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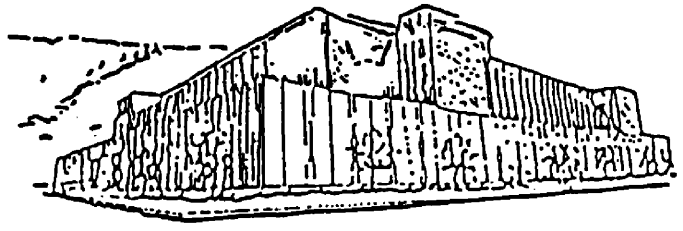
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**Stand Dynamics of *Cinnamomum burmannii*,
an Invasive Tree, on O'ahu, Hawaii**

by

Andy T. Horcher

B.S. The University of Illinois Urban-Champaign, 1995.

presented in partial fulfillment of the requirements

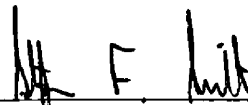
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Master of Science

The University of Montana

2000

Approved by



Chairperson



Dean, Graduate School

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Stand Dynamics of *Cinnamomum burmannii*, an Invasive Tree, on O'ahu, Hawaii.
(32 pp.)

Director: Stephen F. Siebert

SFS

Cinnamomum burmannii (C.G. & T. Nees) Blume is an alien tree species that is invading native forests throughout the Hawaiian Islands. An analysis of *C. burmannii* stands was conducted to provide insight into potential impacts associated with its invasion in Hawaii and similar island environments. *Cinnamomum burmannii* stand structure and understory composition data were gathered in 15 plots from two sites in the Nuuanu Valley and one site in Pauoa Flats on the island of O'ahu. Sites were selected based on terrain, accessibility, and dominance of *C. burmannii*. Physiological data were collected from a single site in the Nuuanu Valley to assess the shade tolerance of *C. burmannii*.

While between and within site variance was high, a general trend of *C. burmannii* self replacement is evident, with reverse J-shaped diameter distributions observed in all three sites. In addition, *C. burmannii* seedling densities were greater than any other species in 59 of 60 1m² sample plots (densities ranged from 2 - 1,432 seedlings/m²). Other shade tolerant, alien tree species maintained reverse J-shaped diameter distributions similar to *C. burmannii*, but were relatively uncommon and usually lacked seedlings. The dominant native forest tree species of Hawaii, *Metrosideros polymorpha* and *Acacia koa*, and shade intolerant, alien tree species had no stems in lower diameter classes and few seedlings. Physiological data collected on a single *C. burmannii* tree and surrounding seedlings, suggest that the species can tolerate extreme shade and maintain high CO₂ assimilation in full sun.

Given its shade tolerance and reverse J-shaped diameter distribution, it appears that *C. burmannii* will continue to colonize and dominate native Hawaiian forests. Native tree species appear to be unable to compete with *C. burmannii* and thus are likely to decline unless active management is undertaken. Further research is needed to determine specific impacts of and possible management approaches to control *C. burmannii* invasion.

Table of Contents

Introduction	pg. 1
Method	pg. 4
Sites	pg. 4
Stand Measurements	pg. 6
Physiology	pg. 7
Caveats	pg. 8
Results	pg. 9
Understory	pg. 9
Stand Measurements	pg. 10
Physiological Data	pg. 16
Discussion	pg. 20
Conclusion	pg. 25
Acknowledgments	pg. 28
Literature Cited	pg. 29

List of Figures and Tables

- Figure 1. Site Map of Nuuanu Valley and Pauoa Flats on O'ahu, Hawaii. pg. 5
- Figure 2. Mean number of *C. burmannii* seedlings (m^{-1}) less than 2m in height observed in five 0.049ha circular plots in each of three *C. burmannii* stands on O'ahu, Hawaii. pg. 10
- Figure 3. Mean basal ($m^2 ha^{-1}$) area observed in three forest stands on O'ahu, Hawaii. pg. 11
- Figure 4. Mean percent of *C. burmannii* by 5cm diameter classes observed in three forest stands in O'ahu, Hawaii. pg. 12
- Figure 5. *Cinnamomum burmannii* mean diameter distribution in each of three stands on O'ahu, Hawaii. pg. 13

- Figure 6. *Citharexylum caudatum* and *Psidium cattleianum* mean diameter distributions in 11 and six 0.049 ha circular plots, respectively, in *C. burmannii* stands on O'ahu, Hawaii. pg. 13
- Figure 7. *Syzygium jambos* diameter distributions in two 0.049ha circular plots in a *C. burmannii* stand in the Pauoa Flats on O'ahu, Hawaii. pg. 14
- Figure 8. *Psidium guajava* and *Schefflera actinophylla* mean diameter distributions in eight and four 0.049ha circular plots, respectively, in *C. burmannii* stands on O'ahu, Hawaii. pg. 14
- Figure 9. *Metrosideros polymorpha* and *Acacia koa* diameter distributions in two and one 0.049ha circular plots, respectively, in *C. burmannii* stands on O'ahu, Hawaii. pg. 15
- Figure 10. *Eucalyptus spp.*, *Casuarina equestifolia*, and *Fraxinus uhdei* mean diameter distribution in five, two, and three 0.049ha circular plots, respectively, in *C. burmannii* stands on O'ahu, Hawaii. pg. 16

Figure 11.	<i>Cinnamomum burmannii</i> shade grown seedling light response curve using artificial light with a LAI 6400.	pg. 18
Figure 12.	Light response data and Michaelis-Menten model estimates of net photosynthesis on <i>Acer platanoides</i> and <i>Acer saccharum</i> seedlings at Walnut Springs in Pennsylvania.	pg. 18
Figure 13.	Adult <i>C. burmannii</i> canopy sun leaves light response curve using artificial light with a LAI 6400.	pg. 19
Figure 14.	Photosynthetic light-response curves for open-grown and understory-grown branches of <i>Pseudotsuga menziessii</i> seedlings near Okanagan Falls, British Columbia.	pg. 19
Table 1.	Abundance of plant species less than 2m in height in 60 1m ² plots in <i>C. burmannii</i> stands.	pg. 9

Table 2. *Cinnamomum burmannii* leaf nitrogen content and specific leaf area based on analysis of a single adult tree in the Nuuanu Valley on O'ahu, Hawaii.

pg. 20

Introduction

The establishment of exotic species can result in ecological and economic devastation (Karevia 1996). This damage may result from a reduction in stream flow and ground water (Scott and Lesch 1997), an increase in soil salinity (Halverson 1992; Macdonald et al. 1989), alteration of fire regimes (D'Antonio & Vitousek 1992) or an assortment of other ecosystem changes. Alien species challenge members of the environment that they invade and are capable of disrupting natural processes on an ecosystem level (Vitousek 1992; Smith 1989).

Trees, due to their size, relatively long life, and impact on their surroundings, can be especially detrimental when invading an ecosystem. Whether reducing stream flow and ground water reserves (Scott and Lesch 1997), altering soil nitrogen levels (Vitousek & Walker 1989), increasing erosion rates (Meyer 1996), or reducing the amount of sunlight which penetrates the canopy (Meyer 1996), alien trees have impacted many ecosystems.

The majority of weed science and alien invasion research focuses on shade intolerant species. Intolerant species tend to have rapid growth rates due to their efficient use of direct sunlight and as a result are often introduced for forestry or agricultural purposes (Kozlowski et al. 1991; Zobel 1987). Due to their high light requirements, some kind of disturbance is usually needed to initiate intolerant species establishment. In contrast, shade tolerant invasive species can establish in the low light levels characteristic of undisturbed forests and persist as dominant members of the ecosystem (Kimmins 1987; Kozlowski et al. 1991), therefore posing a greater invasion risk. Shade tolerant species have relatively high leaf area indexes, which reduce the amount of sunlight

reaching plants below them (Oliver & Larson 1996). Depending on the physiology of native species, their regeneration and growth may be severely limited beneath shade tolerant alien canopies. In addition, shade grown root to shoot ratios tend to be lower (Kramer & Kozlowski 1979) which can alter native disturbance regimes through events such as windthrow.

Alien invasion impacts are most severe in island ecosystems (Loope 1992). These ecosystems evolved in isolation from many powerful selective forces, such as large grazers and humans, which repeatedly shaped most continental environments (Loope 1992). This lack of selective forces has resulted in the loss of aggressiveness (Loope 1992). Due to their isolation, islands typically possess fewer taxa from which the ecosystem developed and increased vulnerability to extinction in even the best of circumstances (Loope 1992).

The Hawaiian islands are the most isolated archipelago in the world and contain more than 5,000 plant species, including approximately 1,200 native and over 4,000 introduced species (Smith 1985; Smith 1989). Of these alien species, less than 15% are likely to establish beyond cultivation (Smith 1985) and less than 2% are believed to threaten native ecosystems (Wester 1992). The native wet and mesic forests of Hawaii are located on upper elevation and windward portions of the islands. These forests are interspersed in a matrix of agricultural lands, development, and alien stands. This results in islands within the islands, increasing the vulnerability of native ecosystems.

Most invasive species require some type of disturbance such as fire or grazing to become established (Loope 1992). However, a few species do not need disturbance to spread (Loope 1992; Mueller-Dombois & Fosber 1992). These exceptions are significant

because they threaten the few native Hawaiian communities, which have not been disrupted (Mueller-Dombois & Fosber 1998) and increase the need for active management of natural areas (Stone et al. 1992a).

The native mesic and wet forests of Hawaii are comprised of two dominant endemic canopy species, *Metrosideros polymorpha* (ohia) and *Acacia koa* (koa), which are especially susceptible to invasive disturbance due to their extreme isolation for millions of years (Vitousek 1990). *Metrosideros polymorpha* exhibits intolerant to intermediate shade tolerance, depending on the variety (Adee & Conrad 1990), and *Acacia koa* is shade intolerant (Whitesell 1990). Unlike many continental forest ecosystems, Hawaii lacks an indigenous dominant shade tolerant tree species.

Compounding the potential susceptibility of Hawaii's native ecosystems is its tourist and commercial role as the "crossroads of the Pacific" (Stone et al. 1992b). As people from all over the world move to or visit Hawaii, the chances of alien invasions tend to increase (Stone et al. 1992b).

Cinnamomum burmannii is an invasive alien in the Hawaiian archipelago (Wester 1992). A member of Lauraceae, its native range is Southeast Asia, including Indonesia and China (Purseglove 1968; Smith et al. 1992). In Hawaii, this species frequently forms monotypic stands and threatens unique, native ecosystems (C. Smith, University of Hawaii, Honolulu, HI, Pers. Comm.; Pers. Obs.).

Little is known about the ecology, growth, distribution, or physiology of *C. burmannii*, even within its native range. Published details of Hawaiian populations are limited to location notes and taxonomic descriptions (Meidell et al. 1997; Wagner et al. 1990). Most information from its native range focused on the production of *C. burmannii*

bark as a cash crop (Ardha 1976; Aumeerudy & Sansonnens 1994; Smith et al. 1992).

No data are available on stand structure, understory species, or soils within *C. burmannii* stands. This lack of information limits our understanding of possible ecosystem effects and management options. Whether on state watershed reserves (used to protect Hawaii's fresh water resources), state natural areas, national parks, or on private land, managers have little information on *C. burmannii* populations.

The objectives of this study were to characterize the general structure and understory composition of *C. burmannii* stands on O'ahu, Hawaii and to better understand *C. burmannii* invasive potential in forest ecosystems of Hawaii and other tropical forests.

Methods

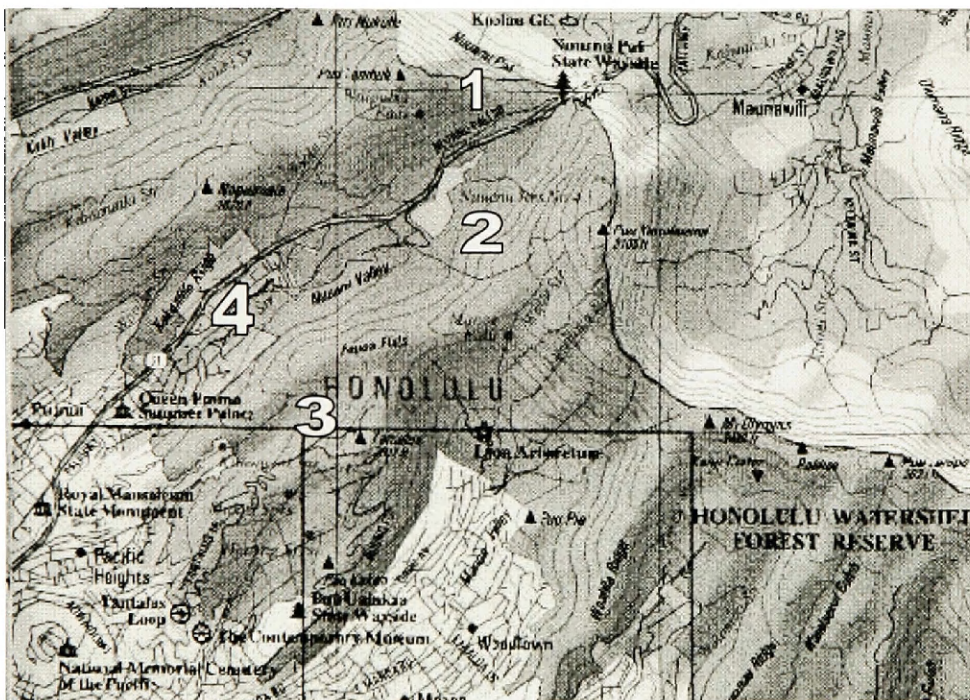
Sites

Three sites were selected for detailed study in the Honolulu Forest Watershed Reserve within the Nuuanu Valley and Pauoa Flats in the Ko'olau range on the island of O'ahu, Hawaii (N 21° 21', W 157° 49'). Sites were chosen based on accessibility, terrain, and *C. burmannii* abundance. The Nuuanu Valley and Pauoa Flats receive approximately 2 – 4m of rainfall annually (Giambelluca & Schroeder 1998). Strong prevailing northeasterly winds flow down both the valley and flats; while maximum and minimum temperatures average near 30° C and 16° C, respectively (Giambelluca & Schroeder 1998).

Site one, a *C. burmannii* stand of approximately 15ha, was on the northwest side of the Upper Nuuanu Valley and was bordered by the Pali Lookout frontage road on the southeast and by steep forested mountains on the northwest (Figure 1). The surrounding

forest was comprised of both native and alien species. Slopes varied from 10 – 50%, had a west and southwest aspect with occasional ravines; the elevation was approximately 365m. The overstory was primarily *Eucalyptus robusta* Sm. with a canopy around 30m. *Cinnamomum burmannii* formed a dense lower canopy around 8m. *Cordyline fruticosa*, commonly known as ti, was abundant in the understory and canopy gaps. Feral pig activity was light to moderate, increasing toward the northwest.

Figure 1. Site Map of Nuuanu Valley and Pauoa Flats on O’ahu, Hawaii



(Hawaii Atlas & Gazetteer 1999)

Site two, a 3ha *C. burmannii* stand surrounded by a mixture of native and alien forest species, was also in the Upper Nuuanu Valley, but on the southeast side, near the upper reservoir (Figure 1). The elevation was 330m and slopes varied from 0 – 30% with some ravines. In site two, the overstory canopy was primarily *C. burmannii* of varying size with numerous canopy gaps. The understory was dense and includes both native and

exotic species. There was widespread evidence of feral pig activity with heavy disturbance in localized areas.

Site three was in the Pauoa Flats, one valley east of Nuuanu, with an elevation of 425m and had slopes of 0-30% with some ravines (Figure 1). This *C. burmannii* dominant stand covered about 15ha and formed a dense canopy of about 15m in height; there was little leaf litter or understory growth present. The stand was surrounded by both native and alien forest species. There was widespread evidence of feral pig activity throughout the stand.

A fourth site in the Nuuanu Valley was selected for a limited physiology study. Located in a residential area, this site was comprised of a single *C. burmannii* tree and saplings growing along the Nuuanu Stream (Figure 1). Due to its proximity to the Kimo Bridge, the canopy and lower leaves were easily reached for analysis.

Stand Measurements

Five 25m diameter circular plots were located randomly beneath *C. burmannii* canopies in each of the three sites. Plots were not placed in large canopy gaps and were at least 30m from trails or roads and 10m from the edge of the stand. All plant species within the 15 plots were identified. The diameter of woody plants over 2m in height were measured at 1.3m to the nearest 0.25cm, except for *C. fruticosa* which was grouped in diameter size classes of 0 – 5, 5 – 10, and 10 – 15cm. The height of all woody stems over 2m was measured to the nearest 0.3m using a clinometer. If the tree forked below 1.3m then each fork was measured (Harrington and Ewel 1997). Percent canopy closure was estimated in each plot by visually surveying the canopy within the plot.

In addition, four 1m² understory sample plots were established in each 25m diameter plot. These plots were located 5m from plot center in each of the four cardinal compass directions. Species, species abundance, and litter depth were recorded in each plot (Harrington & Ewel 1997). Litter depth was measured to the nearest 0.5cm by recording three random samples placed within each 1m² plot and one soil core (20cm deep x 2cm wide) was taken in each of the 60 plots. For each soil core, general soil horizon development was recorded to a maximum depth of 30cm and a minimum of 8cm, depending upon presence of underlying rock. The four cores from each 1m² plot were combined to form one composite sample. The coarse material was removed, and the composites were air-dried. Samples were then sent to the Cornell Nutrient Analysis Laboratories for analysis of organic matter, exchange acidity, NO₃-N, P, K, Mg, Ca, Fe, Al, Mn, Zn, and Cu. Analysis methods were as follows: organic matter through loss on ignition; exchange acidity through extraction with barium chloride/triethanolamine solution buffered at pH 8.0 with subsequent titration of excess base; NO₃-N and P through colormetric resolution of automated hydrazine reduction and stannous chloride reduction, respectively; and K, Mg, Ca, Fe, Al, Mn, Zn, and Cu through atomic absorption.

Physiology

To ascertain approximate light requirements of *C. burmannii*, light response data were recorded on two mornings in early September using a LiCOR™ LAI 6400. Using artificial light on the LAI 6400, measurements were taken from individual leaves of a single tree and surrounding saplings at site four. Ambient light data was collected from the same adult tree, and leaves were sampled from varying heights in the canopy. Dr. M.

Clearwater of Hawaii Agriculture Research Center derived the light response curves using the Photosyn Assistant (Ogren & Evans 1993).

In addition to light response curves, specific leaf area and leaf nitrogen samples were collected for sun leaves, shade leaves, and seedling leaves. Twenty-five to 45 leaves of each group were collected. Leaves used in light response sampling were included in each appropriate grouping, along with additional leaves, which were gathered haphazardly. Leaves were sealed in a plastic bag, photocopied within 24hr of collection, air dried for three to four days, oven dried at 35⁰ C for 6hr, and weighed. Photocopied pages were measured and weighed; leaves were cut out and weighed, and known weight per unit area and dry leaf weight was used to estimate specific leaf area (Bannister 1986). The dried leaf samples were sent to the University of Hawaii, Agricultural Diagnostic Service Center for leaf nitrogen content. Analysis was conducted using block digestion, which is equivalent to the micro-Kjeldahl digestion system (Schuman et al. 1973).

Caveats

There are a number of limitations in this study due to the methods employed and the distribution and accessibility of *C. burmannii* stands. First, the study sites were not located at random and were not necessarily representative of all *C. burmannii* invasion areas. The sample sites were selected on the basis of accessibility and were on relatively gentle terrain in comparison to many other *C. burmannii* stands. In addition, variance between and within the plots was likely to be high in some stands (Shiver & Borders 1996); nevertheless it provided useful information regarding general stand structure and characteristics. Finally, the light response, specific leaf area, and leaf nitrogen data

collected from a single tree and saplings beneath it, may not reflect other *C. burmannii* trees on O'ahu, but provide a rough idea of how the species may be functioning.

Results

Understory

In 59 of the 60 understory plots *C. burmannii* seedlings were more abundant than any other species, both herbaceous and woody. Of the 18 identified species in the 1m² plots, two were endemic to the Hawaiian Islands and two were indigenous; all other species were aliens (Table 1). The native species occurred in low densities compared to the alien species.

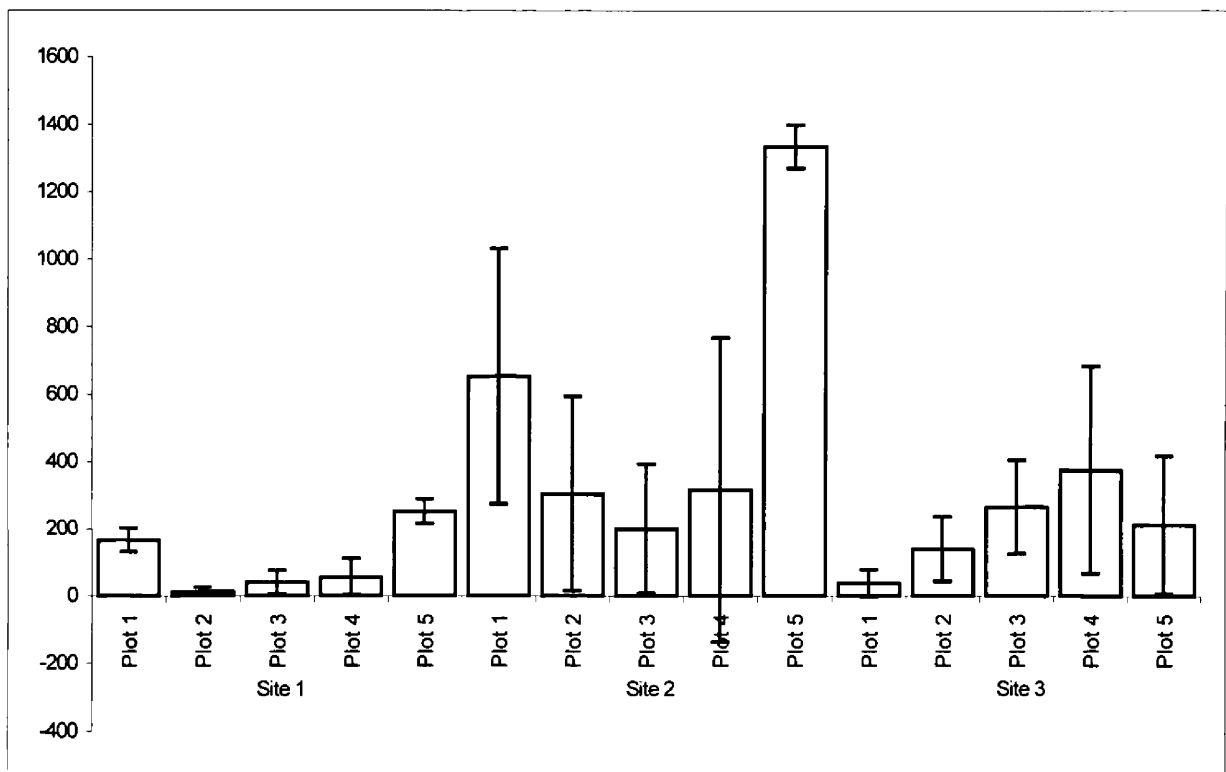
Table 1. Abundance of plant species less than 2m in height in 60 1m² plots in *C. burmannii* stands.

Species	Total	# Plots	Life Form	Status
<i>Acacia koa</i> A. Gray	5	2	T	E
<i>Cinnamomum burmannii</i> (C.G. & T. Nees) Blume	17486	60	T	A
<i>Christella dentata</i> (Forssk) Brownsey & Jermy	38	13	F	A
<i>Citharexylum caudatum</i> Linn	89	20	T	A
<i>Clidemia hirta</i> D. Don	1	1	H	A
<i>Cordyline fruticosa</i> (L.) A. Cheval	37	15	S	A
<i>Grevillea robusta</i> A. Cunn.	1	1	T	A
<i>Hedychium</i> spp	177	12	H	A
<i>Nephrolepis cordifolia</i> (L.) Presl	1	1	F	I
<i>Ophiderma pendula</i>	1	1	F	I
<i>Oxalis regnellii</i> Miq.	5	1	H	A
<i>Oxalis</i> spp.	3	1	H	A
<i>Paspalum conjugatum</i> Berg.	90	12	H	A
<i>Polypodium pellucidum</i>	1	1	F	E
<i>Psidium guajava</i> Linn.	4	3	T	A
<i>Schefflera actinophylla</i> Harms	1	1	T	A
<i>Setaria palmifolia</i> (Koenig) Stapf	20	3	H	A
<i>Syzygium jambos</i> (L.) Alston	26	5	T	A
Unidentified 1	10	4	H?	?
Unidentified 2	2	2	H?	?
Unidentified 3	2	2	H?	?

*Life Form: T = tree, S = shrub, H = herbaceous, F = fern. Status: A = alien, E = endemic, I = indigenous.

Mean *C. burmannii* densities ranged from 14 to 1336 seedlings m^{-2} within the 15 circular plots (Figure 2). While this variability is high, populations of over 1,400 seedlings m^{-2} in individual 1m^2 plots indicates a tolerance of high density conditions.

Figure 2. Mean number of *C. burmannii* seedlings (m^{-1}) less than 2m in height observed in five 0.049ha circular plots in each of three *C. burmannii* stands on O'ahu, Hawaii.

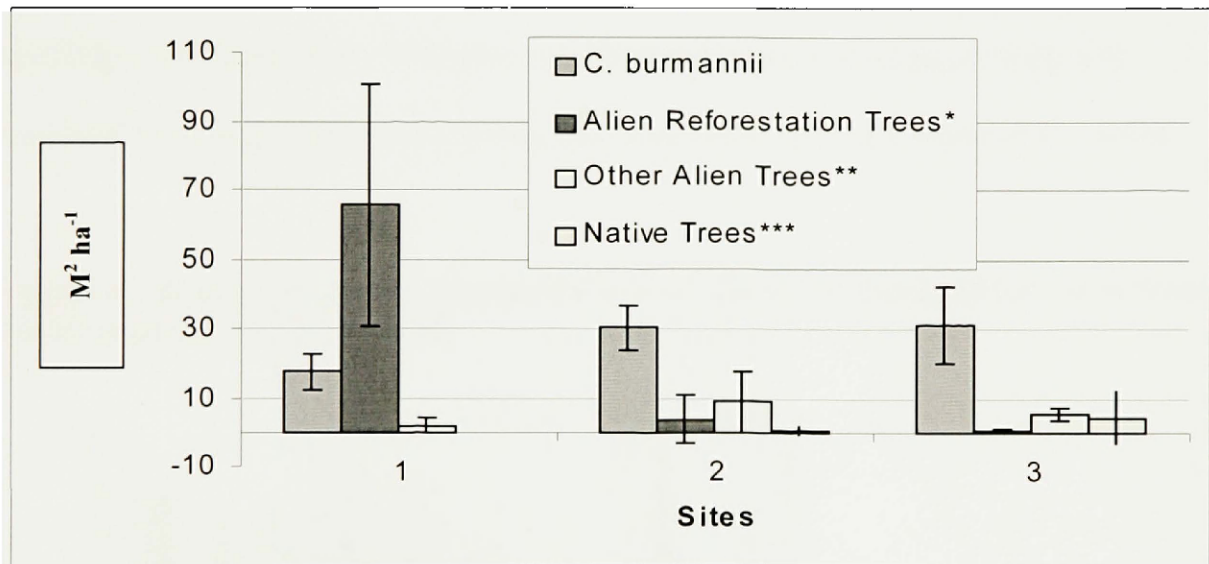


Stand Measurements

Cinnamomum burmannii comprised the majority of the basal area in both site two and three, while it comprised the second most basal area in site one, following the sizeable basal area from the declining *Eucalyptus* overstory (Figure 3). The total basal areas for sites two and three are similar to the maximum basal area found in *A. koa* forest

studied on Kauai at $42\text{m}^2\text{ ha}^{-1}$ (Harrington et al. 1995). Total basal areas of *M. polymorpha* stands on Maui were also similar to total basal areas of sites two and three (Kitayama et al. 1998). Kitayama et al. (1998) also reported a *M. polymorpha* basal area similar to the total in site one. This indicates that *C. burmannii* stands have basal areas similar to native forests.

Figure 3. Mean basal ($\text{m}^2\text{ ha}^{-1}$) area observed in three forest stands on O'ahu, Hawaii.



*Alien Reforestation Trees = *Bischofia javanica* Blume, *Casuarina equestifolia* J. R. Foster & G. Foster, *Eucalyptus* spp., & *Fraxinus uhdei* (Wenzig) Lingelsh. **Other Alien Trees = *Aleurites moluccana* Willd., *Ardisia elliptica* Thunb., *Citharexylum caudatum*, *Psidium cattleianum* Sabine, *Psidium guajava*, *Syzygium cumini* (L.) Skeels, *Syzygium jambos*, and *Schefflera actinophylla*. ***Native Trees = *Acacia koa*, *Hibiscus tiliaceus* Linn., *Hedyotis termanlis* (Hook & Arnott) W. L. Wagner & D. R. Herbst, & *Metrosideros polymorpha* Gaudich.

Cinnamomum burmannii comprised 50% or more of the stems in all but the upper most size classes (Figure 4). While there was considerable variability within the sites, the diameter distributions of *C. burmannii* (Figure 5) were reverse J-shaped in all three sites. Of the tree species associated with *C. burmannii* only the alien species, *Citharexylum caudatum*, *Psidium cattleianum* (Figure 6), *Syzygium jambos* (Figure 7), *Psidium*

guajava, and *Shefflera actinophylla* (Figure 8) maintained similar diameter distributions. However, none of these species were as abundant as *C. burmannii*, and most, with the exception of *S. jambos*, were more commonly associated with gaps in the *C. burmannii* canopy. It was not surprising that *C. burmannii* stems were more abundant in the selected stands since the stands were selected for the presence of *C. burmannii*. However, recruitment of *C. burmannii* seedlings in these sites was far greater than any other alien trees (Table 1), with the exception of the east and west 1m² plots of site 3, plot 1, where *S. jambos* had 7 and 10 seedlings, respectively, compared to the 6 and 11 seedlings of *C. burmannii*. This plot was affected by heavy feral pig activity and overland flow during heavy rain events; that may favor the larger seeds of *S. jambos*.

Figure 4. Mean percent of *C. burmannii* by 5cm diameter classes observed in three forest stands in O’ahu, Hawaii.

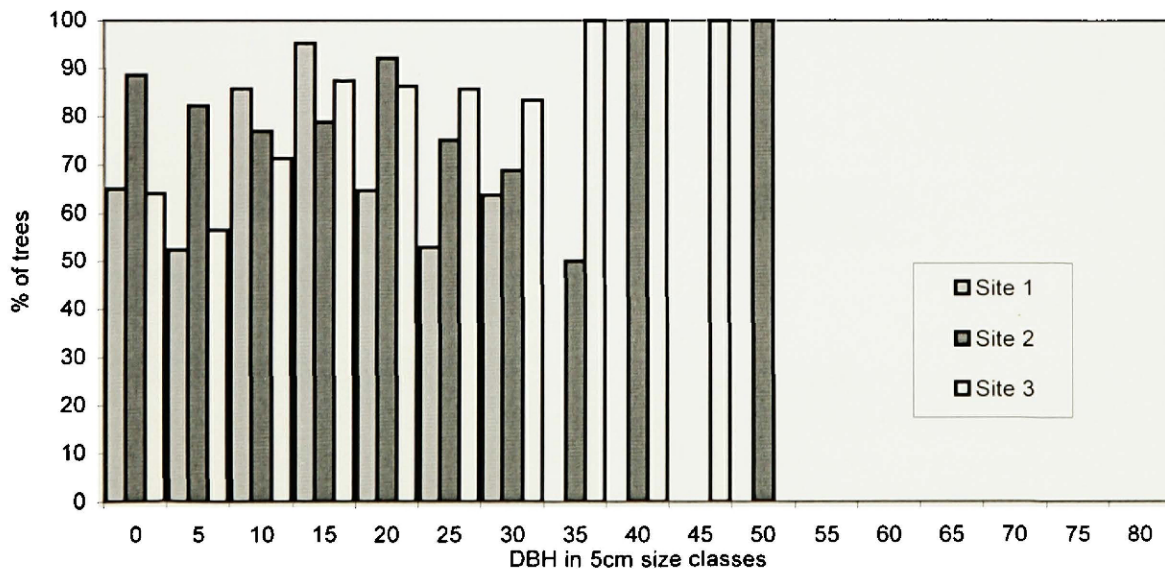


Figure 5. *Cinnamomum burmannii* mean diameter distribution in each of three stands on O'ahu, Hawaii.

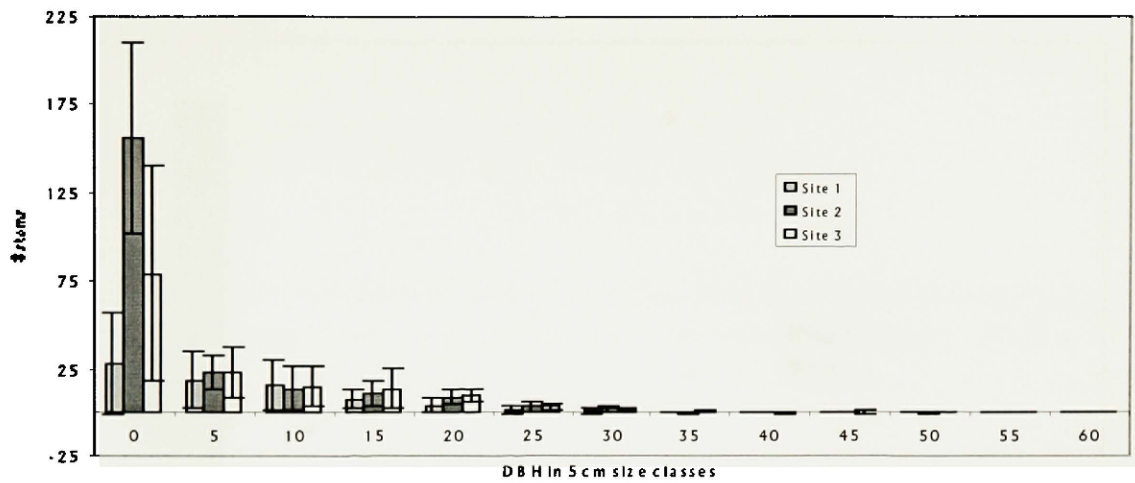


Figure 6. *Citharexylum caudatum* and *Psidium cattleianum* mean diameter distributions in 11 and six 0.049ha circular plots, respectively, in *C. burmannii* stands on O'ahu, Hawaii.

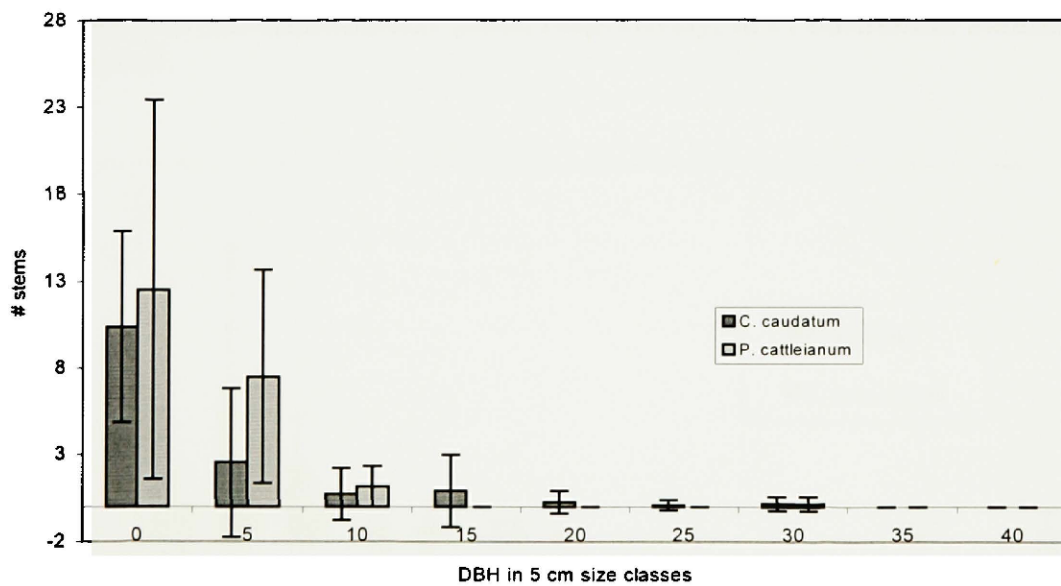


Figure 7. *Syzygium jambos* diameter distributions in two 0.049ha circular plots in a *C. burmannii* stand in the Pauoa Flats on O'ahu, Hawaii.

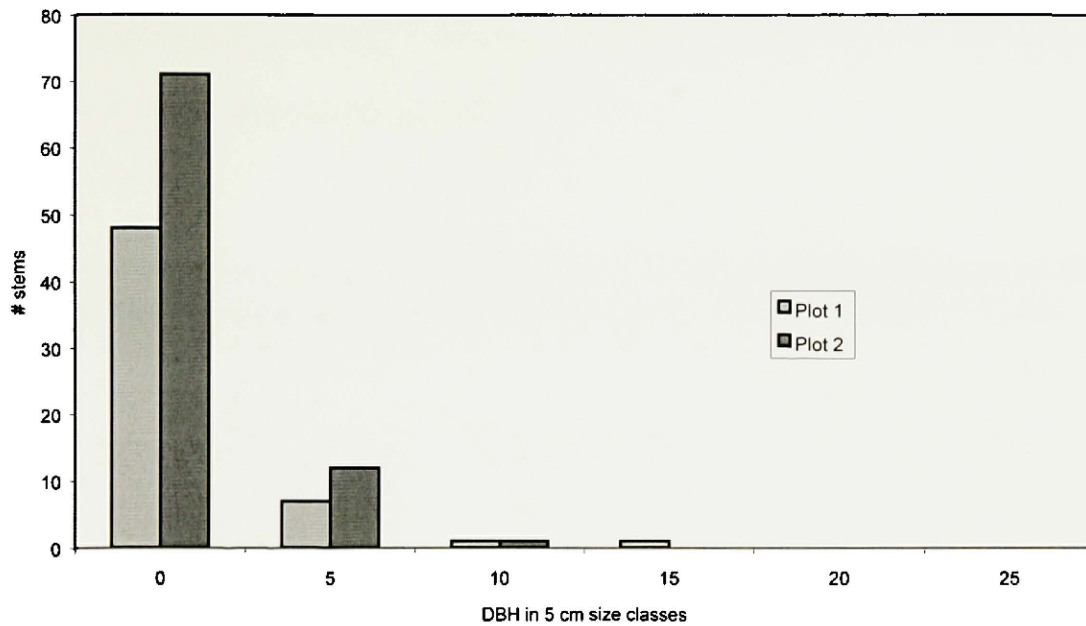
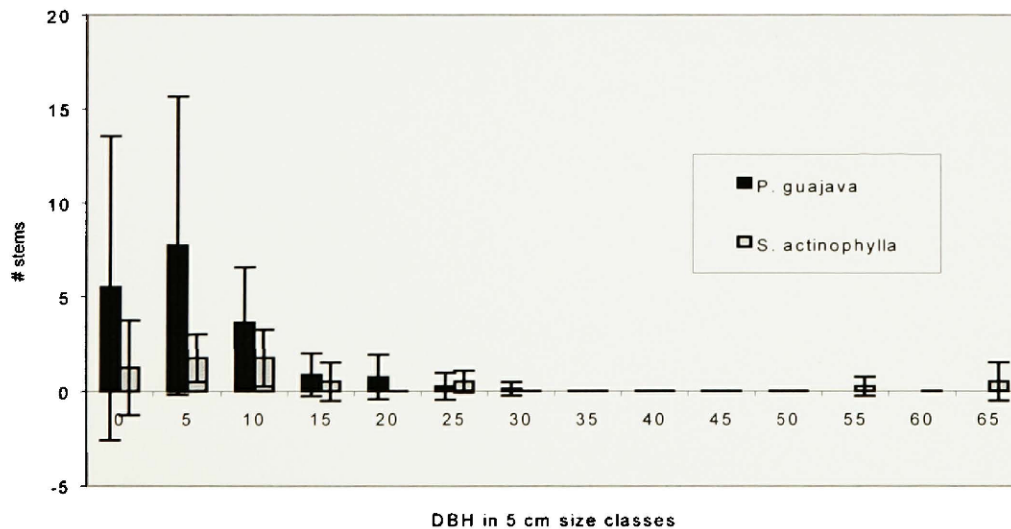


Figure 8. *Psidium guajava* and *Schefflera actinophylla* mean diameter distributions in eight and four 0.049ha circular plots, respectively, in *C. burmannii* stands on O'ahu, Hawaii.



The native *Metrosideros polymorpha* and *Acacia koa*, as well as shade intolerant alien tree species, had few, if any, stems in the lower size classes (Figure 9 & 10). In fact, *A. koa* seedlings were found in only two of the 60 1m² sample plots (Table 1), and these were beneath a large, declining adult tree.

Figure 9. *Metrosideros polymorpha* and *Acacia koa* diameter distributions in two and one 0.049ha circular plots, respectively, in *C. burmannii* stands on O'ahu, Hawaii.

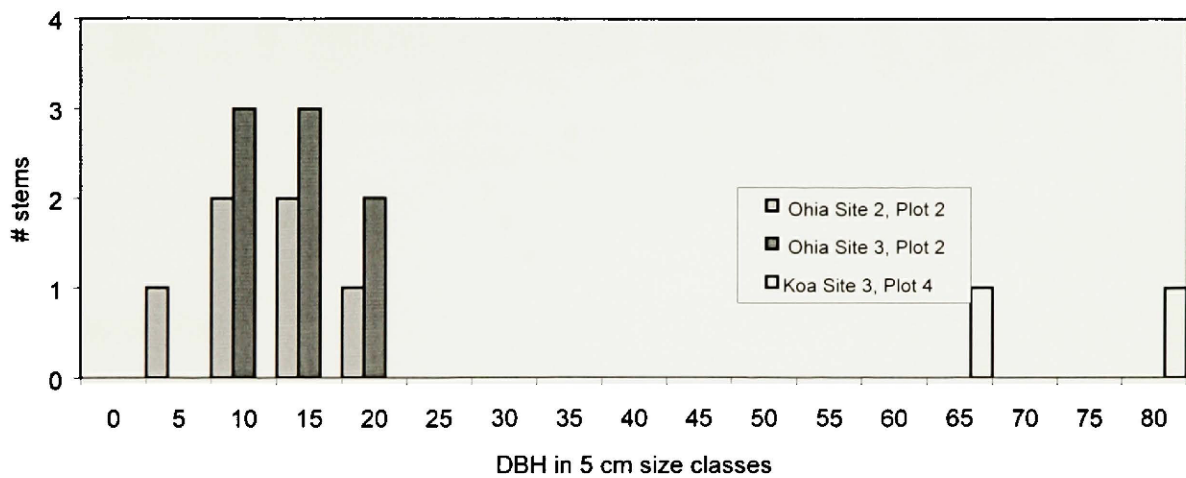
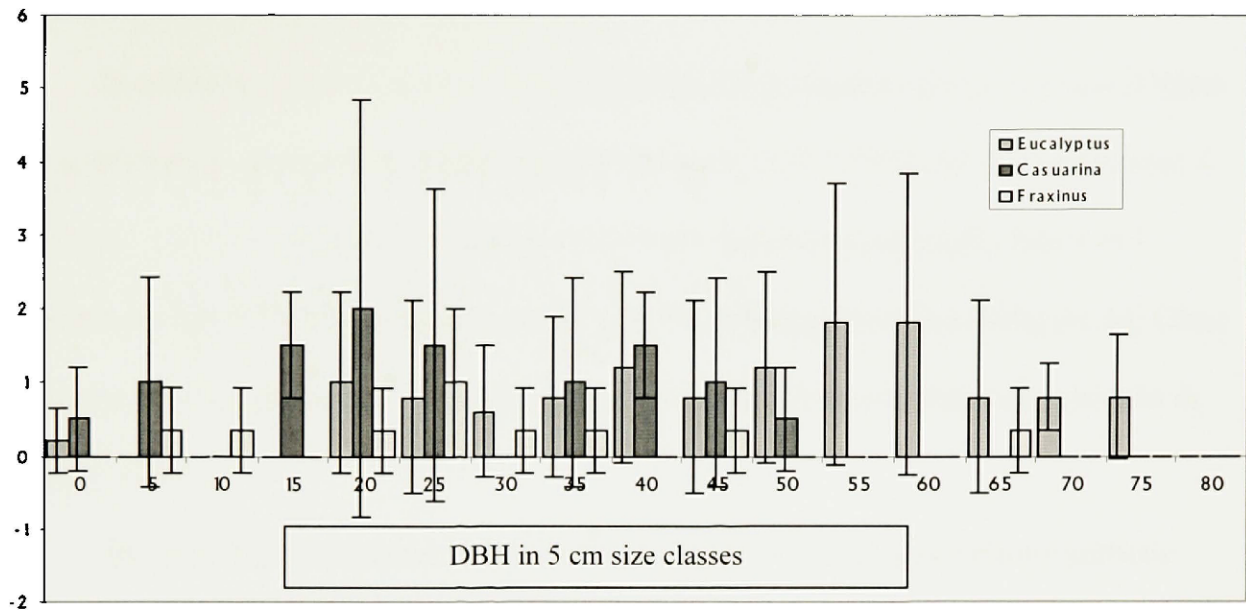


Figure 10. *Eucalyptus* spp., *Casuarina equestifolia*, and *Fraxinus uhdei* mean diameter distribution in five, two, and three 0.049ha circular plots, respectively, in *C. burmannii* stands on O’ahu, Hawaii.



Physiological Data

The seedling light response curve suggests that *C. burmannii* seedlings are very shade tolerant, and able to assimilate CO₂ under very low light conditions (Figure 11). In fact, *C. burmannii* appears to have a relatively low light compensation point (i.e., where photosynthesis is equal to leaf respiration), in comparison to *P. cattleianum* (1.75 to 3.4 $\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$, respectively; Pattison et al. 1998). Compared to very shade tolerant, continental species *Acer saccharum* (Kozlowski & Pallardy 1997b) and *Acer platanoides* (Figure 12; Kloeppe & Abrams 1995), *C. burmannii* seedlings appear to approach a similar maximum CO₂ assimilation rate with a higher level of convexity. Since the photosynthetically active radiation (PAR) is more likely to be greater beneath a *Quercus* canopy with an intermediate level of shade tolerance (Kozlowski & Pallardy 1997b) than beneath the bridge and shade tolerant canopy of *C. burmannii* (Aumeerudy &

Sansonnens 1994; Oliver & Larson 1996), found at site four, *C. burmannii* seems to be better adapted to shade than *Acer saccharum*, because it has a similar maximum assimilation rate at lower light levels.

In addition, sun leaves of *C. burmannii* have high rates of photosynthesis (Figure 13); substantially greater than those found by Pattison et al. (1998) for *P. cattleianum*, *C. caudatum*, and *H. terminalis*, an endemic Hawaiian species occasionally found in *C. burmannii* stands. The same pattern exists with *Pseudotsuga menziesii* (Figure 14; Chen & Klinka 1997), a continental species with intermediate shade tolerance (Kozlowski & Pallardy 1997b).

The low light compensation point for shade leaves, and higher photosynthetic capacity for sun leaves suggests that *C. burmannii* may have photosynthetic plasticity, or greater ability to utilize light over a range of intensities, than many of its competitors, either native or alien. This plasticity may be advantageous for *C. burmannii* by enabling it to survive in very low light levels, while attaining high rates of photosynthesis when exposed to full sun, as in the case of windthrow. However, the small sample size of *C. burmannii* measurements and variation in growing conditions between the greenhouse experiment of Pattison et al. (1998) and field conditions of Kloepfel and Abrams (1995), Chen and Klinka (1997), and this study warrant caution in extrapolating these results.

Figure 11. *Cinnamomum burmannii* shade grown seedling light response curve using artificial light with a LAI 6400.

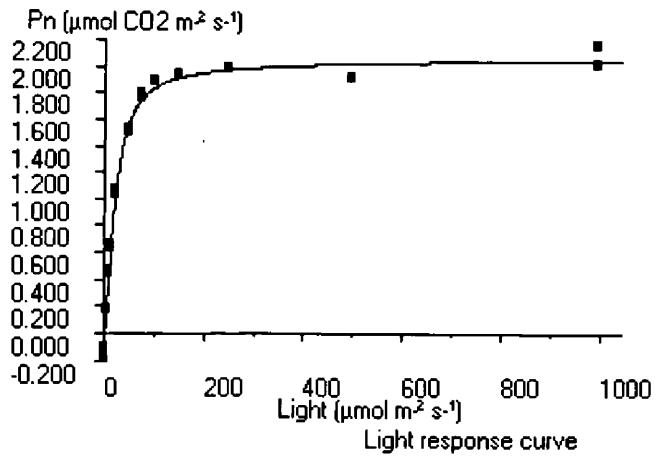
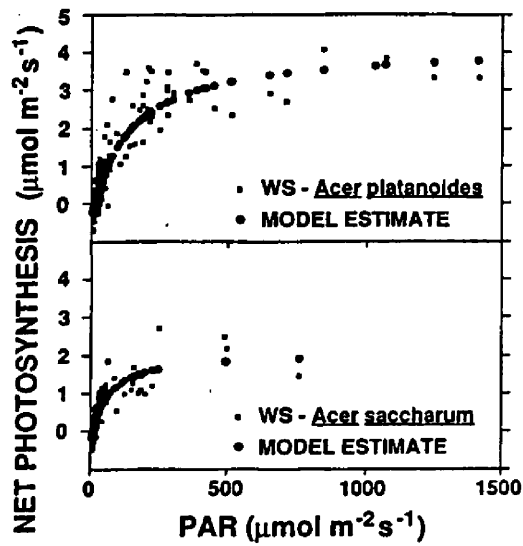


Figure 12. Light response data and Michaelis-Menten model estimates of net photosynthesis on *Acer platanoides* and *Acer saccharum* seedlings at Walnut Springs in Pennsylvania.



From Kloeppel & Abrams 1995

Figure 13. Adult *C. burmannii* canopy sun leaves light response curve using artificial light with a LAI 6400.

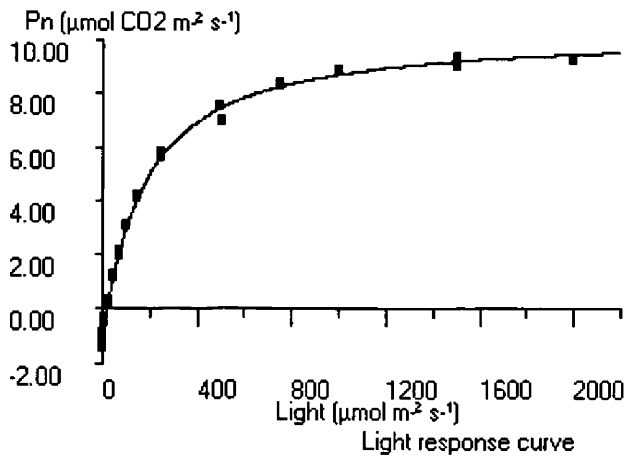
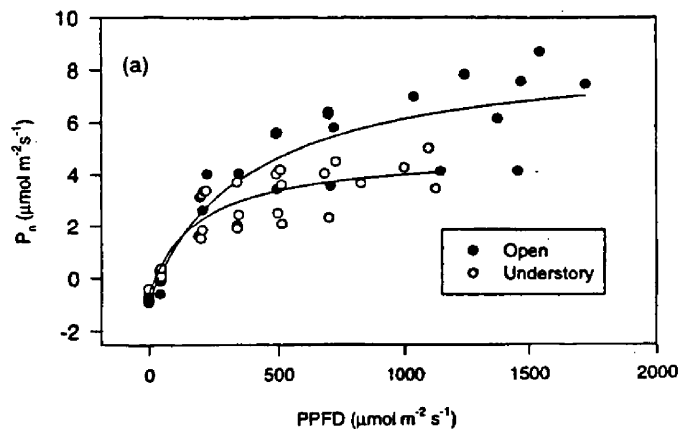


Figure 14. Photosynthetic light-response curves for open-grown and understory-grown branches of *Pseudotsuga menziesii* seedlings near Okanagan Falls, British Columbia.



From Chen & Klinka 1997

Although the physiology data was recorded on a single day and may not be representative of the entire year, further analysis indicated that the results were close to what should be expected over an extended period. By applying leaf nitrogen and specific leaf area data (Table 2) to the regression equation developed by Reich et al. (1998), the resulting A_{\max} (maximum photosynthetic rate) was 15.70 and $9.59 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the

adult tree's sun and shade leaves, respectively. The results derived with Photosyn Assistant using adult tree, ambient light, response data indicate an A_{\max} of $14.0 \mu\text{mol m}^{-2} \text{s}^{-1}$. Since the ambient data was collected using a combination of sun and shade leaves, it is reasonable to presume that this predicted A_{\max} would fall between the predicted sun leaves A_{\max} and shade leaves A_{\max} . By falling within this range one can expect the data to be a reasonable representation of the photosynthetic properties of this tree. However, given the small sample size, the results should be considered as only estimates when extrapolating to other *C. burmannii* trees.

Table 2. *Cinnamomum burmannii* leaf nitrogen content and specific leaf area based on analysis of a single adult tree in the Nuuanu Valley on O'ahu, Hawaii.

Leaf Type	% Leaf N	SLA (cm^2/g)
Adult Sun Leaves	2.10	31.7
Adult Shade Leaves	1.45	40.7
Seedling Shade Leaves	1.30	58.4

Discussion

While shade tolerance is a relative term, which cannot be directly measured, it can be inferred through observations and physiological data (Kozlowski & Pallardy 1997a; Kimmins 1987; Oliver & Larson 1996). *Cinnamomum burmannii* is considered to be a shade tolerant species in its native habitat of Indonesia (Aumeerudy & Sansonnens, 1994). In this study, the high density of regeneration beneath *C. burmannii* canopies (Figure 2), reverse J-shaped diameter distribution (Figure 5), as well as the low light compensation point estimated, indicates that *C. burmannii* is highly shade tolerant on O'ahu. Indeed, high densities of regeneration beneath its own canopy is a common indicator of shade tolerance (Kimmins 1987). This point is enforced by the reverse J-

shaped diameter distribution, indicating long term survival below the canopy. Finally, the estimated light compensation point of *C. burmannii* was below that of *P. cattleianum*, the most shade tolerant species in the Pattison et al. (1998) study. These facts further support the proposed high degree of shade tolerance exhibited by *C. burmannii*. Accompanying a high degree of shade tolerance is low light beneath the canopy (Oliver & Larson 1996). Therefore, the high degree of shade tolerance suggests that few existing alien or native trees, aside from *C. burmannii* itself, will survive beneath a *C. burmannii* canopy.

While other exotic species exhibited diameter distributions similar to that of *C. burmannii* (Figure 5, 6, & 7), stem and seedling populations of these species in *C. burmannii* stands were low. *Syzygium jambos* was the only exception, and heavy overland flow and feral pig activity may have favored seedlings of this species in two of the 15 sample plots. *Cinnamomum burmannii* seeds are approximately 5mm diameter (S. Laughlin, University of Montana, Missoula, MT, Pers. Comm.) and may be washed away by heavy rains. Furthermore, seedlings appear to be adversely impacted by pig activity. In contrast, the larger, 2 – 2.5cm, seeds of *S. jambos* (Wagner et al. 1990) may not be dispersed as easily by rainfall, and the larger, fleshy fruit may be preferred, and deposited by pigs. This might reduce the number of *C. burmannii* establishing, while increasing the likelihood of *S. jambos* establishment.

The other species had less than half the number of stems in each diameter class and very low seedling densities in comparison to *C. burmannii*. *Citharexylum caudatum* had the second greatest number of seedlings with an average of 4.45m⁻² in the 20 1m² plots where it was found (Table 1), while *P. gaujaya* had no seedlings. These tree

species were commonly associated with gaps in the *C. burmannii* canopy and many of the stems were the result of vegetative reproduction or low branching. Whether or not *C. burmannii* canopy gaps will be closed by *C. burmannii* cannot be determined. However, given its high seedling density, ability to coppice, shade tolerance, and photosynthetic plasticity, *C. burmannii* is certainly well poised to dominate mesic and wet forest sites and out compete other alien species.

The diameter distributions of native and alien forestry trees indicate that most are unable to grow beneath *C. burmannii* canopies. Native species had few, if any trees in smaller size classes. This was expected since shade tolerant species, such as *C. burmannii*, will cast deeper shade than shade intolerant species (Oliver & Larson 1996). Less tolerant trees, such as *M. polymorpha* (Adee & Conrad 1990) and *A. koa* (Whitesell 1990) simply cannot survive in the shade cast by shade tolerant species (Oliver & Larson 1996) such as *C. burmannii*.

Metrosideros polymorpha and *A. koa* are the dominant native canopy trees of Hawaii (Adee & Conrad 1990; Whitesell 1990) and both function as pioneer and climax species in their native environments (Adee & Conrad 1990; Gerrish 1989; Whitesell 1990). Stands of *M. polymorpha* will establish in an area and dieback in large or small patches, allowing new seedlings to develop into canopy trees (Gerrish 1989). The introduction of shade tolerant tree species may disrupt this process. Through avian dispersal mechanisms (Laughlin 2000), shade tolerant species, such as *C. burmannii*, may establish beneath the native canopy and reduce the sunlight reaching plants below. The reduction in light may explain the low number of native tree species found in *C. burmannii* stands. However, it is also possible that native trees may not have been

abundant in these stands prior to the introduction of *C. burmannii*, due to prior displacement through human or animal activity, or through the invasion of other alien species. Nevertheless, native trees are unlikely to survive in *C. burmannii* stands due to the ability of *C. burmannii* to tolerate high seedling densities, the deep shade cast by *C. burmannii*, and the inability of shade intolerant and intermediate native trees to tolerate deep shade.

The establishment of shade tolerant tree species can result in many ecosystem changes. Aside from the displacement of less shade tolerant native species, higher rates of windthrow may also occur. Root to shoot ratios are known to decrease with increasing shade in many tree species (Kramer & Kozlowski 1979), and low root to shoot ratios are believed to result from low light conditions below the canopy, where many of these trees develop (Geldenhuys 1986; Geldenhuys et al. 1986). In this study, many *C. burmannii* had been uprooted, exposing a shallow root system which created gaps for advance *C. burmannii* regeneration, epicormic shoot growth, and stump sprouts, thereby allowing *C. burmannii* to replace itself. Shallow rooting may be typical of *C. burmannii* in both its native Indonesian range and in Hawaii; however, environmental conditions differ in the two regions. Hawaiian forests are subject to strong trade winds and occasionally hurricanes (Giambelluca & Schroeder 1998), while equatorial Indonesia is not subject to strong wind patterns (Sanchez 1976). This alteration of disturbance patterns could result in increased erosion.

In addition to the advantage of shade tolerance, *C. burmannii* may have an additional advantage of co-evolution with alien pathogens. The alien soil pathogen, *Phytophthora cinnamomi*, found in Hawaii and once considered a possible cause for the

decline of *M. ploymorpha* (Hodges et al. 1986), was originally isolated in *C. burmannii* in Sumatra (Sinclair et al. 1987). *Phytophthora cinnamomi* infects more than 900 species of plants around the world, and regularly causes decline and death (Sinclair et al. 1987).

Warm, moist soils are ideal conditions for this pathogen (Sinclair et al. 1987), and occur regularly in Hawaii's mesic and wet forests. If *C. burmannii* and *P. cinnamomi* have co-evolved, then *C. burmannii* may be better adapted to *P. cinnamomi* infections.

Another important invasive species of undisturbed forests on moist tropical islands is *Miconia calvescens* (Meyer 1996). While *M. calvescens* has received considerable attention (Meyer 1996; Stone et al. 1992a), *C. burmannii* has not, despite the fact that they have similar invasive traits. Both species are shade tolerant, which permits growth in undisturbed forests (Meyer 1996; Aumeerudy & Sansonnens 1994), and both can produce seed within four years (Meyer 1996; Aumeerudy & Sansonnens 1994). Short juvenile periods are correlated with increased likelihood of tree invasiveness (Rejmanek & Richardson 1996). Furthermore, birds facilitate dispersal of both *C. burmannii* and *M. calvescens* seeds (Laughlin 2000; Meidell et al. 1997; Meyer 1996) which may accentuate their invasive potentials (Kruger et al. 1986). Finally, both *M. calvescens* and *C. burmannii* form monotypic stands which produce deep shade under which their own seedlings tend to dominate (Meyer 1996; Pers. Obs.).

The most important differences between *M. calvescens* and *C. burmannii* are probably seed crop size and growth rates. *Miconia calvescens* often exhibit rapid growth rates, and a single adult is thought to produce up to 5 million seeds per year (Meyer 1996). In contrast, seed crops produced by *C. burmannii* adults were found to produce an estimated maximum of approximately 133,000 seeds per year (Laughlin 2000). The

growth rate of *C. burmannii* is not known, but probably is not as rapid as *M. calvescens*. These differences suggest that *C. burmannii* may spread at a slower pace than *M. calvescens*, but ultimately form similar monotypic stands.

Conclusion

The lack of shade tolerant dominant native forest tree species, along with the introduction of alien dispersers (Laughlin 2000), has enabled *C. burmannii* to establish in some Hawaiian mesic and wet forest sites. Taxonomic disharmony is commonly used to describe native island ecosystems, such as those of Hawaii, and refers to the low species numbers relative to similar continental ecosystems (Loope 1992). This is often applied to the lack of climax and gap replacement species (Loope 1992). Taxonomic disharmony results from evolution in isolation, where a few species fill a broad range of ecosystem niches, such as *M. polymorpha* and *A. koa* which function as both pioneer and climax species (Adee & Conrad 1990; Loope 1992; Whitesell 1990). As a result, shade tolerant aliens, such as *C. burmannii* and *M. calvescens*, out compete native species by reducing the level of sunlight penetrating the canopy and limiting the reproduction and growth of native tree species.

Cinnamomum burmannii is shade tolerant, a characteristic not common to dominant, native, forest trees in Hawaii. Because of its ability to create and grow in deep shade it appears to have become a new “climax” species in some Hawaiian forests. Alien pathogens, which may have co-evolved with *C. burmannii*, such as *P. cinnamomi*, may provide *C. burmannii* with an additional advantage over native species. Wind events and canopy dieback may further favor advance regeneration or stump sprouting by *C.*

burmannii. Such self replacement can result in the establishment of monotypic stands, which can be biologically unstable and threaten the existence of native forest species.

As these monotypic stands continue to expand, land managers will have many concerns. The stands examined in this study lie within the state managed Honolulu Forest Watershed Reserve, which is the water source for much of Honolulu and surrounding communities. The presence of *C. burmannii* could increase the amount of available water by providing a dense canopy and increasing occult precipitation, or reduce water availability through high transpiration rates. If an effective pathogen or pest were introduced, the *C. burmannii* stands could be decimated. Although this could aid in the restoration of native forests, it could also result in landslides and a reduction in water quality, heavily impacting communities like Honolulu, which lie below *C. burmannii* stands.

While this study provides a rough sketch of *C. burmannii* stands on O'ahu, additional research is needed to assist land managers in prioritizing and abating alien species invasions. The detrimental effects of *C. burmannii* establishment must be weighed against the effects of other alien species and management options. This would allow land managers to allocate scarce resources more wisely. Additional physiological and silvicultural studies could assess the impact on forest water resources by providing transpiration and growth rates. Light and stand measurements should be recorded over time to determine the reduction in light levels and the impact on both native and exotic species. Rooting habit and windthrow studies of both native and alien species could provide an estimate of disrupted and native disturbance regimes. Effective means of control should be investigated including mechanical, chemical, and biological methods.

Possible uses for the species, such as specialty lumber and cinnamon production should be further investigated to possibly subsidize alien species abatement.

Considering the high seedling densities, ability to coppice, and shade tolerance, eradication of established *C. burmannii* stands would be extremely challenging. The dense canopy of *C. burmannii* will tend to exclude other species, especially native Hawaiian trees. However, *C. burmannii* is not the only example of shade tolerant alien tree species that threaten native ecosystems. *Miconia calvescens* in the Pacific (Meyer 1996) and *Acer platanoides* in eastern North America (Wyckoff & Webb 1996; Kloepfel & Abrams 1995) are also shade tolerant alien invasives, with the ability to establish and disrupt closed native forests.

With much of invasive research focusing on species that have rapid growth rates and require disturbance to establish, shade tolerant invaders frequently go unmentioned. Thus, they continue to spread and disrupt the closed forest communities that many land managers consider “safe” reserves. While isolated ecosystems, such as those in the Pacific, are among those most at risk, the Wyckoff and Webb (1996) study illustrates that even continental forests can be invaded. Species with shade tolerant characteristics warrant more attention from researchers and land managers. As shade grown crops such as coffee and cacao are encouraged in areas where they are alien, few consider the possibility of their invasion into natural or reserve areas. Widespread naturalized coffee populations in the Hawaiian Islands help to emphasize this point (Wagner et al. 1990). While coffee and cacao do not reach the height obtained by *C. burmannii*, the dense canopy of any shade tolerant species may greatly inhibit regeneration of native species.

As this study suggests, even relatively slow growing, shade tolerant aliens, like *C. burmannii*, have the potential to drastically alter forest communities.

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