55: 225-230.
- Clarkson, B. D. 1990. A review of vegetation development following recent (<450 years) volcanic disturbance in New Zealand. *New Zealand Journal of Ecology* 14: 59-71.
- Clements, F. E. 1916. *Plant succession: an analysis of the development of vegetation*. Carnegie Inst. Wash. Publ. 242. Carnegie Institution of Washington, Washington, D. C.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Amer. Nat.* 111: 1119-1144.
- Corn, C. 1972. Seed dispersal methods in Hawaiian "Metrosideros". In J. A. Behnke [ed.], *Challenging biological problems: directions toward their solution*, 422-435. Oxford University Press, New York.
- _____, and W. M. Hiesey. 1973. Altitudinal variation in Hawaiian Metrosideros. *American Journal of Botany* 60: 991-1002.
- _____. 1979. Variation in Hawaiian Metrosideros. Ph.D. Dissertation. University of Hawaii, Honolulu.
- Cremer, K. W. 1965. Dissemination of seed from Eucalyptus regnans. *Australian Forestry* 30: 33-37.
- _____. 1977. Distance of seed dispersal in eucalypts estimated from seed weights. *Australian Forestry Research* 7: 225-228.
- Crocker, R. L., and J. Major. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. *Journal of Ecology* 43: 427-448.
- Darwin, C. 1859. *On the origin of species by means of natural selection*. John Murray, London, England.
- Dawson, J. W. 1970. Pacific capsular Myrtaceae 2. The Metrosideros complex: M. collina group. *Blumea* 28: 441-445.

- _____, and R. L. Stemmermann. 1990. Metrosideros Banks ex. Gaertn. In: W. L. Wagner, D. H. Herbst, and S. H. Sohmer [eds.], Manual of the flowering plants of Hawaii. Bernice P. Bishop Museum, Honolulu.
- de Foresta, H., and M. Prevost. 1986. Vegetation pionniere et graines du sol en foret Guyanaise. Biotropica 18: 279-286.
- Debussche, M., J. Escarre, and J. Lepart. 1982. Ornithochory and plant succession in Mediterranean abandoned orchards. Vegetatio 48: 255-266.
- _____, J. Lepart, and J. Molina. 1985. La dissemination des plantes a fruits charnus par les oiseaux: role de la structure de la vegetation et impact sur la succession en region mediterraneenne. Acta Oecologica; Oecologia Generalis 6: 65-80.
- Doty, M. S. 1967. Contrast between the pioneer populating process on land and shore. Bulletin of the Southern California Academy of Sciences 66: 175-194.
- Drake, D. R., and I. A. Ungar, 1989. effects of salinity, nitrogen, and population density on the survival, growth, and reproduction of Atriplex triangularis (Chenopodiaceae). American Journal of Botany 76: 1125-1135.
- Drury, W. H., and I. C. T. Nisbet. 1973. Succession. Journal of the Arnold Arboretum 54: 331-368.
- Eggler, W. 1971. Quantitative studies of vegetation on sixteen young lava flows on the island of Hawaii. Tropical Ecology 12: 66-100.
- Egler, F. E. 1954. Vegetation science concepts. 1. initial floristic composition: a factor in old-field vegetation development. Vegetatio 4:412-417.
- Enright, N. 1985. Existence of a soil seed bank under rain forest in New Guinea. Australian Journal of Ecology 10: 67-71.
- Ewel, J., C. Berish, B. Brown, N. Price, and J. Raich. 1981. Slash and burn impacts on a Costa Rican wet forest site. Ecology 62: 816-829.
- Fenner, M. 1980. Germination tests on thirty-two East African weed species. Weed Research 20: 135-138.

- _____. 1985. Seed Ecology. Chapman and Hall, New York.
- _____. 1987. Seed characteristics in relation to succession. pp. 103-114 In: A. J. Gray, M. J. Crawley, and P. J. Edwards [eds.], Colonization, succession, and stability. Blackwell Scientific Publications, Oxford, England.
- Finegan, B. 1984. Forest succession. *Nature* 312: 109-114.
- Forbes, C. N. 1912. Preliminary observations concerning the plant invasion on some of the lava flows of Mauna Loa, Hawaii. *Occasional Papers of the Bernice P. Bishop Museum* 5:15-23.
- Ford, E. D. 1975. Competition and stand structure in some even-aged plant monocultures. *Ecology* 63: 311-333.
- Fosberg, F. R. 1967. Observations on vegetation patterns and dynamics on Hawaiian and Galapageian volcanoes. *Micronesica* 3: 129-134.
- Frankland, B., and R. Taylorson. 1983. Light control of seed germination. pp.428-456. In: W. Shropshire Jr. and H. Mohr [Eds.], *Photomorphogenesis*. Springer-Verlag, New York.
- Friend, D. J. 1980. Effect of different photon flux densities (PAR) on seedling growth and morphology of *Metrosideros collina* (Forst.) Gray. *Pacific Science* 34: 93-100.
- Gagné, W. C., and L. W. Cuddihy. 1990. Vegetation. pp. 45-114. In: W. L. Wagner, D. R. Herbst, and S. H. Sohmer [eds.], *Manual of the flowering plants of Hawaii*. University of Hawaii Press and Bishop Museum, Honolulu.
- Garwood, N. C. 1983. Seed germination in a seasonal tropical forest in Panama: a community study. *Ecological Monographs* 53: 159-181.
- _____. 1989. Tropical soil seed banks: a review. pp. 149-210. In: M. A. Leck, V. T. Parker, and R. L. Simpson [eds.], *Ecology of soil seed banks*. Academic Press, Inc., New York.
- Gentry, A. H. 1982. Patterns of neotropical species diversity. *Ecol. Biol.* 15: 1-84.

- Giambelluca, T. W., M. A. Nullet, and T. A. Schroeder. 1986. Rainfall atlas of Hawai'i. State of Hawaii, Department of Land and Natural Resources, Division of Water and Land Development, Honolulu.
- Gleason, H. A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* 53: 7-26.
- _____. 1927. Further views on the succession-concept. *Ecology* 8: 299-326.
- _____. 1939. The individualistic concept of the plant association. *American Midland Naturalist* 21: 92-110.
- Grubb, P. J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Reviews of the Cambridge Philosophical Society* 52: 107-145.
- _____. 1986. The ecology of establishment. pp. 83-97 *In* A. D. Bradshaw, D. A. Goode, and E. Thorp [eds.], *Ecology and landscape design*. Blackwell Scientific Publications, Oxford, England.
- Guevara, S., and A. Gomez-Pompa. 1972. Seeds from surface soils in a tropical region of Veracruz, Mexico. *Journal of the Arnold Arboretum* 53: 312-335.
- Guppy, H. B. 1906. *Observations of a naturalist in the Pacific between 1896 and 1899*. Macmillan and Co., London, England.
- Hall, J. B., and M. D. Swaine. 1980. Seed stocks in Ghanaian forest soils. *Biotropica* 12: 256-263.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, London, England.
- _____, and M. Obeid. 1967. Influence of seed size and depth of sowing on the establishment and growth of varieties of fiber and oil seed flax. *Crop Science* 7: 527-532.
- _____, J. T. Williams, and G. R. Sagar. 1965. The behaviour of seeds in soil. I. The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. *Journal of ecology* 53: 273-286.

- Heath, J. P. 1967. Primary conifer succession, Lassen Volcanic National Park. *Ecology* 48: 270-275.
- Hobbs, R. J. 1989. The nature and effects of disturbance relative to invasions. pp. 389-405 *In* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson [eds.], *Biological invasions: a global perspective*. John Wiley and Sons, Chichester, England.
- Hodgkinson, K. C., and R. E. Oxley. 1990. Influence of fire and edaphic factors on germination of the arid zone shrubs *Acacia aneura*, *Cassia nemophila* and *Dodonaea viscosa*. *Australian Journal of Ecology* 38: 269-279.
- Hopkins, M. S., and A. W. Graham. 1983. The species composition of soil seed banks beneath lowland tropical rainforests in North Queensland, Australia. *Biotropica* 15: 90-99.
- _____, and _____. 1984. Viable soil seed banks in disturbed lowland tropical rainforest sites in North Queensland. *Australian Journal of Ecology* 9: 71-79.
- _____, and _____. 1987. The viability of seeds of rainforest species after experimental soil burials under tropical wet lowland forest in north-eastern Australia. *Australian Journal of Ecology* 12: 97-108.
- _____, J. G. Tracey, and A. W. Graham. 1990. The size and composition of soil seed-banks in remnant patches of three structural rainforest types in North Queensland. *Australian Journal of Ecology* 15: 43-50.
- Horn, H. S., 1974. The ecology of secondary succession. *Annual Review of Ecology and Systematics* 5: 25-37.
- Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201-228.
- Hughes, F., P. M. Vitousek, and T. Tunison. 1991. Alien grass invasion and fire in the seasonal submontane zone of Hawai'i. *Ecology* 72: 743-746.
- Jackson, T. A. 1971. A study of the ecology of pioneer lichens, mosses, and algae on recent Hawaiian lava flows. *Pacific Science* 25: 22-32.

- _____, and W. D. Keller. 1970. A comparative study of the role of lichens and "inorganic" processes in the chemical weathering of recent Hawaiian lava flows. *American Journal of Science* 269:446-466.
- Jacobi, J. D. 1983. Metrosideros dieback in Hawai'i: a comparison of adjacent dieback and non-dieback rain forest stands. *New Zealand Journal of Ecology* 6: 79-97.
- _____, 1989. Vegetation maps of the upland plant communities on the islands of Hawai'i, Maui, Moloka'i, and Lana'i. University of Hawaii Cooperative National Park Resources Studies Unit Technical Report 61.
- _____, G. Gerrish, and D. Mueller-Dombois, 1983. 'Ōhi'a dieback in Hawai'i: vegetation changes in permanent plots. *Pacific Science* 37: 327-359.
- _____, _____, _____, and L. Whiteaker. 1988. Stand-level dieback and regeneration in the montane rain forest of Hawaii. *GeoJournal* 17: 193-200.
- Johnstone, I. M. 1986. Plant invasion windows: a time-based classification of invasion potential. *Biological Reviews of the Cambridge Philosophical Society* 61: 369-394.
- June, S. R., and J. Ogden. 1975. Studies on the vegetation of Mount Colenso, New Zealand. 3. The population dynamics of red beech seedlings. *Proceedings of the New Zealand Ecological Society* 22: 61-66.
- Kellman, M. C. 1970. The influence of accessibility on the composition of vegetation. *Professional Geographer* 22: 1-4.
- Kitayama, K., and D. Mueller-Dombois. 1992. Vegetation of the wet windward slope of Haleakala, Maui, Hawaii. *Pacific Science* 46: 197-220.
- Koller, D. 1972. The survival value of germination-regulating mechanisms in the field. *Herbage Abstracts* 34: 1-7.
- Lamont, B. 1985. Dispersal of the winged fruits of Nuytsia floribunda (Loranthaceae). *Australian Journal of Ecology* 10: 187-193.

- Lawton, R. O., and F. E. Putz. 1988. Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology* 69: 764-777.
- Little, T. M., and F. J. Hills. 1978. *Agricultural experimentation*. John Wiley and Sons, New York.
- Lockwood, J. P., and P. W. Lipman. 1980. Recovery of datable charcoal beneath young lavas: lessons from Hawaii. *Bulletin Volcanologique* 43: 609-615.
- _____, P. W. Lipman, L. D. Peterson, and F. R. Warshauer. 1988. Generalized ages of surface lava flows of Mauna Loa Volcano, Hawaii. U. S. Geological Survey Miscellaneous Investigations Series Map I-1908. U. S. Government Printing Office, Washington, D. C.
- Loope, L. L., and D. Mueller-Dombois 1989. Characteristics of invaded islands, with special reference to Hawaii. pp. 257-280 *In* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson [eds.], *Biological invasions: a global perspective*. John Wiley and Sons, Chichester, England.
- MacCaughey, V. 1917. Vegetation of Hawaiian lava flows. *Botanical Gazette* 64: 386-420.
- Macdonald, G. A., A. T. Abbot, and F. L. Peterson. 1986. *Volcanoes in the sea: the geology of Hawaii*. University of Hawaii Press, Honolulu.
- McDonnell, M. J., and E. W. Stiles. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* 56: 109-116.
- McIntosh, R. P. 1985. *The background of ecology: Concept and theory*. Cambridge University Press, Cambridge, England.
- McQuilkin, W. E. 1940. The natural establishment of pine in abandoned fields in the Piedmont Plateau region. *Ecology* 21: 135-147.
- Mark, A. F., K. J. M. Dickinson, and A. J. Fife. Forest succession on landslides in the Fiord Ecological Region, Southwestern New Zealand. *New Zealand Journal of Botany* 27: 369-390.

- Miles, J. 1979. Vegetation dynamics. Chapman and Hall, London, England.
- _____. 1987. Vegetation succession: past and present perceptions. pp. 1-29 In A. J. Gray, M. J. Crawley, and P. J. Edwards [eds.], Colonization, succession and stability. Blackwell Scientific Publications, Oxford, England.
- Miller, H. A. 1960. Remarks on the succession of bryophytes on Hawaiian lava flows. Pacific Science 14:246-247.
- Mohler, C. L., P. L. Marks, and D. G. Sprugel. 1978. Stand structure and allometry of trees during self-thinning of pure stands. Journal of Ecology 66: 599-614.
- Mooney, H. A., and F. Drake [eds.]. 1986. The ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York.
- Mortimer, A. M. 1987. Contributions of plant population dynamics to understanding early succession. pp. 57-80. In: A. J. Gray, M. J. Crawley, and P. J. Edwards [eds.], Colonization, succession, and stability. Blackwell Scientific Publications. Oxford, England.
- Mueller-Dombois, D. 1981. Fire in tropical ecosystems. pp. 137-176 In H. A. Mooney, T. M. Bonnicksen, N. L. Christensen, J. E. Lotan, and W. A. Reiners [eds.], Fire regimes and ecosystem properties. USDA Forest Service General Technical Report WO-26.
- _____. 1983. Canopy dieback and successional processes in Pacific forests. Pacific Science 37: 317-325.
- _____. 1986. Perspectives for an etiology of stand-level dieback. Annual Review of Ecology and Systematics 17: 221-243.
- _____. 1987a. Forest dynamics in Hawaii. Trends in Ecology and Evolution 2:216-220.
- _____. 1987b. Natural dieback in forests. Bioscience 37: 575-583.
- _____. 1992. Distributional dynamics in the Hawaiian vegetation. Pacific Science 46: 221-231.
- _____, and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York.

- _____, and V. J. Krajina. 1968. Comparison of east-flank vegetations on Mauna Loa and Mauna Kea, Hawaii. Proceedings of a Symposium on Recent Advances in Tropical Ecology 2: 508-520.
- _____, and L. L. Loope. 1990. Some unique ecological aspects of oceanic island ecosystems. Monographs in Systematic Botany of the Missouri Botanical Garden. 32: 21-27.
- _____, K. W. Bridges, and H. L. Carson [eds.], 1981. Island ecosystems: biological organization in selected Hawaiian communities. Hutchinson Ross Publishing Co., Stroudsburg.
- _____, J. D. Jacobi, R. G. Cooray, and N. Balakrishnan. 1980. 'Ōhi'a rain forest study: Ecological investigations of the 'Ōhi'a dieback problem in Hawaii. Hawaii Agricultural Experiment Station Misc. Pub. No. 183. College of Tropical Agriculture and Human Resources, University of Hawaii, Honolulu.
- Muller, C. H. 1952. Plant succession in arctic heath and tundra in northern Scandinavia. Bulletin of the Torrey Botanical Club 79: 296-309.
- National Oceanic and Atmospheric Administration. 1990. Local climatological data: annual summary with comparative data, Hilo, Hawaii. National Climatic Data Center, Asheville.
- _____. 1991. Local climatological data: annual summary with comparative data, Hilo, Hawaii. National Climatic Data Center, Asheville.
- Ng, F. S. P. 1980. Germination ecology of Malaysian woody plants. Malaysian Forester 43: 406-437.
- Noble, I. R., and R. O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43: 5-21.
- Norton, D. A., 1983. Population dynamics of Libocedrus bidwilli forests in the Cropp River Valley, Westland, New Zealand. New Zealand Journal of Botany 21: 127-134.

- Ogden, J. 1971. Studies on the vegetation of Mount Colenso, New Zealand. 2. Population dynamics of red beech. Proceedings of the New Zealand Ecological Society 18: 66-75.
- _____. 1985. An introduction to plant demography with special reference to New Zealand trees. New Zealand Journal of Botany 23: 751-772.
- _____, G. M. Wardle, and M. Ahmed. 1987. Population dynamics of the emergent conifer Agathis australis (D. Don.) Lindl. (kauri) in New Zealand II: Seedling population sizes and gap-phase regeneration. New Zealand Journal of Botany 25: 231-242.
- Olson, J. S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. Botanical Gazette 119: 125-170.
- Olsson, E. G. 1987. Effects of dispersal mechanisms on the initial pattern of old-field forest succession. Acta Oecologica; Oecologia generalis 8: 379-390.
- Orozco-Segovia, A., and C. Vázquez-Yanes. 1989. Light effect on germination in Piper L. Acta Oecologica, Oecologia Plantarum 10: 123-146.
- Peet, R. K., and N. L. Christensen. 1980. Succession: a population process. Vegetatio 43: 131-140.
- _____, and _____. 1987. Competition and tree death. Bioscience 37: 586-595.
- Porter, J. R. 1972. The growth and phenology of Metrosideros in Hawaii. Ph.D. Dissertation, University of Hawaii, Honolulu.
- Price, M. V., and S. H. Jenkins. 1986. Rodents as seed consumers and dispersers, pp. 191-235 In D. R. Murray [ed.] Seed dispersal. Academic Press, Sydney, Australia.
- Purata, S. E. 1986. Floristic and structural changes during old-field succession in the Mexican tropics in relation to site history and species availability. Journal of Tropical Ecology 2: 257-276.
- Putz, F. E. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. Ecology 64: 1069-1074.

- Rejmánek, M. 1989. Invasibility of plant communities. pp. 369-388 In J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson [eds.], *Biological invasions: a global perspective*. John Wiley and Sons, Chichester, England.
- Rock, J. F. 1913. *The indigenous trees of the Hawaiian Islands*. 1974 reprint by Charles, E. Tuttle Co., Inc. Rutland.
- SAS INSTITUTE, INC. 1985. *SAS user's guide: statistics, version 5 edition*. SAS Institute, Inc., Cary.
- Saulei, S. M., and M. D. Swaine. 1988. Rain forest seed dynamics during succession at Gogol, Papua New Guinea. *Journal of Ecology* 76: 1133-1152.
- Shreve, F. 1942. The desert vegetation of North America. *Botanical Review* 8: 195-246.
- Simon, C. 1987. Hawaiian Evolutionary Biology: an introduction. *Trends in Ecology and Evolution* 2: 175-178.
- Silvertown, J. W. 1980. Leaf-canopy induced seed dormancy in a grassland flora. *New Phytologist* 85: 109-118.
- _____, 1987. *Introduction to plant population ecology*. Longman Scientific and Technical and John Wiley and Sons, Inc., New York.
- Simpson, R. L., M. A. Leck, and V. T. Parker. 1989. Seed banks: general concepts and methodological issues. pp. 3-8 In: M. A. Leck, V. T. Parker, and R. L. Simpson [eds.], *Ecology of soil seed banks*. Academic Press, Inc., New York.
- Skottsberg, C. 1941. Plant succession on recent lava flows in the island of Hawaii. *Göteborgs Kungl. Vetenskaps- och Vitterhets-samhälles Handlingar Sjätte följdén, ser. B., Band 1, no. 8*.
- Smathers, G. A., and D. Mueller-Dombois. 1974. Invasion and recovery of vegetation after a volcanic eruption in Hawaii. *National Park Service Scientific Monograph Series No. 5*.

- Smith, C. W. 1985. The impact of alien plants on Hawai'i's native biota. pp. 180-250. In: C. P. Stone and J. M. Scott, [eds.], Hawai'i's terrestrial ecosystems: preservation and management. Cooperative National Park Resources Studies Unit, University of Hawaii, Honolulu.
- _____, and J. T. Tunison. 1992. Fire and alien plants in Hawai'i: research and management implications for native ecosystems. pp. 394-408 In C. P. Stone, C. W. Smith, and J. T. Tunison [eds.] Alien Plant Invasions in native ecosystems of Hawai'i: management and research. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu.
- Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15: 353-391.
- Spring, P. E., M. L. Brewer, J. R. Brown, and M. E. Fanning. 1974. Population ecology of loblolly pine Pinus taeda in an old field community. Oikos 25: 1-6.
- State of Hawaii. 1970. An inventory of basic water resources data, island of Hawaii. State of Hawaii, Department of Land and Natural Resources, Honolulu.
- Stemmermann, L. 1983. Ecological studies of Hawaiian Metrosideros in a successional context. Pacific Science 37: 361-373.
- Stewart, G. H., and T. T. Veblen. 1982. Regeneration patterns in southern rata (Metrosideros umbellata) - kamahi (Weinmannia racemosa) forest in central Westland, New Zealand. New Zealand Journal of Botany 20: 55-72.
- Swaine, M. D., and J. B. Hall. 1983. Early succession on cleared forest land in Ghana. Journal of Ecology 71: 601-627.
- Takeuchi, W. 1991. The Metrosideros polymorpha forest of Alakai Swamp: population structure and dynamic trends. Ph.D. Dissertation. University of Hawaii, Honolulu.
- Thompson, K. 1992. The functional ecology of seed banks. pp. 231-258. In: M. Fenner [ed.], Seeds: the ecology of regeneration in plant communities. C. A. B. International, Wallingford, England.

- _____, and J. P. Grime. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology* 67: 893-921.
- Uhe, G. 1988. The composition of the plant communities inhabiting the recent volcanic deposits of Maui and Hawaii, Hawaiian Islands. *Tropical Ecology* 29: 26-47.
- Uhl, C. 1982. Recovery following disturbances of different intensities in the Amazon Rain Forest of Venezuela. *Interciencia* 7: 18-24.
- _____, and K. Clark. 1983. Seed ecology of selected Amazon basin successional species. *Botanical Gazette* 144: 419-425.
- _____, _____, H. Clark, and P. Murphy. 1981. Early plant succession after cutting and burning in the upper Rio Negro region of the Amazon Basin. *Journal of Ecology* 69: 631-649.
- _____, H. Clark, K. Clark, and P. Maquirino. 1982. Succession patterns and processes associated with slash and burn agriculture in the upper Rio Negro region of the Amazon Basin. *Biotropica* 14: 249-254.
- United States Geological Survey. 1986. Hawaii Volcanoes National Park and vicinity. U. S. Geological Survey Map 19155-D3-PF-100. U. S. Government Printing Office, Washington, D. C.
- van der Maarel, E. 1988. Vegetation dynamics: patterns in time and space. *Vegetatio* 77: 7-19.
- van der Pijl, L. 1982. Principles of dispersal in higher plants. Springer-Verlag, New York.
- Vázquez-Yanes, C. 1981. Germinación de dos especies de Tiliaceas arbóreas de la vegetación secundaria tropical: Belotia campbellii y Heliocarpa donell-smithii. *Turrialba* 31: 81-83.
- _____, and A. Orozco Segovia. 1982. Seed germination of a tropical rain forest pioneer tree (Heliocarpa donell-smithii) in response to diurnal fluctuation of temperature. *Physiologia Plantarum* 56: 295-298.

- _____, and _____. 1984. Ecophysiology of seed germination in the tropical humid forests of the world: a review. pp. 37-50 In: E. Medina, H. A. Mooney, and C. Vázquez-Yanes [eds.], *Physiological ecology of plants of the wet tropics*. Dr. W. Junk Publishers, The Hague, The Netherlands.
- _____, and _____. 1987. Fisiología ecológica de semillas en la Estación de Biología Tropical "Los Tuxtlas", Veracruz, México. In: D. A. Clark, R. Dirzo, and N. Fetcher [eds.], *Ecología y ecophysología de plantas en los bosques mesoamericanos*. *Revista de Biología Tropical* 35 (supplement 1): 85-96.
- _____, and _____. 1990a. Seed dormancy in the tropical rain forest. pp. 247-259 In: K. S. Bawa, and M. Hadley [Eds.], *Reproductive ecology of tropical forest plants*. UNESCO, Paris, France.
- _____, and _____. 1990b. Ecological significance of light controlled germination in two contrasting tropical habitats. *Oecologia* 83: 171-175.
- _____, and H. Smith. 1982. Phytochrome control of seed germination in the tropical rain forest pioneer trees *Cecropia obtusifolia* and *Piper auritum* and its ecological significance. *New Phytologist* 92: 477-485.
- Vitousek, P. M. 1988. Diversity and biological invasions of oceanic islands. pp. 181-189 In E. O. Wilson [ed.], *Biodiversity*. National Academy Press, Washington, D. C.
- _____, K. Van Cleve, N. Balakrishnan, and D. Mueller-Dombois. 1983. Soil development and nitrogen turnover in montane rainforest soils on Hawai'i. *Biotropica* 15:268-274.
- _____, and L. R. Walker. 1987. Colonization, succession and resource availability: ecosystem-level interactions. pp. 207-223 In: A. J. Gray, M. J. Crawley, and P. J. Edwards [eds.], *Colonization, succession, and stability*. Blackwell Scientific Publications, Oxford, England.
- _____, and _____. 1989. Biological Invasion by *Myrica faya* in Hawai'i: Plant demography, nitrogen fixation, ecosystem effects. *Ecological monographs*. 59: 247-265.

- _____, _____, L. D. Whiteaker, D. Mueller-Dombois, and P. A. Matson. 1987. Biological invasion by Myrica faya alters ecosystem development in Hawaii. *Science* 238: 802-804.
- Wagner, W. L., D. H. Herbst, and S. H. Sohmer [eds.]. 1990. *Manual of the flowering plants of Hawaii*. Bernice P. Bishop Museum, Honolulu.
- Walker, L. R. 1990. Germination of an invading tree species (Myrica faya) in Hawaii. *Biotropica* 22: 140-145.
- _____, and P. M. Vitousek. 1991. An invader alters germination and growth of a native dominant tree in Hawaii. *Ecology* 72: 1449-1455.
- Wallace, A. R. 1911. *Island Life*. Macmillan, London, England.
- Wardle, P. 1971. Biological flora of New Zealand 6. Metrosideros umbellata Cav. [syn. M. lucida (Forst. f.) A. Rich] (Myrtaceae) southern rata. *New Zealand J. Bot.* 9:645-671.
- Wardle, P. 1980. Primary succession in Westland National Park and its vicinity. *New Zealand Journal of Botany* 18: 221-232.
- _____. 1991. *Vegetation of New Zealand*. Cambridge University Press, Cambridge, England.
- Weiner, J. 1985. Size hierarchies in experimental populations of annual plants. *Ecology* 66: 742-753.
- _____, and S. C. Thomas, 1986. Size variability and variation in plant monocultures. *Oikos* 47: 211-222.
- Wester, L. 1992. Origin and distribution of adventive alien flowering plants in Hawai'i. pp. 99-154 *In* C. P. Stone, C. W. Smith, and J. T. Tunison [eds.] *Alien Plant Invasions in native ecosystems of Hawai'i: management and research*. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu.
- Westoby, M. 1984. The self-thinning rule. *Advances in Ecological Research* 14: 167-225.

- _____, and J. Howell. 1986. Influence of population structure on self-thinning of plant populations. *Journal of Ecology* 74: 343-359.
- White, J. 1980. Demographic factors in populations of plants. pp. 21-48 In: O. T. Solbrig [ed.], *Demography and evolution in plant populations*. Blackwell Scientific Publications, Oxford, England.
- White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Review* 45:229-299.
- Whittaker, R. H., and S. A. Levin. 1977. The role of mosaic phenomena in natural communities. *Theoretical Population Biology* 12: 117-139.
- Willson, M. F. 1988. Spatial heterogeneity of post-dispersal survivorship of Queensland rainforest seeds. *Australian Journal of Ecology* 13: 137-145.
- _____, and F. H. J. Crome. 1989. Patterns of seed rain at the edge of a tropical Queensland rain forest. *Journal of Tropical Ecology* 5: 301-308.
- Wodzicki, K. 1981. Some nature conservation problems in the South Pacific. *Biological Conservation*. 21: 5-18.
- Wood, D. M., and R. del Moral. 1987. Mechanisms of early primary succession in subalpine habitats on Mount St. Helens. *Ecology* 68: 780-790.
- _____, and _____. 1988. Colonizing plants on the pumice plains, Mount St. Helens, Washington. *American Journal of Botany* 75: 1228-1237.
- Woodall, S. L. 1982. Seed dispersal in Melaleuca quinquinervia. *Florida Scientist* 45: 81-93.
- Wright, R. A., and D. Mueller-Dombois. 1988. Relationships among shrub population structure, species associations, seedling root form and early volcanic succession, Hawaii. pp. 87-104 In: M. J. A. Werger, P. J. M. van der Aart, H. J. During, and J. T. A. Verhoeven [eds.], *Plant form and vegetation structure*. SPB Publishing, The Hague, The Netherlands.
- Young, K. R., J. J. Ewel, and B. J. Brown. 1987. Seed dynamics during forest succession in Costa Rica. *Vegetatio* 71: 157-173.

Zar, J. H. 1984. Biostatistical Analysis. Prentice Hall,
Englewood Cliffs.