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Ecophysiological and community-level constraints to the invasion of *Myrica faya*, an alien tree in Hawaii Volcanoes National Park

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University of Hawai‘i, 1994
ECOPHYSIOLOGICAL AND COMMUNITY-LEVEL CONSTRAINTS
TO THE INVASION OF MYRICA FAYA, AN ALIEN TREE
IN HAWAII VOLCANOES NATIONAL PARK

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT
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IN
BOTANICAL SCIENCES (BOTANY)

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ABSTRACT

*Myrica faya* is an alien tree invading the montane and submontane forest and submontane grassland communities of Hawaii Volcanoes National Park. The goals of my research were to identify possible community-level constraints to *Myrica* establishment in rain forest communities within the current range of *Myrica* in the park and to determine the potential for further range expansion of *Myrica*.

Seed germination, seedling mortality and seedling growth were monitored in *Metrosideros* rain forest communities with dense understory cover of the ferns, *Dicanopteris linearis* and *Cibotium glaucum*. These fern understories reduced incoming light to less than 1% of full sun, resulting in low germination, high mortality and low growth rates of seedlings. *Myrica* seedling recruitment appeared to occur primarily in gaps in the understory fern cover. Within the current invasion range of *Myrica*, low light availability in the understory of intact rain forest communities is a predominant factor restricting *Myrica* invasion of these habitats.

The potential for the invasion of *Myrica* beyond its current range was investigated near two invasion fronts; one in the wet montane rain forest and the other in the seasonally dry submontane grassland. Seed inputs, seed germination, seedling survival and growth rates were
determined. While seed inputs were low beyond both invasion fronts, constraining the potential rate of invasion, the response of *Myrica* to particular characteristics of each habitat also limited establishment. In the wet, montane rain forest, seed germination was greatly inhibited, probably due to the interaction of low light availability in the understory and high soil water content. In contrast, establishment in the high light environment of the seasonal submontane grassland was restricted by the susceptibility of seeds and young germinants to high moisture stress during the summer, which resulted in low seed germination and high seedling mortality. Though seedlings growth rates were high during the wet season, growth rates were significantly reduced during the dry summer period.
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PART I: BACKGROUND FOR DISSERTATION RESEARCH
CHAPTER 1
LITERATURE REVIEW AND PROPOSED RESEARCH

Introduction

Increased concern in recent years of the potential alteration of native plant communities by the invasion of alien plants has lead to three areas of study contributing to an understanding of plant invasions: the demographic and physiological traits of successful invaders (Bazzaz 1986, Newsome and Noble 1986), and the investigation of the characteristics of communities which make them susceptible to invasion (Elton 1958, Orians 1986). Recent research has focused on determining the mechanisms of invasion with the objective of investigating the constraints or processes controlling invasion, in order to suggest strategies for control of an invasive species (Luken and Mattimiro 1991, D'Antonio 1993).

*Myrica faya* is an aggressive invader of open canopied seasonal submontane forests and grassland within Hawaii Volcanoes National Park (HAVO) and has recently become established in some rain forest habitats. Vitousek and Walker (1989) suggest that this species does not establish itself readily under a closed overstory canopy. The invasion of *Myrica* may be facilitated by the natural population dynamics of the dominant overstory species
Metrosideros polymorpha, which undergoes canopy dieback, creating a large overstory gap. This dissertation focuses on identifying community-level and ecophysiological constraints to the invasion of Myrica in HAVO, and determining the potential role of Myrica in altering future rain forest community structure. This research is a portion of a larger collaborative effort towards the study of the effect of biological invasions on ecosystem processes in HAVO.

History and distribution of Myrica faya in Hawaii

Myrica faya is native to the Macaronesian Islands where it holds a subcanopy position in subtropical montane forests. In the Lauri-Silva montane forest of the Canary Islands Myrica is a minor canopy species. However, it acts as a secondary successional pioneer on sites disturbed by fire. Erica arborea is the first tree species to establish after a fire followed by Myrica. Myrica faya remains a codominant with Erica in warm environments and on sites disturbed periodically by fire (Mueller-Dombois, pers. comm.).

The introduction of Myrica into Hawaii occurred in the late 1800's when it was probably brought by Portuguese laborers, who were reported to have made wine from its fruits and grew it as an ornamental plant (Little and
Skolmen 1989). In the 1920's and 1930's seed of this species was spread on eroding watersheds in a reforestation effort. The aggressive colonizing ability of this species was noticed in 1944 by the state, and a control program was initiated (Neal 1965). In 1961 a survey revealed that 100 ha of HAVO had been colonized by *Myrica*. By 1985, *Myrica* had spread to 12,200 ha (Whiteaker and Gardner 1985). An intensive resurvey in 1992 revealed that 11,600 ha of HAVO were colonized by *Myrica* (Camrath and Tunison 1992). Areas of barren lava flow that had been included in the 1985 survey were deleted in the 1992 survey, resulting in a lower total range of occupation. However, in the 1992 survey, 2900 ha of new areas of colonization were recorded (Camrath and Tunison 1992).

HAVO is located on the eastern slope of Mauna Loa and the southern slope of Kilauea Volcano on the island of Hawaii (Fig. 1.1). Six major ecological zones were identified within HAVO by integrating climate, topography, substrate, and vegetation characteristics (Fig. 1.2) (Doty and Mueller-Dombois 1966, Mueller-Dombois 1976).

*Myrica* is not present in the alpine, the subalpine, the upper montane and coastal lowland ecosystems of the island of Hawaii (Fig. 1.2). The alpine and subalpine ecosystems lie above an altitude of around 2040 m on Mauna
Loa and have average air temperatures below 9.5°C (Mueller-Dombois and Bridges 1981). The climate is dry with night-frost near the ground. The vegetation is primarily scrub with scattered Metrosideros trees grading into treeless low-scrub and sparse moss and lichens above 2500 m. The coastal lowland, extending from 300 m to sea level, receives 700 to 1700 mm rainfall yr\(^{-1}\) and has an average mean air temperature of 23°C. The coastal lowland has a summer drought to subhumid climate and supports grassland with scrub and dry lowland forests (Doty and Mueller-Dombois 1966). Temperature and rainfall patterns probably play a major role in limiting Myrica invasion into these ecosystems.

The current elevational range of Myrica on the windward side of the island of Hawaii, is between 1335 m and 600 m (Whiteaker and Gardner 1985). Myrica faya is present throughout much of the montane and submontane ecosystems of HAVO (Fig. 1.2) (Whiteaker and Gardner 1985, Higashino et al. 1988, Camrath and Tunison 1992). The montane seasonal zone, extending from 2042 to 1160 m elevation, receives 1100 to 1600 mm rainfall yr\(^{-1}\), and has an average air temperature of 12 to 17°C. The vegetation of the montane seasonal zone is primarily Acacia koa parkland and savannah. Myrica is found on ranchlands and open-canopied forests in the lower part of this zone. The
humid montane rain forest zone, extending from 1160 to 460 m elevation on the east side of Kilauea Volcano, receives 2000 to 3000 mm rainfall yr\(^{-1}\) and has a mean air temperature of 16°C (Mueller-Dombois and Bridges 1981). The major vegetation types in the montane rain forest are predominantly open and closed \textit{Metrosideros} forest with either \textit{Dicranopteris linearis} fern or \textit{Cibotium glaucum} treefern understory (Mueller-Dombois 1976). Invasion by \textit{Myrica faya} is prevalent in some communities, particularly those disturbed by recent ash and cinder fall, but generally, rates of \textit{Myrica} establishment are lower in the rain forest than in the seasonal montane or seasonal submontane zones. Dense native vegetation and low subcanopy light conditions characteristic of these rain forest communities may restrict \textit{Myrica} establishment. The seasonal submontane zone extends from 1160 m to 300 m on the south flank of Kilauea Volcano. The climate is dry in the summer (Doty and Mueller-Dombois 1966). The \textit{Metrosideros} forest is open canopied with sparse understory vegetation. In this habitat \textit{Myrica} invasion has been rapid and extensive. On one site in this zone, \textit{Myrica} has developed into a dense monospecific stand (Vitousek and Walker 1989). Several factors including differences in bird dispersed seed inputs, response to the environmental characteristics of the habitat and species
interactions may account for the different rates of invasion by Myrica observed among ecosystems of HAVO.

**Myrica faya fruiting and seed dispersal**

*Myrica faya* produces a fruit with a fleshy mesocarp surrounding 2 to 5 fused stony endocarps each containing a single seed (Walker 1990). Fruit maturation and fruit drop are strongly seasonal, peaking between September and December (Whiteaker and Gardner 1987). Birds, such as the Japanese white-eye (*Zosterops japonica*), which eat the fruit, are the primary vectors for the dispersal of *Myrica* (Woodward et al. 1990). However, only 0.5% of the fruit produced by *Myrica* is dispersed away from parent trees by birds (Vitousek and Walker 1989).

An association between *Metrosideros* trees and *Myrica* establishment in the seasonal submontane forest was first noted by Smathers and Gardner (1979). Most *Myrica* individuals were found established under open-grown individuals of *Metrosideros*. In seasonal submontane forests, 4.7 *Myrica* seeds m\(^{-2}\) mo\(^{-1}\) were captured under *Metrosideros* trees but none were captured in the open, away from *Metrosideros* trees (Vitousek and Walker 1989). Beneath *Metrosideros* crowns, 1.8 *Myrica* seed m\(^{-2}\) mo\(^{-1}\) were captured at an invasion front of *Myrica* near Hilina Pali, but no seeds were found greater than 0.5 km ahead of the
invasion front (Vitousek and Walker 1989). The distance to the nearest seed source, the density of the seed source and the range and movements of birds feeding on Myrica may strongly influence the rate of Myrica invasion.

Nitrogen inputs by Myrica

In the early stages of soil formation, low nitrogen limits plant growth and nitrogen-fixing plants tend to dominate (Walker and Syers 1976). The early successional communities of HAVO are nitrogen limited (Balakrishnan and Mueller-Dombois 1983, Vitousek et al. 1987, Gerrish et al. 1988) yet few nitrogen-fixing plants are present in the native Hawaiian flora (Vitousek 1990).

Myrica faya has the capability, through an interaction with the actinomycete Frankia, to produce nitrogen for its own use in soils of low nitrogen availability. Nodulation of Myrica roots and total amount of fixed nitrogen on soils of low nitrogen status are high when light availability is not limiting Myrica growth (Turner and Vitousek 1987). Levels of available soil nitrogen can be up to 12 times higher under a Myrica tree than under a Metrosideros tree on young soils. Thus, the nitrogen status of early successional sites in HAVO are be altered with the invasion of Myrica (Vitousek et al. 1987, Vitousek and Walker 1989). The possible consequences of
the alteration of soil nitrogen status by *Myrica* nitrogen inputs may be the increased growth rates of native species and an increased rate of primary succession (Vitousek et al. 1987).

**Response of *Myrica* to light availability**

*Myrica faya* exhibits morphological plasticity in its growth form depending on light availability. In high light environments, *Myrica* takes the form of a large shrub with basitonic branching (Smathers and Gardner 1979). The leaves are small and arranged closely around the branch at an acute angle when grown in full sun. In low light environments *Myrica* takes the form of a tree with one to a few basal branches and leaves are typically large and spaced apart on the branch. This leaf arrangement may ensure the greatest amount of light capture and may allow *Myrica* to persist in partially shaded understory conditions.

High relative growth rates in full sun, suppressed growth in shady habitats and high morphological plasticity in response to light availability are characteristics common to species adapted to high light environments (Loach 1970). However, the light requirements of plants can differ at different stages in their life history. *Myrica faya* can germinate under low light conditions of 4%
full sun. However, optimal germination occurs at 50% full sun and optimal growth at 70% full sun (Vitousek and Walker 1989, Walker 1990). The relative light availability below a *Cibotium* treefern canopy in rain forest communities was found to be less than 2% of full sunlight (Burton 1980, Burton and Mueller-Dombois 1984). *Myrica faya* establishment may be inhibited by light preemption by the mid and upper canopy vegetation in closed canopied rain forest communities. *Myrica faya* can persist for a time in the understory as suppressed individuals (Vitousek and Walker 1989), however if an opening in the understory canopy occurs, such as after the fall of a *Cibotium* tree fern, increasing light availability, seedlings and saplings may respond by increasing rates of growth. Thus, establishment of *Myrica* in the rain forest may occur more readily in understory gaps. Moreover, in communities subject to stand-level dieback of the *Metrosideros* canopy (for further discussion see below, pg. 16), *Myrica* invasion may occur over a larger area. If *Myrica* can readily invade *Metrosideros* forest subject to canopy dieback and can establish before native species become established, the species composition and structure of the community may be altered.
Plant water relations

Responses to seasonal variations in soil water availability and other environmental factors are important determinants of a species growth and distribution (Hinckley et al. 1981). Juvenile plants are more often subject to mortality from an environmental stress than adult plants (Donovan and Ehleringer 1991). Low recruitment may influence a particular species distribution within a region (Parker and Pallardy 1988). The absence of Myrica in drought-prone environments, such as coastal lowlands, suggests an intolerance of water stress in some part of its life history.

The relationship between water availability in different habitats and the response of the turgor and osmotic potentials to changes in plant tissue water content was recognized by Höfler (1920). In environments characterized by seasonal periods of drought, many plants exhibit osmotic adjustment. Osmotic adjustment refers to a decrease in osmotic potential greater than can be accounted for by increased solute concentration by dehydration, through the active accumulation of additional solutes (Turner and Jones 1980). Osmotic adjustment allows plant turgor to be maintained at more negative plant water potentials and lower relative water contents (Turner and Begg 1981). Thus, turgor dependent processes, such as photosynthesis and growth, can continue during
periods of low water availability. Turgor is also influenced by the tissue bulk modulus of elasticity. Plants with a low bulk modulus of elasticity (or high elasticity) exhibit a smaller decrease in turgor for a given reduction in the volume of water in tissues, than plants with more rigid tissues. Thus plants with more elastic tissues tend to maintain turgor over a wider range of declining tissue water potentials and decreasing relative water contents than plants with more rigid tissues (Weatherley 1970, Tyree and Jarvis 1982).

The distribution of some *Quercus* spp. in drought-prone environments in the Eastern deciduous forests of the U.S. is partially attributed to their capacity for active osmotic adjustment during water stress (Parker and Pallardy 1988). Maintenance of turgor during drought periods facilitates the continued growth of roots and subsequent utilization of a greater soil volume. Osmotic adjustment and maintenance of root growth during periods of drought in *Populus trichocarpa* makes this species competitively superior to the co-occurring *Alnus rubra* (Pezeshki and Hinckley 1988). A greater capacity for osmotic adjustment was found in pioneer *Metrosideros* populations than in later successional populations (Stemmermann 1986). *Myrica faya*, which is distributed across habitats of differing soil water availability and
climate, may alter its water relations characteristics in response to seasonal changes in water availability.

**Population structure of *Myrica***

Population structural analysis is a quantitative determination of the structure in age states or size frequency of a species (Ogden 1985). The method is used, in part, to determine the relative stability of a species in a community. The population structure of an invasive species often exhibits a large germinant and seedling population with progressively fewer individuals in larger size classes (Wright and Mueller-Dombois 1988). This population structure is described by a reversed J-shaped basal area or biomass size distribution (Ogden 1985).

Population structure of an invasive species may change to a modal pattern (a reduction in small size classes) when some environmental factor is altered (such as decreased light availability) which reduces population recruitment or increases mortality of small individuals (Mohler et al. 1978, Weiner 1985).

The stand structure of *Myrica* (536 stems ha⁻¹) at Ainahou in the HAVO seasonal submontane forest, has a characteristic reversed J-shaped size distribution of an invading population (Whiteaker and Gardner 1987, Wright and Mueller-Dombois 1988). Here 81% of the
population was below 10 cm diameter. The population structure at Naulu, where density of *Myrica* was 733 stems ha\(^{-1}\), was modally distributed with few individuals in the smallest and largest size classes. Low representation of individuals in small size classes may be attributed to a failure of regeneration during a period of unfavorable environmental conditions at the time of germination (Whiteaker and Gardner 1987). However, it may be that the *Myrica* canopy has begun to shade the understory, inhibiting germination and/or suppressing the growth of plants in the very small size classes. This phenomena is most apparent near Puhimau Crater where *Myrica* has developed into a dense monospecific stand with no vegetation or regeneration in the understory. Thus, it appears that a *Myrica* population may recruit continually until self-shading occurs, so that further *Myrica* recruitment may require the disturbance or breakdown of the overstory. *Myrica* population dynamics in rain forest communities may be different than that observed in open-canopied seasonal submontane forest as the response of *Myrica* to different community structural characteristics and habitats will play a role in recruitment and growth.

Invasion of a new species into an intact community can alter population size and structure of the component species (Johnstone 1986). Though *Myrica* is relatively
shade intolerant compared to other tree species present in the rain forest, its prolific reproduction and fast growth rates facilitate rapid population growth. The development of monospecific stands of *Myrica* prevents the establishment of native species. Thus, the invasion of *Myrica* into forest communities of HAVO threatens to alter the native community composition and dynamics (Smith 1984).

**Succession in Hawaii**

Changes in vegetation structure and species composition over time are relatively predictable in the rain forest environment of Hawaii. On the island of Hawaii, new surfaces are created by lava flows from active volcanoes. Primary succession soon begins on these new, previously unvegetated surfaces. *Metrosideros polymorpha* is a pioneer species that colonizes these new lava surfaces (Smathers and Mueller-Dombois 1974, Mueller-Dombois 1987b). Seedlings of *Metrosideros* establish in cracks in the lava (Mueller-Dombois 1987b) and grow very slowly. Soon, native shrubs such as *Dubautia* spp., *Vaccinium* spp. and *Rumex* spp. become established. As the *Metrosideros* forest develops, the mat-forming fern *Dicranopteris linearis* becomes prominent in the understory. The *Metrosideros/Dicranopteris* community may
exist from 50 to 200 years. As the Metrosideros canopy begins to close, the more shade-tolerant Cibotium tree fern replaces Dicranopteris fern as the dominant understory vegetation (Mueller-Dombois 1987b). Development of a mature Metrosideros/Cibotium forest from a bare lava surface may require 400 years of succession (Atkinson 1970).

**Metrosideros population dynamics**

Metrosideros stands are usually a cohort of individuals (Mueller-Dombois 1987b). These individuals enter stages in their life history as a relatively even-structured group. After maturity, the cohort stand enters a stage of senescence and the stand declines in vigor (Mueller-Dombois 1987b). Metrosideros undergoes a stand breakdown phenomenon known as canopy dieback (Mueller-Dombois 1980). Though stand-level mortality of Metrosideros has been noted since the late 1800's, research of the phenomenon began most earnestly in the 1970's (Kliejunas and Ko 1974, Mueller-Dombois 1983, 1985). In 1977, an assessment of Metrosideros canopy decline on the windward side of the island of Hawaii revealed that 50,000 ha of the Metrosideros forest was in dieback (Jacobi 1983). Dieback was first thought to be the result of some disease-causing agent (Petteys et al.)
1975) but, after an extensive research effort, none was found that could be associated with all dieback phenomena (Papp et al. 1979). Ecological studies by Mueller-Dombois et al. (1980) revealed that dieback appeared to be a natural dynamic process related to the life-history of Metrosideros in the rain forest.

Metrosideros is relatively shade-intolerant and sapling regeneration is rarely found below a closed Cibotium tree fern understory (Mueller-Dombois 1987b). Metrosideros maintains itself as a canopy dominant in rain forest communities through regeneration following canopy dieback (Mueller-Dombois 1983) and/or gap-phase replacement (Jacobi et al. 1983, Burton and Mueller-Dombois 1984, Jacobi et al. 1988).

Analysis of Metrosideros population structure often reveals a sapling gap or a lack of young regeneration in the population structure (Mueller-Dombois 1987a). Low light availability under a closed overstory canopy or dense treefern cover, inhibits the development of Metrosideros seedlings to the sapling stage (Burton and Mueller-Dombois 1984). During dieback, however, the closed canopy begins to open. Stunted seedlings and new regeneration respond to the increased light and nutrient availability. Development of suppressed Metrosideros seedlings after dieback usually leads to the establishment
of a new canopy cohort (Burton and Mueller-Dombois 1984). Along with an increase in *Metrosideros* seedling to sapling development there may be an increase in the regeneration of other native species. Thus, dieback is a population process which has supported rather than hindered the long term maintenance of *Metrosideros* as the dominant overstory tree.

Dieback associated with abundant *Metrosideros* regeneration, has been termed replacement dieback (Mueller-Dombois et al. 1980). However, displacement dieback refers to the displacement of *Metrosideros* by other vegetation, such as the *Cibotium* tree fern, which preempts light and inhibits further *Metrosideros* regeneration (Mueller-Dombois 1988). Several dieback types have been identified according to the habitat in which dieback occurs, the vegetation structure, and the potential for *Metrosideros* reestablishment (Mueller-Dombois et al. 1980, Mueller-Dombois 1986). Other types of dieback have been described in Mueller-Dombois et al. (1980) and Mueller-Dombois (1983).

With the invasion of *Myrica faya* into the Hawaiian Islands, there may come a change in the successional development of the native plant communities affected. *Myrica faya* is known to alter the biological availability of nitrogen on sites it occupies in HAVO (Vitousek et al.
1987) and its presence in the community alters the light environment (personal observation). How succession may proceed with the biological invasion of Myrica is unknown.

Summary

Myrica has become codominant with Metrosideros polymorpha in the seasonal submontane forest of HAVO. Myrica establishment in native plant communities may result in a closed canopy Myrica forest with the potential to replace the native vegetation with Myrica and other alien species. The characteristics of the seasonal submontane forest are very different from the seasonal submontane grassland and the rain forest communities where Myrica has not yet become established or has a much lower rate of establishment than in the seasonal submontane forest (Mueller-Dombois and Fosberg 1974, Whiteaker and Gardner 1985). The potential for Myrica to become incorporated into the existing species assemblage of these communities depends on a number of factors including: seed dispersal, physiological requirements for germination and establishment and response to habitat characteristics. In the following dissertation research proposal I shall discuss a number of studies that have been planned to evaluate the relative potential for the invasion of Myrica into communities within and beyond its current range.
Proposed research

Objectives

The purposes of this dissertation research are four-fold: 1) to determine the potential for further Myrica invasion of communities beyond its current range, 2) to determine if Myrica exhibits a decline in physiological vigor beyond its current range, 3) to identify and evaluate possible community-level constraints to Myrica establishment in rain forest communities and 4) to evaluate the capacity of Myrica for altering rain forest community characteristics.

Questions and Hypotheses

A. Invasion boundaries

Myrica faya may extend its range in HAVO into increasingly warmer and seasonally drier environments (seasonal submontane grassland) and into increasingly wetter montane rain forest than that of its main invasion area in the seasonal submontane forest.

The first question is: Will Myrica invade sites beyond its current invasion front in the seasonal submontane grassland?
The hypotheses to be tested are:

1. The absence or low presence of *Myrica* beyond its current invasion front in the seasonally dry grassland is due to a lack of seed supply.

   This hypothesis will be tested by measuring the relative amount of *Myrica* seed being dispersed at the invasion front in the seasonal submontane grassland. Seed traps will be set up at the invasion front during the fruiting season.

2. The advance of *Myrica* into the seasonally dry submontane grassland is restricted by a limited water supply.

   Seed germination, survival and growth response of seedlings transplanted into grassland communities subject to seasonal drought will be monitored.

   The second question is: Will *Myrica* invade wetter montane rain forest sites (Ola'a tract) ahead of its current invasion front at Volcano village?

   The hypotheses to be tested are:

3. The absence of *Myrica* in the *Cibotium* tree fern forest of Ola'a tract is due to a lack of bird-dispersed seed inputs beyond the current invasion range of *Myrica*.

   The relative amount of seed dispersed into Ola'a tract will be determined by setting out seed traps under the forest canopy.
4. Light levels are too low for Myrica survival and growth under the dense Cibotium subcanopy characteristic of the wet montane Ola'a tract rain forest. This hypothesis will be tested by comparing seed germination, survival, and growth response of seedlings transplanted into Cibotium tree fern forest of Ola'a tract to similar studies at other rain forest sites where light availability is higher.

5. Myrica is intolerant of the periodically saturated soil water conditions that occur in Ola'a tract. This hypothesis will be tested by monitoring the growth of seedlings subjected to high, moderate and low soil water availability in a greenhouse experiment where light and nutrients are not limiting to growth.

B. Community-level constraints to invasion

Myrica invasion of rain forest communities appears low when compared to the intensive invasion of seasonal submontane forest, which suggests that habitat and community characteristics in the rain forest do not as readily favor Myrica establishment. Light availability has been hypothesized as a major controlling factor in Myrica establishment in rain forest communities.
The first question relating to possible community-level constraints within the invasion range of *Myrica* is:

Do *Myrica* seed inputs in the rain forest differ from those in the seasonal submontane forest?

The hypothesis selected for testing is:

6. The invasion of *Myrica* into rain forest communities, within its invasion range, is restricted by lower seed inputs than found in the seasonal submontane forest.

This hypothesis will be tested by comparing seed inputs, using seed traps, to the seed inputs measured in the seasonal submontane forest.

The second question is: In what way does the light regime of rain forest communities limit *Myrica* establishment?

The hypothesis selected for testing is:

7. Subcanopy light availability of *Dicranopteris* and *Cibotium* fern dominated understories of *Metrosideros* rain forest communities is suboptimal for the establishment of *Myrica*.

Community structural characteristics including changes in vegetation cover at different heights through the forest will be measured. Light attenuation downward through the canopy and total light availability at the forest floor will be measured. *Myrica* population
structures on invaded sites will be determined. Seed germination and seedling growth will be monitored in these communities.

A question relating to community dynamics is: Does *Metrosideros* dieback facilitate *Myrica* invasion?

The hypothesis is:

8. Increased light availability after *Metrosideros* dieback facilitates the establishment and growth of *Myrica*.

This hypothesis will be tested by measuring and comparing the light availability in non-dieback and dieback stands of *Metrosideros* and determining the current population structure of *Myrica* in these stands.

These eight hypotheses, five concerning the study of the potential of *Myrica* for invasion beyond its current boundaries and three for the investigation of community-level constraints to invasion provided for the scope of the dissertation research presented here.

Research Plan

A. Invasion boundaries

The potential extension of the current range of *Myrica* beyond two contrasting invasion fronts is one focus of this investigation. One invasion front occurs in the
southern portion of HAVO near 800 m elevation. Grassland vegetation and seasonal drought during the summer are characteristics of this area. The other invasion front selected for study is at the northern end of HAVO near Ola'a tract at 1160 m elevation. Undisturbed rain forest communities are generally closed canopied and year-round precipitation is high. In this area, *Myrica* invasion has been restricted to disturbed sites, such as farmland, where the forest has been removed.

**Study area**

The open canopied seasonal submontane forest lies between 1200 m and 960 m elevation and is the main area of *Myrica* invasion. The invasion front of *Myrica* has currently extended beyond the seasonal submontane forest into the seasonal submontane grassland lower than 960 m elevation near the Kipuka Nene campground. *Myrica* trees are not found below 760 m elevation in this area.

Two sites will be selected for the study of the potential for *Myrica* to extend beyond its current invasion front into the seasonal submontane grassland. One study site will be selected at the current invasion boundary of *Myrica* and the other will be located about 3 km beyond the current invasion boundary. This area of the grassland is subject to periods of summer drought and receives about
1500 mm yr$^{-1}$ rainfall on the average. The vegetation is mostly a grassland community consisting predominantly of *Schizachyrium condensatum* and *Melinis minutiflora* on young, shallow, well-drained ash soils with numerous exposed areas of pāhoehoe lava (Doty and Mueller-Dombois 1966, Mueller-Dombois and Fosberg 1974).

A wetter and cooler environment than that of the seasonal submontane grassland is found in the Ola'a tract, beyond the range of *Myrica* invasion, in the montane rain forest. Ola'a tract is a section of HAVO that is separated from the main park area by Volcano village and the Kilauea Forest Reserve. Ola'a tract lies between 1000 m and 1360 m elevation and receives high year round precipitation (3000 mm yr$^{-1}$ on average). The characteristic vegetation type of this area is a *Cibotium* tree fern forest with scattered old *Metrosideros* trees (Mueller-Dombois and Fosberg 1974, Burton 1980). The soils of Ola'a tract are derived from a deep fine-textured ash believed to have been deposited about 2000 to 1000 years ago with a recent shallow surface deposition of ash resulting from the 1790 eruption of Kilauea (Holcomb 1987). The humic top soil and underlying eutrophic ash contribute to the high nutrient status of the soils in this area (Balakrishnan and Mueller-Dombois 1983). These soils are moderately to occasionally poorly drained.
Metrosideros has undergone stand-level dieback in this area. The light environment under the Cibotium tree fern cover in this area has been shown to be so low as to inhibit the establishment of Metrosideros seedlings, thus reestablishment of the Metrosideros forest has been inhibited (Burton and Mueller-Dombois 1984).

Myrica has not yet invaded Ola'a tract though it is present in other rain forest communities in HAVO and in Volcano village. The invasion front of Myrica near Ola'a tract is about 0.5 km south of the Ola'a tract boundary on adjacent farmlands. A study site will be located in Ola'a tract to determine the potential for Myrica to invade a closed-canopied Cibotium tree fern forest beyond its current invasion range in the montane rain forest zone.

Seed trap study

If Myrica is not currently invading a community it must be determined whether seeds are being dispersed into the community. To test the hypothesis that the absence or low presence of Myrica in communities beyond its current invasion fronts near Kipuka Nene and Ola'a tract is due to low seed inputs, some estimates of seed inputs will be made.

Seed traps will be distributed randomly throughout a 1 ha area within 0.5 km of each invasion front. Material in
these seed traps will be collected every 2 months and seeds found in these traps will be identified to species.

Seed germination study

If a lack of seed input is not the sole limiting factor to Myrica invasion of communities beyond the invasion fronts, other potential limiting factors to Myrica invasion will be examined. To test the hypothesis that seed germination and survival is low beyond the invasion fronts, a seed germination experiment will be conducted. Trays of soil from each study site will be seeded with scarified Myrica seed. The trays with seeds will be placed on study sites beyond the current invasion boundaries previously discussed and will be protected by a wire mesh cage to prevent possible seed predation by rodents. Seed germination and survival of germinants will be monitored once a month.

Field growth response study

To test the hypothesis that the advance of Myrica beyond its current invasion front in the seasonal submontane grassland is limited by seasonal drought and high temperatures during the summer, the growth of seedlings transplanted into this habitat will be determined. The growth of transplanted seedlings will be
monitored by monthly measurements of height and diameter growth. Carbon allocation and total biomass of the seedlings will be determined after 1 year.

The rain forest environment, unlike the seasonal submontane environment, does not have a period of summer drought which could potentially limit plant growth. However, in the rain forest, low light availability may be a factor limiting *Myrica* establishment. To test the hypothesis that light availability in the *Cibotium* tree fern forest of Ola'a tract is too low for *Myrica* establishment, the growth rates of *Myrica* seedlings transplanted into this habitat will be monitored. Height and diameter of transplanted seedlings will be measured monthly. Carbon allocation and total biomass of the seedlings will be determined after 1 year.

Light availability and soil temperatures will be measured at random locations throughout each study site using photo diodes, LICOR quantum sensors, and temperature probes attached to a micrologger. These data will be used to compare the relative differences in light availability and temperature at each site and to correlate these factors with potential differences in seedling germination, growth and survival at each site.

To ensure that the observed responses of seedlings in these habitats is accounted for by the factors measured,
soil differences will also be taken into consideration. Intact soil cores from each site will be placed in 1/2 gallon "grow bags" and brought into the greenhouse. These soil cores will be sown with *Myrica* seed watered with a mist-watering system. Seed germination and seedling growth will be monitored.

**Physiological studies in the field**

The relative tolerance of *Myrica* to moisture stress can be evaluated through measures of stomatal control of water loss and maintenance of leaf turgor. Diurnal measurements of stomatal conductance will indicate degree of stomatal control over water loss. Xylem water potential, predawn and midday, will elucidate the relative ability of *Myrica* growing in drought-prone seasonal submontane environments to maintain turgor under water stress. Photosynthesis and stomatal conductance will be measured on established *Myrica* trees at the invasion front in the seasonal submontane grassland during the summer drought period, to determine stomatal conductance and water use efficiency of *Myrica*. To determine the degree of water stress experienced by naturally established *Myrica*, predawn and midday xylem water potential also will be measured on these trees.
Water relations study

Tolerance of *Myrica* seedlings to different degrees of soil moisture availability will be determined in a greenhouse experiment. To test the hypothesis that the vigor of *Myrica* is reduced when exposed to very high or very low soil water availability, I will set up a greenhouse experiment to which four watering treatments will be imposed on *Myrica* seedlings. *Myrica* seedlings will be planted into 12 liter pots of soil/cinder mix for which the field capacity (FC) and permanent wilting point (PWP) of the soil will be determined. Treatments will include: 1) waterlogged, 2) 75% of FC to field capacity, 3) near 50% of FC and 4) near PWP. Pots will be watered to field capacity at the beginning of the experiment and weighed every few days to determine the point at which they have reached the specified treatment level, taking into account the weight of the pot and the plant. Waterlogged plants will be on a continuous watering system.

*Myrica faya* seedling response to these treatments will be measured in terms of growth rates and biomass allocation. Periodic measurements of plant water status on plants of each treatment, using leaves of the same age, will be taken. At the end of the treatment cycle, the pressure-volume technique will be used to determine the
degree of osmotic adjustment in the PWP treatment, with the FC treatment as a control.

B. Community-level constraints

*Myrica faya* has become established in some rain forest communities but is absent from others occupied by the *Dicranopteris* fern and/or by closed *Cibotium* tree fern understories. A number of studies are planned to determine what factors of the existing rain forest vegetation may offer resistance to *Myrica* invasion.

**Study area**

A representative successional sequence of *Metrosideros* rain forest communities was selected for the study of community-level constraints within the invasion range of *Myrica*. The three rain forest communities selected for this study, between 1131 m and 1180 m elevation, resulted from the 1790 explosive eruption of Kilauea Volcano which destroyed the former forest and deposited a 40 to 50 cm layer of ash and cinder (Holcomb 1987). The different successional stages represented by each community are believed to have resulted from different rates of plant colonization after the eruption (Mueller-Dombois, pers. communication). The rain forest communities under selected for this study are characterized as 1) a young
and vigorous stand of Metrosideros with a Dicranopteris fern understory, 2) a mid-successional Metrosideros forest with a Cibotium tree fern understory and 3) a late successional forest with an overstory Metrosideros canopy that has undergone dieback and where there are now only a few standing Metrosideros trees.

The mean annual rainfall for these communities, recorded at the nearest climate station (Park Headquarters), is 2620 mm. Generally the rainfall pattern is slightly seasonal with a wetter winter than summer, but no month receives less than 100 mm of rainfall on the average (Giambelluca et al. 1986).

Seed trap study

The absence of Myrica from rain forest communities characterized by a Dicranopteris understory suggests either that seeds are not being dispersed into the community or some other factor is limiting establishment. To test the hypothesis that the absence or low presence of Myrica in some rain forest communities is due to low seed inputs, some estimates of seed inputs will be made. Seed traps will be distributed randomly throughout a 1 ha area within each rain forest community selected for study. Material in these seed traps will be collected every 2
months and seeds found in these traps will be identified to species.

**Seed germination study**

*Myrica* establishment may be limited by low germination and survival in the mesic rain forest. To test this hypothesis a seed germination experiment will be conducted. Trays of soil from each study site will be seeded with scarified *Myrica* seed. These trays will be placed under the forest canopy of each study site and will be protected by a wire mesh cage to prevent possible seed predation by rodents. Seed germination and survival of germinants will be monitored once a month.

**Community structure, light availability and seedling growth**

To test the hypothesis that the structural characteristics of rain forest communities limit light availability at levels critical for *Myrica* growth, community structural characteristics, light availability through the canopy and seedling growth in the understory will be determined.

The relevé and count-plot methods described by Mueller-Dombois and Ellenberg (1974) will be used to determine the structural characteristics of each site. The percent cover of plant species will be sampled, in 1
ha plots, by strata and the density of all tree species. The leaf area index will be determined using a LICOR plant canopy analyzer.

The light environment within and under the forest canopy of each community will be measured at 1 m height intervals using LICOR quantum sensors. This measurement permits the determination of light attenuation through the canopy which can be related to stand structural characteristics. The light sensors will be attached to a micrologger which will monitor and record light intensity throughout the day. A reference light sensor will be placed in full sunlight in order to determine the relative light intensity passing through the canopy. The light regime will be compared to the potential response of *Myrica* to light availability as measured by Walker (1990).

*Myrica faya* seedlings will be transplanted into each rain forest community and their growth will be monitored by monthly measures of height and diameter. Carbon allocation and total biomass of the seedlings will be determined after 1 year of growth.

*Myrica invasion of Metrosideros dieback stands*

To test the hypothesis that increased light availability with *Metrosideros* canopy dieback facilitates the establishment of *Myrica*, the potential for *Myrica*
germination, survival and growth at study sites characterized by the dieback of *Metrosideros* will be determined. The density and population structure of established *Myrica* will be determined by the count-plot method (Mueller-Dombois and Ellenberg 1974).

C. Future community dynamics

Species population structures reflect the relative stability of their position in a successional sequence. Incorporation of a new species into a plant community can, through competition, alter the population structure of the component species. An analysis of the population structure of the tree species in a forest community will assist in the understanding of future community composition.

For the determination of the population structures of rain forest tree species, 1 ha plots will be established in each community. Seedlings, saplings and trees will be enumerated in subplots. The height and diameter of all tree species (predominantly *Metrosideros polymorpha, Myrica faya, Ilex anomala*) will be measured. Seedlings will be classified according to height from 0.1 to 0.5 m. Saplings will be classified similarly from 0.5 to 5 m. Trees are those greater than 5 m in height.
Schedule of activities

<table>
<thead>
<tr>
<th>Activity</th>
<th>Schedule (prepared March 1990)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seed trap</td>
<td>Started July 1989, sampled once every 2 months, finish August 1990.</td>
</tr>
<tr>
<td>Seed germination (field)</td>
<td>Started October 1989. Germinants counted periodically, the number of ungerminated seeds determined after 1 year.</td>
</tr>
<tr>
<td>Light and temperature</td>
<td>Six days measurement on each site to monitor relative light availability and temperature.</td>
</tr>
<tr>
<td>Topic</td>
<td>Description</td>
</tr>
<tr>
<td>------------------------------</td>
<td>--------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>Stomatal conductance</td>
<td>In good weather, May and June 1990, one diurnal determination of photosynthesis and stomatal conductance. Plant water potential measured on 3 different days.</td>
</tr>
<tr>
<td>Laboratory analysis</td>
<td>September to November 1990.</td>
</tr>
<tr>
<td>Data analysis</td>
<td>December to February 1991.</td>
</tr>
<tr>
<td>Write dissertation</td>
<td>March to July 1991.</td>
</tr>
</tbody>
</table>
Equipment and facilities

1. HAVO Research Center

The Research Center provided office space, a plant drier for dry weight determinations and a Fisher digital scale for weight determinations. The office contains a computer for data entry and a Delta leaf area meter. The center has greenhouse facilities for seed germination experiments and has a soil sterilization facility.

2. University of Hawaii-Hilo

UHH Department of Tropical Agriculture provided indoor greenhouse space for the water relations experiments. The UHH Department of Soils provided a soil pressure chamber for water content and soil water potential determinations.

3. University of Hawaii-Manoa

Dr. D. Mueller-Dombois (with Dr. Vitousek, Stanford University) of the Botany department provided microloggers for monitoring light levels for the determination of forest light regimes, a plant pressure chamber for determination of plant water potentials, and LICOR leaf
area index meter, and other field equipment, such as shovels, soil corers, and soil cans. Dr. Friend provided a LICOR photosynthesis meter for measurements of gas exchange.
Fig. 1.1. Location of Hawaii Volcanoes National Park in reference to the State of Hawaii and the Pacific basin.
Fig. 1.2. Location of ecological zones in Hawaii Volcanoes National Park and invasion range of *Myrica faya* (thatched area), (modified from Camrath and Tunison 1992.)
Literature cited


Vitousek, P.M. 1990. Biological invasions and ecosystem processes: Towards an integration of population biology and ecosystem studies. Oikos 57:7-143


PART II: ORIGINAL DISSERTATION RESEARCH
CHAPTER 2
STRUCTURE AND DYNAMICS OF MYRICA FAYA IN MESIC RAIN FOREST COMMUNITIES OF HAWAII VOLCANOES NATIONAL PARK

Abstract

The population dynamics of the invading alien tree *Myrica faya* in closed canopied rain forest communities was investigated in Hawaii Volcanoes National Park. Bird-disseminated seed inputs, seed germination and seedling growth were monitored. Seed inputs did not appear to be a major factor limiting *Myrica* invasion of the rain forest sites under study. However, *Myrica* seed germination was low under dense fern cover (11 to 25%) compared with germination of the control (60%). Also, *Myrica* seedling survival and growth was much lower under the fern cover than on open canopied sites. The native understory fern cover was found to influence light availability to seedlings and saplings by reducing incoming light to 2% of full sun. While recruitment does not occur under intact *Dicranopteris* fern, recruitment has occurred in gaps in the understory fern cover. Infilling of the mid-canopy by the crowns of established *Myrica* in *Metrosideros/Cibotium* tree fern forest increased the LAI of these communities which further reduced light availability to the forest floor. The population development of *Myrica* may begin to
stagnate as lower light availability reduces the understory recruitment of seedlings and saplings. The bell-shaped size distribution of Myrica in the rain forest indicates that there is an initial establishment and growth of trees into larger size classes followed by the suppression of new regeneration.

Native community dynamics may change with the colonization of Myrica. The development of a subcanopy of Myrica reduces the potential for Metrosideros regeneration and reestablishment after dieback of the cohort of Metrosideros in the overstory. The addition of Myrica increases the canopy leaf area index and reduces light availability to the forest floor. Metrosideros polymorpha, which is less shade-tolerant than Myrica, may not remain the dominant canopy tree in the rain forest, where potential reestablishment of Metrosideros after canopy dieback is inhibited by the occurrence of Myrica in the new canopy.
Introduction

The nature of the native plant communities in the Hawaiian Islands, biotically impoverished and structurally simplistic, often predisposes them to invasion by aggressive alien weeds (Loope and Mueller-Dombois 1989). The invasion of the alien tree *Myrica faya* into the montane forests of Hawaii has been relatively recent (Whiteaker and Gardner 1985) and presents a threat to the maintenance and continued existence of the native state of these forests (Smith 1984). The goal of this study was to determine potential constraints to the invasion of montane rain forests by *Myrica.*

The process of invasion is a function of both the population ecology of the invading species and the suitability of the habitat (Mooney and Drake 1989). The recent invasion of *Myrica* into the open canopy forests of Hawaii Volcanoes National Park (HAVO) has lent support to this concept. Copious seed production, dispersal by birds, and rapid growth rates in open canopy forests, which provide suitable light and temperature conditions for germination and growth, have facilitated the rapid establishment of this invading species (Vitousek and Walker 1989). However, in closed canopy rain forest communities, where light availability in the understory is low (Burton and Mueller-Dombois 1984), the establishment
of *Myrica* has been limited. The habitat and structural characteristics of rain forest communities may present a barrier to the invasion of *Myrica*.

Most of the montane forests of Hawaii are characterized by a presence of a monodominant tree, *Metrosideros polymorpha* in scattered, open canopied, or closed canopied stands, often with an understory layer of dense fern cover (Mueller-Dombois 1980). Observations and measurements of the natural population and community dynamics of *Metrosideros* in the rain forest have shown that the native fern cover can inhibit the establishment of *Metrosideros* by reducing light availability at the forest floor (Mueller-Dombois 1980, Burton and Mueller-Dombois 1984). However, a particular aspect of the population dynamics of *Metrosideros* is canopy decline or dieback, a phenomenon in which an entire mature stand exhibits a synchronous decline in vigor (indicated by a gradual reduction in the crowns of individuals) and dies within a relatively short period of time (Mueller-Dombois 1980). Young saplings and trees on the same site have little or no crown reduction or decline (Mueller-Dombois et al. 1980) compared to overstory trees. The opening of the overstory during canopy decline can increase *Metrosideros* regeneration and the establishment of alien plants (Jacobi et al. 1988).
Certain aspects of the biology of *Myrica*, such as low seed germination and limited survival under the low light conditions (Vitousek and Walker 1989) commonly found in the understory of the rain forest (Burton and Mueller-Dombois 1984), may reduce the invasion potential of this alien weed into closed canopied rain forest habitat. However, canopy dieback of *Metrosideros* and subsequent opening of the overstory canopy may play a role in increasing the establishment of *Myrica*. Seed inputs, seed germination, and seedling growth were measured to determine the potential for *Myrica* invasion with regard to the characteristics of rain forest habitat and community structure. I hypothesized that the community structure of intact rain forest communities would influence light availability in such a way as to present a barrier to the invasion of *Myrica*.

**Study area**

The study was conducted in HAVO on the Island of Hawaii (155° 14' lat and 19° 24' long) between 1116 and 1182 m in elevation (Fig. 2.1). A representative successional sequence of *Metrosideros* rain forest communities was selected for the study of community-level constraints within the invasion range of *Myrica*. The
three rain forest sites selected for this study, developed after the 1790 explosive eruption of Kilauea Volcano which destroyed the forest and laid down a layer of ash and cinder (Holcomb 1987). Young, mature and *Metrosideros* forest in a dieback state characterize sites 1, 2 and 3, respectively. The different successional stages represented by each site are believed to have resulted from different rates of plant colonization and community development after the eruption (Mueller-Dombois, pers. comm.).

Two other sites were selected for a study of the *Myrica* seedling growth and population development. The vegetation at site 7 (Fig. 2.1), near Keanakakoi Crater, is an open canopied *Metrosideros* forest which lies in the transition zone between the rain forest and submontane forest environments. Site 8, near Puhimau Crater, also located in the transition zone between the rain forest and submontane forest environments, is characterized by a closed canopied *Myrica* forest.
Methods

Community composition and structure

Vegetation cover and species composition were determined using point and line intercept methods (Mueller-Dombois and Ellenberg 1974) along a 100 m transect established in each 1 ha plot.

Leaf area index and percent cover of vegetation by height class were measured for a determination of community structural characteristics. Leaf area index was measured in 1 m intervals from 0 to 6 m from the forest floor using a LICOR plant canopy analyser on very cloudy days. Percent cover of vegetation by height class, at sites 1, 2 and 3, were determined using the optical point quadrat method of MacArthur and Horn (1969) using a Minolta 35 mm camera, telephoto lens and lens grid.

Population structure

The population size structures of Myrica and of Metrosideros polymorpha and Ilex anomala were determined for a quantitative assessment of population status and natural regeneration success. The three 1 ha plots were divided into 10 x 10 m subplots on sites 1, 2 and 3. A stratified random sample of fifteen to twenty 10 x 10 m subplots was selected on the basis of number of
individuals represented on each site (more than 50 but less than 100 individuals were counted) to determine tree density, height and basal diameter of each species. Basal diameter was measured above the butt swell with a diameter tape. Height was measured using a clinometer and distance tape. Mature trees were defined as those over 5 m tall with a basal diameter greater than or equal to 5 cm. Saplings were defined as those from 1 to 5 m tall or less than 5 cm in basal diameter. Plants less than 1 m but greater than 10 cm in height were considered seedlings. Eight 10 x 10 m subplots and four 5 x 5 m subplots were selected to determine the density and height of saplings and seedlings, respectively, at each site. The number of dead standing trees was also determined for Metrosideros as a measure of the degree of canopy dieback at each site. Site 8 was also selected for this study. Here, a nearly monospecific stand of Myrica faya has developed, which is about 1.5 ha in size (Aplet, unpublished). In this stand, a transect of ten 10 x 10 m continuous subplots was established. Due to the advanced degree of decay of remnant Metrosideros stems, the number of dead standing trees was not determined at this site. The Kolmogorov-Smirnov goodness of fit test for a normal distribution was performed on frequency data in 2 cm basal diameter size classes.
Growth rates of naturally established trees

Basal diameter growth rates of established trees of *Myrica faya* and *Metrosideros polymorpha* were monitored at sites 1, 2 and 3 for one year. Fifteen to 20 trees of each species at each site were selected to represent a range of basal diameter size classes. Permanent paint was used as a marker where basal diameter was measured on each tree to assist in the accuracy of remeasurement.

Seed inputs

*Myrica faya* seed inputs into the three rain forest communities (sites 1, 2 and 3) were determined in a seed trap study. Twenty seed traps were randomly set up under the forest canopy in each of the 1 ha plots and monitored over 1 year. Each seed trap was made of pvc pipe and was built as a 40 x 25 cm frame standing on four 30 cm high legs. A very fine nylon mesh bag (40 x 25 x 15 cm deep) was attached. The immediate species cover over each seed trap was noted. Thus, some seed traps were placed directly under *Myrica* crowns while other traps were under the crowns of other tree species. Total *Myrica* seed inputs were determined for each site.
Seed germination

Seed was collected in July, August and September 1989 from *Myrica* adults growing at site 7 for a study of seed germination and germinant survival at sites 1, 2 and 3. In October 1989, three plastic trays (55 x 28 x 20 cm deep) each with 38 cups were situated under the canopy of each site and filled with soil from that site. Each cup of each tray was sown with 10 *Myrica* seeds for a total of 380 seeds per tray. Each tray was partially buried in the ground and a box made of 1 cm x 1 cm wire mesh was built around each tray to prevent seed predation.

Seed germination and seedling survival were monitored over 10 months. A greenhouse control was kept to determine the number of viable seeds germinating under optimal conditions of light and moisture.

Seedling transplant experiment

*Myrica faya* seedlings were transplanted into the study sites to determine seedling growth and mortality under different habitat conditions. Hundreds of young *Myrica* seedlings were collected from near Keanakakoi Crater during the month of September. These seedlings were planted in trays of soil and maintained in the greenhouse for 6 weeks until there were enough seedlings 5 cm in height to outplant. These seedlings were utilized where
few or none were present at the study sites. In November, *Myrica* seedlings of uniform size were outplanted. Fifteen seedlings were spaced 1x1 m apart on each of 15 m² plots at each site. There were 45 seedlings planted per site. The height and basal diameter of these seedlings were measured monthly from December, 1989 to November, 1990.

Seedlings were also transplanted back to site 7 to compare seedling growth in an open canopied habitat considered optimal for *Myrica* establishment with seedling growth at the closed canopied rain forest sites.

In a release experiment the *Dicranopteris* understory at site 1 was removed from above half of the seedlings, randomly selected, that were still surviving in July, 1990. In November, 1990, all remaining seedlings were harvested for biomass determinations.

**CO₂ assimilation and stomatal conductance of *Myrica***

A better understanding of the ability of *Myrica* to photosynthesize in shade was needed to help interpret seedling survival and growth under low light availability. CO₂ assimilation for sun- and shade-grown *Myrica* plants at different levels of light availability was experimentally determined under controlled conditions in a greenhouse. *Myrica* branches were excised from sun- (exposed) and shade-grown trees, ends cut under water, and 6 sample
branches of each type were put in water-filled flasks and placed under shade cloths of different densities. Quantum flux (PAR), temperature, relative humidity, and gas exchange rate were determined using a LI-COR 6000 portable photosynthesis meter. The age of the leaves measured was kept as similar as possible by counting to the 14th and 15th leaf below the new foliage.

**Soil characteristics and light availability**

To determine the characteristics of the habitat in each community that might be important in influencing *Myrica* establishment, soil moisture content and light availability were measured.

Soil moisture content, bulk density, pH, and soil N were compared between study sites. Soil core samples were taken from the 5 to 10 cm soil depth twice a month for about 10 months.

The difference in light environments with height through the canopy at each site was characterized from May to July, 1990. Light levels at the ground level and to a height above the fern cover were measured using LI-COR quantum sensors and GaAsP photodiodes (with a spectral response range between 300-680 nm) on each of three plots at each study site. Sensors were set upon poles at 6.5 m, 4 m, 3 m, 2 m, 1 m and at ground level and attached to a
Campbell CR-10 micrologger for data collection. The poles were anchored by guy wires which assisted in leveling the sensors. LICOR quantum sensors were also placed in a nearby open area to attain quantum readings for ambient fully exposed conditions. Measurements were taken every 10 s and averaged over one minute for 3 to 6 full days.

Results

Community composition and species cover

Metrosideros polymorpha is the dominant canopy tree species at all sites with varying degree of canopy cover and density (Tables 2.1 and 2.2). Invasion of Myrica in this area of the rain forest has occurred within the past 15 to 20 years and the degree of Myrica establishment varies between the study sites.

Each study site is characterized by a particular assemblage of species though there are often species common to each. Subcanopy tree species commonly found in rain forest communities include Ilex anomala, Myrsine lessertiana and Coprosma ochracea (Table 2.1) which do not reach heights greater than 10 m (Table 2.2). Vaccinium calycinum is a common shrub and Lycopodium cernuum is a common club moss (Table 2.1). Cibotium glaucum and Dicranopteris linearis often form distinct and dense understory fern layers.
A dense stand of *Metrosideros* and an understory of *Dicranopteris linearis* are conspicuous features of the vegetation of site 1 (Table 2.1). *Dicranopteris*, a mat-forming fern, grows best where the overstory is relatively open and light availability is high. This fern typically produces a thicket 1 to 2 m in height. *Myrica faya* is becoming established in patches of *Lycopodium cernuum* where there is little *Dicranopteris* cover, in communities such as site 1, and also in patchy areas of past pig disturbance of the *Dicranopteris* fern cover. In these pig-disturbed areas much of the understory is now dominated by the alien grass *Erharta stipoides*.

*Cibotium glaucum*, the tree fern, is the dominant understory component of site 2. It produces a nearly horizontal layer of fronds ranging from 3 to 6 m in height. *Myrica faya* has become well established at this site (Table 2.2). The cover and density of *Metrosideros* is much lower here than at site 1 and some trees appear to be undergoing crown decline.

Canopy dieback of *Metrosideros* is extensive at site 3 resulting in low overstory cover values (Table 2.1). *Myrica faya* is quickly becoming the dominant canopy tree at this site. The understory consists of a dense cover dominated by *Cibotium* and supplemented with the presence
of young saplings and small trees of *Metrosideros, Myrica, Ilex, Coprosma* and *Myrsine*. Dense mats of mosses and lichens are often found on decaying logs and on the ground.

The vegetation at site 7 is an open canopied *Metrosideros* forest that was thinned by cinder fall during the 1959 eruption of Kilauea Iki. Though *Myrica* is found at this site, management efforts over the past seven years have aimed at removing most of the *Myrica* population. Shrubs common to the seasonal submontane forest are found in the understory: *Styphelia tameiameiae, Dodonaea viscosa, Carex wahuensis, Machaerina angustifolia* and *Andropogon virginicus* (Table 2.1). Also, the *Metrosideros* canopy is relatively open and various lichen species can be found on the ground.

A dense stand of *Myrica* occupies site 8 (Table 2.2). Most of the *Metrosideros* which was once present at this site has died and decaying stumps of trees remain. There is relatively little understory (Table 2.1). A few alien species can be found around the edge of the stand where the overstory is less dense.

**Community structural characteristics**

The native rain forest is stratified into two predominant layers: the upper canopy of *Metrosideros* and
an understory layer of fern (Fig. 2.2). *Metrosideros* polymorpha and *Ilex anomala* are canopy codominants with *Dicranopteris linearis* as the dominant understory species at site 1 (Fig. 2.2A). The *Cibotium* tree fern layer between 3 to 6 m is a dominant feature of the vertical profile of site 2 (Fig. 2.2B). Plant species in the understory are relatively sparse and composed mostly of grasses and mosses. The reduced cover of the upper canopy of *Metrosideros* is evident when compared to the younger stand at site 1 and *Myrica* is becoming a dominant component of the mid-canopy between 5 and 15 m. Reduction of *Metrosideros* overstory cover values is particularly evident at site 3 (Fig. 2.2C). Here also, tree ferns are the dominant cover between 3 to 6 m and the understory is composed primarily of *Sadleria cyatheoides*, *Lycopodium cernuum* and various grasses, sedges, liverworts and mosses. Young *Myrica* trees have grown above the tree fern layer and are now becoming the predominant tree species in the canopy.

Rain forest LAI and light availability

The leaf area index of the upper *Metrosideros polymorpha* canopy ranged from 2.5 m\(^2\) m\(^{-2}\) to less than 1 m\(^2\) m\(^{-2}\) depending on the degree of *Metrosideros* canopy decline or canopy gaps (Table 2.3, Fig. 2.3). Table 2.3 compares
changes in LAI at the ground surface and above 6 m at different rain forest sites with varying degrees of Myrica present in the canopy. The LAI at site 1 was fairly low throughout the relatively open Metrosideros canopy (Table 2.3), except at 1 m where the prominent Dicranopteris mat fern cover increased the LAI to 6.3 m² m⁻² (Fig. 2.3, Table 2.3). Where gaps occur in the Dicranopteris fern cover, the LAI above 6 m increased with the presence of Myrica in the canopy, while LAI at the ground level decreased in the absence of Dicranopteris fern (Table 2.3).

The understory fern layer of Cibotium added considerably to the canopy leaf area index at sites 2 and 3 (Fig. 2.3). The open overstory canopy and low overstory LAI above the tree fern layer at site 3 (the dieback site) provided a striking contrast to the much higher LAI at site 2 in which the Metrosideros overstory was still relatively intact and Myrica was present in the subcanopy (Fig. 2.3). When comparing Metrosideros/Cibotium forest or Metrosideros/Dicranopteris forest, with and without the presence of Myrica, it appeared that the invasion of Myrica in these communities has added about 1 m² m⁻² of leaf area to the total canopy LAI (Table 2.3). Where Myrica had developed into a closed canopied monospecific stand at site 8, the LAI is around 5 m² m⁻².
There was more light in gaps (Fig. 2.4A) than under full *Dicranopteris* cover (Fig. 2.4B) at site 1. Under the *Dicranopteris* fern, 57% of the measurements of the photosynthetically active radiation (PAR) during midday hours were less than 5 \( \mu \text{mol} \, \text{m}^{-2} \, \text{s}^{-1} \), whereas in gaps only 6% of the measurements were in this range. The occurrence of *Myrica* in gaps, where the *Dicranopteris* thicket has broken down, but not within an intact thicket, suggests that light levels below the *Dicranopteris* fern are too low for *Myrica* establishment. Very low light levels occur at site 2 under *Cibotium* mixed with *Myrica* (Fig. 2.4C), where 68% of the measurements of PAR during midday were below 5 \( \mu \text{mol} \, \text{m}^{-2} \, \text{s}^{-1} \). Light availability in the understory is similar at both the *Metrosideros/Cibotium* site without *Myrica* invasion (Fig. 2.4D) and site 3 (the dieback site) (Fig. 2.4E) indicating the strong influence of the tree fern cover on understory light availability. Light levels under a monodominant canopy of *Myrica* (Fig. 2.4F) were also very low (58% of the measurements of PAR at the forest floor were less than 5 \( \mu \text{mol} \, \text{m}^{-2} \, \text{s}^{-1} \) during midday). The light availability (Fig. 2.4G) under the volcanically thinned *Metrosideros* canopy at site 4, where the understory cover was rather open and scattered, was similar to that determined under a canopy gap in the rain forest (Fig. 2.4A).
**CO₂ assimilation**

Sun-exposed *Myrica* leaves had a light compensation point of around 10 PAR μmol m⁻² s⁻¹ and a light saturation point around 1500 μmol m⁻² s⁻¹. The maximum rate of CO₂ assimilation for sun-exposed leaves at light saturation was 13.5 μmol m⁻² s⁻¹ (Fig. 2.5). Leaves of *Myrica* trees growing in shaded habitats had a light compensation point of 6.5 μmol PAR m⁻² s⁻¹ and a light saturation point of 350 μmol PAR m⁻² s⁻¹ (Fig. 2.5 A,B). The maximum rate of CO₂ assimilation of shade grown leaves was about 7 μmol m⁻² s⁻¹.

**Population structure**

Certain aspects of *Metrosideros* stand development can be discovered when comparing density (Table 2.2) and size class distribution between sites (Fig. 2.6). A young dense stand of *Metrosideros* has developed at site 1 (*Dicranopteris* in the understory) (Fig. 2.6A). The median basal diameter size is 14.5 cm. Seedling and sapling recruitment of *Myrica* was low and recruitment into larger size classes is discontinuous (Fig 2.6B). Invasion of *Myrica* onto the site is recent and only a few individuals are currently producing seed.

The population of *Metrosideros* at site 2 (mature *Metrosideros/Cibotium* stand with incipient canopy
breakdown) has undergone a considerable reduction in density compared to site 1 (Fig. 2.6D). The median diameter size of 24.1 cm indicates that this is an older stand than that found at site 1 (Table 2.2). Regeneration and recruitment of young *Metrosideros* trees into larger size classes is low. *Myrica faya* is well established in larger size classes and mortality of established canopy trees is low. However, *Myrica* seedlings are abundant but few appear to survive to grow above the tree fern canopy (Fig. 2.6E). The frequency of trees greater than 5 cm basal diameter fits a normal distribution, (Kolmogorov-Smirnov, $D(.05) = .08060$), indicating a wave-like pattern of recruitment characteristic of cohort establishment (Mueller-Dombois 1986).

The density of *Metrosideros* has been greatly reduced at site 3 (dieback site) (Fig. 2.6G). Though there are abundant small *Myrica* seedlings, mortality is high and recruitment into larger size classes is low (Fig. 2.6H). An analysis of the frequency distribution of *Myrica* trees indicates a normally distributed population cohort ($D(.05) = .08118$) at site 3.

Strong evidence for the wave-like pattern of establishment of the *Myrica* population in the rain forest is also indicated by the striking bell-shaped distribution ($D(.05) = .0507$) (Fig. 2.6K) at site 8. Here *Myrica* has
developed into a dense monospecific stand with only a few stems remaining of the original Metrosideros forest which once occupied this site. There is no seedling or sapling regeneration of Myrica or Metrosideros in the understory.

The populations of Ilex anomala at site 1 (Fig. 2.6C) and site 3 (Fig. 2.6I) are well established and relatively stable. At site 2 (Fig. 2.6F), the size structure of Ilex shows a disruption from the seedling to the sapling stage, indicating that some factor limits sapling development at this site. This population structure is typical of the less abundant tree species which are common in this rain forest.

Myrica seed inputs into the rain forest

Seed capture at site 1 was much lower than secondary inputs from the seed rain of established trees at other sites. As there were no fruiting Myrica at site 1, seed inputs here are assumed to be primarily from bird dispersal. Twenty Myrica seeds were captured in site 1 during the monitoring period, representing an input of 100,000 seeds ha\(^{-1}\) yr\(^{-1}\). An estimated input of 33,367,500 seeds ha\(^{-1}\) yr\(^{-1}\) at site 2 and 37,090,000 seeds ha\(^{-1}\) yr\(^{-1}\) at site 3 are mostly of secondary seed inputs from established trees. Less than 3% of the total Myrica seed
inputs at sites 2 and 3 were collected from under the crowns of tree species other than *Myrica*.

**Seed germination**

Seeds planted into trays at site 1 germinated 2 weeks ahead of those planted into trays at site 2 and 3. The percentage of viable seeds germinated at site 1 (Table 2.4) was almost three times greater than at sites 2 and 3. The greatest survival of germinants occurred at site 1. The *Dicranopteris* layer was about 0.5 m deep over the seed trays (LAI 3 m$^2$ m$^{-2}$), and light reaching the seed trays was greater than at sites 2 and 3. Under conditions of high light and moisture availability in the greenhouse, 60% of the seeds germinated.

An average of six naturally established *Myrica* seedlings (about 10 cm in height) were recorded at each of three 10 x 10 m plots cleared of *Dicranopteris* fern 2 years earlier. Neither *Myrica* seedlings nor saplings were found occurring naturally within full *Dicranopteris* cover but many *Coprosma* tree seedlings, a native understory tree, were detected under the fern mat.

**Growth**

Relative basal diameter growth rates for classes below 5 cm tended to be greater for *Myrica* at site 1 than at
sites 2 and 3, however basal diameter growth rates were not statistically different (Table 2.5). Overall, the growth of seedlings and saplings of Myrica on sites 2 and 3 tended to be lower than at site 1. Measures of relative height growth of Myrica seedlings and saplings at site 2 (Fig. 2.7) indicated that by 3.5 m in height, growth had stopped. A strong suppression of the growth of young Myrica seedlings and saplings below the tree fern layer, which is between 3 and 6 m in height, is indicated. Overall, the relative growth rates of Myrica trees were greater than those of Metrosideros (Table 2.5).

The relative growth rates of transplanted Myrica seedlings were not significantly different among sites 1, 2 and 3 (Fig. 2.8) but were significantly lower than the relative growth rates of seedlings at site 7. Site 7, transitional between the rain forest and seasonal submontane zone (Fig. 2.1), is drier and more nutrient limited than the rain forest sites (Table 2.6). The higher growth rate of transplanted seedlings at site 7, compared to that at rain forest sites, is believed to be due to higher light availability here than found in the rain forest.
Discussion

There is substantial evidence that an individual invading species can alter the characteristics of native ecosystems (Vitousek 1986). Establishment of the invading nitrogen-fixing tree Myrica in HAVO ecosystems has been occurring over the past 30 years and has been shown to increase soil nitrogen status on nitrogen poor young volcanic sites (Vitousek et al. 1987, Vitousek and Walker 1989). However, another potential effect of the invasion of Myrica faya into Hawaiian ecosystems is to alter the structure and composition of native communities. Myrica faya stands of 733 and 1000 trees ha\(^{-1}\) have been reported in the open-canopied seasonally dry Metrosideros forest (Whiteaker and Gardner 1987, Vitousek and Walker 1989). In the transition zone between rain forest and seasonal submontane forest, a monospecific stand of 1838 trees ha\(^{-1}\) has developed. Characteristics of Myrica, such as the ability to rapidly invade open-canopied sites and form dense stands, which results in the displacement of native species, suggests that Myrica could become the dominant tree in some Hawaiian ecosystems. In the Hawaiian rain forest however, Myrica does not colonize sites as readily. The maximum density of Myrica found in the mesic rain forest during this study was 365 trees ha\(^{-1}\) and further population recruitment was limited. Low growth rates and
high mortality of *Myrica* in the understory of intact Hawaiian rain forest communities will probably prevent it from becoming the dominant tree in these communities. Seed inputs into rain forest communities, characterized by the low presence of established *Myrica*, were not limiting to *Myrica* invasion. While secondary seed inputs from established trees were found to be much greater than primary inputs by birds, bird dispersed seed inputs under non-*Myrica* crowns (100000 seeds ha\(^{-1}\) yr\(^{-1}\)) in the rain forest were within the range calculated by Vitousek and Walker (1989), 23700-254000 seeds ha\(^{-1}\) yr\(^{-1}\), for open-canopied sites where bird dispersal of *Myrica* seed has been observed and where the *Myrica* population growth is high.

Seed germination rates were relatively high in the rain forest, 11 to 25% (though much lower than in viability tests), compared to the results of Walker and Vitousek (1989) for volcanically disturbed sites where high soil temperatures and low moisture availability reduced germination to less than 0.12%. Moderate temperatures (18 to 20\(^{\circ}\)C) and high relative humidities (75 to 80%) under the rain forest canopy probably contribute to higher germination rates than on open, volcanically disturbed sites.
It has long been recognized that forest canopy structure, particularly LAI, affects light penetration though the canopy. The total leaf area indices of the rain forest communities in this study (LAI 5 to 6) were comparatively low for tropical rain forests (LAI≈8) (Larcher 1991). The low LAI of the canopy (1.7 to 2.3) and open crown structure of the overstory Metrosideros in these communities allows a large proportion of incident light through to the understory. On the other hand, the fern layers in the understory attenuate a large proportion of incoming light to the forest floor and add a substantial amount of leaf area to the total LAI. Myrica seedlings have been found to have very low growth rates but have high survival when grown under light conditions of less than 4% of full sun (Vitousek and Walker 1989). However, much of the light available (70% of measurements) at the forest floor, in rain forest communities, was less than 2% of full sun, which probably led to the high mortality rates of seedlings (85%) observed in this study. Shade-adapted seedlings of Myrica can survive for a few months under the low light conditions found under the cover of Cibotium tree fern or Dicranopteris fern. However, 68% of midday light measurements at the forest floor were below the light compensation point, 6.5 μmol m\(^{-2}\) s\(^{-1}\), for shade-adapted Myrica, which resulted in very
low growth rates and high mortality of transplanted seedlings. An analysis of Myrica population structure shows that under the dominant fern layer, there is little recruitment of Myrica from seedling to sapling stages.

The dense closed understory of Dicranopteris fern or Cibotium tree fern cover also presents a barrier to the development of Metrosideros seedlings to the sapling stage (Burton and Mueller-Dombois 1984). Though Metrosideros seedlings grow slowly under light conditions as low as 0.6% of full sun, long term survival under such conditions not been studied (Friend 1980). However, at 10% of full sun, mortality of Metrosideros seedlings is about 14% per year (Burton and Mueller-Dombois (1984).

Myrica faya colonization of rain forest sites appeared to occur in gaps particularly in the fern understory where individual Cibotium have fallen; characteristically producing a gap 4 to 5 m in diameter. Also, Myrica has been observed in gaps of the Dicranopteris fern cover where pig activity has damaged and interrupted the fern cover and promoted the invasion of alien grasses (Stone et al. 1992). The removal of dense overstory on a transitional rain forest site, through the artificial creation of gaps, resulted in the establishment of 150 Myrica seedlings and saplings per hectare within 3 years (Aplet 1993). The influence of canopy gaps on Myrica
establishment in the rain forest was also evident in the case of the natural dieback of the overstory tree *Metrosideros*. Dieback of the *Metrosideros* canopy increases light availability through the canopy to the tree fern layer. However, falling trees and wind damaged tree ferns create gaps in the fern understory, increasing light levels at the forest floor. Thus, invasion of *Myrica* into rain forest communities appears to require some gap-creating disturbance of the fern understory.

*Myrica faya* has begun to take a mid-canopy position in the rain forest. With the colonization of *Myrica*, gaps in the *Metrosideros* canopy are reduced and the consequential reduction in light availability at the forest floor suppresses *Myrica* seedling growth and lowers the likelihood of seedling development to the sapling stage. Light levels under a monospecific stand of *Myrica* are so low as to prevent recruitment not only of its own progeny but also of almost any other species.

The community dynamics of the rain forest are changing with the colonization of *Myrica*. *Metrosideros polymorpha* has maintained its dominant canopy position in the Hawaiian rain forest probably due to the the evolution of subspecific types which function as successional replacers (Mueller-Dombois 1987). Specific aspects of the life history and natural population dynamics of *Metrosideros*
predispose this species to the development and synchronous death of cohort stands (Mueller-Dombois 1986, 1987).

During the decline of a mature cohort stand of *Metrosideros*, a new wave of *Metrosideros* regeneration usually becomes established and the redevelopment of a new cohort stand may begin. However, with the invasion of *Myrica* into dieback stands of *Metrosideros*, light availability and soil characteristics are being altered. *Metrosideros polymorpha* germination is inhibited by *Myrica* litter (Walker and Vitousek 1991) and seedling survival and growth of *Metrosideros* is dependent on light availability (Burton and Mueller-Dombois 1984). Further reductions in light availability with the colonization of *Myrica* into stands characterized by the dieback of *Metrosideros* will most likely inhibit the development of a new *Metrosideros* regeneration. *Metrosideros polymorpha* may lose its position as the dominant canopy species in HAVO rain forests with the invasion of *Myrica*. 
Table 2.1: Species composition and percent plant cover determined by point and line intercept methods on five study sites in HAVO. Taxonomic nomenclature follows Wagner et al. (1990).

<table>
<thead>
<tr>
<th>Species</th>
<th>Site 1</th>
<th>Site 2</th>
<th>Site 3</th>
<th>Site 7</th>
<th>Site 8</th>
</tr>
</thead>
<tbody>
<tr>
<td>Metrosideros polymorpha</td>
<td>74.6</td>
<td>52.7</td>
<td>11.3</td>
<td>48.9</td>
<td>8.8</td>
</tr>
<tr>
<td>Myrica fae</td>
<td>1.0</td>
<td>83.7</td>
<td>24.0</td>
<td>11.3*</td>
<td>89.8</td>
</tr>
<tr>
<td>Ilex anomala</td>
<td>27.8</td>
<td>0.6</td>
<td>6.8</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Cibotium glaucum</td>
<td>0.8</td>
<td>79.3</td>
<td>92.1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Dicranopteris linearis</td>
<td>63.8</td>
<td>0</td>
<td>0.6</td>
<td>0</td>
<td>0.1</td>
</tr>
<tr>
<td>Coprosma ochracea</td>
<td>7.8</td>
<td>0.8</td>
<td>11.7</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lycopodium cernuum</td>
<td>7.8</td>
<td>0</td>
<td>2.2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Sadeleria cyathoeides</td>
<td>0.8</td>
<td>0.8</td>
<td>16.1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Occhanta stipoides</td>
<td>2.1</td>
<td>3.2</td>
<td>3.8</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Vaccinium calycinum</td>
<td>0.4</td>
<td>0.2</td>
<td>2.1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Myrsine lessoniana</td>
<td>0.7</td>
<td>0.1</td>
<td>0.6</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Spagghlotitis plicata</td>
<td>0.7</td>
<td>0</td>
<td>0.4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Isachne distichophylla</td>
<td>0</td>
<td>0.7</td>
<td>0.4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Carex wahusisis</td>
<td>0.2</td>
<td>0.2</td>
<td>1.9</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Salaria gracilis</td>
<td>2.8</td>
<td>0</td>
<td>2.2</td>
<td>0</td>
<td>0.3</td>
</tr>
<tr>
<td>Machaerina angustifolia</td>
<td>0.1</td>
<td>0</td>
<td>2</td>
<td>1.5</td>
<td>0</td>
</tr>
<tr>
<td>Sphaerocionium lanceolatum</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Phalis tankervilliae</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pteridium aquilinum</td>
<td>0</td>
<td>0</td>
<td>0.6</td>
<td>0.5</td>
<td>0</td>
</tr>
<tr>
<td>Psidium guajava</td>
<td>0</td>
<td>0</td>
<td>0.4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Smilax melostomifolia</td>
<td>0</td>
<td>0</td>
<td>0.4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Odontoschisma gracile</td>
<td>0</td>
<td>0</td>
<td>0.2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Ophioglossum pendulum</td>
<td>0</td>
<td>0</td>
<td>0.05</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pellonum campulatum</td>
<td>0</td>
<td>0</td>
<td>0.05</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Cibotium hawaiense</td>
<td>0.5</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Vaccinium reticulatum</td>
<td>0.5</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Hypericum degeneri</td>
<td>0.1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Hedychium gardnerianum</td>
<td>0.1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pellonum nudum</td>
<td>0.1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Eraphoglossum hirtum</td>
<td>0</td>
<td>0.2</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Astelia menziesiana</td>
<td>0</td>
<td>0.4</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Styphelia taniameaeae</td>
<td>0</td>
<td>0</td>
<td>5.6</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Dodonea viscosa</td>
<td>0</td>
<td>0</td>
<td>3.9</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Andropogon virginicus</td>
<td>0</td>
<td>0</td>
<td>1.4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Gahnia gahnumiformis</td>
<td>0</td>
<td>0</td>
<td>1.4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Anemone hupehensis</td>
<td>0</td>
<td>0</td>
<td>0.5</td>
<td>0.2</td>
<td>0</td>
</tr>
<tr>
<td>Sporobolus africanus</td>
<td>0</td>
<td>0</td>
<td>1.2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Wilksstromia phillyreifolia</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.2</td>
<td>0</td>
</tr>
<tr>
<td>Coprosma erinoidoides</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.6</td>
<td>0</td>
</tr>
<tr>
<td>Rubus argutus</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.2</td>
<td>0</td>
</tr>
<tr>
<td>Rubus rosiifolius</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.1</td>
</tr>
<tr>
<td>Basania sp.</td>
<td>0.6</td>
<td>0.4</td>
<td>6.2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Leucobryum seemanii</td>
<td>0</td>
<td>0.2</td>
<td>2.6</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Racomitrium langinosum</td>
<td>0</td>
<td>0</td>
<td>1.4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Cephaloza sandwicensis</td>
<td>0.2</td>
<td>0.8</td>
<td>0.8</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Calypoleta sp.</td>
<td>0</td>
<td>0.2</td>
<td>0.8</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Rhyzogonium sp.</td>
<td>0</td>
<td>5.4</td>
<td>3.8</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Cladonia sp.</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.9</td>
<td>0</td>
</tr>
<tr>
<td>Cladina sp.</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1.9</td>
<td>0</td>
</tr>
<tr>
<td>Sterocaulon volcani</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1.1</td>
<td>0</td>
</tr>
</tbody>
</table>

*Mechanically removed.
Table 2.2: Density, median basal diameter and median height of the five most common tree species in the rain forest of HAVO.

<table>
<thead>
<tr>
<th>Species</th>
<th>Density (trees ha(^{-1}))</th>
<th>Median basal diameter (cm)</th>
<th>Median height (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td><em>Metrosideros polymorpha</em></td>
<td>1540</td>
<td>591</td>
<td>352</td>
</tr>
<tr>
<td><em>Myrica faya</em></td>
<td>76</td>
<td>365</td>
<td>253</td>
</tr>
<tr>
<td><em>Ilex anomala</em></td>
<td>256</td>
<td>48</td>
<td>211</td>
</tr>
<tr>
<td><em>Myrsine lessertiana</em></td>
<td>4</td>
<td>13</td>
<td>58</td>
</tr>
<tr>
<td><em>Coprosma ochracea</em></td>
<td>92</td>
<td>152</td>
<td>242</td>
</tr>
</tbody>
</table>


Table 2.3: Leaf area index (LAI), above 6 m and at the ground level, of different forest sites with different degrees of *Myrica* invasion. Values are means of 5 measurements using the LAI-2000 plant canopy analyzer at three different locations at each site, with standard error in brackets.

<table>
<thead>
<tr>
<th></th>
<th>LAI (m² m⁻²)</th>
<th>Above 6 m</th>
<th>Ground level</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Metrosideros/ Dicranopteris</strong></td>
<td>0.69</td>
<td>6.30</td>
<td>(.13) (.14)</td>
</tr>
<tr>
<td><strong>No Myrica</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Site 1</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Gap in Dicranopteris</strong></td>
<td>1.68</td>
<td>3.37</td>
<td>(.24) (.23)</td>
</tr>
<tr>
<td><strong>Metrosideros/ Myrica</strong></td>
<td>3.75</td>
<td>5.00</td>
<td>(.18) (.10)</td>
</tr>
<tr>
<td><strong>Site 2</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Metrosideros/ Cibotium</strong></td>
<td>2.3</td>
<td>4.47</td>
<td>(.12) (.12)</td>
</tr>
<tr>
<td><strong>with Myrica</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Site 2</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Metrosideros dieback/ Cibotium</strong></td>
<td>.425</td>
<td>4.90</td>
<td>(.02) (.70)</td>
</tr>
<tr>
<td><strong>with Myrica</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Full Myrica cover</strong></td>
<td>5.55</td>
<td>5.49</td>
<td>(.12) (.14)</td>
</tr>
<tr>
<td><strong>Site 8</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2.4: *Myrica faya* seed germination and seedling mortality in trays placed under the canopies of three rain forest sites, October, 1989 to August, 1990. Values are means with standard error in brackets. Germination is the percentage of viable seeds sown. Mortality is the percentage of all seeds germinated and died during the 10 month study period.

<table>
<thead>
<tr>
<th>Site</th>
<th>Germination (%)</th>
<th>Mortality (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>25.2 (1.4)</td>
<td>85.9 (2.7)</td>
</tr>
<tr>
<td>2</td>
<td>11.4 (0.5)</td>
<td>88.9 (1.3)</td>
</tr>
<tr>
<td>3</td>
<td>13.3 (0.7)</td>
<td>64.9 (3.4)</td>
</tr>
</tbody>
</table>
Table 2.5: Relative basal diameter growth rates (cm cm\(^{-1}\) yr\(^{-1}\)) of established trees (≥ 5 cm basal diameter) and saplings (<5 cm basal diameter) of *Metrosideros polymorpha* (data from three sites combined) and *Myrica faya* at three rain forest sites. Values are means of 3 to 6 individuals with standard errors in brackets.

<table>
<thead>
<tr>
<th>Basal Diameter Class (cm)</th>
<th><em>M. polymorpha</em></th>
<th><em>M. faya</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>All sites</td>
<td>Site 1</td>
</tr>
<tr>
<td></td>
<td>M. polymorpha</td>
<td>M. faya</td>
</tr>
<tr>
<td>20-25</td>
<td>0.015(^a)</td>
<td>0.066(^b)</td>
</tr>
<tr>
<td></td>
<td>(0.005)</td>
<td>(0.004)</td>
</tr>
<tr>
<td>15-20</td>
<td>0.029(^a)</td>
<td>0.058(^a)</td>
</tr>
<tr>
<td></td>
<td>(0.008)</td>
<td>(0.011)</td>
</tr>
<tr>
<td>10-15</td>
<td>0.028(^a)</td>
<td>0.150(^b)</td>
</tr>
<tr>
<td></td>
<td>(0.010)</td>
<td>(0.041)</td>
</tr>
<tr>
<td>5-10</td>
<td>0.043(^a)</td>
<td>0.227(^b)</td>
</tr>
<tr>
<td></td>
<td>(0.012)</td>
<td>(0.045)</td>
</tr>
<tr>
<td>0-5</td>
<td>0.094(^a)</td>
<td>0.416(^b)</td>
</tr>
<tr>
<td></td>
<td>(0.023)</td>
<td>(0.052)</td>
</tr>
</tbody>
</table>

\(^a\)Comparisons of means in a row (t-test) are significantly different (P<0.05) except those with a common superscript.
Table 2.6: Soil characteristics of 5 study sites in HAVO. Values of bulk density, soil water content are means of samples taken over 10 months with standard error in brackets. All others n=3.

<table>
<thead>
<tr>
<th>Site</th>
<th>Bulk density (g cm⁻²)</th>
<th>Soil water content (%)</th>
<th>Soil pH</th>
<th>Soil N (NH₄⁺NO₃) (ug/g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.34 (.03)</td>
<td>60.67 (2.16)</td>
<td>5.8</td>
<td>3.3 (.5)</td>
</tr>
<tr>
<td>2</td>
<td>0.88 (.04)</td>
<td>29.96 (1.8)</td>
<td>5.6</td>
<td>5.7 (.9)</td>
</tr>
<tr>
<td>3</td>
<td>0.47 (.05)</td>
<td>47.65 (1.80)</td>
<td>5.6</td>
<td>2.9 (.3)</td>
</tr>
<tr>
<td>7</td>
<td>0.49 (.04)</td>
<td>14.16 (1.10)</td>
<td>6.3</td>
<td>1.0 (.2)</td>
</tr>
<tr>
<td>8</td>
<td>1.10 (.06)</td>
<td>33.5 (1.2)</td>
<td>5.7</td>
<td>6.6 (.9)</td>
</tr>
</tbody>
</table>
Fig. 2.1. Location of study sites in Hawaii Volcanoes National Park.
Hawaii Volcanoes National Park

KILAUEA CALDERA

Observatory

Puhimau Crater

0 1 2 km
Fig. 2.2. Vertical profiles of A) site 1, B) site 2 and C) site 3 indicating the percent cover of important species in 5 m height intervals and the understory cover less than 1 m. Legend:

- Metrosideros polymorpha,
- Myrica faya,
- Ilex anomala,
- Dicranopteris linearis,
- Cibotium glaucum,
- Other species,
Fig. 2.3. Vertical profile of leaf area index (LAI) from 0 to 6 m in height through the forest. Legend: ○ - site 1, □- site 2, ● - site 3.
Fig. 2.4 Frequency of light interception at ground level arranged in intervals of photosynthetic photon flux density (\text{umol m}^{-2} \text{s}^{-1}) for A) Site 1 - gap in \textit{Dicranopteris} cover prior to \textit{Myrica} invasion, B) Site 1 - under full \textit{Dicranopteris} cover, C) Site 2 - \textit{Cibotium} site with \textit{Myrica} invasion, D) \textit{Cibotium} site with no \textit{Myrica} invasion, E) Site 3 - \textit{Metrosideros} dieback site, F) Site 8 - \textit{Myrica} stand, G) Site 7 - open \textit{Metrosideros} forest.
Fig. 2.5. A) CO₂ assimilation of Myrica leaves at different levels of light (PAR, photosynthetically active radiation) availability adapted to growing in the sun (open circles) and shade (closed circles). B) Detail of graph A. Fitted line to sun-adapted leaves is \( Y = 1.516643 + 0.008166 \times X - 19.5667/X \), (\( R^2 = 0.8759 \)). Fitted line to shade-adapted leaves is \(-2.07426 + 1.094543 \times \ln (X)\), (\( R^2 = 0.9303 \)).
Fig. 2.6. Population structure (number of individuals per hectare in representative 2 cm basal diameter classes) of *Metrosideros polymorpha* (A-J), *Myrica faya* (B-K), and *Ilex anomala* (C-I) on site 1, site 2, site 3 and site 8. Closed bars are live trees, open bars indicate dead standing trees. Top number in left corner of panel indicates number of seedlings ha$^{-1}$ and the number below indicates number of saplings (2-4 cm basal diameter).
Fig. 2.7. Relative growth rates (mg g$^{-1}$ day$^{-1}$) for *Myrica* seedlings transplanted onto 4 sites and monitored over 11 months: Site 1- (○), site 2- (□), site 3- (●) and site 7- (■).
Fig. 2.8. Relative height (O) and basal diameter (●) growth rates (mm cm⁻¹ day⁻¹) of suppressed *Myrica* saplings established naturally on site 2.
Literature cited


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


CHAPTER 3
ECOLOGICAL FACTORS LIMITING MYRICA FAYA INVASION IN THE
SEASONALLY DRY SUBMONTANE GRASSLAND OF HAWAII VOLCANOES
NATIONAL PARK

Abstract

Myrica faya, an introduced tree, has been actively invading the montane and submontane ecological zones of Hawaii Volcanoes National Park (HAVO) since 1961. This study was designed to determine mechanisms controlling invasion into the seasonally dry submontane grassland of HAVO where an active invasion front of Myrica is present. Seed inputs at the invasion front were very low. Germination and early survival was promoted under partial and full shade provided by Melinus minutiflora, a fire-adapted alien grass present over much of the grassland. However, competition between Myrica seedlings and Melinus grass for soil moisture during the dry season resulted in increased mortality and reduced growth of young Myrica. Ahead of the invasion front, on sites subject to an extended summer drought period, germination, seedling survival and growth were even further reduced. While drought decreases Myrica seedling survival and growth rates, the potential for seedling recruitment and establishment still exists in these drought-prone
environments, though the rate of establishment is expected to be very slow. Low seed inputs and low soil moisture availability during the summer are factors which appear to control the rate of invasion into the grassland.

Within the active invasion area of the seasonal submontane grassland, seasonal adjustments in osmotic potential and tissue bulk elasticity of established trees appear to facilitate the maintenance of leaf turgor during periods of extended summer drought. Increased photosynthetic capacity in the grassland population resulted in the maintenance of higher photosynthetic rates at lower stomatal conductance values when compared to values determined for a rain forest population. Thus, physiological adjustments in Myrica saplings and trees growing under drought conditions during the summer in the seasonal submontane grassland, appear to facilitate survival and growth during periods of low soil water availability. The Myrica population is expected to increase in density within its invasion range in the grassland. Myrica faya may continue to colonize sites towards the drier westward end of the seasonal submontane grassland as more trees mature and seed inputs increase.
Introduction

Myrica faya, a tree adapted to moist submontane elevations in its native Macaronesian Islands (Lausi et al. 1989), is an aggressive invader in some montane and submontane habitats of the Hawaiian islands. The presence of this alien tree in native Hawaiian ecosystems is of particular concern in HAVO where park officials are mandated to preserve park ecosystems in as natural a state as possible (Houston 1971, Loope 1992). The first individuals of Myrica in HAVO were reported in 1961 (Doty and Mueller-Dombois 1966). Despite control efforts, Myrica now covers 11,600 ha of HAVO and is found in montane and submontane habitats (Camrath and Tunison 1992).

The most intensive invasion of Myrica in HAVO has been in the seasonal submontane environment in open-canopied Metrosideros polymorpha forest and in rain forest habitat where the Metrosideros canopy has been thinned by volcanic cinderfall (Smathers and Mueller-Dombois 1974). In one area of the seasonal submontane forest, a dense monospecific stand of Myrica has developed and replaced the Metrosideros forest that was once present.

Myrica seed is primarily bird dispersed, however dispersal of Myrica seed is of relatively short range and bird movements are partially influenced by the density of
fruiting trees and availability of perches (Vitousek and Walker 1989). Birds known to eat Myrica fruit and common to the seasonal submontane forest include: the common Myna (Acridotheres tristis), the house finch (Carpodacus mexicanus), the Japanese white-eye (Zosterops japonicus), and the 'amakihi (Hemignathus virens) (LaRosa et al. 1985, Vitousek and Walker 1989, Woodward et al. 1990). Of those mentioned, the native 'amakihi has the highest local density of 1250 birds ha⁻¹ at Ainahou Ranch and has been seen eating Myrica fruit where there is dense Myrica colonization (LaRosa et al. 1985). Established Myrica individuals are most often found under the crowns of Metrosideros trees (Vitousek and Walker 1989). Myrica has also been found growing under dead crowns of the alien shrub Buddleja asiatica on volcanically created, early successional habitats (Mueller-Dombois and Whiteaker 1990). The association of Myrica with other species may be related to the intensity of Myrica seed drop under the crowns of other species and a requirement of partial shade for optimal germination in these habitats (Vitousek and Walker 1989, Walker 1990).

Range expansion of Myrica has been recently documented in the seasonal submontane grassland of HAVO (Camrath and Tunison 1992). Myrica faya was mapped at the eastern end of the grassland, in the area of Ainahou Ranch, in 1978
(Clark 1979). Since then, *Myrica* has increased in density at Ainahou Ranch and the invasion of *Myrica* has proceeded westward across the grassland. In 1985, the western limit of *Myrica* invasion in the grassland was slightly southeast of Kipuka Nene Campground (Whiteaker and Gardner 1985) where *Myrica* was present in low densities. At the time of this study in 1991 *Myrica* had invaded 2 km west of Kipuka Nene Campground. The rate of spread has been about 0.29 km year\(^{-1}\).

The length of the summer drought period, which increases from east to west across the grassland, may influence the range expansion of *Myrica* downslope towards the drier lowlands. At the eastern edge of the grassland, which is rarely subject to summer drought, *Myrica* has spread downslope from an elevation limit of 750 m determined in 1985 (Whiteaker and Gardner 1985) to an elevation of 580 m (Camrath and Tunison 1992). However, west of Kipuka Nene Campground, where the summer drought period usually lasts 2 months, invasion has been restricted to an elevational band between about 780 to 870 m. The pattern of establishment in the seasonal submontane grassland suggests that *Myrica* invasion is partially influenced by the duration of summer drought.

This study addresses two questions: 1) Will *Myrica* invasion advance beyond its current invasion range in the
seasonal submontane grassland and towards lower, drier elevations and 2) Will *Myrica* density increase in the seasonal submontane grassland to develop into a *Myrica* forest? These questions were addressed by examining ecological and physiological characteristics of *Myrica* and determining mechanisms controlling invasion in the seasonal submontane environment. Bird-dispersed seed inputs and the potential for seed germination, early survival and seedling growth rates in the seasonal submontane grassland of HAVO were studied to evaluate *Myrica* potential for further invasion of the grassland and dry lowland habitats. Habitat-specific patterns of gas exchange and water-use efficiency in *Myrica* growing in the seasonal submontane and rain forest environments were determined to furnish information concerning the response of *Myrica* to variations in habitat moisture availability and to seasonal drought. The results of these studies suggest that determining the ecological and physiological requirements of an invading species may provide a predictive tool of its invasive potential in different habitats. Moreover, such information has practical implications for the effective control of invasive species near their ecological limits.
Study area

Study sites

Research was conducted on the Island of Hawaii, in HAVO, on the south flank of Kilauea Volcano, between 660 m and 1180 m elevation. Most of the study was situated in the seasonal submontane grassland, between 1160 m and 300 m elevation. The climate of this area is summer-dry (Doty and Mueller-Dombois 1966). The mean annual precipitation at the eastern side of the seasonal submontane grassland is around 2200 mm year\(^{-1}\) and around 1000 mm year\(^{-1}\) at the western side. The underlying substrate is a discontinuous shallow ash layer (0 to 1.0 m in depth) over 500 to 750 yr old pāhoehoe lava flows (Holcomb 1987). Increased fire frequency, due to the invasion of fire-adapted alien grasses in the seasonal submontane forests of HAVO, has reduced the open canopied *Metrosideros* forest (Doty and Mueller-Dombois 1966) to scattered patches and increased the spread of the grassland (Hughes et al. 1991).

To determine the potential of *Myrica* for continued range expansion, with respect to habitat requirements for germination and growth and physiological tolerance to seasonal declines in water availability, three study sites were selected (Fig. 3.1). Site 5 (3 km southwest of Kipuka Nene Campground), was located at 800 m elevation at the western edge of the invasion range of *Myrica* in the
grassland. Site 6 was located 4 km west of the Kipuka Nene site at 660 m elevation downslope from the end of Halina Pali road. The vegetation at site 5 and site 6 consisted primarily of the alien grasses *Melinus minutiflora* (60% and 33% cover, respectively) and *Schizachyrium condensatum* (14% and 33% cover, respectively). *Sophora chrysophylla*, *Styphelia tameiameiae* and *Dodonaea eriocarpa* are shrubs commonly found around the Kipuka Nene area but are absent at site 6. Few *Metrosideros polymorpha* trees are found near these sites. Both sites were burned in a fire in March 1987 (Tunison, pers. comm.) and differences in vegetation recovery may have resulted from different fire intensities, habitat moisture availability and seed availability following the fire. An initial reconnaissance of a 0.5 km$^2$ area at site 5 found eight established *Myrica* individuals and only one of these was mature. *Myrica* was not present at the site 6.

To determine the physiological response of *Myrica* to differences in habitat water availability in terms of *Myrica* water relations characteristics, photosynthetic gas exchange and water-use efficiency, a rain forest population was selected for comparison to the response of the seasonal submontane grassland population. Site 3, at 1176 m elevation, receives around 2500 mm yr$^{-1}$ mean annual
precipitation and is located in the rain forest environment.

Climate

Precipitation and air temperature were monitored by HAVO personnel at climate stations located at Kipuka Nene Campground (892 m elevation) and near the end of Halina Pali road (720 m elevation). Climate diagrams were prepared after the method of Walter (1957). The monthly totals for precipitation and the monthly average air temperature have been averaged over a number of years and are plotted for a year. The scale is such that 1°C corresponds to 2 mm of precipitation. In such a way, the temperature curve serves as an indicator of the evaporative power of the air so that humid and drought periods can be identified. Climate diagrams for sites 5 and 6 (Fig. 3.1), indicate a short period of summer drought. However, during the 1990, winter rainfall was higher than normal and summer rainfall was lower than normal. The summer drought period lasted 3 to 4 months in 1990.
Methods

Habitat

To determine soil moisture availability for seedling growth during the experimental period, soil water content was monitored from December 1989 to November 1990 at site 5 and site 6. Two soil samples were taken from 5 to 10 cm below the soil surface every two weeks. Moisture release curves were developed from psychrometric determinations of soil water potential from soil water content using a soil thermocouple psychrometer (Rawlins and Campbell 1986).

Seed capture

Peak fruiting of Myrica occurs from August to November in the seasonal submontane forest (Whiteaker and Gardner 1987). To evaluate Myrica seed inputs into site 5, at the invasion front where the density of established Myrica was low and the closest fruiting individual was 0.5 km east of the study site, a seed trap study was initiated during the fruiting season from July to November, 1990. Seed traps were set under 20 Metrosideros trees and under 10 Sophora chrysophylla and 10 Styphelia tameiameiae shrubs, the most common shrubs in the 3 ha sample area, and monitored bimonthly. Each seed trap consisted of pipe frame made from pvc (40 x 25 cm rectangle) and lined with a very fine
nylon mesh bag. The frames were positioned 30 cm above the ground using pvc pipe as legs for the frame.

**Seed germination**

Two germination experiments were undertaken to examine the field germination potential and germinant survival of *Myrica* in the seasonal submontane environment and the influence of the degree of natural grass cover on *Myrica* germination.

In the first experiment, seeds were collected from fruiting trees near Kipuka Nene Campground in July, 1989. These seeds were lightly scarified using fine sand paper to remove the mesocarp (Walker 1990) and stored at room temperature. In September 1989, three plastic trays (55 x 28 x 20 cm deep) each with 38 cups were partially buried in the ground at sites 5 and 6. The cups were filled with soil from the experimental site. Each cup of each tray was sown with 10 *Myrica* seeds for a total of 380 seeds per tray. A cover made of 1x1 cm wire mesh was built around each tray to prevent seed predation. The trays were lightly covered with dry *Melinus* grass to prevent detection from passersby on nearby roads or trails and are thus considered as being placed under partial shade.

Germination was defined as seedling emergence above the ground with the presence of cotyledons. Seed
germination and seedling survival were monitored every 2 weeks over 10 months, and seedlings were marked as they emerged. A greenhouse control was kept to determine the number of viable seeds germinating under optimal conditions of light and moisture.

In a second experiment, seeds were collected from fruiting trees near Kipuka Nene Campground in July 1990. They were then lightly scarified using fine sand paper to remove the mesocarp and stored at room temperature. Three potential germination sites for Myrica seed were identified according to the degree of Melinus minutiflora grass cover: open (<20% cover of Melinus grass), partial (20 to 60% cover) and full (100% cover of Melinus grass). At site 5, three replications of 100 seeds each were placed directly on the soil under the different degrees of Melinus cover and covered with wire mesh to prevent predation in August 1990. Also, at site 6, three replications of 100 seeds each were placed under partial Melinus cover only and protected by wire mesh to prevent rodent predation. Germination was monitored every 2 weeks, as in the first experiment, until December, 1990. Also, surviving germinants were enumerated once more in March, 1991. A greenhouse control was kept to determine the number of viable seeds germinating under optimal conditions of light and moisture.
Seedling growth

To determine seedling growth potential in the seasonally dry grassland, seedlings were transplanted into experimental plots. First, naturally established seedlings were collected in September, 1989 from a nearby site where seedlings were abundant. These seedlings were transported to a greenhouse and maintained until there were enough seedlings, 5 cm in height, to be planted at the sites 5 and 6.

At each site, 15 seedlings of uniform size were planted, in November 1989, with 1 x 1 m spacing into three randomly placed 5 x 3 m plots (45 seedlings in total). Height and basal diameter of the seedlings were measured monthly from December, 1989 to November, 1990.

Competition for soil moisture during the dry season in the summer, between Myrica seedlings and the dense cover of Melinus grass present at the study sites was tested by monitoring seedling growth with or without Melinus grass removal. At site 5, additional seedlings were planted in plots in which the Melinus grass cover was removed. Seedlings of uniform size were transplanted in three plots randomly placed at site 5 in November, 1989. Six seedlings spaced 1 x 1 m apart were transplanted in each plot (18 in total). The plots were cleared of Melinus grass in March, 1990 and maintained until the end of the
experiment. At site 6, of the original three plots of 15 transplanted seedlings, six randomly selected individuals in each plot were cleared of Melinus grass in March, 1990. Height and basal diameter of the seedlings were measured monthly from December to November, 1990.

**Stand structure**

To determine the demographic characteristics of the Myrica population within the active invasion area near Kipuka Nene Campground, a 200 m transect of 20 continuous 10x10 m plots was established. Basal diameter of Myrica seedlings, saplings and trees was measured in each plot for an analysis of population size distribution and structure.

**Water relations**

To compare potential alterations in Myrica water relations as influenced by the habitats of different moisture availabilities, pressure-volume analysis was performed on individuals selected from the seasonal submontane and rain forest environments of HAVO.

The study sites were selected to represent a range of soil moisture availability based on environment and season; i.e. reduced water availability from pronounced seasonal drought in the seasonal submontane grassland to
high year-round soil moisture availability in the rain forest. Individuals were selected for study from the seasonal submontane grassland near the Kipuka Nene Campground and from the rain forest near Thurston Lava Tube. Measurements were made on 9 to 12 individuals in April and September, 1990, before and after the dry season, for determination of seasonal and habitat-related adjustments in tissue water relations.

Tissue water relations of *Myrica* adults were determined using the pressure chamber technique modified from Tyree and Hammel (1972). Branches were collected, recut under water, and allowed to resaturate in distilled water overnight. After their saturated weights were obtained, the branches were allowed to dry under ambient conditions on a laboratory bench. Periodic weight and water potential measures were made until the water content of each branch had declined to about 60% of its original fresh weight. Water potential measures were made with a PMS Inst. Co. model 1000 pressure chamber. Weights were measured with a Satorius electric digital balance. Water relations parameters were determined using a pressure-volume curve analysis program (Shulte 1990).
Assimilation and stomatal conductance

Gas exchange characteristics provide a measure of plant physiological performance under various external environmental conditions. The ratio of instantaneous rates of CO₂ assimilation (A) and stomatal conductance (g), a measure of intrinsic water-use efficiency, is directly related to the ratio of intercellular to atmospheric partial pressure of CO₂. This relationship provides a means of determining the mechanisms that control water-use efficiency (Meinzer et al. 1992). Measurements of CO₂ assimilation (A), stomatal conductance (g), the ratio of intercellular to ambient CO₂ partial pressure (pᵢ/pₐ) and intrinsic water-use efficiency (WUE) were determined under ambient conditions with a portable photosynthesis system (Li-6200, LI-COR, Inc.). Gas exchange measurements were carried out in July 1990 on naturally established adults and juveniles growing in the seasonal submontane environment near Kipuka Nene and in the rain forest environment near Thurston Lava Tube. Three leaves on each of 3 to 5 adult and 3 to 5 juvenile individuals from each population were marked and their gas exchange was followed over a 9 hour period from 800 to 1700 h. Measurements were performed on the most recent fully expanded leaves growing under full sun conditions. Leaves were collected at the end of the measurement day.
for determination of their area and dry weight. Leaves from 5 different individuals from each site were also collected for determination of N content. Leaf N content was analyzed by the Agricultural Diagnostic Service Center at the University of Hawaii.

Results

Seed capture

Two *Myrica* seeds were caught in traps representing a capture area 4 m$^2$ over 3 ha at site 5. Seed dispersed by birds, at this invasion front of *Myrica*, was calculated to be 1667 seeds ha$^{-1}$ during the fruiting season. These *Myrica* seeds were captured in traps placed under *Metrosideros* trees; no seeds were captured in the open or under shrubs. Though seed inputs by birds were expected to be low due to the absence of fruiting trees in the immediate vicinity and low bird density in the area (Jacobi, pers. comm.), the small capture area of the seed traps may result in an over or under represent actual seed inputs.
Seed germination and survival

Germination of Myrica seed for determination of seed viability under greenhouse conditions, was 60% for the first experiment and 52% for the second experiment. In the first experiment, where seeds were maintained in trays under partial shade, germination and survival was lower at site 6 than at site 5 (Table 3.1).

In the second experiment, where seeds were placed under different degrees of Melinus cover, germination was higher under increasing shade. Also, survival of germinants increased with increasing shade. Germination of Myrica seed under partial cover at the site 6 site was similar to the open and partially covered treatments at site 5. Lower available moisture may account for low germination and survival at site 6. The survival of germinants increased with increasing Melinus cover. The Melinus grass cover may provide somewhat cooler and moister microsite conditions more favorable to young germinant survival than microsites without Melinus cover.

Soil water availability and seedling growth

Soil water potential was high during the winter months but declined continuously over the summer period from May to September at both site 5 and site 6 (Fig. 3.2A). Precipitation from May to August 1990, in the seasonal
submontane grassland, was lower than normal, producing an extended period of drought. Though total precipitation for the year was greater than normal, most of the precipitation in 1990 fell during the winter months. Lower summer precipitation and more negative soil water potentials at site 6 indicated that this habitat had lower moisture availability than site 5. A sharp decline in the relative growth rates of transplanted seedlings occurred during the dry season from July to October at site 5 and site 6, which corresponded to decreased soil water availability (Fig. 3.2).

The effect of competition on relative growth rates of Myrica seedlings growing in the presence of Melinus grass is evident in the later part of the dry season at site 5 (Fig. 3.2B). Growth of transplanted seedlings was greater in plots cleared of Melinus cover during the dry season than those in competition with Melinus at site 5. At site 6, seedling relative growth rates were similar in both treatments, however, growth rates here were lower than at site 5. During an extended drought the Melinus grass may have become dormant, thus reducing the further effects of competition for soil moisture with Melinus on Myrica growth rates.

Mortality of transplanted seedlings began 6 months after planting in May, at the onset of the dry season in
the seasonal submontane grassland (Table 3.2). Mortality of *Myrica* transplants in both cleared and uncleared plots was significantly greater at site 6 than at site 5.

**Population growth**

Estimates of seed inputs, germination, and survival of seedlings at the Kipuka Nene invasion front are summarized to provide an estimate of population growth. An abundance of seedlings <1 cm diameter is evident in the stand structure diagram of *Myrica* near Kipuka Nene Campground (Fig. 3.3). However, the 0 to 5 cm basal diameter class represents only those individuals <1 cm basal diameter and lacks individuals between 1 and 5 cm basal diameter. These individuals may have been lost during the fire of March 1987. The stand structure at Kipuka Nene Campground was used to determine potential survivorship in to adulthood. The demographic flow chart (Fig. 3.4), suggests that at the current rate of seed inputs at the invasion front, 0.66% of the seed dispersed each year may result in 11 mature individuals within 7 to 8 years (assuming a basal diameter growth rate of 1.5 cm yr\(^{-1}\)).

**Water relations**

Seasonal adjustments in tissue water relations were pronounced in the naturally-established *Myrica* population
growing in the seasonal submontane grassland. Tissue elasticity tended to increase (decreased $E_{\text{max}}$) from the wet to dry season in the seasonal submontane environment (Table 3.3). Also, saturated osmotic potential ($\pi_s$) declined about 0.1 MPa from the wet to the dry season for Myrica in this environment. Greater tissue elasticity and more negative osmotic potential may assist in maintaining turgor as soil water availability decreases during the summer. In contrast, moisture availability was high throughout the year in the rain forest environment and no seasonal changes in the water relation characteristics were observed in the rain forest population.

The tissue osmotic ($\pi_s$) and elastic ($E_{\text{max}}$) properties of Myrica growing in the rain forest as compared to those of Myrica growing in the seasonal submontane environment differed significantly (Table 3.3). The maximal values of turgor pressure for Myrica trees in the seasonal submontane grassland (1.95 MPa) were significantly higher than those of the growing in the rain forest (1.66 MPa), during the summer (Fig. 3.5A and 3.5B). Higher turgor pressure in the seasonal submontane trees resulted from a more negative tissue osmotic potential ($\pi_s$) than found in rain forest trees (Table 3.3). However, turgor pressure declined more rapidly with decreasing relative water content in seasonal submontane trees than in rain forest
trees. This difference was reflected in the higher tissue elastic modulus ($E_{\text{max}}$) (less elastic) for trees in the seasonal submontane than in the rain forest zone (Table 3.3).

Differences in osmotic and tissue elastic modulus ($E_{\text{max}}$) resulted in higher turgor loss points at lower water potentials for *Myrica* growing in the seasonal submontane zone than in the rain forest, during the summer (Fig. 3.5C and 3.5D) even though the relative symplastic water contents ($R_s$) were similar (Table 3.3).

**Assimilation and water-use efficiency**

Comparison of leaf-gas exchange measurements revealed that there is a substantial difference between *Myrica* populations from the rain forest and seasonal submontane environments (Fig. 3.6). CO$_2$ assimilation ($A$) was lower over much of the day for adults and juveniles in the seasonal submontane population than for those from the rain forest population. Low assimilation at both sites near the end of the day was a result of developing cloud cover. Assimilation ($A$) was greatest in the morning hours in the seasonal submontane population when leaf-air vapor pressure deficits were low and midday assimilation declined with increasing leaf-air vapor pressure deficit. Stomatal conductance ($g$) of trees growing in the seasonal
submontane zone were much lower than those growing in the rain forest.

Two distinct patterns emerged when examining the relationship between CO₂ assimilation (A) and stomatal conductance (g) (Fig. 3.7). In the seasonal submontane population, A increased steeply with g as g approached a maximum value around 0.4 mol m⁻² s⁻¹. A increased less steeply with g and approached much higher maximum value around 1.0 mol m⁻² s⁻¹, in the rain forest population. Thus for a given g (up to 5 mol m⁻² s⁻¹), A was higher in the seasonal submontane population. The relationship was not correlated to leaf N content (Table 3.4).

The differences in the relationship between A and g in the two populations is also reflected in water-use efficiency. The water-use efficiency of the seasonal submontane population was significantly greater than the rain forest population (Table 3.4). Lower \( \frac{p_i}{p_a} \), and higher rates of A at a given g are associated with a higher photosynthetic capacity in the seasonal submontane population.
Discussion

*Myrica* invasion into the seasonally dry submontane grassland is influenced by a variety of factors. The expansion of *Myrica* beyond its current invasion range is restricted by low seed inputs. Though fruit production of a mature female *Myrica* tree is abundant, averaging over 400,000 fruits yr\(^{-1}\) (Whiteaker and Gardner 1987) only 0.5\% may be dispersed away from the parent by birds. Dispersal is relatively short-ranged and seed is usually not found >0.5 km ahead of an invasion front (Vitousek and Walker 1989). In this study, low seed dispersal beyond the invasion front is most likely influenced by the low density or complete absence of nearby seed bearing trees and low availability of other food sources, which in turn, influence bird population density and dispersal patterns.

Germination of *Myrica* is promoted by the shade provided by the alien grass *Melinus minutiflora*, which forms a dense continuous cover 30 to 50 cm in height on ash deposits over much of the seasonal submontane grassland (Hughes et al. 1991). Hughes and Vitousek (1993) found that native shrub colonization was inhibited by low light availability under dense grass cover. However, without the shade of other vegetation, such as *Melinus* grass, *Myrica* germination would most likely be low at the invasion front. Adequate microsite conditions for
Myrica germination and growth have also been found under native Metrosideros trees where partial shade and litter accumulation ameliorate the dry, high temperature conditions of surrounding lava or cinder substrate (Walker and Vitousek 1991). Though germination is high under the protective cover of Melinus grass, mortality of germinants and seedlings increases during extended periods of drought. This was evident at site 6, where the drought period was about 1 month longer than at site 5. Also, growth rates of transplanted seedlings declined at the onset of drought. During the wet season growth rates averaged 18 to 19 mg g^{-1} day^{-1} while during the summer drought growth rates declined to an average of 4 to 6 mg g^{-1} day^{-1}. Competition with Melinus grass for soil moisture was evident at site 5 during drought. Thus, long periods of drought in this area present a potential limit to the further progression of Myrica into the summer-drought environment of the lowlands.

Establishment of Myrica within its current invasion range in the seasonal submontane grassland is expected to increase. The demographic flow chart, summarizing survivorship to reproductive age, suggests that despite low seed inputs, population development is possible at the current invasion front. Though the flow chart is based on experimental data that may not accurately represent
natural conditions, the estimated population growth at the invasion front is supported by similar determinations of population growth derived from the actual population structure within the invasion range of Myrica in the grassland. As individuals become established and mature at the invasion front, seed inputs will increase, thus increasing the rate of population development.

In its native habitat in the Canary Islands, Myrica often becomes the first invading tree after fire in the Lauri-Silva forest (Mueller-Dombois, pers. comm.). However, increased fire frequency in the seasonal submontane grassland zone may slow the rate of invasion by Myrica. The current stand structure within the invasion area of the grassland lacks individuals between 1 and 5 cm basal diameter. These individuals may have been lost during the fire of March 1987 (Tunison, pers. comm.) but mature trees appear to have survived. Personal observations of mature fire scarred Myrica indicates that Myrica can basally resprout after fire even if all living aboveground plant material is removed by fire. Increased fire prevention efforts by HAVO personnel may favor increased population growth of Myrica in the grassland.

Maximum CO₂ assimilation in Myrica (7 to 13.5 μmol m⁻² s⁻¹) is within the range determined for other tropical
broadleaved trees; 3.2 to 15.1 \( \mu \text{mol m}^{-2} \text{ s}^{-1} \) (Larcher 1991) and 6.3 to 18.9 \( \mu \text{mol m}^{-2} \text{ s}^{-1} \) (Koyama 1981). However, another Myrica species, Myrica cerifera, has much higher maximum assimilation rates (35 \( \mu \text{mol m}^{-2} \text{ s}^{-1} \)) (Young 1992), than Myrica faya, though maximum stomatal conductance values of Myrica cerifera (0.433 \( \mu \text{mol m}^{-2} \text{ s}^{-1} \)) are similar to that found in Myrica faya (0.51 \( \mu \text{mol m}^{-2} \text{ s}^{-1} \)). Decreases in stomatal conductance (and corresponding decreases in assimilation) in Myrica cerifera were noted when the leaf-air vapor pressure deficit was greater than 1.5 kPa (Young 1992). In this study, increasing leaf-air vapor pressure deficit greater than 2 kPa resulted in a decline in assimilation due, in part, to decreasing stomatal conductance.

Within the invasion area in the grassland, established Myrica exhibits some degree of drought tolerance. In this area both established adults and juveniles (saplings) exhibit high intrinsic water-use efficiency compared to rain forest populations. Stomatal conductance is relatively low for Myrica growing in the seasonal submontane grassland. However, despite low values of stomatal conductance, CO\(_2\) assimilation is generally higher for a given value of stomatal conductance than for Myrica growing in moister rain forest habitats. Two mechanisms may be responsible for increased water-use efficiency.
One appears to be a reduction in stomatal conductance which would increase the stomatal limitation of CO$_2$ and lower $p_i/p_a$. This would result in reduced rates of CO$_2$ assimilation and growth. An alternative means of enhancing intrinsic water-use efficiency is through increased photosynthetic capacity at lower levels of stomatal conductance, which would result in the maintenance of high CO$_2$ assimilation (Meinzer et al. 1992). The latter appears to be true for Myrica growing in the seasonally dry grassland. A high photosynthetic capacity with low stomatal conductance may provide for the maintenance of growth during the summer-drought period.

Other aspects of drought tolerance in Myrica include seasonal changes in water relations characteristics. In the rain forest where Myrica is not subject to seasonal drought conditions, tissue osmotic and elastic properties do not change seasonally. However, in the seasonal environment, osmotic adjustment and increased tissue elasticity during summer drought permit Myrica to maintain turgor to relatively low tissue water potentials. Also, Myrica maintains a relatively high symplastic water content at the turgor loss point. While pronounced dehydration will eventually cause drought injury, relative water contents between 1 and 0.5 are and can permit rapid recovery of turgor without significant metabolic stress if

Juvenile plants are under potentially different selective pressures than reproductive plants (Grubb 1977) particularly in drought-prone environments where juveniles may be exposed to greater variability in soil water availability (Donovan and Ehleringer 1991). Mortality is high in *Myrica* germinants in the seasonal submontane environment, particularly during extended periods of drought. The vulnerability of this lifestage to drought will limit *Myrica* invasion into the summer-drought environment of the lowlands of HAVO.

Though it has been demonstrated in this and other studies (Vitousek and Walker 1989) that *Myrica* has characteristics common to successful invaders, such as efficient dispersal mechanisms and morphological and physiological phenotypic plasticity which may facilitate its invasion into differing habitats (Bazzaz 1986), these characteristics do not insure its successful invasion into all habitats. Both biotic (availability of seed and range of seed dispersers) and abiotic factors vary with habitat and influence the degree and rate of establishment of *Myrica*. Low germination and high mortality in the early lifestages of *Myrica* limit its invasion potential into drought-prone environments.
Table 3.1: Germination and seedling survival of *Myrica* sown in trays and on the substrate under different levels of *Melinus* grass cover.

<table>
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<tr>
<th>Treatment</th>
<th>Germination* (%)</th>
<th>Seedling survival (%)</th>
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<tbody>
<tr>
<td>Site 6</td>
<td></td>
<td></td>
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<tr>
<td>In tray</td>
<td>2.30 (1.0)</td>
<td>12.3* (5.1)</td>
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<td>Soil surface</td>
<td></td>
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<tr>
<td>partial cover</td>
<td>9.0 (4.3)</td>
<td>20.0# (16.3)</td>
</tr>
<tr>
<td>Site 5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>In tray</td>
<td>12.0a (1.3)</td>
<td>39.2* (24.2)</td>
</tr>
<tr>
<td>Soil surface</td>
<td></td>
<td></td>
</tr>
<tr>
<td>open</td>
<td>10.3a (5.2)</td>
<td>17.5 # (14.3)</td>
</tr>
<tr>
<td>partial</td>
<td>10.3a (7.0)</td>
<td>57.1 # (41.0)</td>
</tr>
<tr>
<td>closed</td>
<td>61.0b (21.0)</td>
<td>62.0 # (16.9)</td>
</tr>
</tbody>
</table>

*Germination is expressed as the percentage of viable seed sown; survival is a percentage of the maximum number of seed germinated. Values are means (n=3 plots or trays) and one standard error in brackets. Values were arcsine transformed prior to chi-square analysis. Percentages followed by the same superscript letter are not significantly different (P<0.05).

*Survival to 10 months, # Survival to 6 months.
Table 3.2: Mortality (%) of *Myrica* seedlings planted into cleared and uncleared plots at site 5 and site 6. Values are means with a standard error in brackets, (N=3 plots).

<table>
<thead>
<tr>
<th>Locality</th>
<th>Mortality (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site 5</td>
<td></td>
</tr>
<tr>
<td>Cleared</td>
<td>11.1 (4.6)a</td>
</tr>
<tr>
<td>Uncleared</td>
<td>15.8 (4.8)a</td>
</tr>
<tr>
<td>Site 6</td>
<td></td>
</tr>
<tr>
<td>Cleared</td>
<td>27.8 (4.5)b</td>
</tr>
<tr>
<td>Uncleared</td>
<td>33.3 (13.9)b</td>
</tr>
</tbody>
</table>

Values were arcsine transformed prior to chi-square analysis. Percentages followed by the same superscript letter are not significantly different (P<.05).
Table 3.3: Tissue osmotic potential at full hydration ($\pi_s$), water potential ($\Psi_{tlp}$) at the turgor loss point, tissue elastic modulus near full hydration ($E_{\max}$), symplastic water fraction ($R_s$) and sample size ($n$) of Myrica in April and September, 1990 growing in the rain forest and seasonal submontane zones. Values are means with one standard error in brackets.

<table>
<thead>
<tr>
<th>Locality</th>
<th>$\pi_s$ (MPa)</th>
<th>$\Psi_{tlp}$ (MPa)</th>
<th>$E_{\max}$ (MPa)</th>
<th>$R_s$</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rain forest</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>April</td>
<td>-1.63$^a$</td>
<td>-2.19$^a$</td>
<td>14.3$^a$</td>
<td>.67$^a$</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>(.03)</td>
<td>(.04)</td>
<td>(.90)</td>
<td>(.01)</td>
<td></td>
</tr>
<tr>
<td>September</td>
<td>-1.66$^a$</td>
<td>-2.20$^a$</td>
<td>15.0$^a$</td>
<td>.68$^a$</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>(.05)</td>
<td>(.06)</td>
<td>(.50)</td>
<td>(.03)</td>
<td></td>
</tr>
<tr>
<td>Seasonal Submontane</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>April</td>
<td>-1.85$^b$</td>
<td>-2.27$^a$</td>
<td>22.9$^c$</td>
<td>.65$^a$</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>(.05)</td>
<td>(.06)</td>
<td>(1.0)</td>
<td>(.02)</td>
<td></td>
</tr>
<tr>
<td>September</td>
<td>-1.95$^b$</td>
<td>-2.65$^b$</td>
<td>17.6$^b$</td>
<td>.68$^a$</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>(.06)</td>
<td>(.08)</td>
<td>(1.2)</td>
<td>(.02)</td>
<td></td>
</tr>
</tbody>
</table>

$^a$ Within column means are significantly different (t-test) ($P<.05$) where identified by a different superscript.
Table 3.4: Water-use efficiency (WUE) (μmol mol⁻¹), ratio of internal to ambient partial CO₂ pressure (pi/pa) and Leaf N content (mmol N m⁻²) of juvenile and adult *Myrica* plants growing in the rain forest and seasonal submontane grassland. Values are means and standard error in brackets (n=9 to 12 individuals), except leaf N content where n=3.

<table>
<thead>
<tr>
<th>Locality</th>
<th>WUE (μmol mol⁻¹)</th>
<th>Pi/Pa</th>
<th>Leaf N content (mmol N m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rain forest</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juvenile</td>
<td>30.9</td>
<td>0.75</td>
<td>n/a</td>
</tr>
<tr>
<td></td>
<td>(1.6)</td>
<td>(0.01)</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>20.4</td>
<td>0.80</td>
<td>176.3</td>
</tr>
<tr>
<td></td>
<td>(1.6)</td>
<td>(0.02)</td>
<td>(0.009)</td>
</tr>
<tr>
<td>Seasonal submontane</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Juvenile</td>
<td>52.4</td>
<td>0.68</td>
<td>n/a</td>
</tr>
<tr>
<td></td>
<td>(3.6)</td>
<td>(.01)</td>
<td></td>
</tr>
<tr>
<td>Adult</td>
<td>47.9</td>
<td>0.68</td>
<td>178.3</td>
</tr>
<tr>
<td></td>
<td>(1.2)</td>
<td>(.02)</td>
<td>(.005)</td>
</tr>
</tbody>
</table>
Fig. 3.1. Locations of study sites in HAVO. Site 5 and site 6 are seasonal submontane grassland sites. Site 3 is a rainforest site. Weather diagrams for site 5 and site 6 were created from precipitation and temperature data collected during 1990. Black area represents rainfall in excess of 100 mm mo$^{-1}$. Striped area indicates humid period. Stippled area represents a period of drought. Total rainfall is represented as the top number in the right hand corner. Climate diagrams are from data collected over a 14-year period.
Fig. 3.2. (A) Soil water potential (MPa) during the 1990 study period at site 5 (●) and site 6 (■). A substantial rainfall in the last week of September is not reflected in the soil water potential data as sampling occurred prior to the rainfall event. Values are means (n=4) and error bars are one standard error. (B) Relative growth rate (mg g⁻¹ day⁻¹) of *Myrica* seedlings at site 5 with *Melinus* cover (●) and without *Melinus* cover (○) and (C) at site 6 with *Melinus* cover (■) and without *Melinus* cover (□). Values are means and error bars are one standard error.
Fig. 3.3. Stand structure of *Myrica* at the Kipuka Nene campground area. Density per hectare is indicated in the right-hand corner. Solid line represents a power function which describes survivorship between size classes.
Fig. 3.4. Flowchart of the demography of an invading Myrica population in the seasonal submontane grasslands calculated from data obtained of seed inputs, germination, survival and growth from experiments performed at site 5 and determination of current stand structure within the invasion area at Kipuka Nene campground. Seed germination and mortality derived from estimates of these values obtained under partial cover treatment.
Seed inputs
1667 seed ha\(^{-1}\)

\downarrow

Germinants
100 ha\(^{-1}\)

\downarrow

Seedlings to one year
51 ha\(^{-1}\)

\downarrow

Mature trees
11 ha\(^{-1}\)
Fig. 3.5. Relationship between turgor pressure (MPa) and relative water content and plant water potential (MPa) for Myrica trees growing in the seasonal submontane grasslands and the rain forest in May(--) and September (--).
Fig. 3.6. Leaf-air vapor pressure deficit (VPD), assimilation (A) and stomatal conductance (g) for adults (open symbols) and juveniles (closed symbols) growing in the seasonal submontane grasslands and the rain forest habitat. Values are means and error bars are one standard error.
Seasonal submontane

Rain forest

Leaf-Air VPD (kPa)

A (umol m⁻² s⁻¹)

g (mol m⁻² s⁻¹)

Time (hr)
Fig. 3.7. Relationship of assimilation (A) to stomatal conductance (g) for *Myrica* from a seasonal submontane population (O) and from a rain forest population (●). Solid lines are fitted from equations for the seasonal submontane population, \( A = 0.199 + 54.23g - 49.97g^2 \), \( R^2 = .95 \) and rainforest population, \( A = 2.35 + 24.60g - 13.44g^2 \), \( R^2 = .90 \).
Literature cited


Hughes, F. and P.M. Vitousek. 1993. Barriers to shrub reestablishment following fire in the seasonal submontane zone of Hawai'i. *Oecologia* 93:557-563


CHAPTER 4
CONSTRAINTS TO THE INVASION OF MYRICA FAYA INTO MONTANE RAIN FOREST COMMUNITIES CHARACTERIZED BY CANOPY DIEBACK

Abstract

Myrica faya, an alien tree in the Hawaiian islands, has readily colonized open, seasonally dry forests and some mesic rain forest sites in Hawaii Volcanoes National Park (HAVO), Hawaii. However, an invasion limit to the expansion of Myrica appears to have developed in the montane rain forest zone. This study examined the mechanisms controlling the invasion of Myrica into two different rain forest communities within HAVO. Both communities were characterized by the dieback of the Metrosideros overstory and the presence of a dense subcanopy of Cibotium tree fern. However, one community had active Myrica invasion and was located within the current invasion range of Myrica and the other had no Myrica invasion and was located just beyond the invasion boundary of Myrica in the montane rain forest.

The potential constraints to Myrica invasion differed between the sites; constraints related to seed dispersal (seed inputs and proximity to an abundant seed source) and related to the ecophysiological response of Myrica to the characteristics of each habitat (soil water content and
light levels at the forest floor). Beyond the current invasion front (>0.5 km) in the wet montane rain forest of Ola'a tract, no *Myrica* seed was captured in seed traps. The density of birds, known to feed on *Myrica* seed, may be somewhat reduced due to the low density of trees and potential food sources in areas of *Metrosideros* dieback. However, within the current range of *Myrica*, seed rain from existing mature trees was very high. Germination of *Myrica* seed in Ola'a tract was strongly inhibited, apparently by high soil water content, which may have reduced oxygen diffusion to the seed. Germination of seed was found to be lower under the *Cibotium* canopy at the more mesic Thurston site than in the greenhouse (where temperatures and light availability were higher). However, large seed inputs from established *Myrica* trees at Thurston still led to a large number of young naturally established seedlings. Relative growth rates and biomass production of *Myrica* seedlings are suppressed by low light availability in the forest understory, and mortality is high, so that few seedlings survive to the sapling stage.
Introduction

Many investigators have evaluated the demographic or physiological traits of successful invaders (Bazzaz 1986, Newsome and Nobel 1986) while others have pointed out the characteristics of communities which make them susceptible to invasion (Orians 1986). Successful invaders are generally characterized as having efficient dispersal mechanisms and morphological and physiological phenotypic plasticity which facilitate their invasion into differing habitats (Bazzaz 1986). However, the ability to determine the potential spread and ecological limits of an invasive species is limited by a lack of information on species-specific and habitat-specific mechanisms controlling invasion (D'Antonio 1993).

The dominant canopy tree in Hawaiian montane rain forests is *Metrosideros polymorpha*, which can form a closed overstory. The understory is often dominated, on the island of Hawaii, by dense tree fern (*Cibotium* sp.) or matted fern (*Dicranopteris linearis*) cover (Mueller-Dombois et al. 1980, Mueller-Dombois 1987). Light availability below the fern understory cover is often less than 2% of full sun (Burton and Mueller-Dombois 1984). *Metrosideros polymorpha* undergoes a population phenomenon of dieback under a natural disturbance regime which results in the synchronized thinning of the *Metrosideros*
overstory (Mueller-Dombois 1983, 1985). Suppressed *Metrosideros* seedlings respond to an increase in light and nutrient availability after dieback with increased growth rates (Burton and Mueller-Dombois 1984). Often, this leads to the establishment of new cohorts and the subsequent development of a new monodominant stand of *Metrosideros* (Burton and Mueller-Dombois 1984). In this way, *Metrosideros* maintains itself as the dominant canopy species in most rain forest communities through abundant regeneration following canopy dieback (Jacobi et al. 1983, Mueller-Dombois 1986, 1987). In mature rain forest, other native forest trees become established in the shade of the *Metrosideros* canopy and become minor subcanopy components (Drake and Mueller-Dombois 1993). However, optimal *Myrica* growth occurs in 70% of full sun (Vitousek and Walker 1989) and *Myrica* invasion of rain forests undergoing canopy dieback may be facilitated with gap development in the overstory and the potential increase in light availability to the forest floor.

I examined factors controlling invasion of *Myrica* into two montane rain forest communities which were characterized by: 1) *Metrosideros* canopy dieback and 2) different degrees of *Myrica* invasion. *Myrica faya* invasion was active in one community while the other community had no *Myrica* invasion (though there was
invasion on nearby sites). Seed availability and the potential for seed germination, early survival and growth were determined to evaluate potential constraints to invasion.

Study area

Research was conducted in the montane rain forest of HAVO on the island of Hawaii (155° 14' lat and 19° 24' long) between 1180 m and 1230 m elevation (Fig. 4.1). Two study sites, located 3.5 km apart, were selected for the study of *Myrica* invasion into rain forest communities within and beyond the current invasion range of *Myrica* in the montane rain forest in communities characterized by dieback of the canopy tree *Metrosideros*.

Site 4 was located in Ola'a tract (1230 m elevation), a portion of HAVO, separated from the main park area by the village of Volcano. The mean annual temperature is around 16°C. The mean annual precipitation is 3028 mm (based on a 25 year record). Heavy cloud cover is common (Burton and Mueller-Dombois 1984). The soils of Ola'a tract are derived from a deep fine-textured ash believed to have been deposited 2000 to 1000 years ago with a shallow top ash layer 200 years old (Holcomb 1987). The humic top soil and underlying eutrophic ash contribute to
the high nutrient status of the soils in this area (Balakrishnan and Mueller-Dombois 1983). These soils are moderately to occasionally poorly drained. The *Metrosideros* forest in this area has undergone displacement dieback (e.g. Mueller-Dombois 1986), the displacement of *Metrosideros* from the site by other native vegetation. The dense subcanopy layer of tree ferns (*Cibotium*), which grow vigorously on eutrophic ash, preempts light and suppresses the growth of *Metrosideros* seedlings, preventing the establishment of a new *Metrosideros* forest (Burton and Mueller-Dombois 1984).

Though *Myrica faya* is present on farmland and along roadsides within 0.5 kilometer of Ola'a tract, an invasion boundary appears to have developed in the wet montane rain forest and *Myrica* is not found in Ola'a tract.

Site 3, behind Thurston Lava Tube, at 1180 m elevation, has a lower mean annual rainfall of around 2500 mm and a similar mean annual temperature of around 16°C. The *Metrosideros* forest on this site is about 200 years old, having developed after the 1790 explosive eruption of Kilauea which destroyed the forest and left a 0.5 m layer of ash substrate over the area (Holcomb 1987). Recent canopy dieback of *Metrosideros polymorpha* has occurred on this site and the open canopy structure has facilitated
abundant *Metrosideros* regeneration. Also, *Myrica* invasion of this site has been relatively aggressive.

**Methods**

**Seed capture**

To assess *Myrica* seed dispersal within and beyond its current invasion range at the two rain forest study sites, a seed trap study was initiated in August, 1989. Twenty seed traps were randomly set up under the forest canopy, over an area of 1 ha, within Ola'a tract, near the Ola'a tract boundary, adjacent to the farmland. The closest fruiting individual was 0.5 km south of the boundary. Each seed trap was a frame constructed of pvc pipe (40 x 25 cm rectangle) and lined with a very fine nylon mesh bag. The frames were positioned 30 cm above the ground using pvc pipe as legs for the frame. Seed traps were also set up in a similar manner over a 1 ha area at site 3 where there is active *Myrica* invasion.

**Seed germination**

Field germination experiments were undertaken to compare the potential for germination and survival of young *Myrica* seedlings on the two study sites. Seeds were collected from fruiting *Myrica* trees in the Devastation
area, an area of rain forest thinned by the 1959 eruption of Kilauea Iki. These seeds were lightly scarified using fine sand paper to remove the mesocarp (Walker 1990) and stored at room temperature. In September 1989, three plastic trays (55 x 28 x 20 cm deep) each with 38 cups were placed in the field at both study sites. The cups were filled with soil from each study site and each cup of each tray was sown with 10 Myrica seeds for a total of 380 seeds per tray. A cover made of 1 cm x 1 cm wire mesh was built around each tray to prevent seed predation. Seed germination and seedling survival were monitored twice a month over 10 months.

A second germination trial, performed under uniform greenhouse conditions, was set up to test the effect of soils from the two study sites on seed germination. Seeds obtained from fruiting Myrica trees, were germinated on intact soil cores taken from each site. Thirty replicate cores from each site were placed into soft plastic pots, each seeded with 15 Myrica seeds. The pots were placed under a mist watering system in the greenhouse; temperature averaged 20°C ± 4°C and light availability was 60% of full sunlight. Also, a control was established to determine germination on vermiculite, a neutral substrate. Three perforated plastic trays (51 x 25 x 5.4 cm deep)
with 48 cups were filled with vermiculite and each cup was sown with four seeds for a total of 192 seeds/tray.

Field growth

To compare the potential for plant growth at Ola'a tract and at Thurston, naturally established Myrica seedlings were collected from a nearby open canopied rain forest site and grown to about 5 cm in height in the greenhouse. Then, seedlings of uniform size were transplanted 1 m apart into three randomly placed 5 x 3 m plots on sites 3 and 4 with 15 seedlings per plot. A total of 45 seedlings was transplanted per site. The height and basal diameter of the transplants were measured monthly from December, 1989 to November, 1990. All transplants were harvested in November, 1990. Leaf, stem, and roots were separated and oven-dried at 60°C until a stable dry weight was reached. Analysis of variance was used to compare differences in plant growth parameters between sites.

Myrica stand development

The stand structure of the Myrica population at site 3 was determined to analyze the demographic characteristics of the invading population. A 100 m transect of 10
continuous 10 x 10 m plots was established. All *Myrica* were enumerated and their basal diameter measured.

**Greenhouse growth experiment**

The frequently waterlogged soils at Ola'a tract may have presented a barrier to the growth of *Myrica*, which establishes mostly on more mesic sites. An experiment to test the effect of excessive soil moisture regimes on *Myrica faya* seedling growth was undertaken at the University of Hawaii Tropical Agriculture farm, Volcano, Hawaii adjacent to the Ola'a tract. *Myrica faya* seedlings were grown in 12 liter pots containing an Ola'a soil:cinder mixture in a greenhouse under conditions of natural light, temperature and humidity. The experiment began January 9, 1991 and ended June 21, 1991. Two different treatment regimes were selected: waterlogged plants (WL) were subject to a water level maintained within 10 cm of the top of the pot using heavy plastic bags around the pot to retain the water while water was refreshed twice daily, and well-watered plants (WW) were watered every second day. There were 15 plants per treatment. Some extra pots with seedlings were maintained for determining biomass parameters for each treatment level during the experimental period. Pots were labeled by treatment level and randomly placed on three greenhouse
benches. The positions of the seedlings were shifted every 2 weeks to avoid any effect of variability in greenhouse conditions on plant growth. Height and diameter of the seedlings was monitored once a month for 6 months and harvested for determining leaf, stem, root and total biomass as well as total leaf area per plant.

Allometric equations were used to determine the relationship between height and diameter measurements and the biomass data taken from harvests at the beginning, middle and end of the experiment. The equations were based on the logarithmic transformation, \( \ln(Y) = \ln(a) + b\ln(X_1) + c\ln(X_2) \) where \( Y \) is dry weight (g), \( X_1 \) is basal diameter (cm) and \( X_2 \) is height (cm). These equations were corrected for bias, inherent in lognormal transformations of data, according to Sprugel (1983).

From the biomass data, the following growth parameters were derived according to the methods described by Hunt (1978) and Beadle (1985):

\[
RGR = \frac{\ln(W_2) - \ln(W_1)}{T_2 - T_1}
\]

\[
ULR = \frac{(W_2) - (W_1) \cdot (\ln A_2 - \ln A_1)}{T_2 - T_1 \cdot (A_2 - A_1)}
\]
Relative growth rate (RGR) (mg g\(^{-1}\) day\(^{-1}\)) is used to compare the effects of treatments on dry-matter production. Unit leaf rate (ULR) (g m\(^{-2}\) day\(^{-1}\)) is a measure of the net gain in dry weight of the plant per unit leaf area. It is a function of both photosynthesis and respiration. Leaf area ratio (LAR) (m\(^{2}\) kg\(^{-1}\)) is a ratio describing the amount of leaf area produced per unit of plant mass present.

The equations presented above to estimate ULR and LAR assume dry weight and leaf area are linearly related (Hunt 1978). Regression analysis from the harvests of plants under the four treatment regimes revealed that a linear relationship did exist between these two parameters.

Also derived from biomass data were the shoot-root ratio (shoot/root, shoot dry weight/root dry weight (g g\(^{-1}\))) and specific leaf area (SLA, leaf area/leaf dry weight (m\(^{2}\) kg\(^{-1}\)), a measure of leaf thickness.

Analysis of variance was used to compare differences in plant growth parameters between treatments.

**Habitat characteristics**

Soil moisture and light availability were monitored to determine differences in these factors between sites and
their potential effect on *Myrica* establishment. Soil core samples were taken from soil depths of 5 to 10 cm twice a month for about 11 months to determine soil water content. Moisture release curves were developed from psychrometric determinations of soil water potential at different soil water contents using a soil thermocouple psychrometer (Rawlins and Campbell 1986). The relative difference in light environments between the two study sites was determined at the ground level using LI-COR quantum sensors and GaAsP photodiodes (with a spectral response range between 300-680 nm) on each of three plots on each study site. Sensors were attached to a Campbell CR-10 micrologger for continuous data collection. Light measurements were taken every 10 s and averaged over 1 minute for 3 sunny days in May, 1990 at each site.

Climate data for weather diagrams was collected by the personnel of HAVO and the University of Hawaii Department of Tropical Agriculture at the Volcano farm.

**Results**

**Habitat**

Greater than average rainfall occurred during 1990, the year in which this study was conducted. The Volcano research farm adjacent to the Ola'a study site and the
park headquarters near the Thurston study site received 4580 mm and 4187 mm of rainfall, respectively (Fig. 4.1). Soil water content (g H2O/g soil dry weight(*100)) was 60 to 80% and 50 to 70% during the study period at Ola'a and Thurston, respectively. Soil water potential was around -0.05 MPa at site 4 during the study period, while at site 3, soil water potential ranged from -0.1 to -0.3 MPa (Fig. 4.2).

Light availability (Fig. 4.3) at ground level during midday was somewhat greater at site 4 than at site 3. Nearly 80% of the relative light availability at the forest floor was less than 5% of full sunlight at site 3, while at site 4 only 44% of the incoming light was less than 5% of full sunlight. Though the general vegetation structure is similar on both sites (Table 4.1), the recent development of *Myrica* in the canopy at site 3, may have begun to further reduce light availability at the forest floor here.

**Seed capture**

There was no *Myrica* seed captured during the year that the seed traps were monitored at the Ola'a tract boundary. Seeds from other forest trees such as *Cheirodendron trigynum* (Gaud.), *Ilex anomala* Hook. & Arnott, *Myrsine lessertiana* A. DC and *Coprosma ochracea*, as well as seeds
of other locally abundant species such as *Perottetia sandwicense* and *Rubus ellipticum*, were captured. At Thurston, *Myrica* seed inputs from established fruiting individuals was estimated at 3.7 million *Myrica* seeds ha\(^{-1}\) yr\(^{-1}\). At a nearby rain forest site, an estimated 100,000 *Myrica* seeds ha\(^{-1}\) yr\(^{-1}\) was dispersed onto the site by birds.

**Seed germination**

Seeds planted in the field had significantly lower germination rates than in the greenhouse (Table 4.2). Three different attempts to germinate *Myrica* seed in trays placed under the forest canopy and another attempt to germinate seeds on the forest floor at site 4 in Ola'a tract, were unsuccessful. However 11% of the seed germinated at site 3. Germination of *Myrica* seed was not significantly different on Ola'a tract and Thurston soil cores in the greenhouse but germination in both these treatments were somewhat lower than the vermiculite control (Table 4.2).

**Seedling growth**

Light availability was an important factor influencing seedling growth rates. At Thurston (site 3), the fall of one large tree fern early in the study resulted in a
partial opening of the canopy above one plot of 15 transplanted seedlings. RGR, ULR, and LAR of transplanted seedlings growing in the partial opening were significantly greater than seedlings growing under full tree fern cover (Table 4.3). The growth rates of transplanted seedlings at site 4 were not significantly different from those in the partial opening at the site 3. SLA was greater under full canopy cover at site 3 and under partial cover. RGR was influenced mostly by changes in ULR rather than LAR under different light regimes.

In the greenhouse experiment, waterlogging did not significantly alter the RGR, ULR, LAR or SLA of seedlings compared to the well watered control (Table 4.4). Though waterlogging reduced root and nodule mass, aboveground growth was not inhibited, resulting in a higher shoot-root ratio and greater biomass than the control (Table 4.5). Growth rates of greenhouse seedlings were significantly greater than those growing in the field probably due to greater light availability and warmer temperatures within the greenhouse.

Discussion

*Myrica faya* has many characteristics of a successful invader; early reproduction, rapid growth, abundant seed
production (Vitousek and Walker 1989). However, the dependence on birds for seed dispersal can limit *Myrica* invasion by influencing the range and habitats into which propagules are dispersed. Though *Myrica* seed was available at the invasion front, about 0.5 km from the site where seed traps were set up, seed inputs into the wet montane dieback forest of Ola'a tract appeared to be very low. Alien birds, such as the Japanese white-eye (*Zosterops japonica*), are known to feed on *Myrica* fruit and disperse seed (Woodward et al. 1990), however, the presence of these birds in areas of *Metrosideros* dieback may be somewhat reduced due to the low density of trees and potential food sources resulting in very limited *Myrica* seed dispersal ahead of the invasion front (Sakai, Cuddihy, pers. comm.). Though no *Myrica* seed was captured in seed traps placed beyond this invasion boundary, reports over the past 10 years of two *Myrica* saplings found a kilometer beyond the invasion boundary in the rain forest provide some indication that a limited amount of seed dispersal must occur beyond its current range (Tunison, pers. comm.). Abundant sources of *Myrica* seed in close proximity to the dieback forest behind Thurston Lava Tube probably contributed to a high degree of seed rain onto that site.
Limits to *Myrica* invasion of the montane rain forest also include: the suppression of germination, growth or survival of *Myrica* by existing vegetation and potential adverse affects of abiotic factors on germination and growth. Lower light availability and lower temperatures in the field trials probably reduced germination compared to germination in the greenhouse. Also, seed germination was more strongly inhibited at site 4 in Ola'a tract than at site 3 behind Thurston Lava Tube, though light availability was slightly higher at Ola'a tract. Higher rainfall and more frequently waterlogged soils at Ola'a tract may promote fungal growth on *Myrica* seed or reduce oxygen availability to the embryo (when seeds are in water or coated with a film of water for prolonged times). The inhibition of seed germination due to reduced oxygen diffusion though a film of water around seed in waterlogged soils has been demonstrated in plants unadapted to such conditions (Dasberg and Mendel 1971). While most studies of *Myrica* germination have focused on the effect of one factor (i.e., light), further studies of the interaction of soil water content, temperature and light availability need to be done to fully understand the potential influence of the combination of these factors on *Myrica* seed germination.
Light preemption by the *Cibotium* subcanopy limits *Myrica* seedling growth. Optimal *Myrica* growth occurs in 70% of full sunlight (Vitousek and Walker 1989) and seedlings exhibit suppressed growth under very low light availabilities. Survival of seedlings for up to 5 months under 1% of full light, characteristic of the understory light regime of many closed canopied forest sites, has been recorded in a related study done by this author. The stand structure of *Myrica* at site 3 indicated that abundant young seedling regeneration occurs but few seedlings survive to become saplings. Therefore, further recruitment of saplings to canopy tree status is unlikely.

While *Myrica* seedling growth rates were very low under the *Cibotium* treefern cover, growth can increase in response to changes in light availability following the development of a gap in the treefern cover. LAR, the ratio of photosynthetically active area to total plant biomass, remained relatively unchanged from habitat to habitat while ULR, the net gain in dry weight of the plant per unit leaf area, was strongly influenced by light levels and explained most of the variation in RGR. Reduced photosynthesis under conditions of low light availability was the most likely cause of low growth rates and biomass production. In montane rain forest communities in which the overstory and understory are
intact, the suppression of Myrica growth may be greater than that observed in this study where the overstory has been lost through dieback.

High soil water availability and periodically waterlogged soil conditions at Ola'a tract appeared to restrict germination but not Myrica growth. Waterlogged soils, which tend to have a low rate of oxygen diffusion, are often characterized by toxic concentrations of Fe$^{2+}$ and Mn$^{2+}$ (Talbot et al. 1987). Analysis of Ola'a soils indicated relatively low levels of these ions (Balakrishnan and Mueller-Dombois 1983). However, the montane rain forests on the slopes of Mauna Loa receive 3000 to 5000 mm rainfall yr$^{-1}$ (State of Hawaii 1970). There are many poorly drained sites in which soils have potentially toxic levels of these ions and hypoxic conditions which may restrict Myrica establishment (Balakrishnan and Mueller-Dombois 1983).

While low seed inputs would control the initial rate of invasion into new habitats, abiotic factors also play an important role in limiting Myrica establishment in montane rain forest sites. High rainfall and poor soil drainage, coupled with low light levels at the forest floor, limit germination and restrict growth in wet, montane rain forest habitats. Myrica has abundant seed production and tremendous growth potential (Vitousek and
Walker 1989) which has ensured its successful invasion in some habitats. However, biotic and abiotic factors vary with the habitat and community development and have different degrees of influence on the invasive potential of Myrica.
Table 4.1: Canopy and understory plant cover (%) at site 3 (Thurston) and site 4 (Ola'a).

<table>
<thead>
<tr>
<th></th>
<th>Site 4</th>
<th>Site 3</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Canopy</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Metrosideros polymorpha</em></td>
<td>2.9</td>
<td>11.3</td>
</tr>
<tr>
<td><em>Myrica faya</em></td>
<td>0</td>
<td>24.0</td>
</tr>
<tr>
<td>Other tree species</td>
<td>11.3</td>
<td>19.1</td>
</tr>
<tr>
<td><strong>Understory</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cibotium glaucum</em></td>
<td>94.3</td>
<td>92.1</td>
</tr>
<tr>
<td>Herbs and shrubs</td>
<td>27.6</td>
<td>26.0</td>
</tr>
</tbody>
</table>
Table 4.2: Germination (%) of *Myrica faya* seeds in the greenhouse (in soil cores from each site) and in trays placed in the field at sites 3 and 4. Means of 3 replications with standard error in brackets.

<table>
<thead>
<tr>
<th></th>
<th>Greenhouse soil core</th>
<th>Field</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site 4</td>
<td>32.4&lt;sup&gt;a&lt;/sup&gt; (3.4)</td>
<td>0.0</td>
</tr>
<tr>
<td>Site 3</td>
<td>43.3&lt;sup&gt;a&lt;/sup&gt; (4.2)</td>
<td>11.0</td>
</tr>
<tr>
<td>Control</td>
<td>61.6&lt;sup&gt;b&lt;/sup&gt; (3.8)</td>
<td>n/a</td>
</tr>
</tbody>
</table>

<sup>a</sup>Chi-square analysis of arcsine transformed data. Superscripts with the same letter are not significantly different (P<.05).
Table 4.3: Relative growth rate (RGR, mg g\(^{-1}\) day\(^{-1}\)), unit leaf rate (ULR, g m\(^2\) day\(^{-1}\)), leaf area ratio (LAR, m\(^2\) kg\(^{-1}\)), specific leaf area (SLA, m\(^2\) kg\(^{-1}\)) and final biomass (g) of transplanted Myrica seedlings grown over an 11 month period at site 3 (under partial and closed cover) and site 4. Values are means with standard deviation in brackets.

<table>
<thead>
<tr>
<th>Locality</th>
<th>RGR</th>
<th>ULR</th>
<th>LAR</th>
<th>SLA</th>
<th>Biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site 4</td>
<td>4.87a</td>
<td>0.674a</td>
<td>7.11a</td>
<td>20.13a</td>
<td>0.65a</td>
</tr>
<tr>
<td>n=45</td>
<td>(.19)</td>
<td>(.012)</td>
<td>(.29)</td>
<td>(.43)</td>
<td>(.09)</td>
</tr>
<tr>
<td>Site 3</td>
<td>2.87b</td>
<td>0.452b</td>
<td>6.45b</td>
<td>21.3b</td>
<td>0.31b</td>
</tr>
<tr>
<td>closed</td>
<td>(.20)</td>
<td>(.03)</td>
<td>(.20)</td>
<td>(1.0)</td>
<td>(.04)</td>
</tr>
<tr>
<td>n=26</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>partial</td>
<td>5.40a</td>
<td>0.697a</td>
<td>7.85a</td>
<td>20.3a</td>
<td>0.55a</td>
</tr>
<tr>
<td>n=15</td>
<td>(.30)</td>
<td>(.04)</td>
<td>(.25)</td>
<td>(1.3)</td>
<td>(.20)</td>
</tr>
</tbody>
</table>

a All comparisons in a column are significantly different (P<.05) except those with a common superscript.
Table 4.4: Relative growth rate (RGR, mg g\(^{-1}\) day\(^{-1}\)),
unit leaf rate (ULR, g m\(^2\) day\(^{-1}\)), leaf area
ratio (LAR, m\(^2\) kg\(^{-1}\)), specific leaf area (SLA, m\(^2\) kg\(^{-1}\)) of Myrica seedlings grown in pots
experimentally treated in a greenhouse. Myrica seedlings were subjected to two
treatments: well watered (WW) and
waterlogged soils (WL). Values are means
with standard error in brackets.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>RGR</th>
<th>ULR</th>
<th>LAR</th>
<th>SLA</th>
</tr>
</thead>
<tbody>
<tr>
<td>WW</td>
<td>21.21(^a)</td>
<td>3.87(^a)</td>
<td>5.79(^a)</td>
<td>9.86(^a)</td>
</tr>
<tr>
<td>n=15</td>
<td>(.70)</td>
<td>(.29)</td>
<td>(.29)</td>
<td>(.17)</td>
</tr>
<tr>
<td>WL</td>
<td>22.32(^a)</td>
<td>4.04(^a)</td>
<td>5.82(^a)</td>
<td>9.92(^a)</td>
</tr>
<tr>
<td>n=15</td>
<td>(.49)</td>
<td>(.31)</td>
<td>(.32)</td>
<td>(.25)</td>
</tr>
</tbody>
</table>

\(^a\)All comparisons in a column with a common
superscript are not significantly different
(P<.05).
Table 4.5: Mean dry weights (g plant$^{-1}$) of leaves, shoots, roots, and nodules, total plant leaf area (m$^2$), shoot/root ratio and final biomass of Myrica seedlings grown in well watered (WW) and waterlogged soils (WL). Standard errors in brackets, n=15.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Leaf</th>
<th>Stem</th>
<th>Root</th>
<th>Nodule</th>
<th>Leaf area</th>
<th>Shoot/Root</th>
<th>Final biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>WW</td>
<td>81.9a</td>
<td>60.4a</td>
<td>26.3a</td>
<td>4.3a</td>
<td>0.79a</td>
<td>4.7a</td>
<td>173.0a</td>
</tr>
<tr>
<td></td>
<td>(4.6)</td>
<td>(3.9)</td>
<td>(1.2)</td>
<td>(.5)</td>
<td>(.04)</td>
<td>(.3)</td>
<td>(9.1)</td>
</tr>
<tr>
<td>WL</td>
<td>115.4b</td>
<td>87.5b</td>
<td>21.4b</td>
<td>2.9b</td>
<td>1.1b</td>
<td>8.3b</td>
<td>231.2b</td>
</tr>
<tr>
<td></td>
<td>(5.5)</td>
<td>(4.9)</td>
<td>(1.7)</td>
<td>(.5)</td>
<td>(.07)</td>
<td>(.4)</td>
<td>(11.9)</td>
</tr>
</tbody>
</table>

All comparisons in a column are significantly different (P<.05) except those with a common superscript.
Fig. 4.1. Location of site 3 behind Thurston Lava tube and site 4 in the Olaa tract of Hawaii Volcanoes National Park. Weather diagrams for 1990 are also presented. Curve of mean monthly temperature is the stipled line. Curve of mean monthly precipitation is the solid line. Black area indicates mean monthly precipitation ≥ 100 mm. Vertical shading indicates a season of adequate rainfall (after Walter 1957). Total precipitation for 1990 and the average total precipitation over 15 years given in the top right hand corner of the weather diagram.
Fig. 4.2. Soil water potential (MPa) at site 3 (●) and site 4 (○) measured from January to November 1990.
Fig. 4.3. Relative light availability during midday hours, as a percent of full sun, averaged over a three day period at site 3 (solid bars) and site 4 (thatched bars).
Fig. 4.4. Stand structure of *Myrica* actively invading the dieback forest behind Thurston Lava tube (site 3). Arrow indicates sapling gap in stand structure.
Literature cited


CHAPTER 5
SYNTHESIS

The nature of the native plant communities in the Hawaiian Islands, low in species diversity and structurally simplistic, often predisposes them to invasion by aggressive alien weeds (Loope and Mueller-Dombois 1989). Many alien plant invasions in Hawaii have been successful and those species that have naturalized amount to 47% of Hawaii's flowering plant flora (Wagner et al. 1990). Invasive alien plants present a threat to the maintenance and continued existence of remaining natural plant communities of Hawaii that have so far escaped the destructive effects of development, agriculture or grazing (Smith 1984, Cuddihy and Stone 1990).

An invasive tree which has attracted a great deal of attention and concern in Hawaii for its recent explosive increase on several islands and its ability to invade nearly intact plant communities is *Myrica faya* (Cuddihy and Stone 1990). *Myrica faya*, an actinorrhizal nitrogen fixing tree native to the Macaronesian islands, was probably introduced during the late 1880's to Hawaii (Fosberg 1937). On Hawaii island, *Myrica* invasion has been particularly rapid in Hawaii Volcanoes National Park (HAVO). First discovered there in 1961, it has spread
rapidly over 11,000 ha of the park (Camrath and Tunison 1992) (Fig. 5.1). Myrica faya invasion has occurred in young volcanic cinder habitats, open canopied seasonal montane forest and grassland and in closed canopied montane rain forest (Whiteaker and Gardner 1985, Camrath and Tunison 1992). Copious seed production, seed dispersal by birds, and rapid growth rates in open canopied forests (which provide suitable light and temperature conditions for germination and growth) have facilitated the rapid establishment of Myrica faya (Vitousek and Walker 1989). However, particular aspects of the biology of Myrica, such as low seed germination and limited survival under the low light conditions (Vitousek and Walker 1989, Walker 1990) that are commonly found in the understory of rain forests (Burton and Mueller-Dombois 1984), appear to reduce the invasive potential of this alien weed into closed canopied rain forest communities.

HAVO resource managers are involved in an active program for the control of Myrica. To allocate resources and facilitate management efforts, information concerning Myrica population development in the rain forest and potential community-level alterations with Myrica invasion would provide some indications of potential problems that may be addressed through management. Also, determining the potential for further range expansion of Myrica and
the identification of habitats in which Myrica has reached its ecological limits would direct future control efforts.

This study was designed to determine the community-level and ecophysiological constraints to Myrica invasion and to analyze its potential for further range expansion in HAVO. Locations of research sites are indicated in Figure 5.2. Two major hypotheses were addressed: 1) that the structural characteristics of closed canopied communities, would present barriers to the invasion of Myrica and 2) that Myrica has reached its ecophysiological limits at its current invasion boundaries in the wet montane rain forest and seasonally drought prone grassland. It is predicted that invasion of new habitats beyond its current range of Myrica will be restricted. I review factors that would potentially limit Myrica invasion including seed inputs, germination and seedling growth within and beyond the current invasion range of Myrica.

Community-level constraints to invasion

The montane rain forest of HAVO is dominated by a closed overstory canopy of Metrosideros polymorpha with a well developed understory of mixed native tree species and ferns. Particularly dominant in the understory is the treefern, Cibotium glaucum, which forms a dense layer of
fronds between 3 and 6 m above the forest floor in mature and overmature *Metrosideros* forests. In young *Metrosideros* forests, a mat-forming fern, *Dicranopteris linearis*, develops dense thickets from the ground to about 1 m in height. *Myrica* invasion of these forests has been limited to trail and roadsides, heavily disturbed sites, areas in which either the *Dicranopteris* or *Cibotium* fern cover has been disturbed by pig activity and on sites in which canopy trees have undergone stand-level decline. While certain rain forest sites show some invasion of *Myrica*, *Myrica* is absent from others, most notably, from sites containing an intact understory of *Dicranopteris* fern. The low establishment of *Myrica* in the rain forest contrasts *Myrica* establishment in open canopied seasonal submontane forest and volcanically disturbed rain forest where *Myrica* density ranges from 1000 to 1800 trees ha\(^{-1}\) in places. The activity of feral pigs in the rain forest, uprooting *Cibotium* and *Dicranopteris* fern and exposing the soil, has facilitated the invasion of many alien species in the rain forest including *Myrica* (Stone et al. 1992). It has been suggested that past pig activity destroyed much of the *Dicranopteris* fern cover in the Puhimau area, which lead to the development of a dense monospecific stand of *Myrica* at that site. Feral pigs were removed from certain areas of the rain forest in HAVO by 1980.
through an intensive management program initiated by resource managers however, population development of *Myrica* and other alien trees has continued (Stone et al. 1992).

Three rain forest communities, which developed after the 1790 explosive eruption of Kilauea Volcano that destroyed the forest and laid down a layer of ash and cinder, were selected for a study of community-level constraints to invasion. Site 1 was characterized by the development of a young *Metrosideros* stand with a dense understory of the matted fern, *Dicranopteris*. Site 2 was characterized by a mature stand of *Metrosideros* with developing subcanopy of *Myrica* and an understory of *Cibotium* tree fern. Site 3 was characterized by dieback of the *Metrosideros* overstory, a dense understory of *Cibotium* and an advanced development of a population of *Myrica*. The different successional stages of *Metrosideros* stand development represented by each site are believed to have resulted from different rates of plant colonization and community development after the eruption.

First, I examined whether the absence of *Myrica* at sites containing *Dicranopteris*, represented by site 1, was due to a lack of seed inputs or from some factor limiting establishment. A seed trap study revealed that seed inputs into site 1 were relatively high. In plots where
the Dicranopteris cover was manually removed, the presence of naturally established Myrica seedlings (17 in 30 m² after 2 years) indicated a strong potential for Myrica invasion in the absence of Dicranopteris fern.

I hypothesized that the presence of the dense cover of Dicranopteris fern, restricted Myrica invasion by reducing the amount of incoming light to below that needed for Myrica germination, growth and survival. I tested Myrica seed germination, seedling survival and seedling growth under the Dicranopteris fern. Light levels were also measured and it was determined that 72% of the light reaching the soil surface was below 1% of full sun. While 25% of the seed germinated, 86% of these died in the first 5 months and all were dead after 10 months. Growth of transplanted seedlings was very low (2.7 mg g⁻¹ day⁻¹) and after 8 months 87% of these seedlings had died.

In other rain forest habitats, the dense cover of Cibotium tree fern present in mature Metrosideros forest, also presents a barrier to light availability at the forest floor. Measures of light levels at the forest floor of a Metrosideros/Cibotium forest revealed that 80% of the incoming light is less than 5% of full sun. However, much of the Metrosideros/Cibotium forest has been invaded by Myrica. I believe that disturbance of the understory by pigs, which tend to uproot individual tree
ferns and create gaps in the tree fern cover, increasing light availability to the forest floor, has promoted the invasion of Myrica into these habitats. At site 2, Myrica has become a subcanopy component of the Metrosideros/Cibotium forest. Though the Metrosideros overstory has undergone some crown decline, infilling of the mid-canopy by the crowns of established Myrica has increased the canopy LAI at site 2. This developing Myrica canopy is now strongly limiting the recruitment of its own seedlings and saplings. In germination and seedling growth trials in the understory of site 2, germination of Myrica seed was found to be low (11.4% of viable seed). Seedlings exhibited very low relative growth rates (1.12 mg g⁻¹ day⁻¹) and there was 89% mortality after 6 months. Here, the developing canopy of established Myrica trees has altered light availability to the forest floor, limiting its further recruitment.

With the occurrence of Metrosideros dieback in the rain forest zone, I hypothesized that increased light levels at the forest floor would facilitate Myrica establishment. Most of the Metrosideros overstory at site 3 was lost to dieback. Here, the overstory canopy LAI is very low (<1 m² m⁻²) but below the extensive Cibotium tree fern cover LAI is greater than 5 m² m⁻². Myrica has invaded this site and is beginning to develop a new
canopy. I tested *Myrica* seed germination, seedling survival and seedling growth under the *Cibotium* cover. Light levels were also measured and it was determined that 85% of the light reaching the soil surface was below 5% of full sun. Only 13% of the *Myrica* seed germinated, 86% of these germinants died in the first 5 months and all were dead after 10 months. The relative growth rates of transplanted seedlings were low, 2.9 mg g⁻¹ day⁻¹ under full cover and, where there was a gap in the treefern cover over one plot, growth was nearly doubled to 5.4 mg g⁻¹ day⁻¹. Despite the open overstory, the tree fern cover strongly influences light availability to the forest floor. A structural analysis of the developing stand of *Myrica* at this site indicates that further seedling and sapling regeneration is strongly suppressed. Gaps or partial gaps in the tree fern cover may have facilitated the initial invasion of *Myrica* at this site. However, intact tree fern cover inhibits the establishment of *Myrica* as well as *Metrosideros* by limiting light which is needed for germination and growth.

Overall, *Myrica* invasion is constrained by two main factors: the structural characteristics of the rain forest, particularly the understory fern layer which intercepts much of the incoming light through the canopy resulting in low light levels at the forest floor, and the
low germination potential and low growth and survival of *Myrica* under low light conditions. As a result, *Myrica* invasion can only occur in the rain forest if there is some disturbance of the understory fern layer. Prior to the removal of pigs from the rain forest some *Myrica* became established and are now prominent in mid-canopy positions. Despite predictions by Vitousek and Walker (1989) that in time dense stands of *Myrica* could develop completely displacing the native canopy tree *Metrosideros*, this is unlikely in rain forest habitats. The current population structure of *Myrica* in the rain forest indicates that further reproduction is limited, which suggests that *Myrica* has nearly reached its full potential occupation of these communities.

Ecophysiological constraints to invasion beyond the current range of *Myrica*

**Invasion boundary characteristics**

There are relatively distinct boundaries to the current invasion range of *Myrica* in HAVO. An invasion boundary is evident in the montane rain forest where *Myrica* has not yet invaded wet habitats. A survey of *Myrica* invasion done in 1985 and repeated in 1992 revealed that *Myrica* has not increased its invasion range in the wet montane forest over this period (Whiteaker and Gardner
1985, Camrath and Tunison 1992). Another invasion boundary occurs in the seasonal submontane grassland near Kipuka Nene Campground. This invasion boundary has been slowly progressing across the grassland at an apparent rate of 0.27 km per year (Camrath and Tunison 1992).

The two boundaries of Myrica invasion that were investigated in this study, occur in very different environments and communities. High year-round precipitation and frequently waterlogged soils are characteristic of the wet montane rain forest near the northern invasion boundary of Myrica. The seasonal submontane grassland, at the southern invasion boundary of Myrica, is drier and warmer than the montane rain forest and is subject to a 1 to 2 month (on average) drought during the summer. I hypothesized that the potential for the spread of Myrica beyond its current invasion range is limited by an intolerance of early life stages of Myrica to environmental stresses particular to each habitat (i.e., excess soil water availability in the wet montane forests and the lack of soil moisture during the drought period in the seasonal submontane grassland).

Three sites were selected for the study of constraints to the invasion of Myrica beyond its current invasion range. Within the wet montane rain forest a site was selected in the Olaa tract which lies about 0.5 km beyond
the current range of *Myrica* in the montane rain forest (Site 4) (Fig. 5.2). This late-successional forest is characterized by dieback of the overstory tree, *Metrosideros polymorpha*, and a dense subcanopy of the treefern *Cibotium*. Two study sites were located in the seasonal submontane grassland. Site 5 was located near the current boundary of *Myrica* invasion in the grassland and site 6 was located 3 km beyond the current boundary (Fig. 5.2). While the vegetation at these grassland sites consisted primarily of alien grasses such as *Melinus minutiflora* and *Schizachyrium condensatum*, site 5 also supported scattered native shrubs of *Sophora chrysophylla*, *Dodonaea viscosa* and *Styphelia tameiameiae*.

**Restriction in seed dispersal**

Simultaneously with the study of the potential effects of habitat factors on *Myrica* establishment beyond these two invasion fronts, seed dispersal outside the invasion range of *Myrica* but close to the invasion fronts was also investigated. In a seed capture study near the invasion boundaries in the wet montane rain forest and the seasonal submontane grassland, *Myrica* seed inputs were very low. *Myrica faya* is primarily bird-dispersed and the density of fruiting trees and the feeding behavior of birds may influence the amount of seed dispersed into habitats.
beyond its current range. The presence of a few outliers of *Myrica* scattered beyond the invasion boundaries in these habitats suggests that some dispersal of seed occurs and germination, growth and survival are successful. However, behavior of seed-dispersing birds across these habitats and communities has not yet been studied. Such a study would provide a better understanding of the influence of bird dispersers on the rate of *Myrica* invasion.

**Ecophysiological constraints**

To determine whether *Myrica* reached its ecophysiological limits at these two contrasting boundaries in HAVO, I set up a number of experiments to determine the potential for seed germination and seedling growth and survival in these habitats. Seed germination was monitored in trays filled with soil from each habitat. Young seedlings were also transplanted at each site to determine seedling growth potential and mortality in the contrasting habitats.

In the seasonal submontane grassland beyond its current range of invasion, *Myrica* germination and seedling survival were very low. At site 6, which is drier and warmer than site 5, only 2.3% of the seed sown in trays germinated and 18% of these were alive after 10 months.
At site 5 12% of the seed sown in trays germinated and 39% of these were alive after 10 months. However, germination in the field was significantly lower than in the greenhouse (60%) where seeds were well watered. Low soil moisture availability during the summer appears to be a limiting factor to establishment. In an experiment where seeds were germinated under different degrees of *Melinus* cover, germination was increased by 51% when placed in the shade of full *Melinus* cover compared to germination on unvegetated soil. The shade provided by the cover of the alien grass *Melinus* may create somewhat cooler and moister microsite conditions favorable to young germinant survival than unshaded microsites.

Transplanted seedling growth was greater during the wet season than the dry season in the grasslands. During the wet season, seedling growth was 18.3 mg g\(^{-1}\) day\(^{-1}\) and 19.9 mg g\(^{-1}\) day\(^{-1}\) at sites 6 and 5, respectively. However, growth rates declined significantly during the drought period to 4.0 mg g\(^{-1}\) day\(^{-1}\) and 6.4 mg g\(^{-1}\) day\(^{-1}\) at site 6 and 5, respectively. Also, the results of a competition experiment of *Myrica* seedlings with *Melinus* grass, indicated that competition for soil moisture during periods of drought may result in significant reductions of *Myrica* seedling growth rates. The susceptibility and sensitivity of young seedlings to water stress appears to
be a factor limiting further *Myrica* invasion beyond its current range in the seasonally dry grassland.

In the wet montane forest, seed germination was strongly inhibited. *Myrica faya* seed may not be able to germinate in soil that is frequently waterlogged or where waterlogging is associated with low light levels at the forest floor. In the montane rain forests receiving greater than 3000 mm rainfall yr\(^{-1}\), periodically waterlogged soils may inhibit seed germination through fungal growth on the seed or reduced oxygen availability when seeds are coated with a film of water (Dasberg and Mendel 1971). Transplanted seedlings grew significantly less in the wet montane rain forest (4.9 mg g\(^{-1}\) day\(^{-1}\)) than in the seasonal submontane grasslands during the wet season. However, seedling growth was greater in the wet montane rain forest than growth at mesic rain forest sites (1 to 3 mg g\(^{-1}\) day\(^{-1}\)) where light availability was lower and soils were well drained. While low light availability in the montane rain forest decreases *Myrica* seedling growth rates, my experiments indicated that *Myrica* range expansion into the wet montane forest may be limited by the inability of *Myrica* seed to germinate in excessively wet soils and under low light conditions.

Factors controlling the invasion of *Myrica* in HAVO included: bird-dispersed seed inputs beyond its current
range of invasion, interference by existing vegetation and abiotic stresses. While low seed dispersal beyond the current invasion boundaries limits the rate of invasion the response of *Myrica* to the habitat conditions beyond its invasion range limits its ability to become established. Expansion of *Myrica* into wet, montane rain forest is not expected to occur due to its low germination and survival in these habitats. However, some range expansion may occur in the seasonal submontane grasslands if a number of consecutive wet summers permit the growth and establishment of individual *Myrica* to the adult stage. While very young *Myrica* seedlings are susceptible to drought, older seedlings and adults appear to be relatively drought tolerant. As individuals mature and produce seed, the potential for *Myrica* population growth and expansion increases. However, *Myrica* expansion beyond its current range in drought-prone habitats is expected to be very limited.

Summary of significant findings

1. A large percentage of available light (55 to 70 %) under the *Dicranopteris* fern and *Cibotium* tree fern layers, at midday, is below the light compensation point
for CO₂ assimilation of shade-adapted Myrica. This results in high seedling mortality. Thus, Myrica is unable to establish itself under intact fern understories characteristic of the montane rain forest of HAVO.

2. Disturbance of the rain forest understory fern layer, however, promotes the establishment of Myrica in the rain forest. Disturbance of the Dicranopteris fern cover by pigs or the Cibotium understory by wind throw or pig damage, can increase the levels of incoming light above the light compensation point for Myrica by 40 to 50%.

3. The addition of Myrica in the canopy or subcanopy increases LAI of the rain forest community. Consequential reductions in light levels at the forest floor limit further Myrica establishment on the site and results in the development of a cohort or single generation stand.

4. Dieback of the Metrosideros overstory in the rain forest with dense Cibotium undergrowth does not directly facilitate Myrica invasion. However, wind throw of Cibotium tree ferns in Metrosideros dieback stands can create gaps that facilitate Myrica establishment.
5. Excess soil water appears to inhibit *Myrica* seed germination and limit the potential for *Myrica* invasion in wet, montane rain forest habitats.

6. The early life stages of *Myrica* are most vulnerable to drought in the seasonally dry grasslands, particularly seed germination and young seedling survival. This limits *Myrica* invasion into drought-prone environments.

7. Older *Myrica* seedlings appear to be able to withstand 3 months of drought in the seasonal submontane grassland, though growth rates during drought are very low. Mortality begins in the fourth month of drought.

8. *Myrica* adults growing in the seasonally dry environment have developed the capacity to osmotically adjust and maintain turgor during periods of low water availability. However, increased osmotic potential is an indication of internal stress which may lead to reduced vigor or susceptibility to insect attack.

9. Despite high young seedling mortality, *Myrica* invasion of the seasonal submontane grasslands will continue within the current invasion range as seed inputs from established
individuals increase. However, any range expansion into more drought-prone habitats is not expected.

Suggestions for future research

Study focus on bird-behavior at invasion boundaries

While previous studies of bird feeding behavior have focused on some major habitats, there is little information on their habits at boundaries between forest and grassland or ecotones. For example, habitat and food availability differ between the submontane woodland and grassland communities and also between intact and dieback rain forest communities. Bird use of these habitats and presence and behaviour of potential bird dispersers of Myrica are expected to be different and will affect the spatial dynamics of Myrica.

Study focus on other invasion boundaries in different environments

This study focused on the invasion of Myrica within its current range and invasion into habitats within a few kilometers of its current invasion range in wet montane and seasonally dry submontane environments. However, the current invasion range of Myrica has other boundaries which have not been investigated. Camrath and Tunison
(1992) have noted an increase in the range of *Myrica* on the east slopes of Kilauea towards the warmer and more humid side of the island of Hawaii. Also, the potential for *Myrica* invasion above 1200 m towards higher elevations where habitats are cooler and drier has not been investigated. While this study suggests that *Myrica* has nearly reached its full potential range of occupation between the warm, seasonally dry environment and the wet, montane rain forest, additional information on the potential for *Myrica* invasion beyond these other boundaries would indicate whether *Myrica* has reached its full invasion potential in the landscape of HAVO.

**Study focus on Myrica dieback**

Recent observations of a rapid *Myrica* dieback in an area of intense *Myrica* invasion in HAVO have produced new questions as to the potential ecological limits of *Myrica* invasion. Some researchers have suggested that an insect or insect-vectored pathogen may be responsible for the current *Myrica* dieback in some areas. Other researchers believe that 3 years of drought may have physiologically weakened established *Myrica* trees, making them susceptible to insect attack. Also, a current lack of *Myrica* regeneration in the area where dieback is occurring suggests that the extended drought period is limiting
population development (Tunison, pers. comm.). This dieback phenomenon needs to be investigated further as it is unknown at this time whether Myrica is undergoing a total population collapse or is experiencing a temporary contraction of its range. Concerted efforts between ecologists and pathologists may help resolve the causes of the observed Myrica dieback.
Fig. 5.1. The current distribution of *Myrica faya* in Hawaii Volcanoes National Park (thatched area) (modified from Camrath and Tunison 1992).
Hawaii Volcanoes National Park

Mauna Loa Summit

Alpine

Subalpine

Montane Seasonal

Submontane Seasonal

Rain forest

'Olula Montane Rainforest

Talusan caldera

Coastal Lowland

Hawaii Volcanoes National Park

Pacific Ocean

0 1 2 3 4 5 miles

0 2 4 6 8 km
Fig. 5.2. Location of study sites in HAVO.
Literature cited


PART III: APPENDICES
Appendix A

Species list

Vascular plants

PSILOPHYTA
PSILOTACEAE
Psilotum campulatum Sw.
Psilotum nudum (L.) Beaux.
LYCOPHYTA
LYCOPODIACEAE
Lycopodium cernuum L.
PTERIDOPHYTA
ASPLENIACEAE
Asplenium acuminatum Hook & Arn.
Asplenium lobulatum Mett.
ATHRIACEAE
Athyrium microphyllum (Sm.) Alston
Diplazium sp.
BLECHNACEAE
Sadleria cyaetheoides Kaulf.
DENNSTAEDTIACEAE
Microlepiia strigosa (Thunb.) Presl.
DICKSONIACEAE

*Cibotium glaucum* (J. Sm.) Hook & Arnott
*Cibotium hawaiense* Nakai & Ogura

ELAPHOGLOSSACEAE

*Elaphoglossum hirtum* (Sw.) C. Chr. var. *micans* (Mett.) C. Chr.

GLEICHENIACEAE

*Dicranopteris linearis* (Burm.) Underw.

HEMIONITIDACEAE

*Coniogramme pilosa* (Brack.) Hieron.

HYMENOPHYLLACEAE

*Sphaeroconium lanceolatum* (Hook & Arn.)
*Vandenboschia davallioides* (Gaud.) Copel.

HYPOLEPIDACEAE

*Pteridium aquilinum* (L.) Kuhn var. *decompositum* (Gaud.) Tryon

OPHIOGLOSSACEAE

*Ophioglossum pendulum* L. subsp. *falcatum* (Presl) Clausen

ORCHIDACEAE

*Phaius tankarvilleae* Banks ex L'Hér.

THELYPTERIDACEAE

*Pneumatopteris sandwicensis* (Brack.) Holtt.
MONOCOTYLEDONAE

CYPERACEAE

Carex wahuensis C. A. Mey. var. rubiginosa R.W. Krauss
Cyperus gracilis R. Br.
Gahnia gahniformis (Gaud.) A. Heller
Machaerina angustifolia (Gaud.) Kern

GRAMINEAE (POACEAE)

Andropogon virginicus L.
Isachne distichophylla Munro ex Hillebr.
Melinus minutiflora P. Beauv.
Ehrharta stipoides Labill.
Rynchelytrum repens (Willd.)
Setaria gracilis Kunth.
Setaria palmifolia (J. Konig) Stapf
Sporobolus africanus (Poir.) Robyns

LILIACEAE

Astelia menziesiana Sm.
Hedychium gardnerianum Ker-Gawl.

ORCHIDACEAE

Spathoglottis plicata Bl.

SMILACACEAE

Smilax melastomifolia Sm.
DICOTYLEDONAE

AQUIFOLIACEAE

Ilex anomala Hook & Arnott

ARALIACEAE

Cheirodendron trigynum (Gaud.) Heller

CELASTRACEAE

Perrottetia sandwicensis Gray

ASTERACEAE

Bidens pilosa L. var. pilosa
Dubautia ciliolata (D.C.) Keck
Emilia sonchifolia var. sonchifolia (L.) D.C.
Pluchea odorata (L.) Cass.

EPACRIDACEAE

Styphelia tameiameiae (Cham.) F. Muell.

ERICACEAE

Vaccinium calycinum Smith f. fauriei (Lévl.) Skottsbg.
Vaccinium reticulatum Sm.

FABACEAE

Sophora chrysophylla (Salisb.) Seem

GUTTIFERAEE (CLUSIACEAE)

Hypericum degeneri Fosb.

MYRICACEAE

Myrica faya Ait.
MYRSINACEAE

*Myrsine lessertiana* A. D.C.

*Myrsine sandwicense* A. D.C.

MYRTACEAE

*Metrosideros polymorpha* Gaud. var. *polymorpha*

*Psidium cattleianum* Sabine f. *cattleianum*

*Psidium guajava* L.

PASSIFLORACEAE

*Passiflora mollissima* (HBK). Bailey

RANUNCULACEAE

*Anemone hupehensis* (Lem. & Lem. f.)

ROSEACEAE

*Rubus rosifolius* Sm.

*Rubus argutus* Link.

RUBIACEAE

*Coprosma ernodeoides* Gray

*Copromia ochracea* Oliver var. *rockiana* Oliver

*Hedyotis terminalis* Hook & Arnott

*Hedyotis centranthoides* (Hook & Arnott) Steud.

SAPINDACEAE

*Dodonaea viscosa* Jacq.

THYMELAECEAE

*Wilkstroemia phillyreifolia* A. Gray
Non-Vascular plants

Lichens

Cladina sp.

Cladonia skottsbergii H. Magn.

Stereocaulon volcani (Bory) Ach.

BRYOPHYTA

Rhizogonium sp.

Rhacomitrium lanuginosum Wils.

Leucobryum seemanii Mitt.

CEPHALOZIACEAE

Cephalozia sandwicensis

LEPIDOZIACEAE

Bazzania sp.

Riccardia sp.

Odontoschisma gracile

Calpogeia sp.

Sphaerocionium lanceolatum
Appendix B

Relationship between soil water potential and soil water content for different soils in HAVO

The following are equations derived from thermocouple psychrometry of soil water potential for different soil water contents from different study sites in HAVO.

Equations:

Site 1: Soil water potential (MPa) =
\[-11422.04 \times e\left(\frac{9.07938 - \ln(\%\text{water})}{13.0489}\right),
R^2 = 0.95\]

Site 2: Soil water potential (MPa) =
\[-0.94358 \times e\left(\frac{4.029695 - \ln(\%\text{water content})}{4.397994}\right),
R^2 = 0.90\]

Site 3: Soil water potential (MPa) =
\[-0.90835 \times e\left(\frac{5.854012 - \ln(\%\text{water content})}{3.092959}\right),
R^2 = 0.97\]

Site 4: Soil water potential (MPa) =
\[-61.35912 \times e\left(\frac{-2.18562 - \ln(\%\text{water content})}{-5.72845}\right),
R^2 = 0.95\]

Sites 5 and 6: Soil water potential (MPa) =
\[-191.966 \times e\left(\frac{-10.2138 - \ln(\%\text{water content})}{-27.5016}\right),
R^2 = 0.9801\]

Site 7: Soil water potential (MPa) =
\[-508.47 \times e\left(\frac{-4.47973 - \ln(\%\text{water content})}{-5.97896}\right),
R^2 = 0.97\]
Fig. B.1. Relationship between soil water potential (MPa) and soil water content (%) for soils from six different sites in HAVO. A) Site 1 (+), site 2 (■), and site 3 (●). B) Site 4 (◆), site 5 (○) and site 7 (□).
APPENDIX C

Indirect methods for the estimation of leaf area index

Introduction

Canopy structure, the spatial arrangement of foliage, branches and stems, determines light penetration through a forest canopy. Descriptions of canopy structure are particularly important for determining the amount of light received by individual plants within the canopy and in the understory. Leaf density, leaf orientation, leaf inclination and leaf area index are four parameters of canopy structure that are often measured. However, direct measurements of these parameters, requiring many individual measurements of plant parts, are often laborious and time consuming, particularly in forest canopies. A number of indirect methods for determining canopy structure, most based on the measure of radiation transmission through a canopy, provide a limited amount of information of canopy structure but have the advantage of permitting the rapid sampling of a large areas of canopy (Norman and Campbell 1989).

Leaf area index (LAI) is the most commonly measured canopy structure parameter as it is a useful simplification for the modelling of photosynthesis and productivity with radiation distribution within a plant
canopy (Jones 1992). LAI is defined as the ratio of total leaf area to ground area and is independent of leaf orientation (Welles 1990). A number of techniques have been developed for measuring LAI. These techniques include direct harvesting (Fliervoet and Werger 1984), measures of litterfall (Madgwick and Olson 1974), allometric relationships between tree diameter and leaf area (Whittaker and Woodwell 1968), hemispherical photographs of the canopy (Wang and Miller 1987), optical point quadrats (MacArthur and Horn 1969), and the attenuation of radiation through the canopy (Pierce and Running 1988, Perry et al. 1988). The technique used and mathematical models employed have a strong influence on calculated LAI (Martens et al. 1993). However, using a single technique and mathematical model, relative comparisons of LAI can be made (Martens et al. 1993).

Estimates of LAI from radiation measurements through the canopy are derived from mathematical models based on the transmitted fraction of a beam of radiation incident on the canopy. If the distribution of foliage is homogeneous then the average radiation at any level tends to decrease exponentially with increasing depth into the canopy. The decline in radiation through a canopy can be computed from an equation developed by Monsi and Saeki (1953) called the Beer-Lambert law. This equation is:
\[ \frac{I_z}{I_0} = e^{-k\Sigma L} \]  

(1)

where \( I_z \) = intensity of radiation at a particular canopy depth \( z \), \( I_0 \) is the intensity of radiation above the canopy, \( k \) is the extinction coefficient and \( \Sigma L \) is the cumulative LAI from the top of the canopy down to a reference height \( z \). The extinction coefficient indicates the degree of attenuation of light within the canopy for a given area index. In canopies which have a vertical leaf orientation the extinction coefficient is generally less than 0.5, while in plant communities with broad horizontally oriented leaves the extinction coefficient can be 0.7 to 1.0 (Larcher 1991).

The most accurate indirect estimate of LAI, derived from the measurement of the transmission of radiation through canopy foliage, is accomplished by gap fractions analysis. The gap fraction of canopy is the fraction of view from some direction beneath a canopy that is not blocked by foliage (Welles 1990). An inverted matrix approach is used, where LAI becomes the dependent variable and radiation the independent variable, to estimate LAI and leaf angle distribution (Norman and Campbell 1989). The basic approach is to determine the transmitted fraction \( \frac{I_z}{I_0} \), as in equation (1), of a beam of radiation from a range of zenith angles. By accounting for the variation of the extinction coefficient with
zenith angle one can account for the expected variation in transmitted fraction of radiation (Jones 1992) and permits an estimate of k without harvest or other empirical measures of LAI (Fownes, pers. comm.).

One instrument used for the indirect measurement of LAI is the LAI-2000 plant canopy analyzer. This instrument has an optical system that measures diffuse radiation at five zenith intervals (Welles 1990). The contribution of radiation scattered by foliage is minimized by the use of filtered silicon light sensors that are sensitive only to radiation less than 490 nm. The gap fractions at five zenith angles are measured by obtaining a reference reading above the canopy and a number of readings beneath the canopy (Welles and Norman 1991). The below canopy readings are divided by the above canopy readings for each of the five angles and the resulting ratios are assumed to be equivalent to the canopy gap fraction at each ring's viewing angle (Welles 1990). LAI is calculated as:

\[ \text{LAI} = 2\Sigma - \ln(T(i)) \sin(\theta) \cos(\theta) \, \text{d}\theta \]  

(2)

where \( T(i) \) is the proportion of transmitted radiation \( (I_Z/I_O \text{ in equation (1)}) \) for each zenith angle \( (\theta) \) of each sensor ring \( (i) \). This method assumes that the foliage faces all compass directions with equal probability (azimuthally random) and is randomly positioned in the
canopy, that only sky radiation is seen by the sensor (foliage is opaque and does not scatter light), that the foliage elements are small and that the foliage may be inclined at a variety of angles (Welles and Norman 1991). The LAI-2000 plant canopy analyzer is best used when the sun is obscured to reduce the potential amount of scattering of radiation from sunlit foliage. Also the need for above canopy measurements requires the use of scaffolding or a large canopy opening to obtain above canopy readings of incident radiation as it assumes opaque leaves.

Canopy structure can also be described in terms of foliage height profiles using an optical point-quadrat method developed by MacArthur and Horn (1969). This method provides for the rapid measurement of foliage distribution in forest canopies of all heights and has been used and compared to other methods of determining LAI by Aber (1979 a,b) and McIntyre et al. (1990) in broad-leaved deciduous forests. The optical point-quadrat method is derived from the point-quadrat sampling method first described by Warren Wilson (1959, 1960) but involves the use of a camera with a grid on the viewfinder screen and a telephoto lens used as a view finder. With the camera pointed straight up the cross-sections of the grid become imaginary vertical lines through the canopy.
Height to the lowest leaf covering each grid point is determined. Total canopy LAI and vertical distribution of leaf area is estimated by the equation developed by MacArthur and Horn (1969):

\[ \text{LAI}_{h_1-h_2} = \ln \left( \frac{p(h_1)}{p(h_2)} \right) \]  

where LAI\(_{h_1-h_2}\) is the density of foliage in the height interval between \(h_1\) and \(h_2\), \(p(h_1)\) is the probability of intercepting leaves over height \(h_1\) and \(p(h_2)\) is the probability of not intercepting leaves over height \(h_2\). \(p(h_1)\) and \(p(h_2)\) were estimated from the proportion of point intercept measurements that exceed the heights in question. This method assumes a random horizontal arrangement of leaves in the canopy (\(k=1\) in equation (1)).

Three different indirect measures of estimating the leaf area index of rain forest canopies are compared in this paper.

**Study sites**

Three rain forest study sites were selected for a comparison of indirect methods of measuring LAI. Site 1 is characterized by a short-statured young stand of *Metrosideros* with an understory of *Dicranopteris linearis* fern that forms a dense mat 1 to 2 m in height. Site 2 was characterized by a tall-statured mature stand of
Metrosideros with Myrica faya in the subcanopy. This site had an understory Cibotium glaucum tree fern layer with dense frond cover between 3 to 6 m in height. Site 3 was characterized by very reduced overstory cover due to the dieback of the canopy and an understory of dense Cibotium tree fern.

Methods

Gap-fraction method using the LAI-2000 plant canopy analyzer

One LAI-2000 sensor was used to obtain above and below canopy readings on three rain forest sites. Readings were taken on days of full cloud cover. One above canopy reading was taken in a large gap in the forest canopy and three below canopy readings were taken immediately after obtaining the above canopy reading at each sampling point. Above and below canopy readings were repeated for 3 times at 5 different locations at each site at 0, 1, 2, 3, 4, 5 and 6 meters above the forest floor. For measurements above 1 m the LAI-2000 was mounted on an extending height pole with a level used to keep it horizontally and vertically oriented. The program within the LAI-2000 computer collects and processes the data to obtain an LAI for each sampling point.
Optical point-quadrat method

The optical point-quadrat method of MacArthur and Horn (1969) was used to determine the LAI of the same three rain forest sites. A 200 telephoto mm lens mounted on a Minolta 35 mm camera was calibrated so that it could be used as a rangefinder for measuring distances to within 1 m. A screen with a grid of intersecting lines provided 25 sampling points within the camera's field of view. The camera was pointed up from a tripod 1 m above the ground at each sampling point. The distance to the nearest leaf covering one of the 25 points of the viewfinder was measured by focussing the lens for each point and recording the distance, infinity was recorded for sky intercepts. Eight to ten 10 m long transects were randomly located under the canopy of each forest site. Five locations on each of the transects were randomly selected for sampling. Thus there were a maximum of 50 locations sampled with 25 vertical sampling points each. The number of leaves that a vertical line would intercept is equivalent to the area of leaves relative to the area of ground they cover if leaves are horizontally positioned. The log transform equation (3), developed by MacArthur and Horn, was used to covert the measurement of height to the lowest leaf over each grid point to an
estimate of the leaf area index in 5 m height intervals. MacArthur and Horn (1969) suggest that the measurement of leaf area index below 2 m (ground to 2 m) be measured with a plumb bob. This was not done in this study. Thus, only cumulative LAI above 2 m is presented in this study.

Radiation transmission method

The difference in light environments with height through the canopy at each of three rain forest sites was characterized from May to July, 1990. Photosynthetically active radiation (PAR) levels at the ground level and at 5 m were measured using LICOR quantum sensors and GaAsP photodiodes (with a spectral response range between 300-680 nm) on each of three plots at each rain forest site. Sensors were set on the ground and on poles 1, 2, 3, 4, and 5 m from the forest floor and attached to a Campbell CR-10 micrologger for data collection. Each sensor was vertically oriented. The poles were anchored by guy wires which assisted in leveling the sensors. LICOR quantum sensors were also placed in a nearby open area to attain PAR readings for ambient fully exposed conditions. Measurements were taken every 10 s and averaged over five minutes for 3 to 6 sunny days. Leaf area index was determined from measurements of relative radiation transmission (the PAR intercepted by the quantum sensors
relative to the fully exposed PAR readings) for data taken been 10 am and 2 pm. LAI was determined using equation (1). The extinction coefficient (k) was assumed to be equal to 1, for completely random horizontally arranged leaves in a homogeneous canopy.

Results

The LAI estimates using the optical point-quadrat technique of MacArthur and Horn (1969) and the LAI-2000 plant canopy analyzer are presented in Tables C.1 and C.2, respectively. The optical point-quadrat method was utilized to estimate changes in LAI to the top of the canopy while the LAI-2000 plant canopy analyzer was limited in this respect. A comparison of LAI estimates at different positions in the canopy for the point-quadrat, gap-fraction, and radiation transmission methods for indirect estimates of LAI are presented in Table C.3. There were differences in the LAI estimated by each technique. The optical point-quadrat and the radiation transmission method both had higher estimates of LAI above the understory fern layer (>2 m) relative the estimation of LAI using the gap-fraction technique at site 1. These higher estimates of LAI may be due to an underestimation of the number of gaps in the canopy by the optical point-
quadrat and radiation transmission methods. However, the radiation transmission and gap fraction methods measured similar total LAI for site 1. At site 2 the radiation transmission method and the gap fraction method provided similar estimates of LAI at site 2. The optical point-quadrat method underestimated LAI above 5 m (compared to the LAI estimated by the other methods), which was probably due to the difficulty in making point measurements to individual leaves within the fairly dense multilayered canopy. At site 3, while the radiation transmission method and the gap fraction method provided similar estimates of total LAI, there were large discrepancies in the estimate of LAI with height between methods. This site has large overstory gaps due to the dieback of the overstory canopy. The understory is a fairly complex mixture of dense Cibotium tree fern and low statured (~8 m) trees. The LAI-2000 plant canopy analyzer probably "saw" more gaps in the canopy than the other methods. As at site 2, identifying individual leaves was difficult with the optical point-quadrat method.

The relationship of radiation transmission through the canopy to LAI is presented in Figure C.1. The slope of the lines provides an estimate of the extinction coefficient through these canopies. In the radiation transmission method the extinction coefficient is assumed
to be 1. However, the slopes of these fitted lines are somewhat different from 1. The extinction coefficients for sites 1, 2 and 3 are 0.81, 1.46 and 0.79, respectively which suggests that an extinction coefficient of 1 may be a near approximation for sites 1 and 3 but will largely overestimate LAI at site 2.

Discussion

The MacArthur and Horn method of indirect LAI determination was first used in Hawaiian rain forests by Burton (1980). Burton (1980) utilized this technique to determine changes in LAI with changes in height through the canopy of different rain forest sites subject to different degrees of overstory canopy opening. In this study the MacArthur and Horn technique was compared to other indirect methods of determining LAI of similar rain forest sites. While this technique first appeared to provide a rapid method for determining LAI at different levels in the rain forest canopy it was much slower and more tedious than the other methods employed. The difficulty in seeing individual leaves at any height throughout a fairly dark forest even on clear sunny days probably resulted in a larger degree of sampling error than occurred using the other methods. The Cibotium tree fern understory on sites 2 and 3 made viewing difficult
above 3 m since whole Cibotium fronds often took up the entire camera view. The small leaves of Metrosideros were also difficult to distinguish as individuals above 5 m. Aber (1979) found that estimated LAI was consistently lower using this technique when compared to the LAI determined from litterfall in broad-leaved forests. McIntrye et al. (1990) found that in using this technique expected LAI differences between three study sites were not realized and LAI estimates were inconsistent with direct measures of LAI. In this study, the LAI estimates by the optical point quadrat method were not consistently higher or lower than with the other methods used.

The MacArthur and Horn technique assumes that leaves are randomly dispersed in order to validly use the equations to transform the point-intercept data to estimates of LAI. This assumption is not met in nature as foliage often has a clumped distribution and leaves are inclined at different angles depending on their position in the canopy (Warren Wilson 1960). The validity of using a vertical sampling method alone was questioned by Warren Wilson (1960) who found that vertical sampling could greatly underestimate actual LAI due to the reduced projection of vertically inclined leaves. Warren Wilson (1960) suggested that a number of intercept samples should be taken through the canopy in both the horizontal and
inclined towards vertical directions. Despite the apparent errors involved in determining total LAI by the optical point quadrat method, the estimate of the relative leaf area distribution by height and by species using this method was considered accurate and was recommended by Aber (1979).

The Beer-Lambert model (equation (1)), which defines the radiation transmission through the canopy as proportional to the cumulative LAI, has been used to estimate light penetration in forest stands of different LAI (Gholz et al. 1991). This model estimates LAI on the assumption that the canopy is homogeneously distributed and that the foliage is horizontally oriented (Monsi and Saeki 1953). The extinction coefficient ($k$) is usually estimated from direct measures of LAI and radiation penetration (Gholz et al. 1991). While the Beer-Lambert model assumes that $k$ is constant through the forest canopy, recent research has indicated that this assumption may not be appropriate, particularly if the vertical distribution of foliage in the canopy varies (Sampson and Smith 1993). Decreased light extinction with increased canopy depth was observed by McIntryre et al. (1990). In deciduous forests $k$ will vary seasonally with leaffall (Gholz et al. 1991). In this study of evergreen broad-leaved rain forest, leaf area distribution and $k$ were
assumed to be constant year-round through the canopy. Thus, measures of LAI by the plant canopy analyzer were made in the winter months when heavy cloud cover was present and radiation transmission and optical point quadrats data were taken in the late spring and early summer months. The assumption of a seasonally constant leaf area distribution and k may not be valid as some visible changes in the understory fern cover have been observed. Also, k probably changes through the canopy due to the non-uniform distribution of foliage in different parts of the canopy.

The radiation transmission method used in this study utilizes the Beer-Lambert model for estimating LAI and thus is dependent on the same assumptions used to derive the model. Also the extinction coefficient is assumed to be 1 which may not be valid if the foliage density changes with height through the canopy and the general relationship between LAI and intercepted radiation presented in figure C.1 suggests that k is different between each study site. However, this relationship was derived using average LAI estimated by the plant canopy analyzer and the average of measures of radiation transmission measured by quantum sensors. Since the LAI was determined indirectly, these estimates of the extinction coefficient may be in error.
The zenith angle of the sun will alter the amount of radiation transmitted through the canopy that is measured by quantum sensors and thus will effect determinations of $k$. The radiation transmission method used in this study probably overestimates LAI as it does not take into account the zenith angle of the sun nor the light penetration from various zenith angles through gaps in the canopy. More accurate determinations of LAI by the radiation transmission method can be accomplished by taking radiation measurements at different zenith angles and azimuth directions and using the gap fraction inversion procedure to calculate LAI (Perry et al. 1988, Norman and Campbell 1989).

All the methods employed in this study for the estimation of LAI assume that canopy foliage is horizontally homogeneous. In young stands and open canopied stands such as those represented by sites 1 and 3, the assumption of horizontal homogeneity may not be appropriate and can produce an error in the estimate of LAI for all the techniques used in this study. Mathematical methods for estimating LAI in non-homogeneous canopies have been presented by Lang and Yueqin (1986) and Perry et al. (1988).

The optical point quadrat method is not recommended for determination of LAI in Hawaiian rain forests.
Sampling error can be large due to the difficulty of seeing individual leaves above each grid point and the assumptions of the technique have been shown to be in error. The LI-2000 plant canopy analyzer is a rapid and efficient instrument for measuring LAI. It takes into account varying degrees of radiation penetration through the canopy at different zenith angles thus accounting for more of what a plant would "see" in terms of the light climate in the understory. The radiation transmission method is based on assumptions that result in the probable overestimate of LAI, but a procedure for a more accurate estimation of LAI using this technique is described above. Direct determinations of LAI should be made to determine the error in the estimate of LAI by each of these methods. However, this was not done in this study and estimates of LAI can only be considered as limited approximations.
<table>
<thead>
<tr>
<th>Vertical height through forest (m)</th>
<th>Site 1</th>
<th>Site 2</th>
<th>Site 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>15-20</td>
<td>0</td>
<td>1.5 (0.4)</td>
<td>0</td>
</tr>
<tr>
<td>10-15</td>
<td>2.1 (0.2)</td>
<td>2.6 (0.4)</td>
<td>1.2 (0.5)</td>
</tr>
<tr>
<td>5-10</td>
<td>3.3 (0.1)</td>
<td>3.5 (0.5)</td>
<td>2.5 (0.3)</td>
</tr>
<tr>
<td>2-5</td>
<td>2.1 (0.4)</td>
<td>4.3 (0.3)</td>
<td>5.0 (1.0)</td>
</tr>
</tbody>
</table>

Table C.1: LAI determined by the MacArthur and Horn technique for 5 m height intervals through the canopy of three rain forest sites. Values are means (n=10 transects) with one standard error in brackets.
Table C.2: LAI determined at six different heights by using the LAI-2000 plant canopy analyzer. Values are plot means (n=5) and standard error in brackets.

<table>
<thead>
<tr>
<th>Height</th>
<th>Site 1</th>
<th>Site 2</th>
<th>Site 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>&gt;6</td>
<td>0.9 (0.2)</td>
<td>3.7 (0.2)</td>
<td>0.4 (0.1)</td>
</tr>
<tr>
<td>5</td>
<td>1.0 (0.3)</td>
<td>3.9 (0.1)</td>
<td>0.6 (0.1)</td>
</tr>
<tr>
<td>4</td>
<td>1.2 (0.4)</td>
<td>4.5 (0.3)</td>
<td>1.4 (0.1)</td>
</tr>
<tr>
<td>3</td>
<td>1.6 (0.4)</td>
<td>4.6 (0.2)</td>
<td>3.2 (0.1)</td>
</tr>
<tr>
<td>2</td>
<td>1.8 (0.5)</td>
<td>4.7 (0.1)</td>
<td>3.2 (0.1)</td>
</tr>
<tr>
<td>1</td>
<td>1.6 (0.1)</td>
<td>4.9 (0.1)</td>
<td>3.4 (0.3)</td>
</tr>
<tr>
<td>0</td>
<td>6.3 (0.2)</td>
<td>5.0 (0.1)</td>
<td>4.9 (0.3)</td>
</tr>
</tbody>
</table>
Table C.3: A comparison of cumulative LAI values, determined at different locations within the canopy of three different rain forest sites, derived by three different techniques. Values are means with standard error in brackets.

<table>
<thead>
<tr>
<th>Site</th>
<th>Position in canopy</th>
<th>Optical point quadrat</th>
<th>Gap fraction</th>
<th>Radiation transmission</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Above 5 m</td>
<td>2.8 (0.2)</td>
<td>1.0 (0.2)</td>
<td>2.1 (0.3)</td>
</tr>
<tr>
<td></td>
<td>2-5 m</td>
<td>2.1 (0.4)</td>
<td>1.6 (0.3)</td>
<td>2.3 (0.1)</td>
</tr>
<tr>
<td></td>
<td>Total LAI</td>
<td>na</td>
<td>6.3 (0.2)</td>
<td>6.0 (0.2)</td>
</tr>
<tr>
<td>2</td>
<td>Above 5 m</td>
<td>2.6 (0.4)</td>
<td>3.7 (0.2)</td>
<td>3.2 (0.2)</td>
</tr>
<tr>
<td></td>
<td>2-5 m</td>
<td>4.3 (0.3)</td>
<td>4.4 (0.1)</td>
<td>4.5 (0.2)</td>
</tr>
<tr>
<td></td>
<td>Total LAI</td>
<td>na</td>
<td>5.0 (0.1)</td>
<td>5.2 (0.2)</td>
</tr>
<tr>
<td>3</td>
<td>Above 5 m</td>
<td>1.9 (0.4)</td>
<td>0.4 (0.1)</td>
<td>0.9 (0.1)</td>
</tr>
<tr>
<td></td>
<td>2-5 m</td>
<td>5.0 (1.0)</td>
<td>2.3 (0.1)</td>
<td>3.6 (0.2)</td>
</tr>
<tr>
<td></td>
<td>Total LAI</td>
<td>na</td>
<td>4.9 (0.7)</td>
<td>4.7 (0.1)</td>
</tr>
</tbody>
</table>
Fig. C.1. Relationship between transmitted radiation $(\ln(I/Io))$ recorded by quantum sensors at different levels in the canopy and leaf area index (LAI) determined by the LAI-2000 plant canopy analyzer for three different rain forest sites: Site 1-($\bullet$), $\ln(I/Io)=-0.713-0.81(LAI)$, $R^2=0.99$, site 2-($\square$), $\ln(I/Io)=2.20-1.47(LAI)$, $R^2=0.99$ and site 3-($\blacksquare$), $\ln(I/Io)=-0.604-0.79(LAI)$, $R^2=0.91$. 
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Wang, Y.S. and D.R. Miller. 1987. Calibration of the hemispherical photographic technique to measure leaf area index distributions in hardwood forests. Forest Science 33:210-216


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