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***Myrica faya*: Review of the Biology, Ecology,
Distribution, and Control, Including an
Annotated Bibliography**

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ABSTRACT

The family Myricaceae consists of three or four genera, depending on the classification system followed, of which the largest is *Myrica* with 37-52 species. Members of the genus are typically evergreen shrubs or small trees. The high degree of floral and foliar uniformity within the genus has resulted in confusion and disagreement as to species level classification, and has produced a large number of synonyms. *Myrica* is widely distributed primarily in tropical or subtropical regions of the world, but several species also occur in northern and southern temperate habitats. The greatest concentration of species appears to be in South Africa. Chevalier's Monographie des Myricales, published in 1901, remains the definitive work on the taxonomy of the genus, but is out of date in many respects and in need of revision. No members of the genus are themselves of significant economic value, but several species have received disproportionate research attention because of their anatomically and morphologically unusual floral development and structure, and the ability of *Myrica* spp. to fix atmospheric nitrogen through symbiotic association with the Actinomycete *Frankia*.

In Hawai'i, *Myrica faya* (fayatree) has received considerable attention because of its ability to invade and significantly alter native habitats. It is native to the northern islands of Macaronesia, the Azores, Madeira, and the Canaries in the north Atlantic ocean. It was probably introduced to Hawai'i by Portuguese immigrants from the Azores or Madeira during the period 1876-1886, although there are no apparent ethnobotanical uses that would readily account for such introduction. In Hawai'i, research has concentrated on two general aspects: the ability of fayatree to invade native habitats and to permanently alter the nutrient status of volcanic soils, which are typically deficient in nitrogen, through its nitrogen-fixing ability, potentially encouraging further invasion by other alien species; and the control of fayatree through mechanical, chemical, or biological approaches. Mechanical removal of fayatree is effective on a limited scale, such as in the Special Ecological Areas of Hawai'i Volcanoes National Park, but this approach is labor intensive and not practical on a wider scale. Herbicides, such as imazapyr, were shown to be effective when applied to cut stumps, but are expensive and likewise require intensive labor if applied on a wide scale. Investigations of the native habitats of fayatree have led to the identification of insects and pathogenic organisms that may assist in the biocontrol of fayatree in Hawai'i. Some of these organisms have been introduced into quarantine in Hawai'i for testing. To date, two insects, both moths, have been released, *Strepsicrates smithiana* in 1955, and a second, identified at the time as *Phyllonorycter myricae*, in 1991. These have not effected control, but observations of *P. myricae* are still in progress. Although unrecognized until recently, locally occurring disease organisms, such as the fungus *Botrytis cinerea* may also be limiting fayatree.

INTRODUCTION

Alien plants have been cited as a primary threat to the integrity of Hawai'i's native ecosystems in a recent assessment of risks to these ecosystems (Carpenter and Mitter 1992). More than 4,600 plant species have been introduced by either direct or indirect means to the Hawaiian Archipelago in the approximate 220 years since European discovery (C. Smith 1985). An estimated 861 of these alien species have become naturalized and flourish in Hawai'i's mild climate. Naturalized species comprise nearly 47% of the currently accepted flora of the Hawaiian Islands (those species which are unable to establish and maintain populations without the assistance of humans are excluded in these estimates) (Wagner *et al.* 1990).

Myrica faya Aiton (fayatree, firetree, or firebush) has been recognized as one of the twelve most noxious plants alien to Hawai'i due to its ability to rapidly and aggressively invade and colonize the Hawaiian environment (C. Smith 1985). This species is considered one of the most serious alien plant threats, if not the most serious, on nitrogen-poor sites such as young lava flows and open-canopy xeric and mesic forest ecosystems of the Hawaiian Islands (Taylor and Markin 1992, Vitousek and Walker 1989).

Fayatree affects ecosystem properties by nearly quadrupling the amount of nitrogen entering typically nitrogen-deficient lava substrates (Vitousek 1992). Thus, this invasive species may alter the processes of primary succession and, ultimately, the vegetation composition of the Hawaiian Islands. Disruption of plant communities in turn may adversely affect native fauna such as birds, land snails, and insects which depend on native vegetation for food and habitat.

Fayatree is a vigorous competitor in Hawai'i's ecosystems. It has the apparent potential to exclude the native dominant tree *Metrosideros polymorpha* ('ohi'a) in certain environments (Walker and Vitousek 1991) and form monotypic stands with greatly reduced native understory vegetation (Vitousek 1986). It is also a management problem in agricultural systems such as rangeland and cropland where it readily displaces economic plant species (Little and Skolmen 1989).

Fayatree is capable of producing large numbers of fruits throughout the year. The fruit is consumed by native and non-native birds, alien rodents and ungulates which disperse this species over short and,

presumably, long distances, increasing the density of existing populations and expanding the range of fayatree (LaRosa *et al.* 1985, Woodward *et al.* 1990).

Fayatree is a member of the family Myricaceae, a rather obscure family of woody trees and shrubs, no member of which has known significant economic uses. Fayatree may be the only member of the family which is known to occupy a dominant position in its native habitat. Some of our knowledge concerning the biology of the genus *Myrica* has been compiled by developmental biologists interested in aspects of morphological evolution (such as the development of dioecy) (Macdonald 1977, 1979, 1980). The ability of members of the genus to fix atmospheric nitrogen has also focused considerable research attention on this group (Mian *et al.* 1976, Miguel and Rodriguez-Barrueco 1974, Monz and Schwintzer 1989, Vitousek and Walker 1989).

Because of the particular problems caused by fayatree in the Hawaiian Islands, much of the information concerning the ecology of this species has been gained in Hawai'i (on the island of Hawai'i in particular) as opposed to the native habitat. These studies have focused largely on the invasive ability of this tree as an introduced species (Smathers and Gardner 1979, Vitousek and Walker 1989), as well as on control approaches. The relationships and interactions of fayatree in its native environment are less well understood.

Fayatree is native to three island clusters in the mid-Atlantic Ocean: the Azores, Madeira, and Canary Islands. Collectively, and including the Cape Verde Islands (although fayatree is not known to be native to the latter group), these are known as the Macaronesian Islands. Fayatree also occurs in mesic forests on the southern Portuguese mainland where there is question as to whether it is naturalized or native (see section on Distribution). Only in the Hawaiian Islands is fayatree considered an invasive weed.

It is widely accepted that Portuguese laborers from Madeira and the Azores were recruited as agricultural workers by the Hawai'i Territorial Government beginning in 1878. Many were vineyard growers who had suffered economic hardship from a blight that had attacked the vineyards in the 1850's. Unlike most other immigrants to Hawai'i at that time, the Portuguese frequently transported their entire families with them (McDermott *et al.* 1980). It is conceivable that, in addition to their families, these workers also brought with them some of the plants, including fayatree, important to their lifestyle. The

unpublished report of Yamayoshi (1954), of the Board of Commissioners of Agriculture and Forestry of the then Territory of Hawai'i, is the most precise record available of the initial introduction of fayatree to Hawai'i, although the year of this occurrence is not known.

Fayatree was recognized as a problem species as early as 1937 (Fosberg 1937), and efforts toward its control in Hawai'i have been active since 1944 (Neal 1965). Control remains an on-going concern of state, federal, and private land managers. Mechanical, chemical, and biological control programs have met with varying levels of success. Research and field trial programs continue to explore the most effective and environmentally benign methods to control this plant.

The objective of this review is to assess current knowledge of fayatree and to summarize available information for use by researchers and managers involved in control efforts of this invasive plant in Hawai'i. This compilation of data from technical reports, journals, books, unpublished manuscripts, and personal communications synthesizes information on taxonomy, biology, ecology, distribution, ethnobotanical uses, and control approaches for this species. An annotated bibliography is included.

DESCRIPTIVE BIOLOGY

Systematics

The family Myricaceae is a member of the Division Magnoliophyta, Class Magnoliopsida, Subclass Hamamelidae, and is placed in its own order, the Myricales (J. Smith 1977). The Myricales and six other orders, Fagales, Juglandales, Hamamelidales, Urticales, Leitneriales, and Casuarinales comprise the subclass Hamamelidae, a phylogenetic grouping of orders which are characterized by strongly reduced, often unisexual flowers which either lack or produce a poorly developed perianth (Cronquist 1978). The order Myricales possesses morphological attributes similar to those of the Casuarinales, Fagales, and Juglandales. These four orders are thought to have been derived from the order Hamamelidales (Takhtajan 1969). Phylogenetically, the Myricales are thought to be most closely related to the Juglandales and the Fagales (Takhtajan 1969, Cronquist 1978). Other plant systematists have

placed the Myricaceae in the Juglandales based on similarities in inflorescence morphology (Hjelmqvist 1948) and anatomy (Cronquist 1978).

Members of the Myricales are also included in the Apetalae, an artificial grouping of plant orders which is based on the absence of a perianth. The artificial assemblage Amentiferae forms the central core of the Apetalae. The Amentiferae is characterized by minute, apetalous, unisexual, mostly wind-pollinated flowers clustered in erect or pendant inflorescences referred to as aments or catkins. Current theory posits that the homologous inflorescence morphology in these amentiferous orders is the result of a divergent, yet parallel evolution from entomophily (insect-pollination) to anemophily (wind-pollination) (Abbe 1974, Sporne 1975, Takhtajan 1969). Although the individual flowers of the Amentiferae are greatly simplified, the inflorescences are thought to have become increasingly specialized and complex (Abbe 1974, Takhtajan 1969). The morphological complexity of the Amentiferae has been studied by several taxonomists; many of these studies have been reviewed by Hjelmqvist (1948) and Abbe (1974). Macdonald (1977, 1979, 1980) has examined the morphology and ontogeny of the inflorescence of the Myricales.

The Myricaceae is a family of woody plants native mainly to the subtropical and warm temperate regions of the world. Taxonomists and phytogeographers consider the Myricaceae to be an ancient family dating to the Tertiary Epoch of the Cretaceous Period with the living members representing relicts of once extensive tracts of subtropical forest that spread across the territory that is now central and southern Europe (Sporne 1975, Takhtajan 1969). The family consists of three, or disputedly, four genera and an estimated 37 to 56 species. The base chromosome number throughout the family is eight, with various levels of ploidy present (Macdonald 1989).

Chevalier (1901), who published the initial taxonomic treatment of the Myricaceae, divided the family into three genera: *Comptonia*, *Myrica*, and *Gale*. This classification is based mainly on the nature of the fruit exocarp and the various morphological developments of the pistillate flower bracts during maturation of the fruit. The monotypic genus *Comptonia*, consisting of *C. peregrina*, was once included in the genus *Myrica* (as *M. asplenifolia*). *Comptonia peregrina* has been given generic status due to its unique morphology (Abbe

1974). The fruit exocarp of *C. peregrina* is smooth, lacking the papillate emergences typical of the family; eight lanceolate secondary bracts are persistent at maturity, forming a cupule-like base that overtops the fruit which are thought to aid in wind dispersal of the fruit. The genus *Comptonia* is also distinguished from other myricaceous genera in having stipulate leaves and mostly monoecious plants.

Hjelmqvist (1948) discussed the variation in the floral morphology of *Myrica* and, following Chevalier (1901), divided the genus into three sections: Morella, Cerophora, and Faya. This division was later supported by Abbe (1974) (as discussed under "Distribution").

Section Morella is distinguished by branched (compound) male inflorescences and succulent (fleshy) emergences which cover the fruit. Species of this section are native to eastern Asia; representative species are *M. esculenta* and *M. rubra*. Phylogenetically, it is argued that this group of species is the most primitive of the genus based on the compound, and thus less reduced nature of the male inflorescence (Hjelmqvist 1948) (assuming that phylogenetic development tends toward the minimalist state).

Section Cerophora is characterized by male inflorescences which are either simple, or at least give the appearance of being simple. Based on male inflorescence morphology, section Cerophora is considered to contain the most advanced representatives of the genus. The emergences which develop on the fruits are cerigenous, or waxy. This section, the most extensive of the three in terms of species number, has been subdivided into two subsections, apparently based on the geographical range of its members. *Myrica* species of subsection *Africanae* range from tropical west Africa south to the Cape of Good Hope. Representative species are *M. kandtiana* and *M. serrata*. Members of subsection *Americanae* range from the central eastern coastal plain of the United States and extend south through Central America reaching a southern limit in Chile and Argentina. Representative species are *M. cerifera* and *M. pubescens*.

Section Faya is characterized by male inflorescences intermediate in form between those of section Morella and section Cerophora having either a slightly branched to apparently simple morphology. Papillate fruit emergences are of the waxy type.

Hjelmqvist (1948) noted that in sections Faya and Cerophora, ovaries developing in the tightly clustered pistillate florets of a single pseudanthium can sometimes coalesce to form a syncarpium which matures into a multiple fruit. Members of section Faya are native to the Macaronesian Islands and the western coast of North America ranging north from Vancouver Island, British Columbia south to central California. Based on the morphological similarity of the fruits of sections Cerophora and Faya and developmental similarities, Macdonald (1979) suggested that section Faya might best be included in section Cerophora. Representative species are *M. faya* and *M. californica*.

Gale is a monotypic genus (*G. palustris*) considered by some taxonomists a species of *Myrica*, *M. gale* (Britton and Brown 1970, Fernald 1970, Mabberley 1989, Heywood 1979). Chevalier (1901) placed this plant in a distinct genus as it produces fruits which lack papillae but which do produce two persistent secondary bracts that elongate and mature into broad, wing-like appendages. The separation of *M. gale* into a distinct genus is somewhat problematic taxonomically, as a specimen of *M. gale* was the lectotype used by Linnaeus to initially describe the genus *Myrica* (Abbe 1974). Strict adherence to botanical rules of nomenclature then, would require that the genus *Myrica* be reserved for *M. gale* and that the remaining species be placed in a newly designated genus. Macdonald (1977) has supported Chevalier's (1901) designation of a distinct genus for *M. gale* (based mainly on the ontogeny of the male inflorescence) and recognizes *Gale* and *Comptonia* as the two morphologically most advanced genera of the family.

The discovery of a unique myricaceous plant endemic to New Caledonia prompted the designation of the monotypic genus *Canacomyrca* (*C. monticola*) (Hjelmqvist 1948). This plant has been included in the Myricaceae mainly due to similarities in inflorescence morphology, although several morphological characteristics clearly deviate from those typical of the family. Distinguishing features are stipulate leaves; bisexual flowers; a pendulous, anatropous ovule (an ovule with the body fully inverted) rather than the erect, orthotropous (a straight, or unbent ovule), basal ovule typical of *Myrica*; a six-lobed disk which enlarges in fruit to completely enclose the ovary at maturity; and endosperm in the seeds. *Canacomyrca* may also lack

a nitrogen-fixing symbiont (Cronquist 1978, Heywood 1979, Hjelmqvist 1948, Mabberley 1989).

Anatomy

Whereas the anatomy of *fayatree* itself has not been extensively investigated, Metcalfe and Chalk (1950) provided a comprehensive account of the anatomy of the Myricaceae with some references to *fayatree*. This description was summarized by Metcalfe and Chalk as follows:

Aromatic trees or shrubs which are widely distributed in temperate regions. They usually bear root tubercles containing nitrogen-fixing bacteria. Their aromatic nature is caused by waxy material which is secreted from the leaves by characteristic peltate glands. Uniseriate glandular hairs also occur, and in some species, certain of the epidermal cells with thin, outwardly arched walls also have a secretory function. The ranunculaceous stomata occur only on the lower surface of the leaf. In the stem, cork arises superficially, and the pericycle contains fibres and stone cells arranged in a continuous or interrupted ring. Both solitary and clustered crystals occur.

Vessels (in the wood) are small, usually exclusively solitary, sometimes tending to be ringporous, perforation plates exclusively scalariform or scalariform and simple, intervacular pitting intermediate to alternate, pits to parenchyma round, members of medium length, occasionally moderately long. Parenchyma apotracheal, diffuse. Rays exclusively uniseriate or up to 4-8 cells wide, heterogeneous. Fibres with distinctly bordered pits, of medium length, occasionally moderately long.

The more comprehensive treatment of the anatomy of Myricaceae and related families provided by Metcalfe and Chalk (1950) should be consulted if additional detail is desired.

The nitrogen-fixing ability of the Myricaceae is especially noteworthy. Metcalfe and Chalk (1950) provided the following account of root nodules of this family, summarizing much of the information from the work of Bottomley (1911, 1912):

According to Bottomley, the root nodules of *Myrica gale* originate as lateral branches of the tetrarch roots. Three branches usually arise laterally near the end of each primary nodule, and by repetition of this process, 'cluster' nodules are produced. Bottomley recognized 4 zones in each

mature nodule. (i) An apical meristem. (ii) An 'infection thread' area. (iii) A bacterial zone comprising most of the cortical tissue and consisting of enlarged cells filled with bacteria. The cortical cells become infected before the young branch emerges from the old root. (iv) A basal region devoid of bacteria, composed of cells filled with oil drops. This gradually encroaches on and replaces all of the other zones. Bottomley secured experimental evidence that the bacteria in the nodules are capable of fixing nitrogen.

The structure of the root nodules in certain North American species of *Myrica* has been examined by Youngken (1919, 1923), who was apparently unaware of Bottomley's earlier work. Youngken's examination led to conclusions similar to those of Bottomley, and he identified the organism which occurs in the nodules as an *Actinomyces*. Concerning this organism he says: 'The *Actinomyces* not only confines itself to the cortex of the tubercular root, it later works its way into the tracheae of these structures, passes into the pitted vessels of the main roots, thence into those of the stems, and, conveyed by the transpiration stream gradually upward, is carried through the axes of catkins so as finally to reach the flowers, bracts and fruits. In these it confines its existence to the parts corresponding to the mediocortex of the root tubercles, namely the mesophyll and outer mesocarp regions respectively.'

Growth Form

Members of the Myricaceae characteristically are evergreen, or, less frequently, deciduous aromatic trees or shrubs. Most species have a nitrogen-fixing actinomycete as a symbiont in root nodules. The leaves typically are simple, spirally arranged, dotted with peltate multicellular glands and are aromatic, exstipulate, and often coriaceous. The single seed of the Myricaceae generally lacks endosperm and is protected by a stony endocarp.

Fayatree is an adaptable species that varies in habit from a medium-sized tree up to 20 m in height and 75 cm in diameter to a multi-stemmed shrub up to 10 m in height. The shiny, dark green simple leaves with axial clusters of bright red to purple fruits make *fayatree* an attractive plant that has been grown ornamentally in the Macaronesian and Hawaiian Islands, and the Portuguese mainland.

Reproductive Structures

The reproductive structures of fayatree display the complexity of form and plasticity in structure, development, and function that is characteristic of the Myricaceae. Reduction of the floral structure of *Myrica* apparently is so pronounced that the nature, function, and derivation of individual floral structures have been difficult to determine.

Inflorescence

Flowers of the Myricaceae have been the subject of detailed ontogenetic studies due to their morphological and developmental uniqueness (Abbe 1974, Hjelmqvist 1948, Macdonald 1979). The greenish or yellowish flowers are small, much reduced and generally unisexual, and clustered in short, lateral, generally unisexual inflorescences growing on either monoecious or dioecious plants (Figs. 1-3). The flower lacks a perianth but is subtended by one to eight small bracts. Bracts are not persistent on the fruit at maturity. The staminate flower typically has one to six anthers subtended by a floral disk. The pistillate flower typically consists of a superior ovary with two fused locules, the single chamber containing an erect and straight ovule and a single style with two short stigmatic branches (Fig. 3). The fertilized pistillate flower produces a small, rounded, one-seeded drupe or nutlet.

The inflorescence of fayatree is a catkin-like compound spike of pseudanthia which develop in the axils of the primary bracts. Much previous confusion about the structure of the *Myrica* inflorescence has been the result of the misidentification of the partial inflorescence as a single flower. Such confusion has led to prior estimates of from two to as many as twenty stamens per flower. Pseudanthium structure is further obscured by the overtopping of the partial inflorescence tip by floral components, such as tertiary bracts (Abbe 1974). Various methods have been employed to interpret the structure of the *Myrica* flower.

Hjelmqvist (1948) studied the external morphology of the flowers and inflorescences of *Myrica* and suggested that the flower arising in the axil of a bract is actually a pseudanthium (an inflorescence which simulates a single flower; for example, the Asteraceae inflorescence) that has developed through the union of a number of structurally simple flowers.

From analysis of the vascular anatomy of *Myrica*, Abbe (1974) was able to clarify that the smallest unit of the typical flower consists of either a single stamen or a naked ovary subtended by a single tertiary bract, and that the partial inflorescence, or pseudanthium, is comprised of an aggregate of unisexual florets. Abbe (1974) further posited that the compound inflorescence consists of several pseudanthia varying in position from racemose to cymose on the main inflorescence axis. Abbe viewed the pistillate inflorescence as consisting of an acropetal sequence of partial inflorescences with the youngest and most reduced floret nearest the distal end of the main axis. Abbe discussed, but was not able to explain, the ability of floret primordia to develop into more than one structural form. For example, secondary bract primordia have the potential to form secondary bracts, stamens, papillae, or a portion of the inflorescence axis (Abbe 1974, Macdonald 1979, 1980).

Gardner (1985) described some unusual flower characteristics for fayatree observed in the Hawaiian and Macaronesian Islands. A small number of pistillate flowers was frequently observed growing on predominantly staminate plants, and conversely, staminate flowers were noted growing on pistillate plants. Hjelmqvist (1948) described bisexual inflorescences produced by *Myrica*. These he identified as androgynous catkins, clusters of bisexual florets consisting of a central pistil with three to four stamens connate to and spirally arranged around the pistil. The androecium, in this case, was not viable. The distal ends of the bisexual inflorescences produced unisexual florets of three to four stamens subtended by a single bract. Lloyd (1981) also observed bisexual florets with non-functional stamens that developed infrequently on *M. gale*. Macdonald (1979) noted that 20% to 25% of *Myrica* species are subdioecious (i.e., having some pistillate flowers on predominantly staminate plants and/or staminate flowers on predominantly pistillate plants) and that each section of the genus contains one or more species that is not strictly dioecious.

Macdonald (1979) investigated the development of the pistillate flower and gynecandrous partial inflorescence of *M. californica*, a small tree or shrub closely related to *M. faya* which is native to the coastal regions of Washington to California. Morphological investigation revealed three types of gynecandrous inflorescences, or pistillate

- Figure 1. Flowering branches with staminate flowers of fayatree
- Figure 2. Closeup of staminate flowers
- Figure 3. Closeup of pistillate flowers of fayatree
- Figure 4. Closeup of stamens borne on the surface of immature fayatree fruit
- Figure 5. Fruit clusters on branches of pistillate fayatree. Fruit darkens as it matures.
- Figure 6. Fayatree as a component of a typical dense laurosilva forest on the island of Pico of the Azores
- Figure 7. Young fayatree colonizing abandoned farmland on the island of Pico, Azores
- Figure 8. Older, open stand of fayatree in mid-elevation pastureland on the island of Pico, Azores

inflorescences which produce androecia (referred to as androgynous catkins by Hjelmqvist (1948). Gynecandrous inflorescences of the type produced by *M. californica* and *M. faya* combine the characteristics of the two other types described by Macdonald (1979). These are inflorescences with stamens formed proximally on the pistillate inflorescences (termed "mixed" inflorescences by Lloyd (1981)) and inflorescences with bisexual florets consisting of one or a few stamens inserted on the gynoeical wall or in the axil of the highest order bract associated with the gynoeicum.

Fruit

The gynoeicum of fayatree, with stamens connate to the ovary wall, matures into an unusual drupe with stamens persistent on the exocarp. Gardner (1985) reported fayatree fruits with stamens occurring singly or in small clusters on the surface of the fruit walls (Fig. 4). He observed that these stamens dehisce to release apparently normal pollen. However, Hjelmqvist (1948) and Lloyd (1981) reported non-functional androecia forming on pistillate florets of *M. gale* and *M. faya*, respectively.

Macdonald (1979), through developmental study of the gynoeicum of *M. californica*, demonstrated that the wall enclosing the ovule is composed of tissue developed not only from the growth of gynoeical primordia but also is composed of tissue from the inflorescence axis. Stamens may develop from either axis primordia or gynoeicum primordia. Stamens differentiated from these primordia develop connate to the ovary wall and mature with the fruit to cover the exocarp. The author did not report the functional condition of these stamens.

As alluded to above, numerous wax-secreting papillae cover the exocarp of the mature drupe of the genus *Myrica* (Macdonald 1980, Duke 1985). Papillae are vascularized extensions of the subepidermis and differ from trichomes which are non-vascularized extensions of the epidermis. Papillae differentiate from meristematic tissue of the inflorescence axis. Thus, as inflorescence primordial tissue forms a portion of the gynoeical wall, papillae develop on the ovary wall surface interspersed with the connate stamens, when present (Macdonald 1980).

The waxy substance secreted by papillae of fayatree and other species of *Myrica* of sections Faya

and Cerophora is composed of palmitine, myristicin, and palmitic acid (Duke 1985), compounds which impart an astringent taste to the fruit (Millspaugh 1974). In view of these observations, it is interesting that Macdonald (1980) suggested that the papillae are adaptations for fruit dispersal but did not explain the specific dispersal function of these structures. However, any astringent qualities of the fruit apparently do not deter feeding by birds and mammals in Hawai'i (LaRosa *et al.* 1985, Stone 1985, Woodward *et al.* 1990) or in Macaronesia (White 1993) and presumably elsewhere. The bright red or purple fruits apparently are adapted to animal and bird dispersal (Fig. 5).

Sexual Morphism

Gardner (1985) suggested that the subdioecious condition observed for fayatree, although not specifically studied, may be comparable to the subdioecious condition demonstrated by *M. gale* (Lloyd 1981). In this condition a strongly dioecious plant has a tendency to form bisexual or "mixed" inflorescences, (i.e., inflorescences comprised of both pistillate and staminate pseudanthia). Lloyd investigated the variability of sexual expression by *M. gale* growing in North Wales of the United Kingdom. Lloyd (1981) recorded the distribution of sex in 1,390 individuals of *M. gale* and concluded that mixed inflorescences and opposite sex inflorescences occur with such frequency that variability of sex should be considered a normal condition in sexual reproduction for the taxon. Lloyd suggested that environmental conditions could perhaps induce gender variation, but neither the mechanism for inducing sex variation nor the nature of the environmental influence was known. He did, however, observe a tendency for pistillate plants to be concentrated in wetter habitats. Although periodic sex reversal by species of *Myrica* has been reported (Abbe 1974, Hjelmqvist 1948), Lloyd (1981) concluded that sex reversal in *M. gale* occurs only infrequently. Gardner (1985) found no evidence of sex reversal for fayatree in Hawai'i.

Lloyd (1981) also reported a marked preponderance of staminate plants in *M. gale* (94.3% staminate versus 5.7% pistillate). He credited the disproportionate number of staminate plants over female plants to "staminate reproductive fitness," remarking that androecial reproductive success is limited by access of the pollen to the gynoeicum. In other words, the greater the amount of pollen

produced, the higher the probability an individual staminate plant has of passing its genetic information on to successive generations through the mechanism of fertilization.

Lloyd (1981) demonstrated statistically that phenotypic variation of gender is a reproductive strategy that maintains genotypic diversity. The development of staminate florets on a functionally pistillate plant produces no measurable genetic advantage (assuming that the ratio of female to male plants makes it highly likely that the pistillate plants will be fertilized, and thus that their basic genetic information will be preserved in future generations). But the production of pistillate florets on a functionally staminate plant greatly increases the probability that that plant's genes will be transmitted through its own descendants, and thus will contribute to maintaining the overall genetic homogeneity within a population of *M. gale*. Lloyd based his analysis on the assumption that much of the pollen produced within a population of *M. gale* will not be successful in pollination because the sex ratio is so markedly skewed. The production of florets of the opposite sex on either functionally pistillate or staminate plants does provide a significant advantage for *M. faya* and *M. gale* and other variable sex species to succeed in the establishment of populations in new locations, since one individual has the potential to self-fertilize, presuming the absence of self-incompatibility barriers.

DISTRIBUTION

Myricaceae

As described in greater detail under "Descriptive Biology," the family Myricaceae is usually interpreted to include the genera *Comptonia*, *Canacomyrica*, *Gale*, and *Myrica*, and 37-52 species, most of which are distributed in warm and subtropical regions of the globe (Mabberley 1989). The genus *Comptonia* consists of a single species, *C. peregrina*, a deciduous shrub native to open woodlands of southern Canada and the northeastern U. S. (Fernald 1970). The monotypic genus *Canacomyrica* is presently restricted to the island of New Caledonia in the southwest Pacific (Mabberley 1989), although it is represented by fossils in Eocene sediments in New Zealand, and became extinct there in the Miocene

(Mildenhall 1980). The variable and subcosmopolitan genus *Myrica* is native to east and southeast Asia, southern and tropical west Africa, the Macaronesian islands, and warm temperate and subtropical North, Central, and South America. As discussed under "Descriptive Biology," Abbe (1974), following Chevalier (1901) and Hjelmqvist (1948) divided *Myrica* into three sections corresponding with the geographical regions of distribution. Thus, the section *Morella* contains species from east and southeast Asia, section *Cerophora* contains species occurring in Central America and Africa, and section *Faya* includes species of warm temperate North America and the Macaronesian islands.

In his treatment of the prehistorical biogeography of the Myricaceae, Macdonald (1989) summarized as follows the two views concerning when the family first appeared in the fossil record. According to Muller (1981), *Triatriopollenites* sp., which appears to exhibit diagnostic myricaceous characteristics, was present in the Santonian of the eastern U. S. Muller considered the pollen record for *Myrica* continuous and within the geographic range presently occupied by the family. On the other hand, Chourey (1974) concluded from examination of North American megafossils and a review of the fossil pollen literature, that the family was probably not differentiated sufficiently to identify either myricaceous fossil pollen or megafossils before the Eocene-Oligocene. She considered a large number of megafossils from the Cretaceous through the early Tertiary to have been incorrectly identified as myricaceous. Chourey's (1974) analysis suggested that the family evolved much more recently than had been previously thought. In countering this argument, Muller (1981) postulated that the lack of megafossil evidence until the Oligocene might indicate that *Myrica* did not grow in areas favorable to preservation of plant parts.

Palynological studies in Africa and Central and South America point to a Miocene southward migration of the Myricaceae. *Myrica* was present in the southwestern Cape region of Africa in the Miocene (Coetzee and Praglowski 1984) and had also reached Mexico (Graham 1987). *Myrica* did not reach Colombia until the Pliocene, about 4 million years ago. Speciation of *Myrica* is pronounced in Africa, particularly South Africa (Killick 1969) and along the Andes in South America, much more so than in North America, Europe, and South-East Asia.

This may have been due to disjunctions caused by the long sequence of warming and cooling cycles associated with glaciation, the formation of high elevation, cool habitats, and increased importance of birds as means of dispersal during the Tertiary. Macdonald (1989) considered the evidence for late Tertiary radiation in Africa and South America to support the concept that the Myricaceae differentiated more recently than late Cretaceous.

Tiffney (1986) considered the earliest record of myricaceous fruit to be of *Comptonia otocostata* from the early Maastrichtian of Europe, although alternatively, late Cretaceous *Comptonia* fruit has also been placed into an extinct juglandaceous genus. Myricaceous leaves and fruits are reportedly abundant in European Miocene sediments, with similarities to *Myrica cerifera* and *M. pennsylvanica*, species now confined to eastern North America (Friis 1985).

Present-day distribution of south-east Asian species of *Myrica*, comprising section *Morella*, extends from Japan south through China, the Philippines, Malaysia, and west through Burma, Assam, Nepal, and Punjab (India). Section *Morella* is not found west of northwestern India. There is less differentiation of species among these taxa than among those in Africa and South America (Macdonald 1989). On the other hand, one species of this section, *M. esculenta*, has more varieties than does any other species in the family.

The site of origin of the Myricaceae remains controversial. Chourey (1974) rejected Abbe's (1963) suggestion that the family originated in south-east Asia, since *Myrica* would otherwise have had to originated in the early Cretaceous in order to have migrated to Europe, America, and northern Africa by the Eocene. Chourey (1974) reported that no fossil evidence existed for a south-eastern Asian origin. Macdonald (1977) postulated that the Myricaceae was of Boreotropical origin and probably occurred near the Tethys Sea in the Late Cretaceous. He later modified the suggested time frame to early Tertiary, rather than late Cretaceous as perhaps more reasonable (Macdonald 1989). According to Macdonald (1977), orogenic (i.e., mountain forming) activity and changing climates probably isolated the south-eastern Asia representatives from the remaining members. Similar climatic changes and orogenic activity in the Tertiary in Africa and America also led to the dispersal of the family into southern Africa and, in the Americas, southward into Central and

northern South America. The Myricaceae did not occur in northern South America until after the formation of a continuous land bridge with Central America at the end of the Pliocene. At least in the Tertiary, *Myrica* was not dispersed long distances over water by birds.

Coetzee and Praglowski (1984) suggested the Myricaceae to be of Laurasian (an ancient landmass) origin, but the presence of *Canacomyrica* in New Caledonia and formerly New Zealand (Mildenhall 1980) was considered problematic in determining the place of origin of the family. However, Raven and Axelrod (1984) suggested that the Myricaceae could have migrated relatively recently to Africa and South America, and that *Canacomyrica* may have no direct relationship to Myricaceae.

Myrica faya

Myrica faya, hereafter referred to as fayatree, is endemic to Macaronesia, in the north eastern Atlantic Ocean approximately between 37° to 16° north latitude and 32° to 14° east longitude (Takhtajan 1986). Macaronesia is comprised of four distinct volcanic island clusters: the Azores, Madeira, Canary Islands, and the Cape Verde Islands, and may also include the area of southern Morocco on the African mainland (Sunding 1979). Fayatree occurs in the three northernmost groups but is not found in the Cape Verde Islands. The more southerly Cape Verde Islands have a drier climate and a larger tropical floral element compared to the northern Macaronesian islands. Separated by more than 1,600 km (1,000 miles) of ocean, fayatree presumably either did not become dispersed to the Cape Verde Islands or was not able to survive in the more xeric habitat.

The native flora of Macaronesia consists of an estimated 3,200 species, 680 of which, approximately 21%, are endemic to the islands. The remaining species are also natural components of the flora of the Mediterranean region and the African continent. This flora represents the surviving relicts of a flora which developed and dispersed during the Eocene Era of the Tertiary Period, approximately 60 million years ago. During the Tertiary interglacial period, most of the present Mediterranean region was submersed under the ancient, extensive Tethys Sea. The subtropical vegetation which flourished along the shores of the Tethys Sea was dispersed via marine currents and by migration along the coastal fringes. Mountain ridges ranging from southeastern Africa

into Asia Minor and the Balkan Peninsula provided a land bridge over which this vegetation could disperse and greatly expand its range from that of the Tethys Sea coastal region (Takhtajan 1969, 1986; Sunding 1979).

The ancient Tethyan flora was subtropical, and is dominated by broad-leaved evergreens of the Lauraceae family. Characteristic genera included *Laurus*, *Persea*, *Cinnamomum*, and *Ocotea*. Plant remains identified as belonging to the Myricaceae have been found in fossilized Baltic amber dating to the late Eocene Epoch, indicating the Myricaceae family was also a component of this ancient flora (Takhtajan 1986).

Fayatree is a prominent subdominant component of the laurel forests (regionally referred to as the laurosilva) of Macaronesia. These forests flourish in regions of fairly high average annual precipitation, ranging from 1,000 to 1,500 mm or even as high as 2,500 mm, and are typical to elevations ranging from 500 to 1,200 m on the mountain slopes of the islands (Bramwell and Bramwell 1974, Hodges and Gardner 1985). The endemic species *Laurus azorica*, *Persea indica*, and *Ocotea foetens*, of the family Lauraceae, dominate the forest canopy. Important subdominants, in addition to fayatree, are the endemic *Apollonias barbusana* and *Erica arborea*, a species common throughout the Mediterranean area.

The laurosilva forest is thought to have originated during the late Tertiary period approximately 20 million years ago around what is now the Mediterranean Sea. As these forests became extinct during the Pleistocene glacial period, isolated remnants of unglaciated land along the west coast of Africa served as refugia for the plant species, including fayatree, that colonized the Macaronesian islands over the past 5 million years (Henríquez *et al.* 1986). Remnants of the African laurosilva forest, an area referred to as "Enclosed Macaronesia," still exist in southern Morocco, and contain a number of plants and animals also found throughout the Atlantic islands (Henríquez *et al.* 1986). While the original laurosilva forest is gone from southern Europe, a second species of *Myrica* that might be a remnant of this flora is *M. gale*, which is presently distributed between southern France and the Iberian Peninsula (Spain and Portugal) to the upper latitudes (i.e., British Isles, Canada) of Europe and North America. No phylogenetic studies have been conducted, but it is

possible that *M. gale* is the closest relative of fayatree.

Distribution in Macaronesia

The Azores

The Azores archipelago is the most north-westerly of the Macaronesian islands, between approximately 37° to 39° north latitude and 32° to 25° east longitude, and consists of nine major islands: Corvo, Flores, Graciosa, São Jorge, Terceira, Faial, Pico, São Miguel, and Santa Maria. The Azores are the most isolated of the Macaronesian islands, being located approximately 1,500 km (900 miles) from the nearest continent (Europe) and more than 700 km (420 miles) from Madeira, the nearest island group. The islands have no aboriginal human population and were uninhabited until 1439 when they were settled by the Portuguese, who continue to administer the islands as an autonomous region (Hodges and Gardner 1985). The presence of fossils in volcanic tuff confirms the early presence of fayatree in the Azores (Forjaz *et al.* 1970) and counters speculation (unpublished) that fayatree may not be native to these islands, but was introduced by the early Portuguese settlers.

Palhinha (1966) recorded fayatree throughout the Azores archipelago as a subdominant in the laurosilva ecosystem and also as a frequent element of the coastal vegetation. Although the native laurosilva forest, including fayatree, was described as abundantly distributed throughout the islands, recent visits to the Macaronesian islands have shown that centuries of human habitation have reduced the remaining stands of the original forests to a relatively low level. Hodges and Gardner (1985) reported that fayatree occupied a prominent position in the remaining laurel forest, however. Fayatree was observed growing from sea level on coastal bluffs up to 600 m elevation on mountain slopes. At higher elevations (usually above 600 m) the laurosilva forest typically changes to open grassland referred to as the Brezal zone (Henríquez *et al.* 1986). Detailed observations of fayatree distribution and habitat resulting from recent (since 1984) exploration are summarized as follows:

Pico: Of the four islands of the Azores visited by scientists from Hawai'i since 1984, the most extensive stands of remaining forests were found on the island of Pico (Fig. 6). The island is somewhat

unique in that its population appears to have declined over the past 20 years. Abandoned dwellings and vineyards are commonly observed. Fayatree is often one of the primary invaders of the abandoned farmland (Fig. 7). The abundance of fayatree in part may be attributed to its nitrogen fixing ability, which allows it to readily colonize low-nitrogen soils. The island has an active volcano and is largely composed of recent lava and cinder fields in which fayatree thrives. At lower elevations (below 150 m), the land has been heavily disturbed by agriculture and there is no sign of original laurosilva forests. From 150 to 600 m, there are scattered stands of laurosilva forests (Fig. 8), although these have been heavily degraded by grazing and colonization by alien species such as *Pittosporum undulatum*, or have been replaced by pine plantings. No stand was identified as being undisturbed laurosilva forest, and scattered patches of fayatree could be found between 150 and 600 m almost anywhere roads reached into the interior of the island except in pastures or as an understory in open pine plantations.

Faial: The island of Faial is not as rocky and has apparently richer soil than does Pico. Most of the island has been cleared for agriculture and fayatree was found rarely in representative stands of the original laurosilva forest. Older trees survived in abandoned or poorly maintained pastureland and along fence and hedgerows. Wind-pruned fayatree was also quite abundant in areas inaccessible to livestock such as steep slopes and sea cliffs. The west end of the island contains an active volcano which has recently (late 1950s) covered much of the area with thick volcanic ash. Fayatree has thrived in the ash substrate and has readily colonized older volcanic substrate. Most notably, fayatree was observed as a common primary colonizer of a'a lava flows (Fig. 9). The lichen *Stereocaulon vesuvianum* (or *S. azorica*) was among the few other floral component noted on these sites (Fig. 10). Fayatree was frequently found growing as an understory in open pine plantations (Fig. 11).

Terceira: The island of Terceira is thought to be typical of most of the remaining islands of the Azores. Except for small areas of rough terrain, which are unsuitable for cultivation, the entire lower elevation (below 600 m) has been converted to agricultural and pasture lands. At higher elevations, areas not under cultivation have been planted with introduced species of trees. Fayatree, over most of this island, was found along roadsides and

occasionally in abandoned vineyards, or on cliff faces or in steep gullies.

A large wooded peninsula, Monte Brazil, adjacent to the major town on the island, Angra do Heroismo, is an eroded remnant of a volcanic cone. Most of the peninsula has not been extensively disturbed and still contains a significant stand of laurosilva forest, including fayatree (Fig. 12), although even this has been degraded by introduced trees, shrubs and other weeds. Several of the fungi and insects collected by scientists from Hawai'i for biocontrol purposes were from Monte Brazil.

São Miguel: This is the largest island of the Azores, with the capital city, Ponta Delgada. Accordingly, its vegetation has experienced perhaps the highest degree of modification seen in the Azores. While scattered fayatrees could be found through the island below 600 m, usually on cliffs or in gullies, three areas where fayatree was relatively abundant were suitable as collection sites. 1) The lowest elevation and driest site was a steep cinder cone (probably less than 20 ha in area) on the extreme west end of the island, in an area referred to on the map as Mosteiros. The cinder cone contained a surprisingly intact stand of laurosilva forest. 2) Fayatree was found abundantly in a very large inactive crater on the west end of the island referred to as Caldeira das Sete Cidades. The bottom of the caldera is quite flat and contains several large, shallow lakes. Most of the area is highly modified for parks or homes, and contains extensive plantings of mature faya as an ornamental shade tree, particularly at the lake edges. No remnant of the laurosilva forest as found, however. 3) Fayatree was found at a higher elevation site in the central part of the island (Fig. 13). The stand lay approximately 6 km southeast of the nearest town, Ribeira Grande, at approximately 500 m elevation on the road to the Lombadas mineral spring. It was approximately 2 km beyond the hot spring resort of Caldeiras where the road leaves the farm lands and enters an area of planted pine forest. One of the pine stands had been cleared and a thick stand of shrubs, including laurel and fayatree, had colonized the 100-200 ha site. Although on the moister east end of the island in the vicinity of the mountain Pico Verde the laurosilva forest extends up to approximately 900 m, no evidence was found that fayatree was present above 600 m. The native forest in this area was rapidly being cut and replaced by plantings of alien pine.

Figure 9. Colonization of relatively recent lava flow by fayatree (dark vegetation) on the island of Faial, Azores

Figure 10. Young fayatree (arrow) growing on a recent a'a lava flow on the island of Faial, Azores

Figure 11. Young stand of fayatree as the understory in an open pine plantation on the island of Faial, Azores

Figure 12. Typical association of fayatree with native *Erica arborea* on the island of Terceira, Azores

Figure 13. Dense, mid-aged stand of fayatree at a higher elevation site in the central part of the island of São Miguel, Azores



Although *faytree* is known to occur on other islands of the Azores, these islands (Santa Maria, São Jorge, Graciosa, Flores, and Corvo) have not been visited by scientists from Hawai'i and specific information on the distribution of *faytree* is lacking. However, there is little reason to doubt that the same general patterns of colonization exist on these islands, with similar modifications in the native *laurosilva* forest resulting from human activities.

Madeira

The Madeiran archipelago, also an autonomous region of Portugal, is comprised of the islands of Madeira, Porto Santo, and the Desertas; the latter consisting of three small, rocky, uninhabited islands. The archipelago is located at 33°N latitude 700 km (420 miles) west of the coast of Morocco in northern Africa and slightly south of the latitude of the Strait of Gibraltar. The topography of Madeira, the main island, is very steep with cliffs and slopes up to 580 m above sea level. In the interior, these steep slopes are broken by deeply cut valleys. Notwithstanding the extreme topography, the island of Madeira supports a large human population. Extensive terracing of steep hillsides has enabled cultivation of otherwise unusable land for small garden plots, vineyards, or crops such as bananas, potatoes or cabbages. Vegetation above approximately 1,500 m is open, flat grassland (*brezales*) grazed heavily by sheep. The climate is moderate, annually averaging 19°C at sea level. Freezing temperatures are restricted to the highest elevations and are rare. Average annual precipitation ranges from 500 to 1,000 mm along the drier southern coast to 1,000 to 1,500 mm in all other locales (Hodges and Gardner 1985).

In an early account, Lowe (1868) described *faytree* as growing on the island of Madeira only in vineyards and chestnut forest planted between the elevations of 152 to 762 m. By 1868, however, most of the native laurel forest below 762 m had apparently been cleared, and *faytree* was found most typically at these elevations as an adventitious species. *Laurosilva* forest growing above 762 m was also noted. Lowe (1868) did not list *faytree* on the Deserta Islands nor on Porto Santo. On the island of Madeira, Hodges and Gardner (1985) found *faytree* growing quite abundantly, often on the sides of very

steep canyons and ravines, in undisturbed and successional native forests to about 900 m elevation. *Faytree* was also growing adventitiously along roadsides and in the understory of pine plantations, and occasionally as planted hedgerows on the northern, moister side of the island. In these locations, the tree was found as low as 100 m elevation and extended up to about 1,000 m. Despite extensive surveys, *faytree* was not found on the south and drier side of Madeira.

On Madeira, the driest location in which *faytree* has been found was a north-south ridge along the eastern end of the island. *Faytrees* were scattered over the east face of the ridge, but the area had been so heavily disturbed by terracing for farming or by plantings of pine forests that no remnants of the original *laurosilva* forest remained.

Two areas on Madeira on the north side of the eastern half of the island were found that were easily accessible and had relatively intact stands of *laurosilva* forest. The first was located due east of the small road junction of Portela. A dirt road proceeded due east from this junction at an elevation of approximately 600 m for 10 to 15 km before it turned south and dropped off the ridge. At the point where it left the ridge, the country had been extensively planted to pine forests, but these were mixed with patches of the original forest containing many large *faytrees* 6 to 10 m high. The second stand, and probably the most pristine remaining block of native forest on Madeira is located in the vicinity of Ribeiro Frio. The forest was on a large tract of land of probably several thousand hectares to the east of Ribeiro Frio, but on a very steep north-facing mountain side. Lower portions of the forest, accessible by a trail from Ribeiro Frio, provided some of the best area for collection of native insects on *faytree* during recent surveys (Markin 1991) and in an earlier survey by Krauss (1964). Other stands of *faytree* were found in isolated pockets on steep hillsides scattered along the north coast and along an east-west highway crossing the island between São Vicente on the north coast and Ribeiro Bravo on the south coast. In the vicinity of the pass (approximately 1,000 m elevation), *faytree* could be found scattered along the mountainsides on either side but was much more extensive on the north side of the island as the road descended to the coast.

- Figure 14. Large, mature fayatree of the island of Gomera of the Canary Islands
- Figure 15. Mixed stand of invading fayatree and native 'ohi'a in Hawai'i Volcanoes National Park
- Figure 16. Dense, mature fayatree stand in the Laupahoehoe area of the Hamakua Coast of the island of Hawai'i
- Figure 17. Young fayatree (arrow) growing in close association with *Buddleja asiatica*, both alien colonizers of new lava flows, in Hawai'i Volcanoes National Park
- Figure 18. Young fayatree growing in a recent cinder deposit in the understory of an 'ohi'a forest at Byron Ledge, Hawai'i Volcanoes National Park
- Figure 19. Rapidly developing fayatree growing into the overstory of an 'ohi'a forest at Byron Ledge, Hawai'i Volcanoes National Park



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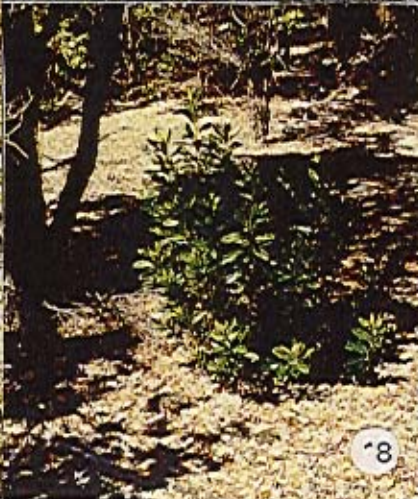
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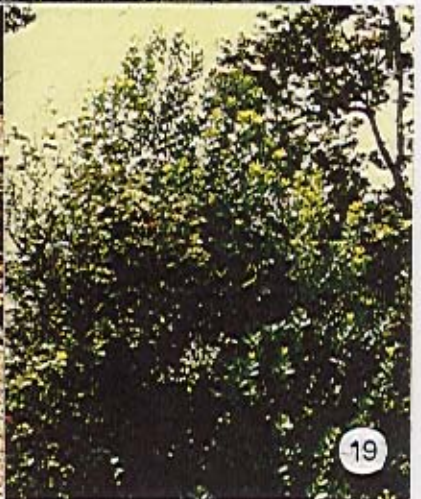
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Canary Islands

The third island group comprising the native habit of fayatree is the Canary Islands, which are located at 28°N latitude, and less than 100 km (60 miles) off the coast of southern Morocco in Africa. The Canary Islands are geographically the most extensive and diverse of the Macaronesian archipelagos. Like the Azores and Madeira, the Canaries are volcanic in origin and its older islands are highly eroded with very steep terrain. The archipelago consists of seven major islands: Tenerife, Gomera, Gran Canaria, Hierro, La Palma, Lanzarote, and Fuerteventura. The two easterly-most islands, Lanzarote and Fuerteventura, are more hilly than mountainous and have extensive areas of sand dunes (Bramwell and Bramwell 1974). These islands were originally colonized by Spain in the late fifteenth century and remain the dominion of Spain.

Generally, the climate of the Canary Islands is mild temperate with mean annual temperatures ranging between 18°C and 25°C, but reaching 35°C on Lanzarote and Fuerteventura (Hodges and Gardner 1985). Vegetation zones range from xerophytic scrub in the lowest and driest elevations to montane scrub above 1,900 m. Two forest zones lie between these extremes: a natural pine forest growing between 1,200 and 2,000 m and an evergreen forest zone (the laurosilva) growing between 400 and 1,300 m (Bramwell and Bramwell 1974, Ceballos and Ortano 1976, Henríquez *et al.* 1986).

In their flora of the Canary Islands, Bramwell and Bramwell (1974) recorded fayatree in a variety of habitats on all islands. They noted that this species was especially common in the native laurel forest and in disturbed forests on all islands excluding the most easterly islands of Lanzarote and Fuerteventura. In the laurel forest and disturbed forest ecosystems, fayatree often grows with *Erica arborea*, a tall evergreen shrub native to forests of the Mediterranean and Macaronesian region, in an association referred to as "Fayal/Brezal". Dominant species in the laurosilva ecosystem of the Canary Islands are *Laurus azorica*, *Persea indica*, *Appollonias barbusana*, and *Ocotea foetens*. Fayatree was reported as rare on the eastern, more xeric islands, presumably limited by lack of moisture or dispersal. The following islands of the Canaries were surveyed during recent exploration by biocontrol scientists from Hawai'i:

Gran Canaria: One of the larger and more central islands of the group is Gran Canaria, which contains the capital city of Los Palmas de Gran Canaria. Unfortunately, in two surveys of the island, only a few scattered fayatrees were found at approximately 1,000 m on the north side. No evidence was found that any of the original laurosilva or other native forest remained.

Tenerife: The largest and highest of the islands, Tenerife has not experienced the same degree of degradation as Gran Canaria. Scattered stands of laurosilva forest exist along the north side of the island, but most of it was not readily accessible. An exception was Valle de la Orotava south of the coastal community of Porta de la Cruz. Fayatree was found extensively in dense stands of *Erica arborea* and *E. scoparia*, but was associated with very little laurel. The higher elevations where the Fayal/Brezal zone would normally occur (Henríquez *et al.* 1986) was being managed for the native pine, *Pinus canariensis*. Shrubby fayatree was found scattered in the understory of these pine plantations from 1,000 to 1,500 m. Beside the road up from Porta de la Cruz, the easiest access to this pine zone was along the highway running up the central ridge from the community of La Lagoona at the east end of the island toward the center and highest point, the volcanic peak of El Tiede which reaches 3,707 m. Hodges and Gardner (1985) found large fayatrees commonly in the Anaga Mountains, which extend from the town of La Laguna to the extreme eastern tip of Tenerife. Another extensive laurel forest between the towns of Erjos and Carrizal Alto on the northwestern tip of the island also contained large, mature fayatrees.

Gomera: The small, almost circular island of Gomera, like most of the islands of the Canaries, contain dry, shrubland vegetation on the east and south parts. The northern portion of the island between the two communities of Hermigha and Vallehermoso is wetter and scattered fayatrees could be found along the edges of fields and pastures from as low as 200 m elevation up to 1,000 m (Fig. 14). There were no remnants of the laurosilva forest in this area, however. The north side of the central high point of the island, Garajonay, a national park with headquarters near the small community of La Palimta, contains the most pristine and extensive stand of native Fayal/Brezal forest, including

abundant fayatrees, found on perhaps any of the Macaronesian islands.

La Palma: A single visit was made to the island of La Palma by a scientist from Hawai'i as part of the biocontrol effort (B. Duffy, *pers. comm.*). Abundant, midsized (3-5 m tall) fayatree was found under pines along the road between the towns of Fuente de la Zarza and Barlovento. Fayatree was also very common along the interior road from Laguna de Barlovento to San Andrés y Sauces, El Charco to Monte de Luna, between Las Caletas to Las Indias, and on interior roads in the Cumbre Vieja Cumbre. Many large trees were found from Fuencaliente toward Santa Cruz. Abundant mature fayatrees, codominant with laurels, were also observed in the Los Tilos Natural Area Reserve.

Cape Verde Islands

The Cape Verde Islands are the southern-most Macaronesian archipelago, at 15°N latitude and located approximately 1,000 km (600 miles) south of the Canaries. Since a laurosilva forest possibly existed on these islands during colder periods of the Pleistocene (Henríquez *et al.* 1986), it is possible that remnant stands of vegetation may have survived on the highest peak, which on Cape Verde island reaches 2,500 m. However, persons at the National Institute for Agricultural Research in the Cape Verde Islands indicated that there has never been a record of fayatree occurring on these islands (M. L. Lobo, *pers. comm.*).

Distribution outside Macaronesia

Portuguese Mainland

Whereas fayatree occurs in mainland Portugal, its status there, as an endemic or introduced species, is disputed. The subject has been reviewed extensively by Queiros (1987). Some authors consider fayatree to be a naturalized species, having been introduced from Portuguese Macaronesia (Pereira 1939), but others recognize this tree as native to Portugal, specifically as a component of the coastal forests of the Serra de Sintra ridge of southern Portugal (Takhtajan 1986, Mabberley 1989). Fayatree frequently has been planted throughout the central and southern portions of Portugal and often escapes cultivation. Whether or not fayatree is native to the Portuguese mainland, human activities likely have been responsible for its present distribution throughout the central and southern regions of the country.

A collection of over 30 specimens of fayatree from mainland Portugal was examined by G. Markin at the Institute Superior de Agriculture herbarium at Lisbon in 1990. Five of the specimens originated near the coastal community of Sintra, located about 30 miles west of Lisbon. The majority, 10+, came from a band concentrated to either side of Figueira da Foz, a coastal community west of Coimbra. Five additional specimens were from the extreme southwestern point of the country in the mountains of Monchique in the Algarve. The remaining specimens appear to have come from scattered locations along the coast south of Lisbon. The following three main areas were visited by scientists from Hawai'i:

Sintra: Sintra is a small community in an isolated pocket of mountains between Lisbon and the Atlantic Ocean. It is a highly developed resort area and suburban community for Lisbon proper. The vegetation appears to be very highly modified. Despite the presence of specimens in herbarium collections from this area, no fayatree was found in a single-day survey.

Coimbra: A 150 km section of coastline west of the city of Coimbra, and stretching from the resort communities of São Pedro de Moel on the south to Palheiros de Mira on the north was visited and found to contain a long but exceedingly narrow band of fayatree. Inland from the coast, the first 5-10 km is mostly sand dunes covered by extensive stands of planted and intensively managed pine trees (the "Pinhal de Leiria"). On the western-most edge of this pine belt, fayatree could be found in a band usually no wider than 1 km, stretching from the edge of the open sand dunes into the pine trees. At no place was fayatree found to be more abundant than a few plants per square hectare, nor were mature trees found, only shrubs or small plants under 5 m high. Fayatree was obviously not a preferred plant in this area, and appeared more as an invasive weed than a native species acting as a pioneer. Numerous recently cut trees were found in this area, but the wood was left on the ground, suggesting that it was not used as firewood. These plants showed no evidence of extensive insect or pathogen attack. Botanists at the herbarium in Lisbon agreed that fayatree was probably not native to this area, but may have been introduced several centuries earlier for use in windbreaks for citrus groves further inland.

Monchique: The isolated pocket of mountains, reaching almost 1,000 m high, in the Algarve region

of the southwestern tip of Portugal contrasts with the relatively flat surrounding landscape. The mountains were formed by a major granitic intrusion and probably once contained a relict forest that may have included remnants of the laurosilva forest that retreated into the mountains as the climate warmed and dried following the last ice age. Herbarium specimens of fayatree had been collected in the mountainous region 30 to 50 years earlier. However, the mountain vegetation was found to be totally modified, the lower elevations had been planted to stands of cork oak and higher elevations planted in pine and eucalyptus. A single fayatree was located on a north slope after a search of several days. Whereas a more intensive search may reveal more plants; no evidence exists that any of the original forest that once covered these mountains still remains.

Morocco

Technicians at Garajonay National Park on the island of Gomera suggested that if stands of fayatree remained from the last ice age on the mainland, another possible place to search for them would be in the higher elevations of the Atlas Mountains of Morocco, an area referred to by Henríquez *et al.* (1986) as "Enclare Macaronésico." Stands of the original laurosilva forests may have existed in this area during periods of glaciation during the Pleistocene and may have migrated upwards into these mountains as the climate warmed and dried. Unfortunately, correspondence with persons who might be familiar with the region in question indicated that there were no records of fayatree in herbarium collections from these mountains, and that, even if any forest had existed at an earlier time, the impact of many centuries of grazing by cattle and goats has probably eliminated any fayatree that may have otherwise survived.

U. S. Mainland

Fayatree as a host of an algal leaf spot disease has been recorded in southern Florida (Ruehle 1936). However, this reference is questionable since no other records of this species on the U. S. mainland are known and recent attempts to confirm the presence of fayatree in Florida have been negative (L. Whiteaker, *pers. comm.*).

Hawai'i

Distribution of fayatree in Hawai'i Volcanoes National Park was mapped in the late 1970s (Clarke

1978), again in 1992 (Camrath and Tunison 1992), and throughout the islands, including Hawai'i Volcanoes National Park, in the mid-1980s (Whiteaker and Gardner 1985, 1992). Stands of this species were found on five of the eight major islands: Hawai'i, Maui, Lana'i, O'ahu, and Kaua'i. Principal concentrations of this tree were found in the Laupahoehoe area of the Hamakua Coast and the Kilauea Volcano summit areas on the island of Hawai'i, the Na Pali-Kona Forest Reserve and the Koke'e State Park areas of the island of Kaua'i, the Palikea area of the Waianae Mountains on the island of O'ahu, and the Kula area of the western slopes of Haleakala on the island of Maui. Presently, an estimated 34,830 hectares (86,000 acres) distributed across the five major Hawaiian Islands are infested with fayatree (Hawaiian Steering Committee on Firetree Control 1989).

Distribution of Other Species of *Myrica* From the Kew Index

The following is a list of species of *Myrica*, together with the years and locations in which they were reported, compiled from the Kew Index:

1735-1885

<i>M. adenophora</i> Hance	China
<i>M. aethiopica</i> L.	Southern Africa
<i>M. alaternoides</i> Crantz = <i>M. cordifolia</i>	
<i>M. altera</i> C. DC. in DC.	West Indies
<i>M. arabica</i> Willd. = <i>Myrsine bottensis</i>	
<i>M. arguta</i> H. B. & K.	Colombia, Venezuela, Ecuador
<i>M. asplenifolia</i> L.	North America
<i>M. australasica</i> F. Muell.	Australia
<i>M. banksiaefolia</i> Wendl. = <i>M. aethiopica</i>	
<i>M. bojeriana</i> Baker	Madagascar
<i>M. brabantica</i> S. F. Gray = <i>M. gale</i>	
<i>M. brevifolia</i> E. Mey. ex C. DC. in DC.	Southern Africa
<i>M. burmani</i> E. Mey.	Southern Africa
<i>M. californica</i> Cham. & Schlecht. in L. California	
<i>M. capensis</i> Hort. ex Steud. = <i>M. aethiopica</i>	
<i>M. caracasana</i> H. B. & K.	Venezuela
<i>M. carolinensis</i> Mill. = <i>M. cerifera</i>	
<i>M. cerifera</i> L.	North America
<i>M. comptonia</i> C. DC. in DC. = <i>M. asplenifolia</i>	
<i>M. conifera</i> Brum. f. = <i>M. aethiopica</i>	
<i>M. cordifolia</i> L.	Southern Africa

- M. domingana* C. DC. in DC. Dominican Republic
M. esculenta Buch.-Ham. ex D. Don = *M. nagi*
M. farquhariana Wall. = *M. nagi*
- M. faya* [Dryand. in] Ait. Canary Islands, Azores
- M. florida* Regel Habitat?
M. frondosa Salisb. = *M. faya*
M. fuscata Rafin. = (synonym uncertain) North America
- M. gale* L. northern temperate region
- M. hartwegi* S. Wats. California
M. heterophylla Rafin. = (synonym uncertain) North America
M. hirsuta Mill. = *M. quercifolia*
- M. humilis* Cham. & Schlecht. Southern Africa
- M. ilicifolia* Burm. Southern Africa
- M. inodora* Bartr. Florida
M. integrifolia Roxb. = *M. nagi*
- M. interrupta* Benth. Venezuela, Colombia, Ecuador
- M. javanica* Benth. Java
- M. kraussiana* Buching. Southern Africa
M. laciniata Willd. = *M. quercifolia*
- M. laureola* Tréc. ex C. DC. in DC. North America
- M. lindeniana* C. DC. Mexico
- M. linearis* C. DC. habitat uncertain
- M. lobbii* Teysm. & Binn. ex Miq. Java
- M. longifolia* Teysm. & Binn. ex C. DC. in DC. Java
- M. luzonica* Vidal Philippines
M. macrocarpa H. B. & K. = *M. arguta*
M. macrophylla Mirb. = *M. javanica*
- M. mexicana* Humb. & Bonpl. ex Willd. Mexico
- M. microcarpa* Benth. West Indies
M. missionis Wall. = *M. nagi*
M. montana Vahl = *Myrsine bottensis*
- M. nagi* Thunb. tropical & subtropical Asia
- M. natalensis* C. DC. in DC. Southern Africa
- M. obovata* Cham. ex C. DC. Florida
- M. octandra* Buch.-Ham. ex D. Don Nepal
- M. ovata* Wendl. f. in Bartl. & Wendl. f. Southern Africa
M. palustris Lam. = *M. gale*
- M. parvifolia* Benth. Venezuela, Colombia, Ecuador
- M. pavonis* C. DC. in DC. Peru
M. pennsylvanica Hort. Reg. ex Lam. = *M. cerifera*
- M. phillyreaefolia* Baker Madagascar
- M. polycarpa* H. B. & K. Venezuela, Colombia, Ecuador
M. polycarpa Mart. & Gal. = *M. xalapensis*
- M. pubescens* Willd. Venezuela, Colombia, Ecuador
M. punctata Griseb. = *M. cerifera*
M. pusilla Rafin. = (synonym uncertain) North America
- M. quercifolia* L. = (synonym uncertain) Southern Africa
- M. rotundifolia* Salisb. = *M. cordifolia*
- M. rubra* Sieb. & Zucc. = *M. nagi*
- M. salicifolia* Boj. ex Baker = *M. bojeriana*
- M. salicifolia* Hochst. ex A. Rich. Abyssinia (Ethiopia)
M. sapida Wall. = *M. nagi*
M. segregata Jacq. = *Forestiera porulosa*
M. serrata Lam. = *M. aethiopica*
M. sessilifolia Rafin. = (synonym uncertain) North America
- M. spathulata* Mirb. Madagascar
M. trifoliata Hort. ex Turp. = *Rhus aromatica*
M. trifoliata L. = *Toddalia lanceolata*
M. trifoliolata Hort. ex DC. = *Rhus aromatica*
M. undulata Rafin. = (synonym uncertain) North America
M. verrucosa Rafin. = (synonym uncertain) North America
- M. vidaliana* Rolfe Philippines
- M. xalapensis* H. B. & K. Mexico
M. xalapensis Peopp. ex Griseb. = *M. microcarpa*
- M. zeyheri* C. DC. in DC. Southern Africa
- 1886-1895**
- M. dentulata* Baill. Madagascar
- M. kilimandscharica* Engl. tropical Africa
- M. meyeri* Johannis Engl. tropical Africa
M. peregrina Kuntze = *M. asplenifolia*
- M. pilulifera* Rendle tropical Africa
- M. rorainae* Oliver Guyana
- M. rugulosa* Baill. Madagascar
- M. spathulata* Baill. Madagascar
- M. usambarensis* Engl. tropical Africa
- 1896-1900**
- M. pumila* Small North America
- 1901-1905**
- M. comorensis* Cheval. Comoro Islands
- M. curtissi* Cheval. North America
- M. dregeana* Cheval. Southern Africa
- M. elliptica* Cheval. Southern Africa
- M. funckii* Cheval. Venezuela
- M. glabrissima* Cheval. Southern Africa
- M. goetzei* Engl. tropical Africa

<i>M. incisa</i> Cheval.	Southern Africa	<i>M. mossii</i> Burt Davy	Transvaal
<i>M. myrtifolia</i> Cheval.	Southern Africa	<i>M. oligadenia</i> Peter in Fedde	Tanganyika Territory
<i>M. nana</i> Cheval.	China		
<i>M. pringlei</i> Greenm.	Mexico	1936-1940	
1906-1910		<i>M. microstachya</i> Krug. & Urb.	Jamaica
		(<i>M. mossii</i> and <i>M. nagi</i> were listed again for an unknown reason)	
<i>M. algarbiensis</i> Gandoger	Lusitania	1941-1950	
<i>M. kandtiana</i> Engl.	Southern Africa		
<i>M. mildbraedii</i> Engl.	Southern Africa		
<i>M. tomentosa</i> Aschers. & Graebn.	Europe, Alaska, Siberia	<i>M. diversifolia</i> Adamson	Southern Africa
		<i>M. holdridgeana</i> Lundell	Puerto Rico
		<i>M. madagascariensis</i> Leroy	Madagascar
1911-1915			
<i>M. cavaleriei</i> Léveillé in Fedde	China	1951-1955	
<i>M. darrisii</i> Léveillé	China		
<i>M. esquirolii</i> Léveillé	China	<i>M. rogersii</i> Burt Davy	Transvaal
<i>M. mairei</i> Léveillé	China		
<i>M. rapaneoidea</i> Léveillé	China	1956-1960	
<i>M. sequini</i> Léveillé in Fedde	China	<i>M. integrifolia</i> Roxb. in Wall.	Nepal
<i>M. shaferi</i> Urb. & Britton	Cuba	<i>M. jamaicensis</i> Howard & Proctor	Jamaica
1916-1920		1961-1965	no new species
<i>M. arborea</i> Hutchinson	Cameroons		
<i>M. auriculata</i> Ridley (= <i>M. esculenta</i> var. <i>ariculata</i> Gamble)	Nepal ?	1966-1970	
<i>M. caroliniana</i> Hort. ex Ettinghausen	North America	<i>M. integra</i> (A. Cheval.) Killick (= <i>M. conifera</i> var. <i>integra</i>)	
<i>M. costata</i> Rusby	Bolivia	<i>M. rotundata</i> Steyer. & Maguire	Venezuela
<i>M. holtzii</i> Engl. & Brehmer	Tanganyika Territory		
<i>M. rubra</i> A. Cheval. (same as <i>M. Nagi</i> from Asia (?))	Saigon	1971-1975	
1921-1925		<i>M. faya</i> Ait. f. <i>nanophylla</i> Kunkel (listed as <i>M. caya</i>)	Canary Islands
<i>M. cacuminis</i> Britton & Wilson	Cuba	<i>M. rothmalerana</i> Pinto da Silva	Portugal
1926-1930		1976-1980	no new species
<i>M. appiculata</i> Urb. & Ekman	Hispanola	1981-1985	
<i>M. phanerodonta</i> Standley	Costa Rica	<i>M. gale</i> subsp. <i>tomentosa</i> (C.DC.) E. Murray (= <i>M. gale</i> var. <i>tomentosa</i>)	
1931-1935		<i>M. rivas-martinezii</i> A. S. Guerra	Canary Islands
<i>M. humbertii</i> Staner & Lebrun	Congo		
<i>M. microbracteata</i> Weimarck	Rhodesia		

1986-1990

Only *M. nagi* C. P. Thunberg ex A. Murray from Japan was listed as a correction of an earlier entry (although the nature of the correction was not apparent)

Species of *Myrica* at Kew Gardens Herbarium

The following is a list of the species of *Myrica*, together with label annotations, at the herbarium of Kew Botanical Gardens, London, compiled by D. E. Gardner and G. P. Markin in September, 1993. The species are loosely grouped according to the region of the world in which they were collected, following the system of the Kew Herbarium:

M. adenophora -- China. "A drink can be made from the fruit."

M. gale -- listed from Japan. This seems questionable, but the specimens seemed typical of this species. Note that Hutchinson listed *M. gale* in *Flora of Tropical Africa*, but a later annotation stated that this species had not been collected in Africa. Specimens were also from eastern Canada; Labrador; New England states; Vancouver Island, British Columbia; Alaska; Sacramento River, California (the latter collected in the mid 1840s).

M. gale var. *subglabra* -- Prince Edward Island

M. tomentosa -- Russia

M. esculenta -- China and Nepal

M. rubra -- Tengyueh (?). Listed by Chevalier as a synonym of *M. nagi*, but the collection was made in 1911 after the publication of Chevalier's monograph.

M. salicifolia -- African Continent, Saudi Arabia, Somaliland, Abyssiani, Ethiopia, and Yemen. Some specimens covered with prominent galls, which appear to have been caused by mites.

M. salicifolia subsp. *mildbraedii* -- Kenya. Some specimens had prominently hairy stems but some did not, apparently this is a variable characteristic.

M. salicifolia subsp. *kilimandscharica* -- Some specimens with abnormal appearing broom-like growths.

M. salicifolia subsp. *meyeri-johannis* (older specimens under the name *M. meyeri-johannis*) -- No location was given for the latter two subspecies.

M. conifera -- Collected by N. L. H. Krauss (1962) at Furnas, São Miguel, Azores. The occurrence of this species in the Azores is questionable. The specimen is probably *M. faya*. The name *M. conifera* has been applied mostly to specimens from East and South Africa. Some specimens from The Cape region of South Africa previously named *M. conifera* have more recently been renamed *M. serrata*.

M. conifera var. *glabra*

M. conifera var. *tomentosa*

M. faya -- Collected by N. L. H. Krauss (1960) at Ribeiro Frio, Madeira.

M. nana -- China

*M. nepalensis**

M. sapida -- Sometimes listed as, or confused with, *M. rubra*, but Chevalier considered it a valid species.

M. videliana -- Formosa. Chevalier also listed this species from the Philippines.

M. farquhariana -- Singapore. Currently listed as a valid species, but it had been previously synonymized with *M. esculenta* or a variety of this species.

M. javanica

M. vidaliana -- The specimens had small leaves, fruit, and flowers, but otherwise typical of the genus.

Myrica sp. -- New Guinea. The leaves were small and rounded.

M. arborea -- Cameroons Mt., Victoria, Africa. This species was described by Hutchinson but not listed by Chevalier.

M. kantiana (some specimens listed as *M. kandtiana*) - Uganda (Nasaka), Africa. This species was listed by Hutchinson but not by Chevalier. Fruits were waxy white or grey.

M. pilulifera var. *goetzei* -- Tanzania. Listed by Polhill** (unpublished) as a valid species and variety.

M. pilulifera var. *puberula* -- Rhodesia

M. serrata -- labeled "East to South Africa." This is the new name used in many instances for specimens from the Cape Region of South Africa previously labeled *M. conifera*.

M. glabrissima -- East and South Africa. Some specimens from East Africa were synonymized with

M. serrata and *M. conifera*. A more recent annotation stated that *M. conifera* "seems to be patterned after the American species *M. cerifera* and therefore not valid." Specimens from South Africa had previously been named *M. africana* var. *integrifolia*.

M. brevifolia -- Portuguese East Africa. Of this species Chevalier stated "inflorescence not known," but the herbarium specimens had prominent inflorescences and fruit.

M. microbracteata

M. bojeriana -- Madagascar. This species was recognized by Chevalier and some specimens with this name were dated as recently as 1975, but on some specimens this name was synonymized with *M. salicifolia*.

M. denticulata var. *comorensis* -- Comoro Islands (near Africa). Originally recognized as two species.

M. phillyreaefolia -- central Madagascar

M. madagascariensis -- This name appears on recently collected (1984) specimens, but a later annotation questioned the use of the name and suggested *M. phillyreaefolia* instead.

M. rugulosa -- central Madagascar

M. spathulata -- central Madagascar. This is an old name but was used as recently as 1991.

M. cordifolia -- Cape Province, South Africa

M. bermannii -- Cape of Good Hope, South Africa

M. dregeana -- South Africa

M. elliptica -- Cape area, South Africa

M. krausiana -- Southwest Cape, South Africa

M. humilis -- South Africa

M. rogersii -- South Africa

M. quercifolia -- Cape Town area, South Africa

M. ovata -- South Africa

M. myrtifolia -- Cape of Good Hope, South Africa

M. aethiopica -- South Africa. Some specimens had been placed in synonymy with *M. salicifolia* and *M. krausiana*.

M. linearis -- Cape Town, South Africa

M. zeyheri -- South Africa

M. natalensis -- Natal, South Africa. Some specimens had been synonymized with *M. conifera*.

M. mossii -- South Africa

M. incisa -- South Africa

M. diversifolia -- Table Mt., South Africa. This species is not listed by Chevalier or Hutchinson.

M. inodora -- Florida, North America

M. obovata -- Florida

M. torreyana -- Florida. Has been considered a synonym of *M. inodora*.

M. cerifera -- Southeastern U. S., Bermuda, and Long Island, New York. A specimen was listed from Europe, but this specimen seems out of place and its identity is questionable.

M. cerifera var. *pusilla* -- Florida. Older specimens labeled *M. pusilla*

M. pensylvanica -- New York

M. asplenifolia -- Northeastern U. S. This name was used for older specimens, but now usually has been synonymized with *Comptonia asplenifolia*.

M. peregrina -- Northeastern U. S. Listed by Chevalier as a synonym of *Comptonia asplenifolia* (sweetfern).

M. carolinensis -- Eastern U. S. The name remained unchanged on some specimens, but was synonymized with *M. californica*, *M. pensylvanica*, and *M. cerifera* on other specimens. Chevalier also synonymized *M. carolinensis* with *M. punctata*. The name *M. heterophylla* also appeared on older specimens but had been placed in synonymy with some of the above names. Chevalier did not recognize *M. heterophylla*.

M. californica -- California. The species is also known from Washington and Oregon. *M. kalapensis* is a name appearing on older specimens of *M. californica*, and was listed by Chevalier as a synonym for *M. pubescens*.

M. hartwegi -- Mariposa County, California, A riparian species at 4,000 ft. altitude.

M. mexicana -- Mexico, El Salvador, Honduras. Sometimes synonymized with *M. cerifera* and *M. xalapensis*. Older specimens were originally named *M. xalapensis*, which was also sometimes synonymized with *M. parvifolia*.

M. pringlei -- Mexico. Chevalier placed this species in the genus *Comptonia*, but specimens were labeled *Myrica*.

M. pubescens -- Costa Rica, Colombia, Venezuela, Ecuador, Peru, Bolivia. This species was synonymized with *M. mexicana* on some specimens, but recognized as a valid species on others. Chevalier recognized it as a separate species. Older specimens of *M. pubescens* were sometimes originally named *M. caracasana*.

M. lindeniana -- Mexico. A tree 5 m high at 2,500 m. One specimen had been referred to as *M. cerifera*.

M. xalapensis -- Mexico, Guatemala. Although the name *M. xalapensis* was also used as a synonym for *M. mexicana* and *M. cerifera* for some specimens, the name had remained unchanged on other specimens, suggesting that the species is recognized as valid and annotated: "Trees 10-15 ft. tall, 6,000 ft. elevation." One specimen collected in swamps.

M. picardae -- Haiti, at 1,540 m. Listed by Chevalier as a valid species from the West Indies.

M. microcarpa -- Puerto Rico, Cuba, Jamaica. Species recognized by Chevalier. Riverbank habitat, 3,000 ft. elevation. Tree up to 25 ft. tall.

M. reticulata -- Santo Domingo. Species recognized by Chevalier. Occurring at 1,300 m elevation. Shrub 2-3 m, or tree 3-5 m tall.

M. cerifera -- Cuba, Dominican Republic, Haiti, Bahamas. *M. cerifera* was also recorded from eastern and southern North America.

M. punctata -- Cuba. Species recognized by Chevalier. One specimen had been renamed *M. cerifera*.

M. arguta -- Trinidad. Listed by Chevalier as a synonym of *M. pubescens*, but recognized on some specimens.

M. arguta var. *tinctoria* -- Colombia, Ecuador. Apparently an older name now usually synonymized with *M. pubescens*, but not by Chevalier.

M. shaferi -- Cuba. Specimen collected in 1910, but the name not used recently. The species was not recognized by Chevalier.

M. pubescens var. *glandulosa* -- Ecuador

M. parvifolia -- Colombia, Ecuador

M. parvifolia var. *obtusa* -- Colombia, Ecuador

M. interrupta -- Colombia. Shrub in cloud forest 4 m tall. The species was recognized by Chevalier as a variety of *M. pubescens*, but a specimen collected in 1988 was named *M. interrupta*.

M. pavonis -- Peru. The species was recognized by Chevalier.

M. macrocarpa -- Colombia. Apparently an older name, now often considered a synonym of *M. pubescens*.

M. arguta -- Ecuador, Bolivia, Peru, Colombia, Venezuela. Sometimes synonymized with *M. xalapensis*, but often retained as a valid name even on older specimens. The name was used as recently as 1961.

M. polycarpa -- Ecuador. An older name; Chevalier listed *polycarpa* as a variety for two different species.

M. pubescens var. *glabra* -- Argentina.

In addition to specimens of *Myrica*, specimens of *Canacomyrca monticola* from New Caledonia were also examined at Kew Herbarium.

Species of *Myrica* from Chile and Venezuela

In addition to specimens of *Myrica* at Kew Herbarium, Gardner and Markin observed *M. parrifolia* and *M. pubescens* in the field near Merida, Venezuela. Specimens of a third species, *M. fankii*, were observed in the university herbarium at Merida. Specimens of northern Chilean species, *M. pavonis*, were observed in the university herbarium at Concepción, Chile.

*Many specimens, those collected prior to 1900 in particular, had little or no descriptive information other than the name.

**Polhill, R. M. Flora of Tropical East Africa. Unpublished and undated manuscript available at Kew Herbarium.

(Myricaceae: "One to three genera, depending on delimitation, with about 40 species, widely distributed, but mostly in temperate regions and tropical highlands, relatively numerous in South Africa. I favour the narrower concept of genera.")

ECOLOGICAL RELATIONSHIPS

The success of fayatree as a general invader in Hawai'i has been attributed to two general factors: 1) biological and physical features of the environment; and, 2) biological attributes of the species itself. Analysis of the potential impacts of fayatree in the Hawaiian ecosystem must consider environmental factors which may enhance or reduce invasion, and characteristics of fayatree itself which promote or limit adaptation to the Hawaiian environment.

Environmental Factors

Environmental factors which can affect the invasive success of an alien species are climate, natural or human-induced disturbance, competition with native flora, nutrient availability, substrate characteristics, and the presence of phytophagous (plant feeding) insects and of other biotic control agents, such as pathogens (Arthington and Mitchell 1986, Barrett and Richardson 1986).

Compatible Climate

The Hawaiian Islands share many climatic and environmental similarities with the Macaronesian islands. These two archipelagos are in the northern hemisphere; share similar latitudes and daylength; soils of volcanic origin; oceanic and subtropical climate; orographically influenced precipitation; habitats are differentiated by wind patterns, elevation, and slope; and incident sunlight is quite uniform year-round (Whitten 1984). These comparable environmental factors may contribute to the successful adaptation of fayatree to a variety of habitats in the Hawaiian Islands. Fayatree grows in a variety of habitats in its native environment, such as on sea cliffs and rocky hillsides, new volcanic soils, among disturbed and undisturbed mesophytic forests and along roadsides and in pastures (Bramwell and Bramwell 1974, Hodges and Gardner 1985). Moisture may be an important limiting factor for distribution of fayatree. In its native habitat, fayatree has been noted to grow more abundantly in areas with moderate annual precipitation averaging 500 to 1,500 mm (Bramwell and Bramwell 1974, Hodges and Gardner 1985, Palhinha 1966). Fayatree is sparsely

distributed in xeric lowland habitats (less than 500 mm average annual precipitation) (Bramwell and Bramwell 1974). However, other factors besides precipitation and available soil moisture may limit fayatree growth in xeric habitats since this species is an abundant primary colonizer of volcanic soils (which are typically porous and do not retain moisture) (Hodges and Gardner 1985).

Considering biological factors, morphological analysis of leaves has demonstrated that fayatree possesses several characteristics adapted to xeric conditions (Lausi *et al.* 1989). Such xeromorphic adaptations include epidermal cells of reduced size (relative to those of mesomorphs) and of isodiametric shape, and a relatively low transpiration rate. In plants which lack these adaptations, water stress decreases cell turgor pressure which causes mechanical tensions between the retreating cell plasma and the rigid cell wall. This tension can lead to cell collapse and death. Reduction in the ratio of cell volume to surface area and equilateral distribution of pressure and tension against the cell diameter are factors thought to increase cell resistance to collapse under water stress (Lausi *et al.* 1989). Reduction in transpiration rate can decrease the amount of water loss through evaporation and may also be a factor which contributes to the adaptation of fayatree to relatively xeric conditions (i.e., annual rainfall of approximately 500 mm).

Fayatree also exhibits an upper elevation and/or precipitation tolerance level, as it rarely occurs above the high-moisture cloud zone in the Macaronesian islands. Depending on other orographic factors such as winds and temperature, this upper limit can range from 600 to 1,500 m. The characteristic plant community within this range is the laurel forest dominated by *Laurus azorica*, *Persea indica*, and *Ocotea foetens* (Bramwell and Bramwell 1974, Hodges and Gardner 1985).

Temperature may be the most significant limiting factor for the distribution of fayatree in its native environment. In the Azores, the most northerly of the Macaronesian islands, this species does not grow above 600 m, just 100 m above the frost zone. Precipitation at 600 m averages 1,870 mm annually. Further south, in Madeira, fayatree has been recorded as abundant in undisturbed and disturbed forests up to 900 m elevation where the average annual temperature is approximately 13.2°C (Hodges and

Gardner 1985). Precipitation averages for these islands were not available. At the southern-most extension of its natural range, in the Canary Islands, *fayatee* is a component of the *laurosilva* forest between 500 and 1,200 m elevation, but additionally, occupies a narrow belt above the forest between 1,200 and 1,500 m. The average yearly temperature of this humid-temperate climate ranges from 12 to 16°C. Precipitation ranges between 500 and 1,000 mm/year (Lausi *et al.* 1989).

In the Hawaiian Islands, *fayatee* displays a similar distribution pattern to that recorded for the Macaronesian islands. In general, *fayatee* readily colonizes old volcanic flows and habitats ranging at elevations between 150 (where it may have been planted and does not reproduce) and 1,310 m (Wagner *et al.* 1990) but it can possibly grow as high as 2,000 m (Markin 1992). Dominant native vegetation community types within these elevation ranges include lowland and montane mesic forests (Wagner *et al.* 1990). Whiteaker and Gardner (1992) reported that *fayatee* is adapted to a wide range of habitats. In Hawai'i Volcanoes National Park, for example, they noted that this species grows on 11 different soil types in 15 different vegetation zones ranging in elevation from 665 to 1,210 m with average annual precipitation ranging from 1,270 to over 2,540 mm and average annual temperature ranging from 15 to 22°C.

Whiteaker and Gardner (1987) previously noted that *fayatee* fruit production was lightest at the wettest and coldest of three study sites invaded by this species and suggested that *fayatee* may not be well-adapted to cold temperature and extremely wet habitats. The apparent low temperature and high precipitation limits for *fayatee* in its native habitat support this observation. Controlled experiments designed to investigate high and low moisture and temperature tolerance levels for *fayatee* could help identify habitats in the Hawaiian Islands which may have a lower invasion threat level by this highly invasive species.

Light Level: *Fayatee* has not been recorded readily invading Hawai'i's dense *Metrosideros polymorpha* ('ohi'a) forests, the closed canopies of which may create a barrier to such invasion (Walker and Vitousek 1991). Their investigation of available light level as a potential limiting factor for *fayatee* invasion of native Hawaiian ecosystems concluded that levels below the optimal 70%, which are typical

within the canopies of mesic and wet Hawaiian forests, may slow *fayatee* establishment by inhibiting germination and subsequent seedling growth. Forests with a closed canopy cover that reduces available light levels below 5% of full sun have not readily been invaded by *fayatee*, indicating that it is shade-intolerant (Walker and Vitousek 1991).

Disturbance: In general, invasive species are often successful where there has been a disturbance of the normal ecosystem (Arthington and Mitchell 1986). Natural or human-induced disturbance within the lowland and montane forest vegetation zones of Hawai'i provide opportunities for *fayatee* to invade (C. Smith 1985). Rapid invasion occurs in habitats disturbed by fire, human activity, feral pig activity, and volcanic eruptions (Gardner 1982, Walker and Vitousek 1991).

Such volcanic areas include Hualalai and Kilauea in Hawai'i Volcanoes National Park on the island of Hawai'i, where *fayatee* has established a competitive relationship with 'ohi'a (Fig. 15) (Wagner *et al.* 1990, Walker and Vitousek 1991). To date, there is no record of invasion of Haleakala Crater on Maui by *fayatee*, however. In areas of secondary succession, *fayatee* has most rapidly and successfully invaded abandoned agricultural lands and pasturelands, especially those of low- to mid-elevations (approximately 150 to 1,500 m) with high moisture levels. Along the Hamakua coast of windward Hawai'i island, within disturbed forest habitat, *fayatee* has formed dense, nearly monotypic stands of trees over 16 m tall (Fig. 16) (Smathers and Gardner 1979).

Competition from Native Flora: Arthington and Mitchell (1986) outlined a three-stage successional process in which an invaded ecosystem is altered by an invading species. The initial stage is invasion into the disturbed habitat. Since species diversity at this stage typically is low, the spread of the invasive species is not significantly inhibited by competition with native species. As species diversity increases and/or the complexity of the vegetation increases, native species interact with and increase competition with the invader species. As the ecosystem adjusts to the invader species, species population flux decreases and the dominant position of the invader species may be reduced.

This model may be examined in relation to ecological studies conducted by several investigators at the Kilauea Iki volcanic eruption area on the island

of Hawai'i (Mueller-Dombois and Whiteaker 1990, Smathers and Gardner 1981, Walker and Vitousek 1991). A 1959 eruption devastated a native forest ecosystem, ranging from montane rain forest in the upper elevations to lowland dry forest in the lower elevations. The eruption blanketed more than 500 m² of forest with a layer of pumice ranging in thickness from 1 to 12 m (Mueller-Dombois and Whiteaker 1991, Smathers and Gardner 1981).

The "snag habitat" site, investigated by Mueller-Dombois and Whiteaker (1990), is an area where the only remaining remnants of the montane rain forest were the upper trunks and crowns of 'ohi'a trees. Fayatree had succeeded in invading this site by exploiting microhabitats created by *Buddleja asiatica*, also an alien species, which, in turn, apparently was able to take advantage of factors such as the slightly higher moisture, shading, or favorable temperature habitat existing underneath the remaining 'ohi'a snags (Fig. 17). Dense clusters of fayatree seedlings recently have sprouted up around the initial invaders and may eventually create dense-canopied, nearly pure stands of fayatree (such as the dense, nearly monotypic stands at Hamakua) if there are no environmental factors to inhibit such growth (Mueller-Dombois and Whiteaker 1990).

Smathers and Gardner (1981) evaluated the competitive relationships between 'ohi'a and fayatree at their Habitat 5 site immediately below the "snag habitat" site. Prior to the eruption, this site was dominated by mesic forest. Fayatree is estimated to have initiated invasion of the area in 1971 (Smathers and Gardner 1981). Observation of fayatree stand vigor at this site indicated that initially, due to rapid germination and growth rate, fayatree threatened to out-compete 'ohi'a. Most fayatrees observed were growing underneath the canopy of established 'ohi'a trees, apparently in direct competition with young 'ohi'a (Fig. 18).

Smathers and Gardner (1979) found that fayatrees at shrub stage were quite aggressive and formed branches which interlocked with young 'ohi'a trees (Fig. 19). Fayatrees attaining tree status (basal diameter > 3 cm), however, displayed a loss of vigor in growth. The number of individuals in this size class was also reduced. 'Ohi'a trees were not observed to experience a loss of vigor as they matured and thus, this native species appeared to be recovering the competitive advantage over fayatree. Low moisture availability in the porous pumice soil

was the limiting factor postulated to inhibit continued fayatree vigor and dominance (Smathers and Gardner 1981).

Walker and Vitousek (1991) evaluated the competitive relationships between 'ohi'a and fayatree at Habitat 5 approximately 10 years after the study of Smathers and Gardner (1981). They concluded that the stands of fayatree were coalescing to form a dense canopy and were threatening to displace the native 'ohi'a. Fayatree at this site had a slightly reduced rate of growth than that found in previous studies, but was still able to grow faster than 'ohi'a. The authors postulated that in time the dense canopies of fayatree would lead to complete displacement of 'ohi'a (Walker and Vitousek 1991).

The invasion succession model postulated by Arthington and Mitchell (1986) does not conform to the pattern of invasion of fayatree into the native Hawaiian ecosystem. These authors suggested that an invader may remain dominant in an invaded ecosystem when it has a competitive advantage over native species. Potential competitive advantages of fayatree in the Hawaiian ecosystem are the absence of agents such as pathogens and phytophagous insects which may serve as limiting factors in the native habitat (Gardner and Davis 1982), the absence of other competing vegetation types, and the ability to fix atmospheric nitrogen, enabling rapid, vigorous growth (Vitousek and Walker 1989).

Nutrient Availability: All Hawaiian soils are of volcanic origin and thus are typically deficient in nitrogen and available phosphorus. Nutrients are rapidly leached due to their high porosity (Cline 1955). Fayatree has a symbiotic association with the nitrogen-fixing actinomycete *Frankia* sp. which enables it to colonize recently formed volcanic substrates better than most native species which are limited by nitrogen deficiencies (Vitousek *et al.* 1987, Vitousek and Walker 1989, Walker and Vitousek 1991). Relatively undisturbed moist montane forest ecosystems with closed canopies and abundant in available soil nitrogen (Cline 1955) may not be threatened with invasion by fayatree (Walker and Vitousek 1991). The high levels of soil nitrogen in these communities is due to the rapid breakdown of detritus in the moist, moderate climate (Cline 1955). Due to the apparent shade-intolerance of fayatree, nitrogen fixation appears to afford this species a competitive advantage only in areas with high light availability. The ability of fayatree to add nitrogen to

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hospitable habitats for other invading species (Aplet 1990, Vitousek and Walker 1989). This factor, coupled with its rapid spread onto old lava flows, has raised concerns that this noxious tree may be able to alter the sequence of primary succession in the Hawaiian Islands and may eventually even alter the species structure of climax forests.

Natural Enemies: Phytophagous insects and other arthropods, pathogens, and herbivorous mammals can alter the success of species establishment through their influence on the vigor of such potential invaders. Since there are no native members of the Myricaceae in the Hawaiian Islands, it is widely assumed that natural enemies specific for fayatree are also absent in this new environment. Surveys conducted in the Azores, Madeira, and Canary Islands for potential biological control agents for fayatree have identified several phytophagous insects and pathogens associated with this species which may contribute to some degree in limiting its aggressiveness in these native habitats (Bianchi 1955, Gardner *et al.* 1988, Hodges and Gardner 1985, Krauss 1964, Markin 1992). No significant native herbivorous vertebrates from these islands have been described. Conversely, it is generally assumed that absence of such control factors may promote the success of this aggressive alien species in the Hawaiian ecosystem, although the degree to which this may be true has not been quantified.

Species Attributes

Plant factors which can contribute to invasive success are mode of reproduction, reproductive capacity, means of dispersal, rate of vegetative growth, tolerance to environmental stress, and, additionally specialized ecophysiological processes such as nitrogen-fixation and allelopathy (Arthington and Mitchell 1986, Barrett and Richardson 1986).

Mode of Reproduction

Fayatree is normally a dioecious plant, but viable stamens sometimes form on pistillate plants, and conversely, viable ovules can develop on staminate plants (Gardner 1985, Lloyd 1981). Thus, this primarily out-breeding species can undergo temporary reversal to self-compatibility by producing functional pistillate or staminate organs on a typically unisexual plant (this form of reproductive plasticity is sometimes referred to as subdioecy (Lloyd 1981). The condition of subdioecy in the genus *Myrica* and

in fayatree specifically, is described in more detail under Descriptive Biology.

This reproductive plasticity is an indication that fayatree individuals contain a high degree of genetic variability, an advantage in a colonizing population of one or a few individuals (Barrett and Richardson 1986). The potential for self-pollination can increase the likelihood of reproductive success during the establishment of new invasive colonies by one or a few individuals since this phenotypic plasticity confers on the plant the ability to produce offspring when compatible mates are lacking or difficult to find (Barrett and Richardson 1986). Comparison of the genetic attributes of fayatree with those of other successful invasive species may help to enhance understanding of the adaptive advantages of invasive species.

An essentially male fayatree has the capacity to produce more than 4,000 fruits/year, compared to more than 37,000 fruits/year for a female tree (Whiteaker and Gardner 1987). At an observed 4% rate of field germination of fayatree seeds observed under open canopy 'ohi'a forest with no leaf litter, a male tree conceivably could produce approximately 160 seedlings annually. An estimated 88 of these seedlings can be expected to survive at the observed seedling survival rate of 55.5% measured 64 weeks after germination (Vitousek and Walker 1989). Clearly, a single male fayatree has the potential to establish a new population.

Reproductive Capacity and Means of Dispersal

One characteristic of an invading species is the ability to increase populations rapidly (Wester 1992). High seed production is one factor which can contribute to the invasive success of an alien species (Groves 1986). The rapid spread of fayatree in the Hawaiian Islands can be attributed, in part, to a high reproductive capacity and to effective short- and long-distance dispersal mechanisms (Smathers and Gardner 1979, Walker 1990, Whiteaker and Gardner 1987). Fayatree has been observed to begin fruiting at an early stage of development (trees with 2 to 3 cm basal diameter and a mean age of 6 years) and to increase fruit production at an incremental rate directly related to the maturity of the tree (Smathers and Gardner 1979, Vitousek and Walker 1989). In Hawai'i Volcanoes National Park the total area invaded by fayatree increased 20-fold over an 8-year

invaded by fayatree increased 20-fold over an 8-year period from 1978 to 1986 an increase attributed to copious seed production and effective dispersal (Whiteaker and Gardner 1992).

Phenological data gathered for fayatree at three sites on the island of Hawai'i indicate that fruit production and maturation occurs year-round with maximum fruit maturation in the month of November and minimum in the month of May (Whiteaker and Gardner 1987). Although peak maturation occurs in November, maturation levels remain high throughout the 5-month period from July through November.

The rate of spread of an invasive plant is also affected by the pattern of its spread. Plants which spread as scattered colonies rather than as an advancing front of an established colony tend to have a faster rate of spread (Auld and Tisdell 1986). Fayatree has established scattered colonies in a diversity of Hawaiian habitats. Fruits not dispersed by animal vectors fall to the soil near the parent tree. Surviving seedlings radiating from these centers of establishment increase the density and expand the invasive front of the existing population (Vitousek and Walker 1989).

Both alien and native frugivorous birds and feral pigs are thought to be responsible for long-distance dispersal (Wagner *et al.* 1985). These fauna consume the fleshy fruits and frequently pass the seeds in viable condition through their droppings in locations often far-removed from the site of consumption (Cuddihy and Stone 1990). Germination experiments on seeds passed by net-captured Japanese white-eyes demonstrated that fayatree seeds remain viable following passage through the gut (Woodward *et al.* 1990). This evidence supports earlier suggestions that there is a correlation between the foraging habits of Japanese white-eye and the invasion pattern of fayatree (Smathers and Gardner 1979).

Birds considered capable of dispersing fayatree include the alien Japanese white-eye (*Zosterops japonica*), house finch (*Carpodacus mexicanus*), North American cardinal (*Cardinalis cardinalis*), common myna (*Acridotheres tristis*), and Nepal kalij (*Lophura leucomelana*); and the native 'oma'o (*Myadestes obscurus*), 'amakihi (*Hemignathus*

virens), 'apapane (*Himatione sanguinea*), and the nene goose (*Branta sandvicensis*) (LaRosa *et al.* 1985, Mueller-Dombois and Whiteaker 1990, Smathers and Gardner 1979, Woodward *et al.* 1990). The 'oma'o and the Japanese white-eye are thought to be the most significant of these due to their frequent foraging visits to trees and to the high number of fruits eaten per visit (LaRosa *et al.* 1985, Woodward *et al.* 1990). Observations of Japanese white-eye behavior in particular (Woodward *et al.* 1990) indicate that these birds often perch in 'ohi'a trees, where they frequently forage on seeds and nectar. The feeding of Japanese white-eye on fayatree fruits, followed by visits to stands of 'ohi'a on recent lava flows or to open-canopy stands of 'ohi'a forest, could be a significant means of transport of fayatree seeds to these native Hawaiian habitats (Fig. 20). Invasion of fayatree has been observed to be most prevalent in sites with both an open canopy and potential perch trees (Vitousek 1990).

The larger gallinaceous birds (such as the nene goose and the Nepal kalij) are thought to be significant dispersal agents. Feral pigs (*Sus scrofa*) are also thought to be effective in short-distance dispersal through the scattering effect of non-ingested seed by their foraging activities (Stone 1985). Other feral alien ungulates which may utilize fayatree fruits as a food source are deer (*Avis avis*) and goats (*Capra hircus*) (LaRosa *et al.* 1985, Mueller-Dombois and Loope 1990, Stone 1985). Alien rats, both the black rat (*Rattus rattus*) and the Polynesian rat (*R. exulans*), may also contribute to dispersal since they have been noted to compete with native birds for fruit food sources (Stone 1985). Black rats are arboreal and are known to consume fruits from small branches of several different native and introduced tree species (Cuddihy and Stone 1990). They may spread fayatree seeds via their scat (LaRosa *et al.* 1985).

Alien herbivores, especially pigs, further aid in establishment of fayatree by creating conditions favorable for fayatree establishment through habitat disturbance. In turn, fayatree enhances alien faunal populations by providing a dependable food source (Stone 1985). Thus, there is a mutually beneficial interaction between the two groups of alien invaders--floral and faunal--into the Hawaiian environment.

Figure 20. Typical growth of a young fayatree at the base of an 'ohi'a tree on an open, recent lava flow in Hawai'i Volcanoes National Park

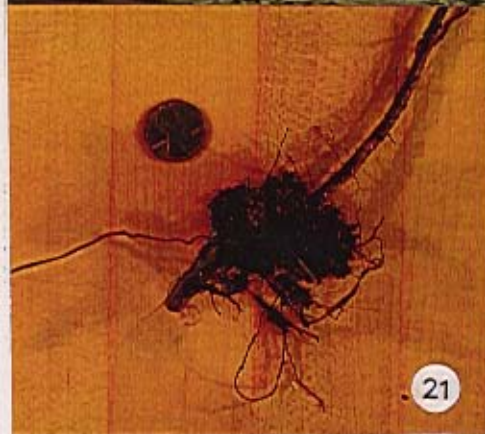
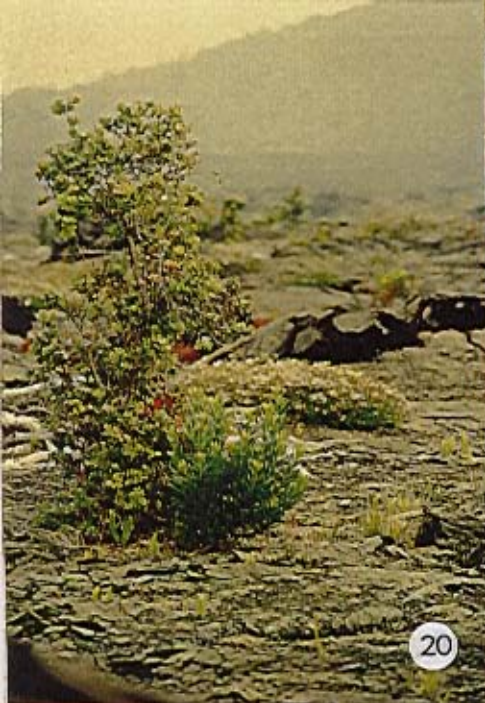
Figure 21. Root nodules of fayatree from Hawai'i Volcanoes National Park

Figure 22. Demonstration of herbicidal treatment of a young fayatree by clear-cutting the tree and spraying the stump with an herbicide such as Tordon RTU

Figure 23. Immature fayatree fruit infested with the larvae of *Carposina atlanticella* on the island of Madeira.

Figure 24. Hollowed fayatree shoot, possibly by a *Carposina atlanticella* larva on Madeira

Figure 25. Fayatree leaf rolling moth *Caloptilia schinella* from the island of Faial, Azores



Rate of Vegetative Growth

Fayatee can grow more than 15 times faster than the growth rate for 'ohi'a in open canopy sites (Vitousek and Walker 1989). This rapid growth rate in large part is due to the ability of fayatee to fix atmospheric nitrogen as discussed above. Mean diameter growth rates for adult individuals in open canopy sites on the island of Hawai'i were 1.5 cm/year, whereas those for 'ohi'a were 0.09 cm/year. No noticeable seasonal diameter growth rate was detected for fayatee (Vitousek and Walker 1989). Observations of the phenological cycle for fayatee indicate that flowering and fruiting occur in seasonal peaks, yet these functions are never completely absent during an annual growth cycle. Leaf flush has been observed to peak during the month of June, but in general, this phenophase also has a rather consistent annual cycle (Whiteaker and Gardner 1992). Steady and rapid growth may combine to give fayatee a competitive advantage over more slowly growing native trees such as 'ohi'a.

Growth rate of fayatee is apparently related to tree size. Trees greater than 5 cm in basal diameter at Habitat 5 of the Devastation Area in Hawai'i Volcanoes National Park showed a marked decline in growth rate and vigor than did younger, smaller trees (Smathers and Gardner 1979). It has been suggested that these decreases may be a function of water stress. As a tree increases in size, there is less soil water available per unit of biomass (Smathers and Gardner 1981). Notwithstanding the decline in growth rate with age, the tree still is able to over-top and out-compete 'ohi'a in open canopy habitats (Walker and Vitousek 1991).

Tolerance to Environmental Stress

Both in its native habitat and in the Hawaiian Islands, fayatee characteristically is an adaptable species able to grow in a variety of habitats and adjust to an array of environmental conditions. It can tolerate a range of moisture regimes and, apparently, is restricted only by the most extreme high and low levels of average annual precipitation. Fayatee can grow and reproduce in a wide range of temperature regimes and is adaptable to several soil types. Tolerance limits for these and other environmental factors have not been quantified for fayatee, although freezing temperatures appear to be a limiting factor in its native environment (Hodges and Gardner 1985).

Nitrogen Fixation

As alluded to above, one of the most significant and prevalent limiting factors for plants adapted to the Hawaiian environment is the low quantity of available nitrogen in the soil (Cline 1955, Hodges and Gardner 1985, Vitousek *et al.* 1987). Symbiotic association with nitrogen-fixing actinorrhizae imparts to fayatee the significant ability to induce and sustain a rapid level of vegetative growth. This constitutes a competitive advantage which is readily apparent in primary successional ecosystems where fayatee successfully out-competes and attains dominance over 'ohi'a, the native primary colonizer of new volcanic soils. The mechanism of nitrogen fixation by fayatee and related species of *Myrica* has been investigated by several researchers (Miguel and Rodriguez-Barrueco 1974, Mian *et al.* 1976, Torrey 1978, Benson and Eveleigh 1979, Callaham *et al.* 1979, Torrey and Callaham 1979, An *et al.* 1985, Schwintzer 1988, Berliner and Torrey 1989, Monz and Schwintzer 1989).

Nitrogen fixation is the conversion of nitrogen gas or atmospheric nitrogen into nitrate, a form of nitrogen which can be metabolized into amino acids and proteins by terrestrial plants. The microsymbionts, in turn, use organic compounds supplied by the plant as an energy source (Raven *et al.* 1986); thus, the two organisms exist in a mutually beneficial, or mutualistic relationship. Fayatee forms a symbiotic relationship with the actinomycete *Frankia* (Procaryota: Actinomycetes: Frankiaceae). Actinomycetes are soil prokaryotic microorganisms in some respects similar to true bacteria, but which morphologically resemble fungi in that they are filamentous, branched, and septate. The hyphal filaments of actinomycetes are finer than are those for most fungi, ranging from 0.5 to 1.0 μm in diameter (Benson and Eveleigh 1979, Raven *et al.* 1987, Torrey 1978). The ability to fix nitrogen allows fayatee and its relatives to thrive in the nitrogen-poor soils typical of recent volcanic flows (volcanic ash), old lava flows, abandoned fields, and roadsides. Conversely, the relatively slow growth of many native species has been attributed in part to nitrogen limitation (Vitousek 1990, Vitousek *et al.* 1983).

No native Hawaiian primary colonizers of volcanic soils are known to have established a symbiotic relationship with a nitrogen-fixing actinomycete. Leguminous trees such as *Acacia koa* and *Sophora chrysophylla* fix nitrogen in symbiotic association

with *Rhizobium* spp. (a genus of true bacteria), but these trees are components of the more intermediate stages of the successional process of Hawai'i's forests (Vitousek 1990).

Although it is not known when or how the symbiont *Frankia* became established in Hawai'i (Vitousek and Walker 1989), this actinomycete may have been already present when fayatree was introduced at the turn of the century, since other non-native woody species which also form a symbiotic relationship with *Frankia*, such as *Casuarina* and *Rubus*, had been introduced before fayatree (Wester 1992).

The fixation of atmospheric nitrogen by vascular plants, such as fayatree, through symbiotic association with soil actinomycetes, has comparable ecological importance to the legume-*Rhizobium* symbiosis as a mechanism for introducing nitrogen into soils (Torrey 1978). Whereas *Rhizobium* is specific to members of the Leguminosae, *Frankia* can form symbiotic relationships with species from several diverse plant families. Beside the Myricaceae, these include the Betulaceae, Casuarinaceae, Coriariaceae, Eleagnaceae, Rhamnaceae, and Rosaceae. Twenty-three genera within these families are reported to develop nitrogen-fixing nodules in association with *Frankia* (Bloom *et al.* 1989).

The ability of fayatree to fix nitrogen was first described by Miguel and Rodriguez-Barrueco (1974) followed by Mian and his associates (1976) who studied the influence of nodulation by *Frankia* on growth rate of fayatree seedlings. Miguel and Rodriguez-Barrueco found that biomass dry weight of six-month old nodulated seedlings was 15-fold greater than that of non-nodulated seedlings.

Cross-inoculation trials have shown that fayatree seedlings develop viable nitrogen-fixing nodules when inoculated with *Frankia* endophyte strains from other species of *Myrica*, notably *M. cerifera*, *M. cordifolia*, and *M. pilulifera* (Mian *et al.* 1976). Inoculation with endophyte from *M. gale* nodules was an exception. Nodulation was induced but nitrogen-fixation was negligible compared with that produced by other *Myrica* endophyte strains. The authors found that not all *Frankia* strains were host-specific and that nodule formation does not necessarily indicate effective nitrogen fixation (Mian *et al.* 1976).

Callaham and his colleagues (1979) described the process of root hair infection and actinomycete-induced nodulation of *M. gale* and *M. cerifera*. The average number of endophytic infections associated with a single nodule is not clearly known although, apparently, only a single infection of a root hair by a *Frankia* strain is necessary for nodule initiation. The initial process of interaction between the host cell and *Frankia* is similar for all species examined in the genera *Myrica*, *Comptonia*, *Alnus*, and *Casuarina*.

The early stages of nodule development in *M. gale* also have been discussed by Torrey and Callaham (1979). The root-like primordium develops endogenously which, as it divides, forms a nodule lobe with vertically upward growing nodule roots. *Myrica* root nodule development is characterized by upward determinate growth of the nodule roots. For example, nodule roots in *M. gale* cease growth at 3-4 cm. The root nodule matures into a highly branched lateral structure with negatively geotropic roots (Benson and Eveleigh 1979, Bond 1952). This negative geotropic pattern is also recorded for *Casuarina* and *Comptonia* (Callaham *et al.* 1979).

Root nodule ultrastructural anatomy for *M. pennsylvanica* was investigated by Benson and Eveleigh (1979). Penetration of a root cell by the *Frankia* hyphae stimulates changes in the host cell substructure. The nucleus enlarges, mitochondria proliferate and hypertrophy, Golgi bodies become more numerous, the amount of starch grains decreases, and vacuolation and associated tannin deposits increase. Once the endophyte has penetrated the host cell, the hyphae form branches which grow radially toward the periphery of the cell lumen. Maturation of the endophyte is accompanied by the formation of vesicles, swollen regions at the hyphal branch tips. This terminal swelling is not separated from the hyphal filament by a cross wall (Benson and Eveleigh 1979). The vesicles may be the site of nitrogenase activity, the enzyme system which catalyses the series of nitrogen fixation reactions. Nitrogenase is synthesized within the cortical layer of the host plant root (Torrey 1978).

The invading hyphae are surrounded by a fibrillar encapsulating material that separates the endophyte from the host cell cytoplasm. The encapsulating material, composed at least in part of pectin, may be consistent in composition with that of the host cell wall (Benson and Eveleigh 1979) or may be formed

by the endophyte itself as a protective barrier (Torrey 1978).

The proliferation of mitochondria and the formation of an encapsulating barrier around the endophyte within the host cell may indicate that the relationship between the endophyte and the host cell is parasitic (Callahan *et al.* 1979). The host plant, as a whole, benefits from the nitrogen gained by association with *Frankia*. Thus, on the organismic level the host plant-actinomycete relationship is symbiotic, but at the cellular-hyphal level, the relationship may be antagonistic. Bloom *et al.* (1989), in evaluating the diversity of *Frankia* strains that infect *M. pensylvanica*, determined that a variety of strains can infect the same host plant.

Nodulation in fayatree is probably similar to that of other species of *Myrica*, but this has not been specifically investigated. Roots of all fayatree individuals examined by Turner and Vitousek (1987) in Hawai'i Volcanoes National Park had *Frankia*-induced root nodules (Fig. 21). These included roots of seedlings less than 2 cm tall and fayatrees growing epiphytically on the trunks of the native tree fern *Cibotium chamissoi*. Nodule clusters examined ranged in size from less than 0.5 x 0.5 cm up to 15 x 8 cm but most clusters varied in the range of less than 0.5 x 0.5 cm to 3 x 3 cm.

Nodule biomass in fayatree was found to vary with age and size of the plant and the amount of canopy cover under which the plant was growing. It tended to be greatest for open canopy sites and decreased in partially shaded and closed canopy sites, respectively. Nodule biomass tended to reach a maximum in trees with approximately 40 cm² basal area. Tree growth beyond this size was not generally accompanied by an increase in nodule biomass (Turner and Vitousek 1987). Fayatrees growing in open canopy sites may produce more nodules due to a higher availability of solar energy for nitrogen-fixation, a greater need for nitrogen by the plant due to a faster growth rate, or because there is less soil nitrogen available since open canopy sites tend to benefit less from leaf and other organic litter as nitrogen sources (Turner and Vitousek 1987). Nitrogen released into the soil from decaying organic detritus increases soil nitrogen levels and may decrease the amount of nitrogen fixation needed by fayatree for growth.

Potential nitrogen-fixing activity is quantified indirectly by measuring the reduction of acetylene to ethylene through the nitrogenase enzyme system

(Turner and Vitousek 1987). Turner and Vitousek (1987) postulated that if nitrogen fixation for root nodules averaged 1 $\mu\text{m N}_2/\text{g/hr.}$, a single tree growing in a partially shaded habitat could produce approximately 14 g $\text{N}_2/\text{yr.}$ Thus, the 1,100 fayatrees trees/hectare recorded at the Devastation Area in Hawai'i Volcanoes National Park could produce 15 kg $\text{N}_2/\text{ha/yr.}$, a substantial amendment to the available soil nitrogen normally present in volcanic ash soils of Hawai'i. Native sources of nitrogen addition to soil (including rainfall, lichens with blue-green algal symbionts such as *Stereocaulon vulcani*, *Nostoc* in bryophyte mats, and algal and bacterial wood and leaf decomposers) average less than 4 kg/ha/yr. Nitrogen fixed by fayatree represents a nearly 4-fold increase in soil nitrogen over that naturally occurring in Hawaiian habitats.

The potential of fayatree to alter primary succession is indicated by results of Vitousek (1990) and Vitousek *et al.* (1983 and 1987) in which artificial addition of nitrogen to 26 and 195 year-old open canopy forest sites doubled the growth of 'ohi'a, whereas fertilization of an approximately 1,000 to 2,000 year-old site (with a much higher level of accumulated nitrogen) had no significant impact on plant growth. Whereas the long-term effects of nitrogen fixation by fayatree has not been determined experimentally, Vitousek *et al.* (1990) have postulated wide-reaching alterations of entire ecosystems.

Earthworms prefer nutrient rich organic litter for food (Nakamura 1990). Aplet (1990) compared earthworm community biomass in a fayatree-dominated community with that in a nearby submontane 'ohi'a forest in Hawai'i Volcanoes National Park. Earthworm biomass levels under fayatree stands were 2- to 8-fold higher than those under 'ohi'a. Nitrogen content of fayatree leaves was nearly three times higher than those of 'ohi'a (Vitousek and Walker 1989). Thus, there may be a direct relationship between earthworm biomass and nutrient content of organic soil detritus. Since earthworms decompose organic litter, an increase in earthworm population can, in turn, increase the rate at which nitrogen from leaf and other organic litter is recycled into the soil and made available for root system uptake. The activity of earthworms in increasing the availability of soil nitrogen may produce a positive effect on vegetation growth (Aplet 1990), but Howarth and Medeiros (1989) considered such alteration deleterious to native systems which are adapted to low nitrogen levels.

Allelopathy

Allelopathy is the production and release of metabolic substances that inhibit germination and retard growth of competitive plants (Mueller-Dombois and Ellenberg 1974). Allelopathy has the potential to decrease plant community species diversity. The absence of other species under dense fayatree canopy, and the fact that allelopathy has been reported for the related species *Myrica cerifera* (Dunevitz and Ewel 1981), has prompted the suggestion that fayatree itself may also have allelopathic characteristics (C. Smith 1985, Whiteaker and Gardner 1992). However, field and greenhouse experiments have not provided conclusive evidence for allelopathy in fayatree. Leachates of both fayatree and 'ohi'a leaf litter reduced fayatree germination (Walker 1990), but no significant differences were found between 'ohi'a germination with water and germination with leachate from fayatree leaf litter (Walker and Vitousek 1991). Whereas removal of fayatree leaf litter stimulated the germination of 'ohi'a seedlings under fayatree canopy (Walker and Vitousek 1991), physical factors such as shading from leaf litter or dense canopy cover probably account for this.

Summary

Periodic volcanic activity in the Hawaiian Islands produces sterile ash soils upon which primary succession occurs, i.e., the formation of a community on a substrate which has not previously supported vegetation (Mueller-Dombois and Ellenberg 1974). Secondary succession occurs in partially disturbed habitats such as pasturelands and timbered forests. Scientists are concerned that fayatree may alter the primary succession sequence and the species composition of secondary succession and ultimately, this species may affect the distribution of native Hawaiian plants--perhaps even contributing to the extinction of some of the more rare and vulnerable species (Wagner *et al.* 1990, Walker and Vitousek 1991, Vitousek *et al.* 1987, Vitousek and Walker 1989). These potential long-term ecological effects of invasion by fayatree on the native Hawaiian ecosystem are the major cause for concern by resource managers.

ETHNOBOTANICAL USES OF FAYATREE

With the prominence of fayatree as an undesirable forest and rangeland weed in Hawai'i, the question is often raised as to the reason this species was introduced to Hawai'i. Other species of *Myrica* (e.g., *M. cerifera*, *M. gale*) have been used for purposes such as soap and candle-making (Elias 1971) or for folk medicine (Moerman 1986). Fayatree was probably introduced between 1876 and 1886 when families of Portuguese settlers from the Azores and Madeira immigrated to Hawai'i as farmers or plantation workers (McDermott *et al.* 1980). While fayatree may have arrived accidentally as seed contaminating implements or clothing the immigrants brought with them, more likely it was deliberately introduced as a familiar plant from the homeland. Actual uses of the plant which could explain its introduction are not readily apparent. In Hawai'i, the only attempt at the beneficial use of fayatree was between 1926 and 1927 when it was tested for its value in reforestation for erosion control. The practice of planting alien species for reforestation was discontinued in the 1940s (Skolmen, unpublished report; Little and Skolmen 1989). No beneficial uses for fayatree are listed in the limited ethnobotanical information available in Hawai'i, and in discussions with some of the oldest Portuguese residents on the island of Hawai'i, none was found who recognized it as a useful plant (G. M., *personal communication with Francis Pacheco*).

Travel to the native habitats of fayatree in search of potential biocontrol agents has created the opportunity to discuss with people in these areas any of the recognized uses or beneficial features which may account for the introduction of fayatree to Hawai'i. In the Azores, particularly on the less developed islands of Pico, Terceira, and Faial, the search for this information was relatively easy since many of the older people there spoke English, having earlier immigrated to the U. S. or the European mainland to seek employment and then returned to the islands to retire. Almost everyone interviewed on these islands immediately recognized fayatree, referring to it by its common name of "faia" or "faia-

de-terra" and knew that it was a common native plant in the islands. On Madeira, habitat disturbance has greatly reduced forested land so that very few residents recognized the plant. The few people who were familiar with fayatree there (where its common name is also faia), knew of no potential uses. The following information therefore was obtained only in the Azores:

Windbreaks

In the Azores, a common use of fayatree is as windbreaks. The dense evergreen foliage and rapid rate of growth make it ideal for this purpose and many small and several rather extensive (up to 0.5 km long) windbreaks were found on the islands of Terceira and Faial (Hodges and Gardner 1985). Most of these were being actively pruned and maintained. Two botanists at the Agricultural College for Portugal in Lisbon, in discussing the history of fayatree in mainland Portugal, mentioned that it was probably introduced a century or more ago from Macaronesian islands as an ornamental, or more likely, that it had been brought in for windbreaks around citrus groves.

Ornamental

Being non-deciduous, and with its variable color (dark green older leaves and lighter green new leaves) and persistent, dense foliage, young fayatrees are attractive as shrubs and frequently have been seen as ornamentals in private yards, parks, and public buildings such as airports. Mature trees observed were generally quite knarled and had more sparse, open foliage. The most abundant stand of these "urban" trees is found in a park on the island of São Miguel in the bottom of the inactive crater "Caldeira da Sete Caidadea".

Grazing and Browsing

Most of the Azores are intensively grazed, utilizing a rotation system with small paddocks enclosed with stone walls. Judging from the observation that fayatree was never found growing inside these paddocks except for a few very old, large trees with branches above the reach of cattle, one might suspect that fayatree is heavily browsed by cattle. Farmers also collected branches of fayatree and placed them into corrals or pastures in the vicinity of the animals, intended as a fodder. Two farmers mentioned that

fayatree foliage was good cattle feed, when it could be obtained, and that their cattle preferred it to grass. These observations are of particular interest in view of the experience in Hawai'i, in which grazing by cattle or goats is not regarded as an effective control measure due to the lack of preference of these animals for this plant (Smith and Lutzow-Felling 1993). Subsequent discussion with farmers on Pico disclosed that the cattle are fed wilted young branches of fayatree. Pollarded trees were observed in one or two areas that serve this use.

Mulch

Observations were made where windbreaks or hedges of fayatree had been trimmed and the branches apparently deliberately scattered on the ground in orchards as a mulch. Unfortunately, no one was present who spoke English who could confirm this as a common practice, or who could explain whether the leaves, which are assumed to be rich in nitrogen, were known to be good for the soil.

Fruit as Animal or Human Food

Approximately half of the people interviewed in the Azores who know something about fayatree mentioned that the fruit was edible. None, however, said that it was used for food, with the exception of one farmer who said that his free-ranging chickens readily fed on the fruit when it was ripe and fell to the ground. Several mothers said that small children would pick the ripe fruit and chew it, but that this practice was discouraged, not because the fruit was thought to be poisonous, but that it made stains that were difficult to wash out of the children's clothes. An occasional account heard in Hawai'i (see Yamayoshi 1954) was that local Portuguese people used fayatree fruit as preserves. This use was not mentioned or confirmed by any of the people interviewed during four visits to the Azores.

Wine

Another often reported account in Hawai'i is that in the Azores the fruit of fayatree is used for making wine. This story apparently also dates back to early references in the Department of Agriculture files (Anonymous 1962) which is the earliest record of this use that could be found, and is still often repeated (Little and Skolmen 1989). In the Azores, all of the people interviewed said that it was never used for wine, explaining that the berries were much too small

to pick and had too little juice. However, several older persons mentioned that it had been used for brandy, and one man was encountered who said that years ago he personally had used fayatree berries as a flavoring for brandy. He would pick ripe berries and soak them in wine for several weeks for their flavor, then distilled it to form brandy. He said that it had been many years since he had last made brandy in this way since none of the older people drink it anymore and the younger generation did not care for the flavor.

Firewood

By far the most common use mentioned for this plant among rural people was that it was an excellent source of firewood, and that in the past it had been used very extensively for this purpose. Fayatree was easy to cut, it burned hot and clean, and regenerated quickly from cut stumps so that it could be continually harvested on a rotation basis. On the islands of Pico and Faial, during visits in the late 1980s and early 1990s, an occasional truckload of what appeared to be fayatree logs was seen coming out of the hills. When asked where the truckloads of firewood were going, those who spoke English replied that the rich people in town liked it for their fireplaces. In general, the use of firewood in rural areas of the Azores for heating and cooking has almost entirely disappeared, having been replaced by propane. An extensive system for distributing and collecting five gallon propane tanks was observed.

Wood

In the Azores, no one familiar with fayatree, including several foresters spoken with, recognized it as having any usable properties as a source of lumber, timber, or other structural wood. According to those explaining the use of fayatree for fence posts, this wood was used more because of its availability than for any particular desirable qualities that it had for this purpose. Fayatree has been observed in the Azores to grow to a full-sized tree, up to 20 m tall with a relatively straight trunk, giving the appearance that lumber could be hewed or sawed from it. However, the few foresters who were asked about it (mostly on the island of Faial) said that they had never heard of its being preferred and knew of no reason why anyone would want to plant or harvest

it as a timber crop. Surprisingly, the Azores appeared to be largely self-sufficient in structural wood. The older homes were made of rock, and more recently of cinder block or concrete, with limited amounts of wood used for rafters and paneling. Wood currently used for these purposes appears to come primarily from extensive plantations of introduced trees such as Japanese cedar (*Cryptomeria japonica*). The prominent ecologist/naturalist Dr. Duarte Furtado, of the University of the Azores, was exceedingly critical of these plantations because most of them were on land from which many of the last remaining stands of the native laurosilva forest were being cleared.

Grapevine Stakes

Whereas the wood of fayatree was not recognized as having any particularly desirable feature in the Azores, in the Canary Islands a technician at the National Park of Garajonay on the island of Gomera explained that in the past, fayatree was the preferred wood for making posts for trellises in vineyards, a use also mentioned by Henriquez *et al.* (1986). A tree, when cut, would promptly recoppice and the new shoots would grow rapidly enough that in 5 to 10 years a new crop of stakes could be taken from the same stump. This technician was one of the few people in the Canaries who could not only recognize fayatree, but also knew anything of its natural history or possible uses. However, he knew of no other uses for this plant in the Canary Islands.

Other Uses

On the occasions when older people were found with whom communication was possible, and who were familiar with fayatree, they were questioned on any known uses for fayatree in folk medicine, magic, songs, or in some other way as part of their folklore. None remembered any such use, although several mentioned that in religious festivals the branches of fayatree were often used for decorations around, or sunshades over, stands or stages. People being interviewed said that this was an early custom but did not know if fayatree was used merely because it was one of the more easily obtained plants, or whether it had any qualities making it especially useful for this purpose.

CONTROL EFFORTS

The need to implement control efforts to prevent the potential widespread invasion of *fayatee* throughout the Hawaiian Islands was recognized as early as 1937 (Fosberg 1937). Specifically, ranchers were beginning to recognize the potential for *fayatee* to rapidly cover livestock rangeland with a dense brush; their economic concerns prompted the then Territory of Hawai'i to become active in the control of *fayatee*. Territorial efforts to control this species were officially instituted by the Board of Commissioners of Agriculture and Forestry in 1945 (Hosaka 1945).

Despite these early control efforts, this aggressive alien has expanded its range throughout Hawai'i at an alarming rate. In 1954, *fayatee* occurred on approximately 3,443 hectares (8,500 acres) (Yamayoshi 1954); by 1985 this area had increased ten-fold to an estimated 34,794 hectares (85,976 acres) (Whiteaker and Gardner 1985).

Fayatee control programs have focused on limiting spread rather than eradication, due mainly to economic and labor restrictions. Mechanical, chemical, and biological control have been used in both native Hawaiian ecosystems and agricultural lands. This section reviews the effectiveness of various control methods. Recommendations for application for each of these techniques, and for further study, are given.

Browsing and Grazing

The effectiveness of *fayatee* control by intensive grazing or browsing by pasture and rangeland livestock was also considered, as was use of goats in National Park areas (*unpublished*). However, in such trials *fayatee* did not appear to be a preferred fodder for livestock, and only the young shoots were selected. After small trees grew to the extent that most new growth was beyond the animals' reach, browsing pressure became negligible. Goats maintained in pens with *fayatee* as the most available food nevertheless avoided *fayatee* and attempted to escape before it was fed upon. These results appear to contrast with the observation described in "Ethnobotanical Uses" that *fayatee* may have been used to some extent for livestock feed in its native habitats. In any case, use of goats or other livestock

for weed control in natural areas such as national parks is impractical as it is inconsistent with management policies for these areas.

Mechanical Control

Mechanical methods of control involve physical removal by cutting the plant at or near its base, digging, or pulling younger plants up. Uprooting by hand is particularly effective in cinder substrates in which young plants have not become firmly established. Plants of considerable size can be removed in this manner under these conditions. Larger trees may be uprooted with a bulldozer where terrain permits, and where damage to other vegetation is not a factor. These techniques were implemented by the Board of Commissioners of Agriculture and Forestry in 1945 when the control of *fayatee* was initiated. At that time, mechanical techniques were the most effective control methods known. The commission recommended that the entire plant be removed with as much associated underground growth as possible. Additionally, disposal by burning was recommended to avoid regeneration (Hosaka 1945).

Although mechanical control methods are effective where judiciously applied, they are labor-intensive and difficult to apply to areas of wide-spread invasion. Additionally, trees growing in areas of rugged terrain, can be difficult or impossible to reach. The care necessary to avoid damage to other vegetation in sensitive areas, such as national parks, negates the use of bulldozers and similar large equipment in these areas.

Nine years after the control program was implemented, the commission reported that *fayatee* was continuing to spread in the Hamakua District of the island of Hawai'i (where it was originally introduced) and was establishing a new population in the Volcano area (Yamayoshi 1954). Mechanical methods were not containing the spread of this invasive species; however, by this time, chemical methods of control were showing some signs of success.

Chemical Control

Several contact and systemic herbicides have been tested for their efficacy in limiting growth and/or killing *fayatee*. Herbicide use was first tried by private landowners as an alternative to mechanical

control (Yamayoshi 1954). Ranchers on the island of Hawai'i treated fayatree with sodium chlorate, 2,4-D, and 2,4,5-T diluted in either water or diesel fuel. These chemicals reportedly produced "good results," and were especially beneficial in steep terrain such as gullies (Yamayoshi 1954), although no records of actual rates of control are known to exist.

A 1967 survey on the island of Hawai'i conducted by the State Department of Agriculture (DOA) showed more than 16,200 hectares (40,000 acres) of forest and rangeland invaded by fayatree (Walters and Null 1970). This invasion of state-owned, agriculturally-zoned land prompted the state to fund fayatree control as a "special project" under the jurisdiction of the DOA (Kim 1969). The same year the survey was conducted, the DOA began testing the efficacy of Tordon 212 and Tordon 22K (formulations of picloram, Dow Chemical Co.)* against fayatree. These herbicides had been previously used in conjunction with mechanical control methods to reduce invasive populations of fayatree and to prevent its further spread (Kim 1969, Walters and Null 1970). Preliminary tests indicated that both herbicides were effective in controlling fayatree. The Department of Agriculture undertook field trials of Tordon 212 while the U. S. Forest Service Institute of Pacific Islands Forestry began field testing of Tordon 22K.

Tordon 212 was mixed with 2,4,5-T amine in a 1:5 ratio and was undiluted for application. The mixture was applied to notches cut around the circumference of the trunks from ground level to 30.5 cm (12 inches) above the ground. Trunks greater than 7.6 cm (3 inches) in diameter had one notch cut for each 7.6 cm of diameter. A hand-held spray gun was used to apply 1 ml of herbicide directly into each of the notches (also called frills). The DOA obtained a successful 95% kill rate of trees treated with the Tordon 212 and 2,4,5-T amine herbicide mixture (*unpublished*). Treated plants showed signs of foliar browning within a month of application and that complete death was evident 3 months after application. Numbers or percentages of trees killed with a single herbicidal application were not reported separately from those requiring more than a single application, resulting in some ambiguity concerning treatment effectiveness, however. Furthermore, the time interval between herbicidal applications was not reported, nor were any experimental control procedures. Between 1967 and 1970 the state began systematically applying these herbicides to fayatree at

the advancing edge of its range, with further efforts, intended to be planned after the initial 3-year project, directed at interior infestations (Kim 1969). Further reference to any such future planning, and if, in fact, this was carried out, is unknown.

Concurrent with Department of Agriculture field trials of Tordon 212 on state lands, U. S. Forest Service Institute of Pacific Islands Forestry began field experimentation with Tordon 22K at the Hamakua Forest Reserve on the island of Hawai'i where fayatree had successfully established a dense population. A 0.8 hectare (2 acre) site with an average of 263 fayatree stems per hectare (650 stems per acre) was selected for herbicide testing. Trees were notched with the same notching technique used by the DOA but herbicide was applied using hand-held oilers rather than spray guns. Undiluted herbicide was applied directly to the cut stems by squeezing the oiler (Walters and Null 1970). Again, no control procedure was described in the field trial report.

As with Tordon 212, foliar browning was observed within 1 month of treatment with Tordon 22K. Ten per cent of the canopy foliage on treated trees was affected within 1 month and 80% of the basal sprouts were defoliated. Within 2.5 months, approximately 77% of the stems were completely defoliated. The Forest Service reported complete canopy kill and 99% control of sprouting from green stems one year after herbicidal application (Walters and Null 1970). Two years following application, 2% resprouting and an average of 4 seedlings per hectare (1.6 seedlings per acre) were recorded (Walters 1970). Based on these results, Tordon 22K was considered effective in controlling fayatree.

Encouraged by the success with Tordon 22K, the USFS-IPIF also conducted field trials with Tordon 212 with the intent to refine application techniques. Although a variety of application techniques and concentrations of the chemical was applied to fayatree stems, Tordon 212 was not found to be effective for the control of this species (Walters 1973). This conclusion was based on an observed average death and dying rate of only 58% of stems treated with undiluted Tordon 212. Treatments of herbicide diluted with water resulted in lowered effectiveness. These results appeared to conflict with the 95% rate of kill with Tordon 212 obtained by the Department of Agriculture. Application methods used by the two agencies were similar. Significantly, the DOA

workers mixed Tordon 212 with 2,4,5-T amine, which may enhance the efficiency of Tordon 212, whereas the Forest Service researchers applied the herbicide without additives. The Forest Service report gives no reference to the results of the Department of Agriculture field trials and Forest Service researchers may have been unaware of them.

The National Park Service began actively investigating mechanical and chemical methods of control for fayatree invasion in Hawai'i Volcanoes National Park in 1973 (Hawai'i Steering Committee on Firetree Control 1989). Hawai'i Volcanoes National Park resource managers found a 4% mixture of Kuron (silvex, Dow Chemical Co.)* in diesel oil applied using hand-held spray guns to be an effective treatment (Gardner 1978, Gardner and Kageler 1982). This method was later abandoned in favor of other chemical treatments, due to the difficulty of working with diesel as a solvent as compared with water, the relatively large quantities of mixture required to kill a tree, the fire hazards of diesel, and the potential to accidentally spray neighboring native vegetation with the mixture. The systemic herbicides Tordon 22K, Kuron, and Roundup (glyphosate, Monsanto Co.)* were tested as possible alternatives to foliar or stem sprays (Gardner and Kageler 1982). Herbicide was applied through a section of rubber latex surgical tubing fitted over a clipped branch of fayatree using squeeze bottles to fill the tube sections with herbicide. This method eliminated contamination of surrounding vegetation caused by conventional spraying techniques and also minimized the amount of chemical delivered to the plant (thus reducing expenditure on chemical) (Gardner and Kageler 1982). Both Roundup and Tordon 22K were effective in killing or severely damaging fayatrees, but Roundup was preferred from a standpoint of practical application since its rapid absorption rate permitted prompt reuse of tube sections to treat other trees (Gardner and Kageler 1982). Furthermore, Tordon 22K was reportedly capable of leaching into surrounding soil through the roots of treated plants, presenting a threat to native vegetation, whereas Roundup was reportedly quickly deactivated in soil (Cuddihy *et al.* 1991). Notwithstanding the advantages of application of chemical through latex tubing for treating individual trees, this technique proved to be labor-intensive and economically inefficient for use on a large scale.

Attempts at large-scale fayatree control were abandoned by the National Park Service in fiscal year 1979-1980 because of inadequate funding. The

impracticality of wide-scale use of herbicides plus the banning from use of the most effective chemicals due to negative environmental impacts led several agencies to band together to evaluate other strategies. Consequently, the National Park Service, The U. S. Forest Service Institute of Pacific Islands Forestry, The Hawai'i Department of Agriculture, the Hawai'i Department of Land and Natural Resources, and the University of Hawai'i agreed to coordinate their weed control activities in an Interagency Steering Committee on Forest Pests. The committee has focused its attention on biological control. In 1988 a diverse local group of ranchers, conservationists, foresters and householders petitioned the state government under the U. S. Department of Agriculture's Resource and Conservation Development to promote an aggressive research program for the control of fayatree (Hawai'i Steering Committee on Firetree Control 1989). This action was taken in conjunction with the recognition by resources managers at Hawai'i Volcanoes National Park that the more than 12,000 hectares (29,652 acres) of invaded park lands could not be adequately managed with available labor and monetary resources. While effective, widespread control measures were under development, resource managers have concentrated control efforts for fayatree and other problematic invasive plants in areas of Hawai'i Volcanoes National Park considered to represent the most ecologically valuable habitats. The selection of these areas, designated special ecological areas (SEAs), was based on factors such as species diversity, concentration of rare species, community intactness, and manageability (Cuddihy *et al.* 1991, Tunison *et al.* 1986, Tunison 1992b, Tunison and Stone 1992). By 1991, approximately 5,460 hectares (13,490 acres) of Hawai'i Volcanoes land were actively managed under the SEA program using a combination of mechanical and chemical control methods (Tunison and Stone 1992). Small fayatree plants were uprooted, while larger plants were severed at the base and the cut stump treated with herbicide (Fig. 22) (Hawai'i Steering Committee on Firetree Control 1989). The application of the Tordon 22K and Tordon RTU (a commercial mixture of picloram and 2,4-D) significantly reduced populations of fayatree in the SEAs (Tunison and Stone 1992).

National Park Service researchers tested the efficacy of five other herbicides for fayatree control in two different ecological areas of Hawai'i

Volcanoes: a dry, open-canopy woodland site (Kipuka Kahali'i) and a wet closed-canopy forest site (Thurston Lava Tube area). The herbicides tested were undiluted Roundup, 9% Chopper (imazapyr, American Cyanamid Co.)* diluted with water, 9% Chopper diluted with citrus oil, 10% and 50% Garlon 3A (triclopyr, Dow Chemical Co.) diluted in water, and 2.8% Escort (metsulfuron methyl, DuPont Co.)* diluted in water. Citrus oil and water were applied as control treatments (Cuddihy *et al.* 1991). Herbicides were applied to freshly cut surfaces of stumps of severed trees (referred to as the cut-stump application method) at both sites and also to notch cuts on large trees at the Thurston Lava Tube site.

Chopper in water or Garlon 3A were the most effective treatments in both wet and dry sites. Chopper produced a 100% kill rate at both sites, and Garlon 3A produced a kill rate of 95% at the wet site and 90% at the dry site. Garlon 3A was also the most effective herbicide for large trees when applied to notches cut at several points around the lower trunks. A 90% kill rate was achieved with this method. Other invasive species, such as strawberry guava (*Psidium cattleianum*), in Hawaiian national parks were also effectively controlled by Garlon 3A (Cuddihy *et al.* 1991).

Hawai'i Volcanoes National Park resource managers and scientists reviewed the SEA program after 4 years of intensive management. Population densities of all alien species targeted for control had declined significantly with *fayatee* populations reduced by an estimated 86%. Although the SEA program successfully decreased invasive plant populations, the review indicated that eradication of target weeds was not possible, primarily because of long-term recruitment from soil seed banks. Indefinite follow-up, and mechanical and chemical control treatments would be required at a low level to maintain densities of alien species in these areas (Tunison and Stone 1992). Thus, a long-term commitment of National Park Service resources would be needed for the continued success of the SEA program.

Whereas the density of *fayatee* within the 5,460 hectares of SEAs was greatly reduced and successfully controlled using a combination of mechanical and chemical methods, this plant continued to spread outside these intensively managed areas. By 1991, excluding those lands within the SEAs, an estimated 12,150 hectares (30,000 acres) of

park lands were colonized by *fayatee* (Cuddihy *et al.* 1991). Potential dispersal of seeds from uncontrolled populations into the SEAs decreases the effectiveness of control efforts in these areas (Tunison and Stone 1992). Long-term control must, therefore, eventually include all invaded areas to prevent reinvasion of controlled areas and colonization of new areas.

Implementation of an intensive statewide control program would require extensive and continuous commitment of federal and state resources. Aware of the monetary limitations for long-term mechanical and chemical control methods, and the fact that eradication efforts using mechanical and chemical means have been successful only in limited, intensively managed areas many state and federal resource managers are hopeful that biological control will provide effective long-term control for *fayatee* and other alien plant species (Gardner and Davis 1982, Gardner and Hodges 1990, Hawai'i Steering Committee on Firetree Control 1989, Markin *et al.* 1992, Tunison and Stone 1992). Concern regarding destruction caused by intensive mechanical and chemical control activity in sensitive areas has also stimulated recent interest in biocontrol of alien species (Gardner 1992). However, Cuddihy *et al.* (1991) reported that carefully conducted herbicidal control procedures have a negligible effect on native vegetation.

Biological Control

Weed biological control (biocontrol) can be defined as the use of living organisms, usually arthropods or disease agents, to reduce or eliminate target species (Strobel 1991). An introduced plant often becomes established in its new environment without its natural predators or associated diseases which can regulate the population density of the plant in its native habitats (Gardner 1990, Gardner and Davis 1982). The intent of classical biocontrol is to restore this balance by introducing such mitigating agents to the new environment of a targeted alien species (Gardner and Smith 1985). Encouragement of the activities of predators and parasites already in the new environment which may also attack the introduced plant is also possible, as an alternative to the introduction of other alien species (biocontrol agents) (Duffy and Gardner 1993, 1994). The goals of a biocontrol program are generally three-fold: 1) find an environmentally compatible alternative to chemical herbicides, 2) find an effective, long-term method of

alien plant control, and 3) develop a less labor-intensive method of control as compared to mechanical and chemical control approaches (Strobel 1991).

The initial task of most classical biocontrol programs is to identify potential control agents which coexist with the targeted plant in its native environment. Often, such organisms have coevolved with the host plant and can be specific to that plant (Strobel 1991). Exploration for pathogens and insect pests of plants related to the target species, even those native to different ecosystems or geographical areas, are also often of value. Whereas many insects and diseases often are found associated with target species, most of these are frequently not suitable as biocontrol agents because they exert little detrimental effect, and/or they are not specific to the target species. Effective biocontrol agents are those capable of exerting a significant controlling effect on the target species, and those which are specific to that species (Gardner 1990).

Once a suitable agent has been approved for release, it is normally initially released into one or a few target areas. The organism, if successfully established, will typically disperse itself naturally from the point(s) of introduction and over time, will increase its population numbers. Once established, no further artificial dispersal of the agent may be required (Gardner 1990).

Fayatree is considered a good candidate species for use of biocontrol measures in Hawai'i because there are no naturally occurring or cultivated members of the Myricaceae in the Islands and because the most influential groups (i.e., visitor industry, agriculture, forestry, native ecosystem managers, naturalists, and conservation) have no objection to its control. Thus, biocontrol of fayatree is not anticipated to cause conflicts or interest or pose other undue problems (Gardner and Davis 1982, Hawai'i Steering Committee on Firetree Control 1989, Hodges and Gardner 1985). The observation that fayatree is not an aggressive species in its native habitat (Gardner, Hodges, Markin; *unpublished*) indicates the possible activity of one or more limiting biological agents. On the other hand, ecological factors such as competition with other species, and environmental influences such as temperature and rainfall may have a significant limiting impact on fayatree in its native environment (Gardner 1984).

The symbiotic association of fayatree with the nitrogen-fixing actinomycete *Frankia*, as discussed under "Descriptive Biology" and "Ecological Relationships", has presented many investigators with what at first appears to be an obvious "Achilles' heel" whereby the plant may be controlled. Considerable initial interest, therefore, has been engendered in the nature of the symbiont and the possibility of deactivating or eliminating it, thus removing the competitive edge of fayatree in the nitrogen-poor sites where it is able to aggressively compete. However, owing largely to the lack of knowledge of the biology of *Frankia*, as well as of potential host-specific means of controlling this and other soil-borne Actinomycetes, these considerations have thus far remained unexplored. The extensive interest in nodulation by *Frankia* among the Myricaceae, however, warrants the review and inclusion in the annotated bibliography of literature references to this area of investigation.

By 1954, intensive efforts of the Hamakua Sugar Mill Company and Kukaiau Ranch, together with those of private landowners on the island of Hawai'i, had failed to prevent the spread of fayatree on their lands (Yamayoshi 1954). The next year, Fred Bianchi, an entomologist with the Hawaiian Sugar Planters' Association, was commissioned by the Territorial Board of Commissioners of Agriculture and Forestry to conduct an exploratory survey of the native habitats of fayatree: the Azores, Madeira, and Canary Islands for potential biocontrol agents (Gardner and Davis 1982). N. L. H. Krauss, a Hawai'i Department of Agriculture entomologist, made further exploratory trips in 1960 and 1962 (Krauss 1964). Subsequent exploratory trips have been made by several scientists beginning in 1984 with funding shared by several Hawai'i state and federal agencies (Gardner 1984, Hodges and Gardner 1985, Gardner *et al.* 1988, Markin 1991).

As outlined above, the biological control program for forest weeds in Hawai'i is overseen by an interagency steering committee. Actions of the steering committee are subject to approval by the U. S. Department of Agriculture Animal and Plant Health Inspection Service. The steering committee facilitates necessary cooperation among agencies and varied interest groups in setting priorities and monitoring control efforts (Markin *et al.* 1992, Smith 1990).

By legal mandate, all plant biocontrol efforts in Hawai'i are under the supervision of the Hawai'i Department of Agriculture, Plant Pest Control Branch. Guidelines on the importation and handling of potential biological control agents differ for insects and pathogens; therefore, these two types of agents will be considered separately.

Insects and Other Arthropods

Several insect species have been investigated for their potential to control fayatree in Hawai'i. Initial exploratory trips resulted in the observation of at least 40 species which feed on fayatree in its native environment (Bianchi, *unpublished correspondence*; Krauss 1964). Insects of four species were sent back to Hawai'i by Bianchi for potential release. These were a thrips (a sap-sucking insect), a leaf miner, a flower-feeding weevil, and a flower-feeding caterpillar (Bianchi, *unpublished correspondence*). Propagation of these insects was unsuccessful and none was positively identified to species. Further attempts at their introduction to Hawai'i were not made at that time (Krauss 1964).

Five years after Bianchi's exploration, Krauss (1964) embarked upon two exploratory trips, in 1960 and 1962. Krauss observed both insects and pathogens but, since he was an entomologist, concentrated his efforts on the insects. He observed at least 36 different insect species feeding on various parts of fayatree. Ten of these were sent back to Hawai'i for propagation, positive identification, and testing for possible release. Krauss (1964) also made exploratory trips to southern Africa (in 1957), Central America (in 1959), and the southern and western coasts of the United States (in 1955-1956 and 1963, respectively) where he observed insects feeding on species of *Myrica* related to fayatree. Insects of five species were shipped to Hawai'i for further investigation as a result of these exploratory trips. As with Bianchi's collections, propagation problems occurred with all but one species identified by Krauss (1964). Reasons for this failure are not known, but may have been the result of faulty handling, disease, parasitic stress, or natural death (Gardner and Davis 1982).

The small moth *Strepsicrates smithiana* was successfully propagated and released in 1955. However, no damage to fayatree resulting from this introduction has ever been reported (Gardner *et al.* 1988). *Strepsicrates smithiana* was introduced from

Florida and southern Georgia where it was observed by Krauss (1964) feeding on the leaves and fruits of wax-myrtle (*M. cerifera*), native to the southeastern U. S. Although this moth has apparently established a population in Hawai'i and was observed feeding on and forming leaf-webs in a small, lowland population of introduced wax-myrtle in the Panaewa area of the island of Hawai'i, it has not been effective against either fayatree or wax-myrtle (Krauss 1964, Hodges and Gardner 1985).

Failures to introduce effective insects for control caused resource managers to focus their control programs on herbicides (discussed above), but the establishment of an insect quarantine facility in Hawai'i Volcanoes National Park in 1984 rekindled interest in the possibility for biocontrol of fayatree (Gardner and Smith 1985). This facility allows for in-state observation and testing of potential insect biocontrol agents. (The facility is not suitable for containment of plant pathogens, however, as most disease organisms are minute fungi that produce microscopic, often airborne spores). Research at the facility focuses upon determining the insect's life-cycle, potential for harboring harmful parasitic agents (which could either decimate the introduced insect and/or which could attack and harm native Hawaiian insects), its host-specificity, and potential to attack native and agricultural plants (Markin *et al.* 1992).

Charles Hodges, a U. S. Forest Service forest pathologist (now retired) and Donald Gardner, a National Park Service plant pathologist, undertook exploratory travel in 1984 to the Macaronesian islands. They visited four of the islands in the Azores, the island of Madeira, and three of the Canary Islands, surveying fayatree in all its major habitats (Hodges and Gardner 1985). Several insects, including one fruit borer, a shoot borer, a leaf-binder, and a few weevils and beetles were observed feeding on fayatree. None of these appeared to seriously limit the tree, however.

The fruit-boring caterpillar found on Madeira was identified in the field as a member of the genus *Carposina*, based on the earlier account by Krauss (1964) of feeding by *C. atlanticella* on immature fruit (Fig. 23) (Gardner 1984). In localized areas where infestation was heavy, an estimated 90% of the fruits were affected by this feeding, which destroyed the seed. Krauss's collections sent to Hawai'i had expired before conclusive results were obtained

(Krauss 1964). A shoot-boring caterpillar, also observed on Madeira, capable of destroying developing meristems of fayatree, was similar in appearance to *C. atlanticella* and was thought to be this species (Fig. 24). Neither the fruit nor the shoot boring activity of this insect was observed on other plants in the vicinity of fayatree, indicating host-specificity.

Upon the rediscovery of *C. atlanticella*, Hodges and Gardner (1985) recommended that this insect be investigated further by entomologists as a biocontrol agent. Although the feeding activities did not appear to decimate populations of fayatree in its native environment, it was suggested that the insect might behave more aggressively in a new environment where its predators and parasites were presumably not present (Gardner 1990, 1992; Hodges and Gardner 1985).

During exploration in the native habitats in 1987, several pathogens, and more than 20 insect species were observed feeding apparently exclusively on fayatree, several of which were considered for further investigation as potential control agents (Gardner *et al.* 1988). An adult of the fruit-boring caterpillar was positively identified as *C. atlanticella*. The insect was observed feeding on fayatree at all the locations on Madeira where fruiting was observed, but fruit development in the Azores (north of Madeira) had not progressed sufficiently at the time of the visit (May) to allow conclusive observation of fruit feeders (Gardner *et al.* 1988). Immature specimens of the tip borer were observed on Madeira, but no adults were found. Damage appeared less prevalent than in 1984. Five candidate insects were imported to the Hawai'i Volcanoes National Park insect quarantine facility for further investigation. Colonies of three of the insects were not successfully established; these were *C. atlanticella* from fruit, the shoot tip borer (thought to be also *C. atlanticella*), and an unidentified staminate flower feeder. Colonies of two of the candidate species, a leaf rolling moth (referred at the time to *Phyllonorycter myricae* but more recently identified as *Caloptilia schinella* (Fig. 25) by specialists in this group at the Natural History Museum, London, and an unidentified leaf looper (Lepidoptera, Geometriidae), were successfully established at the quarantine facility. Whereas *Carposina atlanticella* was initially reported by Markin (1991) to offer promise as a biocontrol agent due to the tight synchronization between its biology and the

phenology of its host, later results (*unpublished*) have indicated that this insect is not limited to fayatree and to be capable of feeding on other host plants, including the native Hawaiian shrub 'ohelo (*Vaccinium reticulatum*).

In the fall of 1988 George Markin also explored in the Azores and Madeira (Markin 1991). He again found *Caloptilia schinella* and *Carposina atlanticella*, and also found two previously undescribed caterpillars: a leaf miner and a twig miner. Feeding activity of the leaf miner was complementary to that of *Caloptilia schinella*. The latter was restricted to young leaves at the shoot apex while the leaf miner appeared to feed only on older leaves. A sufficient number of viable specimens was not collected for shipment to the Hawai'i Volcanoes quarantine facility, however. No evidence of active twig boring by *Carposina atlanticella* was observed in the fall, but evidence of its activity earlier in the season was noted. Markin concluded that the feeding habits of this insect are synchronized with fayatree's spring period of rapid growth (Markin 1991).

Markin (1991) also recommended that a complex of insects that attacks the male inflorescence and a second complex of sap-sucking insects be further studied in the field. Both of these complexes were observed to be active in the Azores. The flower-feeding insects had been observed during exploration in 1955 and 1987 (Bianchi 1955, Gardner *et al.* 1988), in addition to the 1988 trip. Specimens of a pollen-feeding moth were brought to Hawai'i in 1987 but attempts to rear it were unsuccessful (Gardner *et al.* 1988). Markin (1991) hypothesized that this moth may be responsible for reducing pollination, and thus fruit development, in the Azores since the observed fruit production was generally less than that seen in Hawai'i where the moths are absent. The complex of sap-sucking insects observed included aphids, leaf hoppers, plant bugs (true bugs of the order Hemiptera, family Miridae), and scale insects. None of these insects has been studied in detail; it was recommended that a cooperative agreement be established with local scientists in the Azores to conduct field research and to collect specimens for shipment to Hawai'i (Markin 1991).

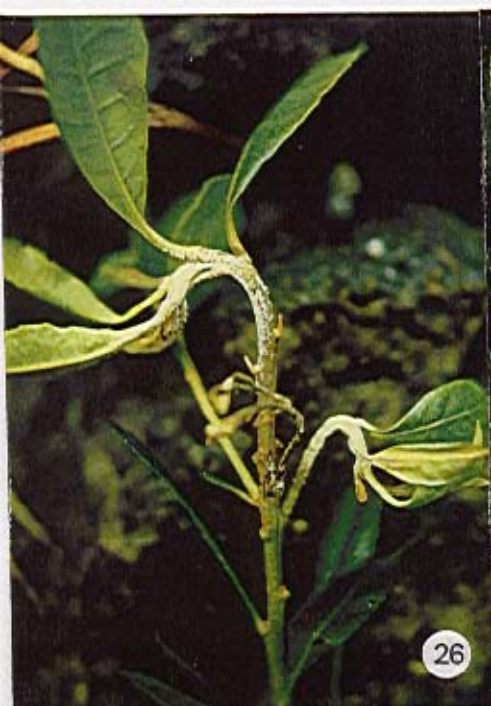
Markin concluded that future exploratory trips to the Azores would not likely yield any new insects that feed on fayatree, and recommended that future efforts be concentrated in Madeira and the Canary Islands, since these regions, the Canaries in

Figure 26. Fayatree shoot infected with the fungus *Ramularia destructiva* on the island of Faial, Azores

Figure 27. Young fayatree severely infected with *Ramularia destructiva* on the island of Tenerife, Canary Islands

Figure 28. Mature fayatree trunk with large canker caused by *Nectria galligena* on the island of São Miguel, Azores

Figure 29. Leaves of fayatree infected with the leaf spotting fungus *Septoria myricae* (?). The fungus was originally isolated from *Myrica cerifera* in North Carolina



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particular, had not been as extensively explored. Furthermore, he suggested expanding the exploration for biocontrol agents to mainland Portugal where fayatree is well established (Markin 1991, 1993). As discussed under "Distribution", the status of fayatree in mainland Portugal, whether native or introduced from the Atlantic islands, is controversial.

Whereas most insects found during exploratory trips to the Macaronesian Archipelago, Africa, and the Americas have not met all of the criteria for introduction to Hawai'i, to date, two insects have been released to control fayatree. As noted above, the moth *S. smithiana* has become established but is unsuccessful in control, and *Caloptilia schinella* was approved in 1991 for release in stands of fayatree on state lands adjacent to Hawai'i Volcanoes National Park. The insect has become established at the release site and is spreading very slowly to other populations of fayatree. Approval was recently granted to release *C. schinella* within Hawai'i Volcanoes National Park (Taylor and Markin 1992). Several scientists (e.g., Brion Duffy, Linda Larrish) have undertaken recent exploratory travel to the Atlantic islands and to mainland Portugal, with consequent introductions of insects to the Hawai'i Volcanoes facility. Evaluations of these collections are currently underway. A contractual agreement also was established through the National Park Service Cooperative Park Studies Unit at the University of Hawai'i with entomologists at the University of the Azores to facilitate long range studies of potential biocontrol agents which can best be carried out by locally established scientists.

Plant Pathogens

Pathogens, particularly fungi, are promising as biocontrol agents because they are often host-specific, destructive to the host, persistent in the environment, and many are easily cultured and dispersed (Gardner 1990, 1992). (As an exception, however, the rust fungi, known for their virulence and host-specificity and therefore otherwise desirable as biocontrol agents, are obligate parasites and cannot be cultured on artificial medium). Additionally, fungi are often free of hyperparasites which plague many insect agents and keep their numbers low. Fungal diseases have been frequently observed on trunks, branches, shoot apices, leaves, and roots of fayatree in the Macaronesian Islands during biocontrol explorations (Bianchi 1954-56; Gardner *et al.* 1988; Gardner and

Hodges 1990; Hodges and Gardner 1985, 1992; Krauss 1964; Markin 1991; B. Duffy, *unpublished*).

Bianchi (1955) was impressed with the virulence of a disease on Madeira causing wilting and necrosis of the stem apices on both young and old fayatrees. The disease, associated with the fungus *Dothiorella* and referred at the time to *D. berengeriana* (later described as the probable imperfect state of *Botryosphaeria ribis*), was not immediately fatal to the infected plant, but substantially inhibited growth and limited flower development. Dr. Natalina de Azevedo, a Portuguese plant pathologist near Lisbon, was contracted to isolate and determine host specificity of the fungus to determine its suitability for importation to Hawai'i (Azevedo 1957, 1960; Rosa 1961). Whereas *D. berengeriana* proved highly virulent to fayatree, Azevedo (1960) found that it also was able to attack several plants of economic importance in Hawai'i, including mango (*Mangifera indica*) and avocado (*Persea americana*). Further consideration of the fungus for biocontrol was subsequently suspended.

Krauss (1964) also observed a twig dieback, associated with *Ramularia destructiva*, which was common throughout the native habitats of fayatree (Fig. 26). This fungus previously had been known on *Myrica gale* in the British Isles, but had not been reported on fayatree. Subsequent observations indicated that certain trees could be severely damaged by *R. destructiva* (Fig. 27). Markin (1991) reported a stand of fayatree on São Miguel island which had been decimated by a pathogen, possibly *R. destructiva*. Elsewhere in its native habitats, severely damaged individual trees have been noted associated with more mildly affected neighboring trees, possibly indicating various levels of genetic resistance to the disease in fayatree populations (Hodges and Gardner 1985, Gardner and Hodges 1990).

Bianchi (1955) observed a widespread canker disease on the trunk, branches, and twigs of fayatree, but the cause could not be determined (Fig. 28). This disease, apparently limited to fayatree, was later found to be caused by a species of *Nectria* (Ascomycetes) (Gardner 1984, Hodges and Gardner 1985). The fungus was referred to *N. galligena*, a bark-infecting pathogen known from woody hosts elsewhere, but reported for the first time on fayatree in the Azores (Gardner and Hodges 1990). Production of infection with *N. galligena* on potted fayatrees from Hawai'i under quarantine has been

difficult to achieve, however. The reason for this is not known, but the restricted space available in the quarantine greenhouse necessitates limitation of the testing to a small number of trees, perhaps representing a population with genetic resistance (Gardner *et al.* 1988, Hodges and Gardner 1992; Gardner, *unpublished data*). The possibility that significant levels of genetic homogeneity may exist in the Hawaiian population of fayatree must be taken into account in all biocontrol considerations, since this population may have arisen from a relatively small number of originally introduced trees.

An unidentified, possibly new, species of the fungus *Cryphonectria* causing a canker disease was observed by Hodges and Gardner (1985) in the Azores in 1984, and was collected and returned to quarantine at the United States Department of Agriculture plant pathogen quarantine facility at Fort Detrick, Maryland, in 1987. Virulence on fayatree was verified at the Fort Detrick laboratory on fresh cut branch sections in 1991 (Hodges and Gardner 1992). Like *N. galligena*, *Cryphonectria* attacks the vascular cambium, causing cankers on the lower stems and branches, eventually girdling the trunk. Recently new collections of the pathogen were returned to quarantine in Hawai'i for further testing (Hodges and Gardner 1992; D. E. Gardner, C. S. Hodges, and E. Killgore, *unpublished data*).

Several other diseases have been observed on fayatree in Macaronesia during exploratory trips to the Azores, Madeira, and Canary Islands (Bianchi

1954-6; Gardner 1984; Krauss 1964; Dennis *et al.* 1977; B. Duffy, *unpublished*), including *Armillaria* root rot caused by *A. mellea* (Hodges and Gardner 1985). While the fungus is known to be pathogenic, this species is already present in Hawai'i, where it has been reported on a wide number of native and nonnative trees, but not on fayatree (Laemmlen and Bega 1974, Raabe and Trujillo 1963). Ruehle (1936) reported *Cephaleuros mycoidea*, a parasitic alga, causing leaf spots on fayatree in southern Florida (Ruehle 1936). This report is probably erroneous, however, since fayatree is not known to occur in Florida (L. Whiteaker, *pers. comm.*) or elsewhere in the continental U. S. Fungal diseases of other species of *Myrica* have also been reported, including those caused by the rust fungi *Gymnosporangium myricatum*, *G. ellisii*, *Cronartium comptoniae*, and others which have not been identified (Gardner and Davis 1982). Like most rust fungi, these species are assumed to be quite host specific and may require alternate hosts to complete their life cycles, but no experimental evidence is available concerning their host range or ability to infect fayatree. Isolates of the leaf spotting fungal pathogen *Septoria* from *M. cerifera* in the southeastern U. S. and from *M. parvifolia* in Venezuela have shown promise in infecting fayatree and causing leaf drop from trees inoculated in quarantine in Hawai'i (Fig. 29). However, results are still preliminary and usefulness of *Septoria* as a biocontrol agent is not known at present (D. E. Gardner, C. S. Hodges, and E. Killgore; *unpublished data*).

*Reference to a company or product name does not imply approval or recommendation of that product by the Cooperative National Park Resources Studies Unit, University of Hawaii, or the National Park Service to the exclusion of others that also may be suitable.

SUMMARY AND CONCLUSIONS

Fayatree, a small to medium tree or shrub, introduced to Hawai'i by Portuguese immigrants from the Azores and Madeira, is of interest to natural resource managers in Hawai'i because it is an aggressive weed which is able to invade and disrupt native habitats on a wide scale. Fayatree roots have the ability to form nodules and to fix atmospheric nitrogen through a symbiotic association with the actinomycete *Frankia*. This ability has been demonstrated to give this species a decided advantage in competition with native species in colonizing newly formed volcanic soils which are poor in nitrogen. The addition of nitrogen to the soil may in turn significantly alter the soil habitat, favoring development of other alien species and further upsetting natural processes. The overriding concern therefore, is in development of effective control measures for fayatree in Hawai'i.

Several approaches have been followed or considered in control of fayatree, primarily by ranchers in attempts to keep pastures clear of the plant, and by resource managers of Hawai'i Volcanoes National Park where the species is one of the highest priority alien weeds targeted for control. Young trees may be successfully pulled from the ground and removed mechanically. Older trees may be clear cut, but the tendency for stumps to resprout profusely necessitates treatment with an herbicide for practical control. Standing trees may also be treated with one of a variety of herbicides which have been found effective, although in natural systems care must be taken to avoid contamination of nearby native vegetation. Chopper in water, or Garlon 3A were found to be two of the most effective herbicides for control of fayatree. Notwithstanding the effectiveness of mechanical or herbicidal approaches to fayatree control, the expense and/or labor-intensive requirements of these methods cause them to be practical only a limited scale. The special ecological areas (SEAs) designated within Hawai'i Volcanoes National Park, were selected to represent ecosystem types or features of particular interest and value and are managed intensively, utilizing mechanical or herbicidal methods of weed control. However, areas of the park outside of the SEAs are subject to rapid colonization and may not be readily accessible for more conventional control activities.

Biological control is considered perhaps the only practical approach for the control of fayatree in these widespread areas. Unlike many other plants considered for biocontrol, fayatree has no commercial value in Hawai'i and therefore presents no conflicts of interest. Furthermore, it has no relatives in Hawai'i which might otherwise be endangered by introduced biocontrol agents. These factors make fayatree especially suitable as a biocontrol candidate. In attempts at classical biocontrol, scientists from Hawai'i have travelled to the native regions of fayatree (i.e., the Azores, Madeira, and the Canary Islands) in search of insects and diseases affecting fayatree in its native habitats which may serve as effective biocontrol agents upon introduction to Hawai'i. These efforts have been coordinated by the Hawai'i Steering Committee on Firetree Control and the Interagency Steering Committee for Forest Weed Control. To date, two insect species have been released in Hawai'i, but neither has yet affected the population of fayatree to any appreciable extent. Exploration for other potential biocontrol agents is continuing, as are efforts at testing other insects and pathogens for virulence and host range under quarantine in Hawai'i. Cooperative agreements and working relationships also have been established with scientists in the Azores and Madeira for the collection and testing potential biocontrol agents on a local basis. The activity of a fungus, already present in Hawai'i, in destroying fayatree fruits and seed, has been recently recognized and may be limiting the spread of fayatree. A decline of fayatree in some parts of Hawai'i Volcanoes National Park of unknown cause appears to be quite effective in controlling the species at present. However, the nature and the cause of this decline must be understood before any conclusions may be drawn as to its long range potential in biocontrol.

To provide a thorough understanding of fayatree, perhaps in indirect support of control approaches, it was desirable to assemble all known information relating to the biology, reproduction, anatomy, physiology, distribution, ecology, and ethnobotanical uses of this species in a single volume. Furthermore, information on other members of the genus *Myrica* and of the family Myricaceae which may be also useful was included as well. The large amount of attention which has been focused on the nitrogen-fixing ability of *Myrica* spp. has become evident throughout this study. This ability in fayatree is frequently seized upon by researchers newly

acquainted with the fayatree problem as an "Achilles' heel" through which the aggressiveness of fayatree in its new environment may be incapacitated. However, the symbiont is not readily obtained in pure culture and direct research has proven difficult. Actinomycetes in general have not previously been targets of control, and little information is currently available concerning their relationships, specificities, and control approaches.

The annotated bibliography is an attempt to include all direct references to fayatree, which are set in boldface type, and in addition to include principal references to the family Myricaceae, to other species of *Myrica*, and other related subjects which may contribute in some way to the scope of this report. The objective in preparing the bibliography was to include sufficient information in each annotation that the subject matter of the report was well-documented

and that the content of each reference was well-represented. Further information, if desired, may then be obtained by consulting the original source.

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ANNOTATED BIBLIOGRAPHY

(Entries in boldface refer to *Myrica faya*, whereas those in normal type refer to other species of *Myrica*, the family Myricaceae, or related subjects.)

- Abbayes, H. des, and C. Hamant. 1946. Répartition et comportement de *Myrica gale* L. dans le Massif armoricain. *Compte Rendu Sommaire Séances Société de Biogéographie* 23:(195)12-17.

In biogeographical studies, *Myrica gale* was reported to occur in the Armorican Mountains (Brittany) as a relic species which spreads along valley floors before it invades the slopes and is actually in regression. Studies of the marshes of l'Erdre demonstrate that this species starts in associations which are inundated in winter in marsh areas. It has been part of two evolutionary divergent series, one of which begins with the magnocariçaie, where it is established at its base. It then ends at the grove where it disappears completely. (in French)

- Abbe, E. C. 1963. The male flowers and inflorescence of the Myricaceae. *American Journal of Botany* 50:632.

The Myricaceae, with three genera, *Myrica*, *Gale*, and *Comptonia*, have structurally unusual staminate inflorescences. The author described in detail variations in structure among the genera and among the sections within the genus *Myrica*, which may form the basis of taxonomic distinctions on the subgeneric level.

- Abbe, E. C. 1974. Flowers and inflorescences of the "Amentiferae". *The Botanical Review* 40:159-261.

Five plant families (Myricaceae, Betulaceae, Fagaceae, Leitneriaceae, and Juglandaceae) comprise the artificial grouping referred to as the Amentiferae. The Amentiferae typically have unisexual, apetalous, bracteate flowers in pendant clusters referred to as aments or catkins, although the author noted that exceptions to this arrangement are so frequent that the term "Amentiferae" may be considered a misnomer. The author explained floral morphology using detailed evidence from ontogeny, phyllotaxy, and vascular anatomy. Fayatree, as a member of the family Myricaceae, is included in the Amentiferae, but this species was not specifically discussed.

- Abbe, L. B. 1963a. Xylem anatomy of the Myricaceae. *American Journal of Botany* 50:632-633.

The wood anatomy of the Myricaceae of the Myricaceae family was examined for about half of the generally recognized 56 species, including *Comptonia* of North America; *Gale*, a palaeartic genus; and representatives from all sections of the bayberry genus *Myrica*, including section *Cerophora*, subsection *Americanae*; section *Cerophora*, subsection *Africanae*; section *Faya*; and section *Morella*. Wood of the Malayan species *M. esculenta farquhariana* was used for assessment of the variation in vessel diameter and length, end wall angles and perforation numbers, and vessel pitting comparisons with other members of the genus and the other genera. *Comptonia* was considered more advanced in having a large proportion of single-pored vessel members, in contrast to the more primitive many-perforate end wall of *Gale*.

- Abbe, L. B. 1963b. Wood anatomy of the bayberry and beech families. *Year Book of the American Philosophical Society* 1963:300-304.

The center of origin for the Myricaceae family was considered to be south-east Asia. (Original reference not seen; citation from Macdonald (1989).)

Adamson, R. S. 1950. Myricaceae Lindl. Pp. 311-314 In: R. S. Adamson and T. M. Salter, eds. Flora of the Cape Peninsula. Juta & Co., Ltd., Cape Town.

The genus *Myrica* is well represented in South Africa. Seven species were described from the Cape Peninsula (in the region of Cape Town): *M. cordifolia* L., *M. burmanni* E. Mey. ex DC., *M. humilis* Cham. & Schlecht., *M. diversifolia* Adamson, *M. quercifolia* L., *M. zeyheri* C. DC., and *M. conifera* Burm.

The author noted that uniformity in floral morphology among species has caused taxonomic distinctions to be based almost entirely on vegetative characteristics. However, this has led to confusion because of the variation in leaf characteristics relative to age, habitat, and environmental interference. Furthermore, species of *Myrica* may hybridize whenever species are associated, such as in South Africa, resulting in intermediate morphological forms. This may explain the apparent difficulty in classification within this genus, as evident in the large number of synonyms and disagreement among authors as to the number of valid species.

Aiton, W. 1798. *Myrica faya*. Hortus Kewensis 3:397.

This is the original description of fayatree. (Original reference not seen; citation from White (1993).)

Alfieri, S. A., Jr., K. R. Langdon, C. Wehlburg, J. W. Kimbrough. 1984. Index of plant diseases in Florida. Florida Department of Agriculture & Consumer Services. Bulletin 11.

Diseases of *Myrica cerifera* (wax myrtle) and the fungi which cause them were included in an index of plant diseases in Florida. They were listed as follows:

- Mushroom root rot caused by *Armillariella* (= *Clitocybe*) *tabescens*.
- Canker caused by *Botryosphaeria dothidea* var. *chromogena* (= *B. ribis* var. *chromogena*).
- Twig dieback caused by *B. quercuum* (= *Phsalospora glandicola*; *P. obtusa*; *P. rhodina*).
- Leaf spot caused by *Calonectria erubescens*.
- Algal leaf spot, green scurf caused by *Cephaleuros virescens*.
- Leaf spot caused by *Cercospora* sp.
- Dodder, *Cuscuta compacta*.
- Dieback caused by *Diplodia* sp.
- Stem lesions caused by *Fusarium* sp.
- Root rot and wilt caused by *F. oxysporum*.
- Stem canker caused by *Fusicoccum* sp.
- Leaf spot caused by *Gloeosporium* sp.
- Leaf spot caused by *Glomerella* sp.
- Rust caused by *Gymnosporangium ellisii*.
- Black mildew caused by *Irene calostroma*.
- Leaf spot caused by *Macrophoma* sp.
- Black mildew caused by *Meliola manca*.
- Nectria erubescens* on leaves.
- Leaf spot caused by *Pestalotia myricae*.
- Leaf spot caused by *Phyllosticta myricae*.
- Root rot caused by *Phytophthora* sp.
- Root rot caused by *Phythium* sp.

Leaf spot caused by *Rhizoctonia ramicola*.
Felt fungus, *Septobasidium castaneum* and *S. sinuosum*.
Leaf spot caused by *Septoria myricae*.
Stem gall and witches' broom caused by *Sphaeropsis tumefaciens*.

An C. S., W. S. Riggsby, and B. C. Mullin. 1985. Relationships of *Frankia* isolates based on deoxyribonucleic acid homology studies. *International Journal of Systematic Bacteriology* 35:140-146.

In a highly technical study, a molecular approach was used to examine the genetic relatedness of 19 *Frankia* isolates by measuring the extent of DNA-DNA homology. *Frankia* from several hosts was tested, including *Myrica pensylvanica*.

Anonymous. 1962. Noxious weeds of Hawai'i. Unpublished file of the Hawai'i Department of Agriculture.

Fayatee was listed as a noxious weed in Hawai'i and a brief description of the plant, its purported uses, and its introduction was given. This is the earliest known printed reference to the supposed use of fayatee fruit for wine making.

Aplet, G. H. 1990. Alteration of earthworm community biomass by the alien *Myrica faya* in Hawai'i. *Oecologia* 82:414-416.

A field study was conducted to determine whether the contribution of nitrogen from fayatee to the soil had any effect on earthworm community biomass. In open forest communities invaded by fayatee, and in nearly pure fayatee stands, earthworm community biomass was three-fold greater than that of non-invaded native forest. The earthworm biomass enhancement was attributed to the increase in nitrogen-rich litter on the forest floor.

Aplet, G., R. Loh, J. T. Tunison, and P. M. Vitousek. Experimental restoration of a dense faya tree (*Myrica faya*) stand. Technical report, University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu. In preparation.

Factors contributing to successful colonization by fayatee were evaluated through experimental restoration of a fayatee stand in Hawai'i Volcanoes National Park. Artificial gaps created in closed faya tree stands were used to predict succession in a closed stand following faya tree mortality resulting from natural causes or management actions. This study indicated that canopy removal or rapid die off would be needed for 'ohia' regeneration. Fayatee would also regenerate to a limited degree along with prolific regeneration of other alien herbs and shrubs. Native tree fern could be encouraged by slow canopy thinning of standing trees. This study demonstrated the need for a cautious approach to ecological restoration of fayatee-colonized areas to avoid reestablishment of fayatee or of other alien species.

Armstrong, R. W., ed. 1983. *Atlas of Hawai'i*. Second Edition, University of Hawai'i Press, Honolulu.

The *Atlas of Hawai'i* is a general account of the geography of the Hawaiian Islands, providing background information on the natural, cultural, and social environments. The distinction among indigenous, endemic, and introduced (or alien) species was clarified. At the time of writing, more than 2,500 kinds of plants were reported endemic to the Hawaiian Islands. The process of species introduction to Hawai'i following contact by Europeans in the late 1700s was described, as was the destruction of habitats and the extinction of native species resulting from such introduction. Although

fayatree was not specifically mentioned among the examples of particularly aggressive, alien (exotic) species introduced (e.g., lantana), this species is currently recognized as belonging to this category.

Arthington, A. H., and D. S. Mitchell. 1986. Aquatic invading species. Pp. 34-53. *In*: R. H. Groves and J. J. Burdon, eds., *Ecology of biological invasions*. Cambridge University Press, Cambridge, Great Britain.

The authors listed climate, natural or human-induced disturbance, nutrient availability, competition with native flora, and the presence or absence of phytophagous insects and of other biological control agents, such as pathogens as factors influencing the invasive success of an alien species.

Arthur, J. C., and G. B. Cummins. 1962. *Manual of the rusts in United States and Canada*. Hafner Publishing Co., New York.

In a compilation of rust fungi in the U. S. and Canada, the authors listed *Cronartium comptoniae* as producing its pycnia and aecia on species of pine and its uredinia and telia on *Comptonia peregrina* (= *C. asplenifolia*) and *Myrica gale*. The fungus reportedly occurs from Nova Scotia to Wisconsin, southward to North Carolina and Missouri, and from Alaska to northern California. *Peridermium comptoniae* was given as a synonym of *C. comptoniae*. *Gymnosporangium ellisii* produces its telia on Juniperaceae (i.e., *Chamaecyparis thyoides*). A uredinial state is absent. The spermogonia and aecia are produced on *Comptonia peregrina*, *Myrica carolinensis*, and *M. cerifera*. The fungus was reported from Massachusetts southward to Florida and Alabama. Synonyms of *G. ellisii* were listed as *Caeoma (Aecidium) myricatum*, *Aecidium myricatum*, and *Podisoma ellisii*.

Auld, B. A., and C. A. Tisdell. 1986. Impact assessment of biological invasions. Pp. 79-88. *In*: R. H. Groves and J. J. Burdon, eds., *Ecology of biological invasions*. Cambridge University Press, Cambridge, Great Britain.

The rate of spread of an invasive plant is affected by the pattern of its spread. Plants which spread as scattered colonies rather than as an advancing front of an established colony tend to have a faster rate of spread.

Azevedo, N. F. D. S. D. 1957. Sobre doenças da *Myrica faya* Ait. Associação Portuguesa para o Progresso das Ciências. Reprint of a presentation given at the Fourth Section of the XXIII Luso-Spanish Congress, Coimbra, 1956. 14 pp.

Fungi isolated from diseased fayatree collected in the Azores and Madeira Islands were identification and described. They included *Pestalozzia cuboniana*, *Pestalotiopsis versicolor*, *Fusarium* sp., and *Coniothyrium fuckelii*. The degree of pathogenicity and potential as a biological control agent was evaluated for each fungus. (in Portuguese with English summary)

Azevedo, N. F. D. S. D. 1960. *Dothiorella* sp. agente de murchidão em *Myrica faya* Ait. Publicações da direção geral dos serviços florestais e aquícolas, Vol. XXVII (II):101-115.

Another fungus, *Dothiorella* sp., was isolated and identified from diseased fayatree reported in Azevedo's 1957 paper. Inoculation trials demonstrated that *Dothiorella* was the responsible agent for the dieback disease. Five strains were identified. Cross inoculation trials showed that certain economic and ornamental trees (e.g., mango [*Magnifera indica*], avocado [*Persea americana*], ironwood [*Casuarina equisetifolia*] of Hawai'i were also susceptible to the disease. Thus, *Dothiorella* was not recommended for importation to Hawai'i as a biological control agent for fayatree. (in Portuguese with English summary)

Baeta Neves, C. M. 1950. A propósito das pragas do samouco, samouqueiro ou faia das ilhas. Reprinted from *Gazeta das Aldeias*, October 16 and November 1, Porto, Portugal. 7 pp.

Fayatree was described as an important species of mainland Portugal because of its ability to increase available soil nitrogen levels, and as a source of tannin to the tannin extraction industry in Portugal. Five insects known to attack fayatree in Portugal were described: *Lycia hirtaria*, *Heliophthrips haemorrhoidals*, *Saissetia oleae*, *Icerya purchasi*, and *Lymantria dispar*. (in Portuguese)

Baeta Neves, C. M. 1958. Nota sobre a entomofauna da *Myrica faya* Ait. *Brotéria* 27(3):99-102.

The author, an entomologist in the native habitat of fayatree, collaborated with Mr. Fred Bianchi, an entomologist from Hawai'i, in search of potential biocontrol insects in the mid 1950s. Insects found associated with fayatree in Madeira and in mainland Portugal were listed. Some of these were also found in later explorations and were familiar, but some were apparently not preserved in collections and their current identities remain uncertain. Insects listed were as follows: Hemiptera, Homoptera Cercopidae, *Philaenum leucophthalmus*, Madeira, Ribeiro Frio, Julho, 1955; Jassidae, *Issus* spp., Madeira, Ribeiro Frio, Julho, 1955; Coleoptera, Anobiidae, *Anobium emarginatum*, Madeira, Ribeiro Frio, Julho, 1955; Chrysomelidae, *Psylliodes cuprea*, Continente (a sul da Figueira da Foz, Junho, 1955); Curculionidae, *Rhynchites coeruleocephalus*, Continente (Pinhal do Urso, Junho, 1955); *Apion pomonae*, Continente (a sul da Figueira da Foz, Junho, 1955) *Apion vorax*, Continente (a sul da Figueira da Foz, Junho, 1955); *Apion (Ceratapion)* sp., Continente (a sul da Figueira da Foz, Junho, 1955); *Brachyderes lusitanicus*, Continente (a sul da Figueira da Foz, Junho, 1955). (in Portuguese)

Baird, J. R. 1969. A taxonomic revision of the plant family Myricaceae of North America, north of Mexico. Unpublished Ph.D. dissertation. The University of North Carolina.

The author revised the taxonomy and discussed the nomenclature of North American species of the Myricaceae, for which he recommended three genera. Since *Myrica gale* is the type species for the family and *Comptonia peregrina* is a distinct monotypic genus, over 90% of the species would have to be assigned to a new genus, *Morella*. This recommendation was not published, however. (Original reference not seen; citation from Macdonald (1989).)

Baker, D., W. L. Pengelly, and J. G. Torrey. 1981. Immunochemical analysis of relationships among isolated *Frankia* (Actinomycetales). *International Journal of systematic Bacteriology* 31(2):148-151.

An immunological study of nine strains of pure-cultured Actinomycetes isolated from symbiotic root nodules was undertaken to establish the taxonomic relationships of these organisms. The isolates were all classified in the genus *Frankia* (family Frankiaceae) and could be divided into two major groups, the first of which was isolated from *Alnus* (family Corylaceae), *Comptonia* (family Myricaceae), and *Myrica pensylvanica* hosts. The second group was isolated from plants of the genus *Elaeagnus* (family Elaeagnaceae). Cross-reaction techniques used in identification of *Frankia* strains are potentially applicable to screening for novel, naturally-occurring strains.

Barrett, S. C. H., and B. J. Richardson. 1986. Genetic attributes of invading species. Pp. 21-33. In: R. H. Groves and J. J. Burdon, eds., *Ecology of biological invasions*. Cambridge University Press, Cambridge, Great Britain.

Environmental factors which can affect the invasive success of an alien species (such as fayatree, although this species is not specifically mentioned) are climate, natural or human-induced disturbance, nutrient availability, competition with native flora, and the presence or absence of phytophagous insects and of other biotic control agents, such as pathogens.

Benson, D. R., and D. E. Eveleigh. 1979. Ultrastructure of the nitrogen-fixing symbiont of *Myrica pensylvanica* L. (bayberry) root nodules. Botanical Gazette 140 (Supplement):S15-S21.

The authors described the ultrastructural detail of the actinomycete symbiont of *M. pensylvanica* root hairs. Also described was the mode of penetration of the endophyte through the host cell wall and its developmental stages within the root nodules. Ultrastructural changes within the host cell in response to symbiont penetration were also discussed.

Benson, D. R., V. A. Greenhut, and D. E. Eveleigh. 1980. Scanning electron microscopy of the nitrogen-fixing actinorhiza of *Myrica pensylvanica*. New Phytologist 83(3):755-760.

A detailed description, based on scanning microscopy, was provided of the filamentous morphology of the nitrogen-fixing endophyte in root nodules of *Myrica pensylvanica*.

Berliner, R., and J. G. Torrey. 1989. On tripartite *Frankia*-mycorrhizal associations in the Myricaceae. Canadian Journal of Botany 67:1708-1712.

The importance of the combined symbiosis of the nitrogen-fixing actinomycete *Frankia* and phosphorus uptake-facilitating mycorrhizae with plant roots of *Comptonia peregrina* and *Myrica gale* was examined. This tripartite symbiosis is common in the legumes. The tripartite association was not observed in field collected and greenhouse inoculated *Comptonia* and *Myrica* plants. No evidence of mycorrhizal-root interaction was observed.

Bianchi, F. A. 1953-1956. Unpublished file of correspondence with the Hawai'i Territorial Board of Agriculture documenting exploration for biocontrol agents in the native habitats of fayatree.

F. A. Bianchi, a Hawaiian Sugar Planters' Association entomologist, conducted the first exploratory travel to the native habitats of fayatree on behalf of the Hawai'i Agricultural Experiment Station, The Hawai'i Cattlemen's Association, and the Board of Commissioners of Agriculture and Forestry of the Territory of Hawai'i in search of potential biocontrol agents for use in Hawai'i. Copies of correspondence principally between Bianchi and Alan Thistle, Director of the Division of Entomology and Marketing of the Territorial Board of Commissioners of Agriculture and Forestry, detailing the activities, findings, and travel of Bianchi among the islands of Macaronesia is included. Also included in the file are copies of correspondence previous to Bianchi's actual travel concerning the fayatree problem in Hawai'i, as well as correspondence concerning the later (1962) exploratory travel of Dr. N. L. H. Krauss to the Atlantic islands.

Big Island Resource Conservation and Development. 1990. Pest alert, firetree. Pamphlet. Big Island Resource and Development, Hawai'i.

The spread of fayatree in Hawai'i was summarized, recent state efforts to control its spread were reported, and suggestions for landowners to prevent further encroachment were presented. The intention of the pamphlet was to increase public awareness of the environmental problems caused by fayatree invasion.

Bloom, R. A., B. C. Mullin, and R. L. Tate, III. 1989. DNA restriction patterns and DNA-DNA solution hybridization studies of *Frankia* isolates from *Myrica pensylvanica* (bayberry). *Applied and Environmental Microbiology* 55(9):2155-2160.

Gel electrophoresis was used to evaluate the diversity of *Frankia* strains that infect *M. pensylvanica*. Results indicated that a variety of strains of *Frankia* can infect the same host plant.

Board of Commissioners of Agriculture and Forestry. 1962. Noxious weeds of Hawai'i. State of Hawai'i, Honolulu. 89 pp.

This reference is a compilation of looseleaf pages describing noxious weeds known in Hawai'i and recommended methods of control. Fayatree was listed as a noxious weed because of its rapid spread and encroachment on agricultural and pastureland. The alien Japanese white-eye and the mynah bird were indicated as the principal means of fayatree spread in Hawai'i. The most effective control method known at the time of writing was to dig out and burn individual plants.

Bond, G. 1952. Some features of root growth in nodulated plants of *Myrica gale* L. *Annales of Botany* 16(64):467-475.

In light of strong evidence that root nodules of *Myrica gale* were functional in fixing atmospheric nitrogen, it was of interest to investigate the unusual features of roots which grew out from the tips of the nodules. Such roots were produced in large numbers and were characterized by vertically upward growth in culture, which was presumably also a condition in the field. Such orientation was reported to be a result of negative geotropism, with evidence indicating that upwardly growing roots facilitate the ventilation of the nodule tissues, which may be of special significance under the bog conditions in which *M. gale* commonly grows.

Bond, G. 1951. The fixation of nitrogen associated with the root nodules of *Myrica gale* L., with special reference to its pH relation and ecological significance. *Annals of Botany* 15(60):447-459.

Under experimental conditions, nitrogen was reported to be fixed by nodulated plants of *Myrica gale*, during the first year of development, of a magnitude comparable to that of legumes under similar conditions. Compared with the legume nodule organism, the *Myrica* organism was found to be markedly adapted to acid soil conditions. Nitrogen fixation was thought to be of considerable ecological importance in the bog habitats frequented by *M. gale*.

Bond, G. 1971. Fixation of nitrogen in two African species of *Myrica*. *The New Phytologist* 70:1-8.

Root nodules of the African species *Myrica cordifolia* and *M. pilulifera* were shown to be capable of fixing atmospheric nitrogen to an extent which was sufficient to sustain good growth of the plants in a rooting medium free of combined nitrogen. This indicated that the nodules of these species have the same properties and physiological significance as the nodules of *M. gale* and *M. cerifera*. This nitrogen fixing ability was considered important in the ability of *M. cordifolia* to flourish on sand dunes.

Bottomley, M. A. 1911. The structure and physiological significance of the root-nodules of *Myrica gale*. *Proceedings of the Royal Society B* 84:215-216.

Nodules on the roots of *Myrica gale* were reported to have been first described by J. Brunchorst in 1886, who stated that they were caused by a fungus with septate hyphae and terminal spores. The fungus was placed in the genus *Frankia* and named *F. brunchorstii* by H. Möller in 1890. It was

considered closely related to a similar fungus in alder nodules. The author investigated nodules from *M. gale* anatomically and also obtained pure cultures of *Frankia* in which he demonstrated nitrogen fixation. From comparisons of young, nonvigorous *Myrica* without nodules with healthy plants with nodules, he concluded that nodules were associated with nitrogen assimilation, and that to the four "families" of nonleguminous plants known to fix nitrogen by means of root nodules (alder, *Elaeagnus*, *Cycas*, and *Podocarpus*), *Myrica* should be added as a fifth.

Bramwell, D., and Z. I. Bramwell. 1974. Wild flowers of the Canary Islands. Excelentísimo Cabildo Insular de Tenerife and Stanley Thornes Publishers, Ltd., London.

Fayatree is listed as the only species of the Myricaceae in the Canary Islands. It occurs on all islands and is locally very common in forests and degraded forest scrub on the West Islands and Gran Canaria from 400 to 1500 m elevation, often in association with *Erica arborea* ("Faya/Brezal"), but very rare on the East Islands.

Britton, N. L., and A. Brown. 1970. An illustrated flora of the northern United States and Canada, Vol. 1. (Republication of the second edition published by Charles Scribner's Sons in 1913 under the title "Illustrated flora of the northern United States, Canada, and the British Possessions"). Dover Publications, Inc., New York.

The taxon *Gale*, considered a monospecific genus by some authors (as *G. palustris* (Lam.) Chev.), is listed as a species of *Myrica*, as *M. gale* L.

Callaham, D., W. Newcomb, J. G. Torrey, and R. L. Peterson. 1979. Root hair infection in actinomycete-induced root nodule initiation in *Casuarina*, *Myrica*, and *Comptonia*. Botanical Gazette 140 (Supplement):S1-S9.

The infection process of root hairs by an actinomycete was described, along with the role of the actinomycete as a stimulant in the morphogenesis of root nodules in *Casuarina*, *Myrica*, and *Comptonia* seedlings.

Camrath, R., and J. T. Tunison. The distribution of fayatree (*Myrica faya*) in Hawai'i Volcanoes National Park, 1992. Technical report, University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu. In preparation.

The distribution of fayatree in Hawai'i Volcanoes National Park as on 1992 was reported, based on the earlier study of Clarke (1978) in which fayatree distribution in Hawai'i Volcanoes National Park was mapped for the first time, and the later report of Whiteaker and Gardner (1985) reporting distribution of fayatree on each of the major islands of Hawai'i. Whereas Hawai'i Volcanoes National Park was included in the latter study, the concentration of the current study in the park resulted in perhaps a more finely tuned up-to-date distribution map applicable by resource management personnel to direct control efforts in the field.

Carpenter, R. A., and W. Mitter, eds. 1992. Environmental risks to Hawai'i's public health and ecosystems. Executive summary. East-West Center, Honolulu.

A recent assessment of risks to native Hawaiian ecosystems identifies invasion by alien plants (such as fayatree) as a primary threat to the integrity of these systems.

Carter, G. A., and D. R. Young. 1993. Foliar spectral reflectance and plant stress on a barrier island. International Journal of Plant Science 154(2):298-305.

Leaf reflectance of *Myrica cerifera* and *Pinus elliotii* was measured in the field on Horn Island, Mississippi, as an estimate of water stress. Visible reflectances and chlorophyll *a* concentrations indicated that *M. cerifera* was not stressed under the conditions of the observations as compared with those of mainland sites.

Chevalier, A. 1901. Monographie des Myricales. Memoirs on the National Society of National Society of Natural Sciences and Mathematics, Cherbourg 32:85-340.

This work is the first comprehensive treatment of the genus *Myrica* on a world-wide basis, listing all species recognized at the time of publication, synonyms, and discussing distribution and the distinguishing morphological characteristics of each species. *Gale* is treated as a separate genus from *Myrica*. (in French)

Chourey, M. S. 1974. A study of the Myricaceae from Eocene sediments of southeastern North America. *Palaeontographica B* 146:88-153.

Members of the Myricaceae were reportedly distributed worldwide on all the major land masses except for Australia and New Zealand, with fruit dissemination largely by birds. From examination of fossils, including fossilized pollen, it was concluded that the family was probably not differentiated sufficiently to identify myricaceous fossils before the Eocene-Oligocene. This analysis indicated that the family had evolved much more recently than had previously been thought. Chourey disagreed with Abbe (1963) that the center of origin of the Myricaceae was south-east Asia. Otherwise, *Myrica* would have to have originated in the early Cretaceous in order to migrate to Europe, America, and northern Africa by the Eocene. Furthermore, no fossil evidence was available for a southeastern Asian origin.

Clarke, G. 1978. The distribution of *Myrica faya* and other selected problem exotics within Hawai'i Volcanoes National Park. (Abstr.) P. 51 In: C. W. Smith, ed. Proceedings, Second Conference in Natural Sciences, Hawai'i Volcanoes National Park. University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu.

The first known survey of fayatree distribution in Hawai'i Volcanoes National Park was reported. The survey was made in conjunction with ongoing efforts at fayatree control through mechanical and chemical means in heavily-infested areas of the park.

Cline, M. G., ed. 1955. Soil survey of the Territory of Hawai'i. Soil survey series 1939, no. 25, U. S. Department of Agriculture, Washington, D. C. and Hawaii Agricultural Experiment Station, Honolulu.

All Hawaiian soils were described as being of volcanic origin and thus are typically deficient in nitrogen and phosphorous. Nutrients and minerals are rapidly leached due to the high porosity of these soils. Although not specifically mentioned, fayatree is successful at colonizing these soils and competing with native plants due to its nitrogen-fixing ability.

Coetzee, J. A., and J. Pragłowski. 1984. Pollen evidence for the occurrence of *Casuarina* and *Myrica* in the Tertiary of South Africa. *Grana* 23:23-41.

A detailed, technical description of *Myrica* pollen was provided. Pollen of both *Casuarina* and *Myrica* was found to be abundant in deposits of the Tertiary age from the Southwestern Cape of South Africa. The Miocene fossil record of *Myrica* pollen could indicate a long history of this genus in that region. The Myricaceae are considered to be of Laurasian (i.e., the ancient landmass) origin with a continuous fossil record from the Santonian onward. The occurrence of the endemic genus *Canacomyrca* in New Caledonia has posed a problem in connection with the question of the place of origin of the family,

although this genus may not be closely related to *Myrica*. Other hypotheses (see Raven and Axelrod 1974) postulate that the Myricaceae may have migrated relatively recently to Africa and South America.

Collins, R. P., and A. F. Halim. 1973. Chemotaxonomy of the Myricaceae. II. Essential oil analysis of three Central American species of *Myrica*. *Lloydia* 36:320-325.

The chemical composition of the leaf oils of *Myrica mexicana* from Provincia de Code, Panama; *M. phanerodonta* from Provincia Alajuela, Costa Rica; and *M. pubescens* from Provincia San Jose, Costa Rica was examined for chemotaxonomic purposes. The analysis indicated that *M. pubescens* and *M. phanerodonta* are very similar to one another and that these species should be regarded as synonymous or at least very closely related. *Myrica mexicana* differed significantly in oil composition from the other two Central American species examined.

Córdoba, L. C. F. de, and F. O. Medina. 1976. Estudio sobre la vegetación y flora forestal de las Canarias occidentales. Capítulo séptimo: Las foraciones de faya y brezo. Excelentísimo Cabildo Insular, Santa Cruz de Tenerife.

A comprehensive description of fayatree, together with its classification, Spanish and Portuguese common names, distribution, and ecology was presented. Flora associated with fayatree in its native habitats, and the localities of other species of *Myrica* were discussed. Cultural uses of fayatree and its relatives, such as for perfume, were described. (in Spanish)

Costa, A. da, and Franquinho, L. de O. 1987. Plantas e flores Madeira. Francisco Ribeiro, Funchal.

Fayatree is listed as a native tree of Madeira, occurring from 0-1,000 m elevation. (in Portuguese)

Cronquist, A. 1978. The evolution and classification of flowering plants. Second edition. Allen Press, Lawrence, Kansas.

The Myricales is among seven orders of higher plants which comprise the subclass Hamamelidae, a phylogenetic grouping of orders which are characterized by strongly reduced, often unisexual flowers which either lack or produce a poorly developed perianth. Phylogenetically, the Myricales was considered most closely allied with the Juglandales and the Fagales. The family Myricaceae was placed in the order Juglandales based on anatomical similarities.

Cuddihy, L. W., G. L. Santos, and C. P. Stone. 1991. Control of firetree (*Myrica faya* Aiton) with herbicides in Hawai'i Volcanoes National Park. Technical Report 82. University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu. 46 pp.

Efforts to find herbicides effective for the control of fayatree in Hawai'i Volcanoes National Park were reviewed. Five herbicide solutions were applied to cut stumps of fayatree at two sites, representing moist and dry locations. These were imazapyr in water, imazapyr in citrus oil, triclopyr, metsulfuron, and glyphosate. All treatments were effective, but at varying levels. Imazapyr in water provided 100% control at both the moist and dry sites tested. Impacts of the herbicides on surrounding native plants were also assessed.

Cuddihy, L. W., and C. P. Stone. 1990. Alteration of native Hawaiian vegetation: Effects of humans, their activities and introductions. University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu.

The authors discussed Polynesian and European impacts on native Hawaiian ecosystems by land-altering activities and by introduction of plant, animal, and insect species alien to Hawai'i. The uses of fayatree as a reforestation species (pp. 51-52), its spread by alien birds (p. 70), its impact on the native ecosystem, and control efforts (pp. 84-85) were described.

Davidson, R. W., W. A. Campbell, and G. F. Weber. 1942. *Ptychogaster cubensis*, a wood-decaying fungus of southern oaks and waxmyrtle. *Mycologia* 34:142-153.

Fungi not previously known to invade living trees were occasionally found in decaying but living hardwoods in the southeastern U. S., indicating weakly pathogenic qualities. Study and comparison of cultures from decaying oaks and from southern waxmyrtle (*Myrica cerifera*) indicated that the same fungus, *Ptychogaster cubensis*, was isolated from these unrelated hosts and thought to be the cause of the decay. It was therefore considered reasonable to expect that the fungus also occurred in other hosts.

Davis, C. J., E. Yoshioka, and D. Kageler. 1992. Biological control of lantana, prickly pear, and Hamakua pamakani in Hawai'i: A review and update. Pp. 411-431 In: C. P. Stone, C. W. Smith, and J. T. Tunison, eds., Alien plant invasions in native ecosystems of Hawai'i: Management and research. University of Hawai'i Press, Honolulu.

Whereas biocontrol programs for the three weed species listed in the title of the paper were considered successful, those for other weeds in Hawai'i, including fayatree, have failed thus far. At the time of writing, no introduced biocontrol insects had been recovered from this species, indicating failure of establishment.

Dennis, R. W. G., D. A. Reid, and B. Spooner. 1977. The fungi of the Azores. *Kew Bulletin* 32:85-136.

Lists of known fungi of the Azores archipelago, native and introduced, were presented including those occurring on fayatree. A few selected species were described and illustrated. It is notable, however, that pathogenic fungi have been found on fayatree in recent explorations for biocontrol agents in Macaronesia which were apparently overlooked by Dennis *et al.* (see Gardner and Hodges 1990).

Deschka, G. 1976. Lithocolletidae von Madeira (Lepidoptera). *Entomologische Berichten* 36:90-96.

A new species of the moth genus *Phyllonorycter* (named *P. myricae*) was described from fayatree from Madeira. Illustrations were provided of the leaf mines made by this species. The new species was described as similar to *P. picturatella* which was earlier reared from leaf mines of *Myrica carolinensis* in the U. S. These two species were reported as the only members of *Phyllonorycter* known at the time of writing to mine leaves of *Myrica* spp. (in German with English abstract)

Dias, E. 1991. Carta da vegetação da ilha Terceira. Jornadas Atlânticas de Protecção do Meio Ambiente. Secretaria Regional do Turismo e Ambiente, Direcção Regional de Ambiente. Camara Municipal de Angra do Heroísmo.

This work constitutes the beginning of the first project of mapping the Azores. The results preliminary work on the island of Terceira were presented here. Fayatree - *Erica azorica* (broom) forests are characterized by a dominance of faya in continuous stands of individuals with medium height and very similar appearance. This results in a well-defined upper stratum and a regular,

closed upper arrangement. The *E. azorica* element of this stratum has a tendency to enlarge its cover with exposure to dominant winds. Since these two species possess only *folhas de luz* (leaves adapted to light), the foliage forms only a narrow but closed tree top. The lower strata - shrubs and herbaceous growth - are poorly defined, of irregular distribution, with low density and diversity. The ecology of fayatree in the Azores was stated to have been discussed for the first time by Guppy (1917) in his description of the vegetation zonation of Pico island. The fayatree zone described by Sjögren (1973) was also referred to. On Pico Matias Simao the fayatree is progressively substituted by *Erica* broom, which eventually becomes the dominant species. The presence of *Pittosporum undulatum* an alien forest species which is capable of replacing native species, was also discussed. (in Portuguese)

Dodge, B. O. 1934. *Gymnosporangium myricatum* in relation to host parenchyma strands. Mycologia 26:181-190.

The author conducted a histological study of the infection of southern white cedar, the "primary" (defined as the economically important) host of the rust fungus *Gymnosporangium myricatum* upon which telia are produced. *Myrica* sp. is the "alternate", or economically unimportant, host upon which spermogonia and aecia are produced. Occurrence of the rust on the alternate host was not discussed in this article. The author considered *G. myricatum* to be synonymous with *G. ellisii*.

Doty, M., and D. Mueller-Dombois. 1972. Atlas for bioecology studies in Hawai'i Volcanoes National Park. Miscellaneous Publication 89. Hawai'i Agricultural Experiment Station, College of Tropical Agriculture, University of Hawai'i, Honolulu. 507 pp.

The authors presented a synthesis of data originally reported in 1966. The physical and biological factors of Hawai'i Volcanoes National Park were described, with a checklist of park flora and fauna. In 1961, when the checklist of vascular flora was compiled by F. R. Fosberg, only a single fayatree was seen in the park on the Crater Rim Trail. This may have been the first published report of fayatree in the park.

Drurg, H. 1869. Handbook of the Indian flora, Vol. III. Richardson and Co., London.

Myrica esculenta var. *sapida* (Wall.) (= *M. sapida* Wall.) and *M. integrifolia* Roxb. were reported from India.

Duffy, B. K., and D. E. Gardner. 1993. Botrytis fruit rot and other disorders of *Myrica faya* in Hawai'i. Abstracts of the 6th International Congress of Plant Pathology, July 28-August 6, 1993; Montreal, Canada.

Biological control approaches should evaluate limiting potentials of agents already present in the environment as well as potential limitations of introduced agents. Fruit rot, caused by *Botrytis cinerea* was the first disease of fayatree identified from Hawai'i. It caused up to 59% fruit loss in 1992. Infection also interfered with dissemination by birds. Fruit infection appeared to be aided by feeding by at least two lepidopteran species. Other disorders of fayatree in Hawai'i noted were leaf spots, dieback, defoliation, and root rots. Causes of these disorders were under investigation.

Duffy, B. K., and D. E. Gardner. 1994. Locally established *Botrytis* fruit rot of *Myrica faya*, a noxious weed in Hawai'i. Plant Disease 78:919-923.

Botrytis (cinerea) fruit rot of fayatree, a newly recognized disease already affecting fayatree in Hawai'i, may be functioning as an effective biocontrol for this alien plant. The fungus appears not to attack the fleshy fruits of associated native shrubs significantly, and thus exhibits host-specificity. Its association with larvae of *Cryptoblabes anidiella* and *Amorbia emigratella*, both lepidopteran species feeding on fayatree, may account in part for distribution and establishment on this species. Exploitation of biocontrol agents already present in the environment was encouraged as an alternative to the cumbersome and lengthy screening process under quarantine necessary for foreign agents prior to their release in the environment.

Duffy, B. K., and D. E. Gardner. 1995. Decline of invasive faya in Hawai'i. Newsletter of the Hawaiian Botanical Society 34:1,3-5.

A decline of fayatree, characterized by chronic defoliation often beginning at the base of the tree, general and extensive chlorosis, and often rapid death in which many leaves remain attached to the branches has been noted in recent years in fayatree-infested areas of Hawai'i Volcanoes National Park. An overview of possible causes of the decline, both biotic, such as insects and diseases of organic origin, and abiotic, such as soil factors and drought, was presented for consideration by readers on a less technical, preliminary basis.

Duffy, B. K., and D. E. Gardner. Spontaneous decline of invasive *Myrica faya* in Hawai'i. (Manuscript in review, 1995).

A technical report was prepared intended for publication in a professional journal detailing the known facts concerning the apparent decline of fayatree in Hawai'i, and describing methods and approaches considered thus far in attempting to determine the nature and cause of the dieback. Such understanding is necessary to assess the potential usefulness of the decline in biocontrol of fayatree.

Duke, J. A. 1985. Handbook of medicinal herbs. CRC Press, Inc., Boca Raton, Florida.

The papillae of fayatree and other species of *Myrica* of sections Faya and Cerophora secrete a waxy substance. The wax produced by *Myrica* is composed of palmatine, myristicin, and palmitic acid.

Dunevtiz, V., and J. Ewel. 1981. Allelopathy of wax myrtle (*Myrica cerifera*) on *Schinus terebinthifolius*. Florida Scientist 44(1):13-20.

Nutrient solutions leached through soil in which wax myrtle (*Myrica cerifera*) was rooted was found to inhibit the growth of *Schinus terebinthifolius*. Aqueous extracts of wax myrtle leaves reduced the vigor of *S. terebinthifolius* and an increase in susceptibility to pests was indicated. The ecological similarity between these two trees in Florida suggested that the native wax myrtle may serve as an effective biological control for *S. terebinthifolius*, an undesirable alien species.

Eleuterius, L. N. 1971. Notes on occurrence of *Gymnosporangium ellisii* in Mississippi. Bulletin of the Torrey Botanical Club 98(5):281-282.

Telial galls of the rust fungus *Gymnosporangium ellisii* was collected from white cedar (*Chamaecyparis thyoides*) in Mississippi. Witches' brooms were also present on the telial host. Aecia were collected on *Myrica cerifera* in the same locations as infected white cedar. The *M. cerifera* was considered an insignificant vegetational component of the forest in these locations, but leaves were reportedly heavily infected by aecia, which formed sori on the lower leaf surfaces and young stems. Of the species of *Gymnosporangium*, only *G. ellisii* was reported to produce its aecial state on a member of the Myricaceae.

Elias, T. S. 1971. The genera of Myricaceae in the southeastern United States. *Journal of the Arnold Arboretum* 52:305-318.

The author did not mention fayatree specifically, but uses of other species, such as *Myrica gale* and *M. cerifera*, for candle wax and in the manufacture of soap are undoubtedly also applicable to fayatree. In addition to his discussion of the Myricaceae of the southeast, the author included a thorough description of the entire family Myricaceae, as well as several references to other studies of the family.

Encyclopaedia Britannica. 1978. Angiosperm. Encyclopaedia Britannica, Inc. London. Vol. 1, pp. 882-883.

The genus *Myrica* is classified as the only genus in the family Myricaceae, which is the only family in the order Myricales (which was probably derived from the Hamamelidales), in the subclass Magnoliida, class Magnoliopsidae, under the division Magnoliophyta (Angiospermae).

Farr, D. F., G. F. Bills, G. P. Chamuris, and A. Y. Rossman. 1989. Fungi on plant and plant products in the United States. American Phytopathological Society Press, St. Paul, Minnesota.

In a comprehensive compilation of fungi on plants in the U. S., the following fungi were listed as occurring on species of *Myrica*:

On *M. cerifera*

- Phytophthora* sp. (root rot)
- Pythium* sp. (root rot)
- Appendiculella calostroma* (black mildew)
- Asterella myricae* (on leaves)
- Asteridiella manca* (black mildew)
- Botryosphaeria dothidea* (dieback)
- B. obtusa* (on limbs)
- B. ribis* (on roots and limbs)
- Calycellina carolinensis* (on leaves)
- Dactylospora stygia*
- Dasyscyphus* sp.
- Glomerella* sp. (leaf spot)
- Gnomonia myricae* (on leaves)
- Hypoxylon rubiginosum*
- H. truncatum*
- Leptosphaeria* sp.
- Mycosphaerella myricae* (leaf spot)
- M. pardalota* (on leaves)
- Nectria erubescens* (leaf spot)
- Trichomerium grandisporum* (sooty mold)
- Valsa ceratosperma*
- Zoellneria callochaetes* (on fallen leaves)
- Gymnosporangium ellisii* (rust)
- Aleurobotrys botryosus* (on dead stems)
- Armillaria tabescens* (root rot)
- Dendrophora versiformis*
- Hymenochaete rubiginosa*
- Microporellus obovatus* (on trunks)

Pachykytospora alabamae (on wood)
Perenniporia tenuis (on dead wood)
Pycnoporus sanguineus (on wood of saplings)
Septobasidium castaneum (parasitic on scale insects)
S. pseudopedicellatum (on scale insects infesting limbs)
Septobasidium sp. (on scale insects infesting limbs)
Stereum hirsutum
S. ochraceo-flavum (on stems)
S. ostrea
Trametes hirsuta
Cercospora sp. (leaf spot)
Chaetochalara aspera (on dead leaves)
Fusarium oxysporum (root rot, wilt)
Fusarium sp. (stem lesions)
Phymatotrichopsis omnivora (root rot)
Ptychogaster cubensis (wound rot)
Ramularia monilioides (leaf spot)
Thozetella cristata
Aplosporella lathamii (on dead twigs)
Diplodia sp. (dieback, twig blight)
Fusicoccum sp. (stem canker)
Macrophoma sp. (leaf spot)
Pestalotia stellata (on leaves)
Phyllosticta myricae (leaf spot)
Septoria myricae (leaf spot)
Sphaeropsis tumefaciens (stem gall, witches' broom)
Rhizoctonia ramicola (leaf spot)
R. solani (seedling blight)

On *M. californica*

Gnomonia myricae (on leaves)
Lophodermium foliicola (on leaves)
Propolis phacidioides (on leaves)
Cronartium comptoniae (rust)
Phellinus ferreus

On *M. gale*

Ciboria acerina (on catkins)
Cryptodiaporthe phomaspora (on dead stems and twigs)
Leptosphaeria myricae (on twigs)
Massarina myricae (on dead twigs)
Trichopezizella barbata
Cronartium comptoniae (rust)
Gymnosporangium ellisii (rust)
Ramularia destructiva (on twigs)
R. monilioides (leaf spot)
Diplodia sp. (dieback, twig blight)
Septoria myricata (leaf spot)

On *M. pusilla*

Stereum ochraceo-flavum (on stems)

On *Myrica* sp.
Eriopezia microspora
Hypoxylon stygium
Nitschkia broomeiana
Corticium floridensis (on wood)
Exidia glandulosa (on bark)
Inonotus rickii (on wood)
Stereum ochraceo-flavum (on stems)
Sporidesmium inflatum (on bark)

Fernald, M. L. 1970. Gray's manual of botany. Eight Edition, D. Van Nostrand Co., New York.

Representatives of the genus *Myrica* in the eastern U. S. were listed as *M. gale* L., *M. gale* var. *subglabra* (Chev.) Fern., *M. pennsylvanica* Loisel., *M. pennsylvanica* x *M. macfarlanei* Youngken, *M. heterophylla* Raf., *M. heterophylla* var. *curtissi* (Chev.) Fern., *M. cerifera* L., and *M. pusilla* Raf. The genus *Comptonia* is also listed as *C. peregrina* (L.) Coult. and *C. peregrina* var. *asplenifolia* (L.) Fern.

Fessenden, R. J., R. Knowles, and R. Brouzes. 1973. Acetylene-ethylene assay studies on excised root nodules of *L.* Proceedings of the Soil Science Society of America 37:893-898.

In a highly technical study, the acetylene reducing activity of excised root nodules of *Myrica asplenifolia* (*Comptonia peregrina*), a low-growing deciduous shrub native to northeastern North America, was measured in the field and the laboratory. Efficiency of sampling methods and assay techniques between field and laboratory studies was compared to determine suitable approaches for obtaining accurate and consistent results of such assays. Field-collected nodules were determined to be unsuitable for physiological experiments unless a large effect of treatments on acetylene reducing activity is large and readily detectable.

Fletcher, W. W. 1955. The development and structure of the root-nodules of *Myrica gale* L. with special reference to the nature of the endophyte. Annals of Botany New Series, 19:501-513.

The status of knowledge and history of investigation of root nodulation in myricaceous species at the time of writing (1955) was reviewed. Various authors had classified the endophyte (symbiont) as fungal, bacterial, actinomycetal, or plasmodial in nature, but the organism had not been conclusively isolated at that time. The name *Actinomyces myricarum* had been applied by one of the earlier investigators. The attempts to characterize the endophyte were described, and a new approach, that of growing test plants from seed in water culture in a greenhouse, was followed in an effort to obtain more reliable results than were considered possible from the previous field-oriented studies.

Fletcher, W. W., and I. C. Gardner. 1974. The endophyte of *Myrica gale* nodules. Annali di Microbiologia ed Enzimologia 24:159-172.

The authors described the morphology and physiology of the nitrogen fixing nodules of roots of *Myrica gale*. The endophyte had as of the date of writing never been successfully obtained in pure culture. The many attempts to do this over the years were reviewed, and possible reasons for the failures discussed. Characterization and identification of the endophyte was stated to be still dependent on cytological studies. Although early opinion varied greatly, in recent years (to the time of writing) the actinomycetal nature of the endophyte had been established. This study included both light and electron microscopic investigations of nodule tissue of *M. gale*, and the relationship between this endophyte and those of other non-leguminous plants was discussed.

Flora of Taiwan Editorial Committee, eds. 1976. Flora of Taiwan, Vol. II. Epoch Publishing Co., Ltd., Taipei, Taiwan.

The species *Myrica rubra* Sieb. & Zucc. occurs in Southern China and Southern Japan, whereas *M. rubra* var. *acuminata* Nakai was listed as occurring in Korea, the Philippines, and Taiwan, where it is found in thickets throughout the island. *Myrica adenophora* Hance occurs in China, whereas *M. adenophora* var. *kusanoi* Hayata is endemic to Taiwan.

Foot, D., and P. Yang. Interference between the two-spotted leafhopper, *Sophonia rufofascia*, and an introduced biological control agent, *Caloptilia schinella*, on non-indigenous faya bush, *Myrica faya*, in Hawaii. Manuscript in preparation intended for publication in a professional journal.

The interaction between the leaf roller, *Caloptilia schinella*, a biological control agent of fayatree, and the two-spotted leafhopper, *Sophonia rufofascia*, an adventive species that has recently begun causing foliar chlorosis and leaf wilt on fayatree in Hawai'i was investigated. Adult female *C. schinella* laid significantly more eggs on healthy fayatree foliage compared to chlorotic leaves resulting from feeding by *S. rufofascia*. Significantly more larvae, pupae, and adult *C. schinella* were recovered from healthy fayatree leaves and the duration of the larval stage was slightly shorter on healthy foliage. Larval survivorship was also significantly higher on non-chlorotic fayatree. Adult sex ratios also differed slightly between healthy and chlorotic leaves. These results suggested that recent feeding activity of the two-spotted leafhopper on fayatree has interfered with the establishment of *C. schinella* and may be limiting its effectiveness as a biological control agent of fayatree in Hawai'i.

Ford, E. J. 1985. Descriptions of the larva and pupa of *Rynchus apiculatus* with biological notes (Coleoptera: Curculionidae). Coleoptera Bulletin 39(1):29-32.

The weevil *Rynchus apiculatus* was reared from wax myrtle (*Myrica cerifera*) from coastal South Carolina. The larval and pupal stages were described and biological notes provided.

Forjaz, V. H., J. L. Monjardino, and N. S. M. Fernandes. 1970. Contribuição para o estudo das jazidas fossilíferas das ilhas do Faial, Pico, S. Jorge e Terceira (Açores). Comunicações dos Serviços Geológicos de Portugal 64:28-37 + 2 plates.

Fossils in lava outcrops on the islands of Faial, Pico, São Jorge, and Terceira of the Azores were identified as representing a number of recognizable endemic plant species, among which was fayatree. The ancient presence of fayatree in the Azores, in association with other laurosilva forest species, was thus established, although specific ages of the fossils were apparently not provided. (in Portuguese with English abstract)

Fosberg, F. R. 1937. Immigrant plants in the Hawaiian Islands. I. University of Hawaii Occasional Paper No. 32. Honolulu. 11 pp.

A brief taxonomic description of fayatree was given, with a discussion of its initial introduction to the Hawaiian Islands. Fayatree distribution is recorded on the islands of Kaua'i, O'ahu, Maui, and Hawai'i. The invasive nature of fayatree was recognized and concern was expressed about its rapid spread on the island of Hawai'i.

Friis, E. M. 1985. Angiosperm fruits and seeds from the middle Miocene of Jutland (Denmark). Det Kongelige Danske Videnskabernes Selskabs Skrifter 24:1-102.

Myricaceous leaves and fruits were reportedly abundant in European Miocene sediments. Some endocarps were preserved showing characteristics similar to *Myrica cerifera* and *M. pensylvanica*, species now confined to eastern North America. (Original reference not seen; information from Macdonald (1989).)

Gardner, D. E. 1978. Evaluation of a new technique for herbicidal treatment of *Myrica faya* trees. Pp. 114-119 In: C. W. Smith, ed., Proceedings of the Second Conference in Natural Sciences, Hawai'i Volcanoes National Park. University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu.

Tests were conducted to determine the potential of the systemic herbicide Round-up as a control agent for fayatree. Results suggested that small, undiluted applications of Round-Up on stems cut close to the main stem could be an effective control method.

Gardner, D. E. 1982. Exotic plants in Hawai'i's National Parks: A major challenge. Park Science 2(2):18-19.

The problem caused by disruptive alien plants in Hawai'i's national parks, and attitudes of the public and park managers toward alien species was discussed. Types of control methods employed by park managers and the relative effectiveness of each was summarized. Fayatree was given as an example of an aggressive and unwelcome alien in the Hawaiian landscape.

Gardner, D. E. 1984. Current biological investigations: exploration for control agents in the native habitats of firetree, and evaluation of rust diseases of *Rubus* spp. in the southeastern U. S. pp. 53-60 In: C. W. Smith, ed., Proceedings of the Fifth Conference in Natural Sciences, Hawai'i Volcanoes National Park, June 5-7. University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu.

An exploratory trip to the Azores, Madeira, and Canary Islands to locate potential biological control agents for fayatree was reported. This was the first in the recent series of trips to Macaronesia since Krauss's exploration in the early 1960s. Several pathogenic fungi and insects were observed and reported.

Gardner, D. E. 1985. Observations on some unusual flowering characteristics of *Myrica faya*. Newsletter of the Hawaiian Botanical Society 24:14-17.

Whereas fayatree tends toward dioecism, that is, a condition in which staminate and pistillate flowers occur on separate plants, a subdioecious flowering condition was observed in Hawai'i Volcanoes National Park, with some staminate flowers occurring on predominately pistillate plants and some pistillate flowers occurring on predominately staminate plants. Furthermore, stamens connate with the fruit exocarp were reported, giving the unusual appearance of individual stamens borne on the fruit surface.

Gardner, D. E. 1990. Role of biological control as a management tool in national parks and other natural areas. Technical Report NPS/NRUH/NRTR-90/01, U. S. Department of the Interior, National Park Service, Washington, D. C.

Both the problems and potential of biocontrol in addressing alien species invasions in national parks and other natural areas (as distinct from agricultural and horticultural application) were described. Fayatree was cited as an example of such an invasive species which has received considerable attention as a subject for biocontrol.

Gardner, D. E. 1992. Plant pathogens as biocontrol agents in native Hawaiian ecosystems. Pp. 432-451 *In*: C. P. Stone, C. W. Smith, and J. T. Tunison, eds. Alien plant invasions in native ecosystems of Hawai'i: Management and research. University of Hawai'i Press, Honolulu.

Fayatee was among the species targeted for biocontrol by the National Park Service. Both early and recent efforts to find potential biocontrol agents in the native habitats of this species were reviewed. Current efforts in the use of pathogens as biocontrol agents, as distinct from insects, were discussed, as were the possibilities of successful control of several other target alien species in native Hawaiian systems through biological approaches.

Gardner, D. E., and C. J. Davis. 1982. The prospects for biological control of non-native plants in Hawaiian national parks. Technical Report 45. University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu. 55 pp.

The potential for introduction of biological control agents (phytopagous insects and phytopathogens) to control a number of noxious alien plant species in the Hawaiian Islands was outlined. The report also reviewed previous attempts at biocontrol in Hawai'i and also discussed National Park Service considerations for introducing biocontrol agents, together with the research and management of such agents. Twenty-five alien species, including fayatee, were mentioned in particular as potential candidates for biological control.

Gardner, D. E., and C. S. Hodges, Jr. 1990. Diseases of *Myrica faya* (firetree, Myricaceae) in the Azores, Madeira and the Canary Islands. *Plant Pathology* 39:326-330.

Five fungi pathogenic to fayatee (*Nectria galligena*, *Cryphonectria* sp., *Ramularia destructiva*, *Botryosphaeria ribis*, and *Armillaria mellea*) most of which were previously unrecorded but found during two exploratory trips (in 1984 and 1987) to the Azores, Madeira, and Canary Islands were reported.

Gardner, D. E., and C. S. Hodges, Jr. 1993. Biocontrol of *Myrica faya* in Hawai'i: Investigation of pathogens from the Azores, Madeira and Canary Islands. Abstracts of the First Symposium "Fauna and Flora of the Atlantic Islands," October 4-9, 1993, Funchal, Madeira, Portugal. p. 25.

Diseases of fayatee found both in earlier exploration for biocontrol agents and in current work include a twig dieback caused by *Dothiorella* sp., leaf spots caused by *Ramularia destructiva*, and stem and branch cankers caused by *Nectria galligena* and *Cryphonectria* sp. The cosmopolitan root-rotting fungus *Armillaria mellea* was also found on fayatee, but its broad host range precluded its consideration for biocontrol. Leaf spots caused by *Septoria* sp. from *Myrica cerifera* in the U. S. may also attack fayatee.

Gardner, D. E., and V. A. D. Kageler. 1982. Herbicidal control of firetree in Hawai'i Volcanoes National Park: A new approach. *Ecological Services Bulletin*, No. 7. U. S. Department of the Interior, National Park Service, Washington, DC. 13 pp.

Results were reported of research on three herbicides (Round-up, Tordon 22K, and Kuron) used for control of fayatee and other problematic introduced species. The methods of applying herbicide directly to cut proximal stems and into holes drilled in the main or major stems were evaluated. Round-up was found to be the most rapidly absorbed herbicide into cut stem ends of the three chemicals tested.

Gardner, D. E., and C. W. Smith. 1985. Plant biocontrol quarantine facility at Hawai'i Volcanoes. *Park Science* 6:3-4.

The newly-completed insect quarantine facility at Hawai'i Volcanoes National Park was described, emphasizing that this was the first such laboratory known to be constructed by a non-agricultural agency for the purpose of addressing weed problems in natural areas. Although not specifically mentioned, fayatree was among the first of the weed species to be considered for biocontrol research in the new facility.

Gardner, D. E., G. P. Markin, and C. S. Hodges, Jr. 1988. Survey for potential biological control agents for *Myrica faya* in the Azores and Madeira. Technical Report 63. University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu. 18 pp.

A field collecting trip to Macaronesia was reported which was a follow-up to a trip made to the Azores, Madeira, and the Canary Islands in 1984. Potential biological control agents for fayatree were sought. Specifically, specimens of the fungi *Ramularia destructiva* and *Nectria* sp. were collected for evaluation. Five insect species which feed on fayatree were also identified as potential biological control agents. Two of these were successfully established in the Hawai'i Volcanoes National Park quarantine facility for further testing.

Gardner, I. C., and G. Bond. 1966. Endophyte adaptation in *Myrica*. *Naturwissenschaften* 53:161.

The ability of the nitrogen-fixing endophyte from a specific host to form symbiosis and fix nitrogen in another host was tested among species of *Myrica*, based on similar previous tests among species of *Alnus*, *Casuarina*, and *Coriaria*. *Myrica cerifera* and *M. cordifolia* were inoculated with endophytes from *M. gale*, with the result that *M. cerifera* and *M. cordifolia* nodules were unable to fix significant amounts when inoculated with the symbiont from *M. gale*. It was concluded that some adaptation to particular host species occurred among *Myrica* endophytes.

Graham, A. 1987. Tropical American Tertiary floras and paleoenvironments: Mexico, Costa Rica, and Panama. *American Journal of Botany* 74:1519-1531.

Fossil pollen records indicated that *Myrica* was among the genera of north-temperate trees and shrubs that were present in eastern Mexico by the late Miocene. *Alnus*, *Myrica*, and *Ilex* were present in the Pleistocene of Panama, and first appeared in South America in the Plio-Pleistocene.

Guba, E. F. 1932. Monograph of the genus *Pestalotia*. *Mycologia* 24(4):353-397.

In a monograph of the genus *Pestalotia*, the author included *P. myricae* with a technical description, as collected on partly fresh leaves of *Myrica cerifera* from Green Cove Springs, Florida in 1882 by G. Martin. The original description of the fungus was reportedly unsatisfactory, with the conidia wrongly described.

Guppy, H. B. 1917. Plants, seeds, and currents in the West Indies and the Azores. Williams & Norgate, London.

The five vegetation zones of Seubert and Hochstetter (1843), including those comprised of fayatree on the island of Pico (Azores), were simplified to three zones. A lower woods zone on Pico, termed the Faya Zone, extended from the coast to between 600 and 660 m elevation. Fayatree, *Erica azorica*, and *Persea azorica* were the most frequent species in this zone. (Original reference not seen; information from Tutin (1953).)

Haggar, J. P. 1988. The structure, composition and status of the cloud forests of Pico Island in the Azores. *Biological Conservation* 46:7-22.

Previous studies of the altitudinal changes in vegetation were at variance with one another. Marler and Boatman (1952) considered that *Myrica-Laurus* forest extended up to 1000 m, where *Erica azorica* dominated. This high altitudinal limit was probably due to the site being on the drier side of Pico and in an area much disturbed by livestock. Tutin (1953) considered the *Myrica-Laurus* forest to reach only to 600 m, with *Erica-Juniperus* forest above this. These studies failed to consider *Ilex* or *Vaccinium* as dominant in the forest associations, or to form a significant component in the vegetation. Man's activities, i.e., clearing and grazing, are important influences leading to differences in observations.

Halim, A. F., and R. P. Collins. 1970. Volatile oil composition of foliage from sweet fern. *Lloydia* 33:7-10.

Taxonomically, the Myricaceae is a confusing group with the number of genera unsettled. Most authors have treated the family as unigeneric (*Myrica*), but others have raised the three subgenera (*Myrica*, *Gale*, and *Comptonia*) to generic rank.

Halim, A. F., and R. P. Collins. 1973. Essential oil analysis of the Myricaceae of the eastern United States. *Phytochemistry* 12:1077-1083.

The family Myricaceae consists of about 50 species of trees and shrubs growing mainly in subtropical to mild-temperate regions of the world. It is represented in North America by eight or nine species, seven or eight varieties, one natural hybrid, and one artificially produced hybrid. More than 45 names have been applied to these plants, indicating the variable nature of the members of this family.

The essential oil content of several members of the Myricaceae was examined for chemotaxonomic purposes. This analysis supported the concept that the family should be divided into three genera. The study also suggested that *Myrica pusilla* and *M. macfarlanei* were not valid species.

Hall, I. V. 1975. The biology of Canadian weeds. 7. *Myrica pensylvanica* Loisel. *Canadian Journal of Plant Science* 55:163-169.

Myrica pensylvanica, commonly known as bayberry, was described as a native shrub occurring mainly along or near the seacoast of the Maritime Provinces of Canada. It was thought to have moved into the Atlantic provinces from the eastern U. S. following the retreat of the last glacial ice. Although the plant has had some beneficial uses, particularly the use of the wax from fruit by early settlers for candle making, *M. pensylvanica* is the major weed problem in lowbush blueberry fields on Prince Edward Island. It was reportedly one of the first species of woody shrubs to invade neglected pastures, but within 15 years is typically shaded out by white spruce. Lateral growth of *M. pensylvanica* is by rhizome, and following burning, new shoots grow from dormant buds of the stem or rhizome. The waxy upper surface of leaves of *M. pensylvanica* resist the effects of salt spray. The herbicides 2,4-D and 2,4,5-T in kerosene or fuel oil applied to cut stumps were recommended for control. The major insect pest of *M. pensylvanica* was reported to be the red-humped caterpillar (*Schizura concinna*), which also feeds on apple in Nova Scotia. Both *Apioportha phomaspora* and *Diaportha eres* have been reported as fungal pests, as well as the leaf spotting fungi *Mycosphaerella myricae*, *Phyllosticta myricae*, and the rust fungus *Gymnosporangium ellisii*.

Hansford, C. G. 1955. Tropical fungi. V. New species and revisions. *Sydowia Annales Mycologici* 9(1/6):1-88.

Notes were compiled on fungi in herbaria from Stockholm, Kew, Paris, and Harvard. Included in an extensive list of fungi, the dark mildew *Irenopsis myricae* had been collected on *Myrica deflexa* in Puerto Rico and was described as a new species.

Haselwood, E. L., and G. G. Motter, eds. 1976. Handbook of Hawaiian Weeds. 4th Printing by Lyon Arboretum Association, Honolulu. 479 pp. (Originally published in 1966 by the Hawaiian Sugar Planters' Association, Honolulu.)

The authors considered *fayatree* a significant weed in the Hawaiian Islands, and included it (pp. 118-119) in a comprehensive list of such weeds with their descriptions and illustrations.

Hawai'i State Department of Agriculture. Monthly Report of the Plant Pest Control Branch. Section: *Noxious Weed Control Activities*.

An unpublished report is prepared each month by the DOA Plant Pest Control Branch detailing control activities (i.e., locations, numbers of plants destroyed, methods of control) for each of several noxious weeds, including *fayatree*.

Hawai'i State Department of Agriculture, Pesticide Branch. (undated). Chemical controls research summary. Mimeographed report. 3 pp.

Fayatree was listed among a number of troublesome weeds in Hawai'i for which herbicidal treatments were recommended. The following recommendation was given for *fayatree*: Garlon 3A 50% v/v in water, continuous frill. Chopper 9% or Garlon 3A 10% v/v in water, cut stump.

Hawai'i Steering Committee on Firetree Control. 1989. Preventing the loss of agricultural and forest lands by controlling the plant pest firetree (*Myrica faya*). Unpublished proposal for the control of *fayatree*. (Bud Doty, Committee Chairman, Volcano, Hawai'i.)

The detrimental effects of *fayatree* on the native ecosystem, rangeland, and natural watershed of the Hawaiian Islands were discussed. Currently used control methods, and those being investigated were reviewed. Specific recommendations for the local control of *fayatree* by mechanical removal and herbicide treatment were given.

Henríquez, M. N. G., J. D. R. Pérez, and C. S. Rodríguez. 1986. Flora y vegetacion del archipelago Canario. Edrica, Las Palmas de Gran Canaria.

The authors compiled a comprehensive treatment of the flora of the Canary Islands, as well as of the phytogeography of Macaronesia. *Fayatree* was listed among the native species of the Canaries, and was included in general discussions of vegetation types and zones throughout the islands, as well as uses of native plants in local culture. (in Spanish)

Henry, M.-F. 1977. Cytologie ultrastructurale de l'endophyto présent dans les nodosités radiculaires de *Myrica gale* L. Bulletin de la Société de France 124:291-300.

Electron microscopic studies of the root nodules of *Myrica gale* were carried out to elucidate the ultrastructure and the nature of the endophyte. The microorganism was seen as filamentous elements, often septated, and sometimes branched. This morphology, the membrane system, and lack of a nucleus limited by a membrane are features consistent with bacterial and actinocycetal ultrastructures. The endophyte was surrounded by capsular material similar to those of other non-leguminous root nodules. (in French with English summary)

Heywood, V. H., ed. 1979. Flowering plants of the world. Oxford University Press, Oxford.

The taxon *Gale*, considered at the generic level by some authors, was recognized here as a species of *Myrica*, as *M. gale* L.

Hjelmqvist, H. 1948. Studies on the floral morphology and phylogeny of the Amentiferae. *Botaniska Notiser Supplement Vol. 2:1-171.*

Floral morphology and development of eight ament-bearing plant families (Myricaceae, Juglandaceae, Balanopsidaceae, Leitneriaceae, Fagaceae, Betulaceae, Corylaceae, and Salicaceae) were described. At the time of writing, the Amentiferae was considered a natural grouping by plant taxonomists. This view has since been amended. The variation in floral morphology of the Myricaceae was described on pp. 11-29. The genus *Myrica* was separated into three sections—Morella, Faya, and Cerophora—based on floral morphology. Fayatree was described as having an unusual morphology as the male inflorescences are compound and the position and orientation of the stamens deviates from morphology typical of *Myrica*. The characteristic fused carpels (syncarps) in fayatree constitute an unusual female floral morphology. The atypical development of androgynous (bisexual) inflorescences was also discussed.

Myrica microbracteata was reported in Zimbabwe, and *M. lobii* (= *M. esculenta* var. *lobbii*) and *M. kilimandscharica* Engl. were reported from South Africa. *Myrica salicifolia* was reported from Africa. *Myrica javanica* was reported in Indonesia, *M. pavonis* in Chile. *Myrica pubescens* and *M. punctata* in Costa Rica to Chile and Argentina.

Hodges, C. S., Jr., and D. E. Gardner. 1985. *Myrica faya*: potential biological control agents. Technical Report 54. University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu. 37 pp.

The first exploratory trip to Macaronesia since Krauss's travel in the early 1960s was made to the Azores, Madeira, and Canary Islands to determine the distribution of fayatree in its native habitat and to investigate potential biological control agents. Six fungi and two insects were identified. Two fungi, *Nectria* sp. and *Ramularia destructiva* were recommended for in-depth study.

Hodges, C. S., Jr., and D. E. Gardner. 1992. Preliminary evaluation of *Cryphonectria* sp. as a biological control agent for *Myrica faya*. *Newsletter of the Hawaiian Botanical Society* 31:8-13.

An unidentified member of the genus *Cryphonectria*, a group of fungi including important bark-infecting pathogens of woody plants, was found in trunk cankers of fayatree in the Azores. Cultures of the fungus were brought to the USDA Plant Disease Research Laboratory at Ft. Detrick, Maryland, where stem sections representing 18 species from 14 families of important woody plants in Hawai'i were inoculated to determine their susceptibility. The fungus did not fruit and developed only slightly or not at all on most species, but developed well on both fayatree and *M. cerifera* (waxmyrtle), indicating host-specificity within the genus *Myrica*.

Hooker, J. D. 1890. *Flora of British India*, Vol. V. L. Reeve and Co., London.

Myrica nagi Thunb. (= *M. integrifolia* Roxb., *M. missionis* Wall., *M. farquhariana* Wall., *M. rubra* Sieb. & Zucc., and *M. sapida* Wall.) was reported from Malaysia, China, Japan, India in the subtropical Himalayas from 3,000 to 6,000 ft., the Khasia Mountains, south to Singapore.

Horie, Y. 1979. New or interesting *Emericella* from herbal drugs. *Transactions of the Myological Society of Japan* 20(4):481-492.

In a survey of plants classified as herbal drugs in Japan, the fungus *Emericella nidulans* var. *dentata* was isolated from a number of hosts, including *Myrica nagi*.

Hosaka, E. Y. 1945. Noxious weeds of Hawai'i. Report to the Board of Commissioners of Agriculture and Forestry, Honolulu.

Faytree was recognized as a noxious weed in the Territory of Hawai'i, and efforts to control this species were officially instituted by the Board of Commissioners of Agriculture and Forestry in 1945.

Hosaka, E. Y., and A. Thistle. 1954. Noxious Plants of the Hawaiian Ranges. University of Hawai'i Extension Bulletin 62. 39 pp.

Several problematic weeds in Hawai'i were described. A brief description of faytree, the reason it was considered a pest, its distribution in the islands, and recommendations for control were given.

Howarth, F. G. 1983. Classical biocontrol: Panacea or Pandora's box? Proceedings of the Hawaiian Entomological Society 24:239-244.

The author addressed the subject of biocontrol, based largely on his and others' experience with this approach in Hawai'i, and provides evidence that uncontrolled introduction of potential biocontrol organisms may result in "biological pollution," or may have other, unintentional but detrimental influences in Hawai'i's environment.

Howarth, F. G. 1985. Impacts of alien land arthropods and mollusks on native plants and animals in Hawai'i. Pp. 149-179 In: C. P. Stone and J. M. Scott, eds. Hawai'i's terrestrial ecosystems: Preservation and management. University of Hawai'i Cooperative National Park Studies Unit, Honolulu.

The author provided a comprehensive discussion of the effects of invasion by alien species on island habitats illustrated by many specific examples. Biocontrol of alien species, an approach intensively developed in Hawai'i, has resulted in some apparently spectacular successes in the control of both weeds and insects. However, the long-range, far-reaching effects of such introductions has not yet been fully evaluated, and may not be favorable. A much more thorough understanding of the ecology of the target pests and the potential biocontrol agent should be gained, prior to introduction, than has been available in the past. It is sometimes difficult to gain a consensus within the community as to what constitutes a pest.

Howarth, F. G., and A. C. Medeiros. 1989. Non-native invertebrates. Pp. 82-87 In: C. P. Stone and D. B. Stone, eds. Conservation biology of Hawai'i. University of Hawai'i Cooperative National Park Studies Unit, Honolulu.

The impact of alien species in Hawaiian environments was described. Although emphasis was placed on invasive invertebrates, many of the problems presented by these organisms are shared by invasive plants as well. Public education is a key to long-range prevention of introduction and control of alien species.

Humphries, C. J. 1979. Endemism and evolution in Macaronesia. Pp. 171-199 In: D. Bramwell, ed., Plants and islands. Academic Press, London.

The Azores were described as much colder and wetter than the southern archipelagos of Macaronesia, and are covered by clouds most of the time. There is some gradual zonation of the vegetation, but no north-south differential. The pattern is more or less the same for all the islands, the only real variation being due to differences in altitude, varied geological conditions (e.g., acidic ash on São Miguel and limestone on Santa Maria) and the forest zones being lower in the wetter western islands. The coastal halophyte communities and lowland xerophytic scrub merge at 100 m into the faytree broadleaved woodland which occurs on most of the islands up to about 500 m. This is replaced up to about 1,350 m by the cloud belt *Juniperus brevifolia* zone, and above this the *Calluna/Daboic*a belt.

Hutchinson, J. 1917. Myricaceae. Flora of Tropical Africa 6(2):307-314.

The author listed a number of species of *Myrica* from tropical Africa, including some (e.g., *M. arborea*, *M. kantiana*) not included by Chevalier in his monograph of the genus.

Hutchinson, J. 1925. Myricaceae. Flora Capensis 5(2):561-572.

The author described *Myrica* as a genus with about 50 species, 15 of which occur in South Africa, six in the Mascarene Islands, 11 in tropical Africa, and the remainder widely distributed throughout the Northern Hemisphere. Species recognized from South Africa included: *M. cordifolia* L., *M. burmanni* E. Meyer ex C. DC., *M. dregeana* A. Chev., *M. humilis* Cham. & Schlecht., *M. elliptica* A. Chev., *M. kraussiana* Buching. ex Krauss, *M. brevifolia* E. Meyer ex C. DC., *M. ovata* Wendl. f., *M. myrtifolia* A. Chev., *M. linearis* C. DC., *M. glabrissima* A. Chev., *M. zeyheri* C. DC., *M. quercifolia* L., *M. conifera* Burm. f., and *M. incisa* A. Chev. (See also Killick 1969).

Index Kewensis. 1895-1990. Genus *Myrica*.

A running list is kept beginning at "the time of Linnaeus" and continuing to the present includes all known species of *Myrica* with their geographic locations.

Ingelog, T., and S. Brakenhielm. 1973. Forests, forestry, and environmental problems on Madeira. Fauna och Flora 68(6):238-249.

The authors provided a brief summary of natural conditions and land use on Madeira, including an outline of problems and issues involving the management of native and commercially established forests. Much of the natural forest currently is found in the steep, inaccessible valleys of the northern side of the island. Tree height does not usually exceed 10 meters. The position of fayatree among other native species, including laurel (*Laurus azorica*), briar (*Erica arborea* and *E. scoparia*), and bilberry bush (*Vaccinium maderense*) was discussed. (in Swedish with English summary)

Jepson, W. L. 1951. A manual of the flowering plants of California. University of California Press, Berkeley.

Myrica californica (West Coast wax myrtle) was listed as a native species of the North American coastal forest, occurring from California north to Vancouver Island.

Keng, H. 1969. Orders and families of Malayan seed plants. University of Malaya Press, Kuala Lumpur.

Myrica esculenta var. *farquhiana* was listed as occurring on the sandy beaches of Malaysia.

Kharbuli, P. P., and R. R. Mishra. 1982. Survey of mycorrhizal association in some trees of northeastern India. Acta Botanica Indica 10(2):192-195.

Myrica nagi and *M. esculenta* were included in a survey of 18 forest species in India for association with mycorrhizal fungi. Seventeen percent of *M. esculenta* roots examined and 8% of *M. nagi* roots were found to be infected.

Killick, D. J. B. 1969. The South African species of *Myrica*. Bothalia 10:5-17.

Myrica was described as a genus of about 56 species, distributed throughout the Northern Hemisphere, the Mascarenes, tropical Africa, and South Africa. At the time of writing, the only comprehensive revision of the genus *Myrica* was stated to be that by Chevalier (1901), who recognized a rather large concentration of

species and varieties from South Africa, often basing his new taxa on single specimens. Hutchinson's (1925) treatment of the *Myrica* spp. of South Africa was also reviewed and compared with the present treatment. Collections made since that time had made Chevalier's species criteria increasingly difficult to apply, necessitating revision. Accordingly, the 19 species of *Myrica* formerly recognized from South Africa were reduced to nine: *M. integra* (A. Chev.) Killick, *M. serrata* Lam., *M. quercifolia* L., *M. diversifolia* Adamson, *M. pilulifera* Rendle, *M. brevifolia* E. Mey. ex C.DC. in DC., *M. cordifolia* L., *M. kraussiana* Buching. ex Meisn., and *M. humilis* Cham. & Schlechtld. Little variation in flower structure among the species could be found upon which to base taxonomic distinctions, necessitating a key based almost entirely on vegetative characters.

Kim, J. Y. 1969. "Myrica faya" control in Hawai'i. Down to Earth 25:23-25.

The problem caused by infestation by fayatree was briefly summarized, and State Department of Agriculture efforts at control were described using a herbicidal mixture of Tordon 212 and 2,4,5-T amine. This silvicide was reported as "very effective" when applied to a frill, or notch, cut into the basal portion of the stem.

Kirkheimer, F. 1932. On pollen from the Upper Cretaceous Dysodil of Banke, Namaqualand (South Africa). Transactions of the Royal Society of South Africa 21:41-50.

Fossil *Myrica* leaves and possibly pollen were found in deposits of the Upper Cretaceous age in Namaqualand, South Africa. (Original reference not seen; information from Coetzee and Prąglowski (1984).)

Kirk, P. M., and B. C. Sutton. 1980. *Henicospora minor*, new genus, new species (Hyphomycetes). Transactions of the British Mycological Society 75(2):249-254.

A new fungal genus, *Henicospora* was established which accommodated the former *Trichocladium cylindrocladium*, occurring on dead leaves of *Myrica rubra*. The new species was described as *H. minor*.

Krauss, N. L. H. 1964. Insects associated with firebush (*Myrica faya* Aiton). Proceedings of the Hawaiian Entomological Society 18:405-411.

Several insect taxa were reported which were introduced from Madeira, Azores, and the Canary Islands to Hawai'i during the years 1955 to 1963 for biological control of fayatree. An annotated list of insects associated with other species of *Myrica* was included from southern Africa, Portugal, Costa Rica, the continental U. S., and Hawai'i (i.e., *M. cerifera*).

Kunth, R. 1928. Repertorium speciorum novorum regeii vegetabilei luitia. Flora Venezuelensis. p. 292.

Myrica arguta, *M. caracasana*, and *M. funckii* were listed as representing the family Myricaceae in the flora of Venezuela. (in Latin)

Lachmund, H. G. 1929. *Cronartium comptoniae* Arth. in western North America. Phytopathology 19:453-466.

About 16 species of pine are primary hosts (spermatogonial-aeial hosts) of sweet fern blister rust, *Cronartium comptoniae*, in the eastern U. S. *Myrica asplenifolia* (= *Comptonia peregrina*), *M. gale*, and *M. carolinensis* were reported as alternate (uredinial-telial) hosts. In the West, the rust has been found on lodgepole pine and *M. asplenifolia* only. On the latter host, the rust reportedly forms yellowish uredinia on the upper leaf surface and brownish telial horns, which develop in dense, more or less matted tufts. Even

with heavy infection, however, little injury was reportedly evident on the host. Observations on *M. californica* in Washington State indicated this species to be immune, indicating that *M. californica* was not instrumental in spreading *C. comptoniae* into Oregon and California.

Laemmeln, F., and R. V. Bega. 1974. Hosts of *Armillaria mellea* in Hawai'i. Plant Disease Reporter 58:102-103.

Armillaria mellea, a root rot fungus with a wide host range among woody plants, was reported in Hawai'i on a number of flowering plants and gymnosperms, but not on fayatree. This information is useful in light of the discovery of *A. mellea* on fayatree in the Azores during exploration for biocontrol agents of potential use in Hawai'i (See Gardner and Hodges 1990).

LaRosa, A. M., C. W. Smith, and D. E. Gardner. 1985. Role of alien and native birds in the dissemination of firetree (*Myrica faya* Ait.—Myricaceae) and associated plants in Hawai'i. Pacific Science 39:372-378.

Foraging behavior of three native and three introduced bird species at two sites in Hawai'i Volcanoes National Park were reported where 'ohi'a and fayatree are codominant. The hypothesis that the alien Japanese white-eye (*Zosterops japonicus*) is a major disperser of fayatree seeds was not supported as these birds were rarely observed ingesting the seeds. Furthermore, in captivity, the Japanese white-eye demonstrated less preference for the firetree seed than in the wild. These results contrast with those of Woodward *et al.* (1990). Seed germination trials conducted in the laboratory did not show a significant increase in germination for ingested seeds over non-ingested seeds.

Lausi, D., P. L. Nimis, and M. Tretiach. 1989. Adaptive leaf structures in a *Myrica-Erica* stand on Tenerife (Canary Islands). Vegetatio 79:133-142.

The authors discussed the effects of ecological variation on plant morphology in a *Myrica-Erica* codominant forest belt on the island of Tenerife in the Canaries. Examination of leaf anatomy of fayatree revealed reduced cell size and isodiametrically-shaped cells. These features were interpreted as adaptations for xerophytic conditions that provide resistance against water stress.

Lee, S. C. 1935. Forest botany of China. The Commercial Press, Ltd., Shanghai.

Myrica adenophora, with the common names young mai and Tsing mai, was reported from Kwantung Forest, China, at elevations between 3,000-5,000 ft. *Myrica esculenta* was reported in Yunnan Province, China, in forests at 4,800 ft. *Myrica nana* was reported in Yunnan Province in forests up to 9,000 ft. *M. rubra* (= *M. nagi*) (strawberry tree) was reported in South China in forests between 3,000-8,000 ft.

Leroy, J. F. 1949. De la morphologie florale et de la classification des Comptes Rendus de l'Academie des Sciences, Paris 259:1162-1163.

The author discussed the usefulness of floral morphology in the classification of the members of the family Myricaceae. The creation of a separate subfamily, the Canocomyricoideae, was suggested for the genus *Canacomyrica*. (Note: see the statement of Adamson and Salter (1950) regarding the lack of usefulness of floral morphology in classification of the Myricaceae.) (In French; original reference not seen, information from Sundberg (1985).)

Lipp, C. C. 1994. Ecophysiological and community-level constraints to the invasion of *Myrica faya*, an alien tree in Hawaii Volcanoes National Park. Ph.D. dissertation, Department of Botany, University of Hawaii at Manoa.

Whereas fayatree is generally characterized as an aggressive invasive alien species in Hawai'i Volcanoes National Park, certain habitats appear to be more successfully or rapidly colonized than are others. Those not readily invaded include undisturbed dense forests with understory fern cover, rain forests, and seasonally dry submontane grassland. Research indicated that low availability of light in the forest understory was the primary factor in limiting fayatree establishment as opposed to lack of dispersal by birds. However, in areas where dieback of 'ohi'a occurs, the dominant native overstory tree, gaps are created in the canopy which allow light to reach the understory and fayatree to become established. Once established, fayatree may in turn shade out 'ohi'a seedlings, which are less shade-tolerant than is fayatree, and eventually replace 'ohi'a as the dominant canopy tree. In rain forest sites, such as Ola'a Tract, high soil moisture may inhibit seed germination and fayatree establishment. In dry grassland habitats, low soil moisture may contribute to fayatree seedling mortality. However, data indicated that fayatree germination and seedling survival were aided by shading by the alien grass *Melinis minutiflora*, although this grass later competed with fayatree for soil moisture under drought conditions. Whereas relatively few seedlings survived in seasonally dry grasslands, physiological adjustments to drought conditions appeared to enable surviving trees to eventually establish a population, which was predicted to increase as trees mature and increased seed input.

Little, E. L., Jr., R. O. Woodbury, and F. H. Wadsworth. 1974. Trees of Puerto Rico and the Virgin Islands, Vol. 2. Agriculture Handbook 449, U. S. Department of Agriculture, Washington, D. C.

Myrica cerifera (= *M. pusilla*, *M. pumila*) common names "waxmyrtle, southern bayberry, candle-berry, tea-box, tea-bark, cerero, árbol de cera, arraiján, cera vegetal" was reported in the West Indies, Florida, Texas, north to Arkansas, and southern Delaware in moist soils. *Myrica holdridgeana* ("palo de cera") was reported from the Luquillo Mountains of Puerto Rico, a locality to which it is restricted. *Myrica mexicana* (common name "cerero") was reported in southeastern continental U. S. along the Atlantic Coast, Florida, Texas, north to New Jersey; Bermuda, the Bahamas, and the Caribbean islands of Cuba, Jamaica, Hispaniola; Mexico and Belize south to Costa Rica.

Little, E. L., Jr., and R. G. Skolmen. 1989. Common forest trees of Hawai'i (native and introduced). Agriculture Handbook 679, U. S. Department of Agriculture, Washington, D. C.

Fayatree was illustrated and described as one of the common forest trees of Hawai'i. Its arrival and history in the islands was briefly outlined. It was planted near Hawai'i Volcanoes National Park and near the Alakai Swamp, on the island of Kaua'i, in 1927 and again in 1940. Since 1940, it has been considered one of Hawai'i's most noxious plants. Because of its ability to fix nitrogen, it has the ability to take over the best pasture land by forming dense thickets. An active eradication program was reported to be underway.

Lloyd, D. G. 1981. The distribution of sex in *Myrica gale*. Plant Systematics and Evolution 138:29-45.

The distribution of male and female inflorescences among stems of *M. gale* was quantified. The author measured a higher ratio of staminate to pistillate inflorescences and determined that the development of staminate or pistillate flowers on phenotypically unisexual inflorescences was an environmentally induced phenomenon. Most pistillate flowers growing on predominantly staminate stems were viable as were most of the staminate flowers developing on predominantly pistillate stems. The author hypothesized that the subdioecious condition in *M. gale* has evolved from monoecious ancestors rather than from bisexual (hermaphroditic) populations. Although fayatree itself was not mentioned in this study, observations on *M. gale* may be applicable to this species as well.

Loh, R., J. T. Tunison, L. R. Walker, and P. M. Vitousek. Population changes of faya tree in three sites, 1986-1993. Technical report, University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu. In preparation.

The authors gathered data through field observations to document changes in fayatree populations in Hawai'i Volcanoes National Park during the period 1986-1993.

Long, R. W., and O. Lakela. 1976. A flora of tropical Florida. University of Miami Press, Coral Gables.

Myrica cerifera (wax myrtle) was reported as indigenous to Tropical Florida.

Loope, L. L. 1992. An overview of problems with introduced plant species in national parks and biosphere reserves in the United States. Pp. 3-28 In: C. P. Stone, C. W. Smith, and J. T. Tunison, eds. Alien plant invasions in native ecosystems of Hawai'i: Management and research. University of Hawai'i Press, Honolulu.

Biological control of weeds had its basis in agriculture, but the National Park Service has taken initiative in applying this approach to control of invasive alien plants in native systems. Fayatree was among the first species to be targeted for biocontrol in this relatively new program.

Loope, L. L., R. J. Nagata, and A. C. Medeiros. 1992. Alien plants in Haleakala National Park. Pp. 551-576. In: C. P. Stone, C. W. Smith, and J. T. Tunison, eds. Alien plant invasions in native ecosystems of Hawai'i: Management and research. University of Hawai'i Press, Honolulu.

Although fayatree was not known to occur within the boundaries of Haleakala National Park at the time of writing, the dense stand on the western slope of Haleakala, the upper reaches of which approach the park boundary, together with its proven ability elsewhere in Hawai'i to rapidly expand its range, were considered cause for concern.

Lowe, R. T. 1868. Manual of the flora of Madeira and the adjacent islands of Porto Santo and the Desertas, Vol. I. Dichlamydeae. John Van Voorst, London.

Fayatree was reported on the island of Madeira only in vineyards and chestnut forest planted between the elevations of 152 to 762 m. By 1868 most of the native laurel forest below 762 m had apparently been cleared, and fayatree was likely most typical as an adventitious species.

Lucas, M. T. 1956. Fungi lusitaniae XIV. Agronomia Lusitana 18:109-122.

The fungus *Lophiostoma desmazierii* was reported as a new species on fayatree in Portugal, although pathogenicity of the fungus was not discussed. (in Portuguese)

Mabberley, D. J. 1989. The plant book. Reprint and correction of 1987 edition, Cambridge University Press, Cambridge, Great Britain.

The taxon *Gale*, considered at the generic level by some authors, was recognized as a species of *Myrica*, as *M. gale* L.

Macdonald, A. D. 1977. Myricaceae: Floral hypothesis for *Gale* and *Comptonia*. Canadian Journal of Botany 55:2636-2651.

The author agreed with Chevalier's (1901) treatment of the Myricaceae in recognizing three genera: *Myrica*, *Gale*, and *Comptonia*. He compared the ontogeny of the staminate flowers of two species of Myricaceae considered to display advanced characteristics, *Gale palustris* (= *M. gale*) and *Comptonia peregrina* with a primitive representative of the family, *M. pilulifera*. The three sections of *Myrica* established by Chevalier were recognized, with *Morella* restricted to southeastern Asia, eastern China, Taiwan, and Japan; *Cerophora*, which contains most species of *Myrica*, is divided into two subsections, *Africanae* and *Americanae*, and spans the equator of the African and North and South American continents. On the basis of wood anatomy and morphology, Section *Morella* is considered the most primitive. Section *Faya*, which contains three species: *fayatree*, restricted to Macaronesia; *M. inodora*, restricted to the southeastern U. S.; and *M. californica*, restricted to the western coast of North America. The genus *Comptonia* is restricted to eastern North America, while *Gale* is circumboreal. The author's anatomical study included *fayatree*, *M. californica*, *M. rubra* from Japan, *M. adenophora* from Taiwan, *M. javanica* from Indonesia, *M. esculenta* from Singapore, and *M. diversifolia*, *M. quercifolia*, *M. kraussiana*, *M. integra*, *M. cordifolia*, and *M. serrata* from Pretoria, South Africa.

Macdonald reviewed hypotheses on the ancient dispersal of Myricaceae in Africa and America. He stated that the fossil record was of little value for determining possible phylogenetic relationships within the Myricaceae. Myricaceous pollen was reportedly similar to that of unrelated families such that it could not be identified reliably in Cretaceous sediments. "Based on climatic-edaphic preferences of extant plants, the present distribution, the limited fossil record, and the earth's tectonic activity, it can be surmised that the Myricaceae is of Boreotropical origin and probably occurred near the Tethys Sea in the late Cretaceous." "...Other lines of evidence also provide little information on the status of the family or on the interspecific relationships."

Macdonald, A. D. 1979. Development of the female flower and gynecandrous partial inflorescence of *Myrica californica*. *Canadian Journal of Botany* 57:141-151.

The author described the organogenesis of the female flower and gynecandrous partial inflorescence, an inflorescence type in which stamens develop on the gynoecium. Adaptive advantages of this inflorescence type could not be explained. *Fayatree* was mentioned as also producing a gynecandrous inflorescence.

Macdonald, A. D. 1980. Organogenesis of the female reproductive structure of *Myrica pensylvanica*. *Canadian Journal of Botany* 58:2001-2006.

Development of the female reproductive structures on *M. pensylvanica* was discussed. Wax-secreting structures which develop on the fruit exocarp were described as papillae, rather than trichomes, since they develop from a ring of meristematic cells immediately below the epidermis of the floral receptacle. The author attributed the function of these wax-secreting papillae to fruit dispersal. *Fayatree* fruits also develop these ceriferous papillae.

Macdonald, A. D. 1989. The morphology and relationships of the Myricaceae. Pp. 147-165 In: P. R. Crane and S. Blackmore, eds. *Evolution, systematics, and fossil history of the Hamamelidae*, Volume 2: 'Higher' Hamamelidae. Systematics Association Special Volume 40B. Clarendon Press, Oxford.

The author provided a comprehensive treatise of the Myricaceae, including a review of the biogeographical evidences for its origin and distribution. The family was characterized as cosmopolitan, with about 50 species, although absent in Australia and New Zealand. Two genera were recognized, *Comptonia*, a monotypic genus, and *Myrica*. *Myrica* reportedly consisted of two subgenera *Myrica* and *Morella*. The base chromosome number for the family is $x = 8$, but *Comptonia* is tetraploid and subgenus *Myrica* is at

least hexaploid. Three sections were included in *Morella*: *Morella*, *Faya*, and *Cerophora*. The status of the genus *Canacomyrica* was reported as problematical, but based on a comprehensive palynological study of 30 species, it was concluded that this genus should not be excluded from the family. This study also provided evidence that *Comptonia* was sufficiently distinct to be retained as a separate genus, but that *M. gale* should not be raised to generic status as *Gale*.

Macdonald stated that many species exhibit a range of morphological variation which has resulted in the naming of a large number of varieties and species of doubtful validity. The essential oils produced by members of the family were found to be particularly useful in resolving these problems. Furthermore, reciprocal inoculation of saprophytic endophytes was useful in taxonomic delimitation.

Speciation of *Myrica* was reportedly pronounced in Africa, particularly South Africa, and along the Andes in South America, much more so than in North America, Europe, and south-east Asia. Fruit dissemination was reportedly largely by water and by birds, although the role of birds in transporting fruit long distances was thought to have been possibly overrated in past accounts.

Mack, R. N. 1992. Characteristics of invading plant species. Pp. 42-46 In: C. P. Stone, C. W. Smith, and J. T. Tunison, eds. Alien plant invasions in native ecosystems of Hawai'i: Management and research. University of Hawai'i Press, Honolulu.

Alien trees in Hawai'i are particularly prominent and diverse in life form. Fayatree was listed as an example of an invasive angiosperm tree.

Mackintosh, A. H., and G. Bond. 1970. Diversity in the nodular endophytes of *Alnus* and *Myrica*. *Phyton* 27(1):79-90.

Unusual combinations of nodule endophytes were examined in the genera *Alnus* and *Myrica*. In *Alnus*, nine of these combinations resulted in functional symbioses as compared with only one in *Myrica*. The endophyte apparently exists in a number of forms, each able to symbiose with a restricted number of unusual host species, whereas in *Myrica* the endophytes showed little or no such ability. Geographical distribution and taxonomic affinity of host species may provide a basis for some of the findings.

Markin, G. P. 1991. Insect survey of potential biological control agents of *Myrica faya* in the Azores and Madeira Islands, Portugal, 1988. Technical Report 75. University of Hawai'i Cooperative National Park Studies Unit, Honolulu.

A 1988 entomological survey of the Azores and Madeira in search of biocontrol insects for fayatree in Hawai'i was reported. A leaf-mining caterpillar, unidentified at the time of writing, was the only new insect observed as a potential biocontrol candidate. More than 12 species of insects which feed on fayatree were surveyed and described. The author recommended further exploration concentrated in the Canary Islands and also on the Portuguese mainland for potential agents.

Markin, G. P. 1993. Visit to Europe and Atlantic islands to continue search for biological control agents for *Myrica faya*. Unpublished report to the University of Hawai'i Cooperative National Park Studies Unit, Honolulu.

Activities during the most recent visits to Madeira and the Azores in conjunction with the fayatree biocontrol program were detailed, and the progress of the collaborators in each of the island groups was evaluated. The disposition of a collection of the insects from fayatree in the Azores was discussed. Markin concluded that no new insects of fayatree were likely to be found in the Azores, and recommended that further exploration there be suspended and redirected to the Canary Islands and possibly to Madeira. A recent collection of fayatree insects from Madeira, submitted by António

Aquiar, should be examined for new insects. If none are found, exploratory work in Madeira was also recommended for suspension. Examination of the *Myrica* collection at the herbarium of Kew Botanical Gardens, London, revealed areas of concentration (e.g., South Africa, South America) of other species which should be sites of future exploration for biocontrol agents of fayatree.

Markin, G. P., and L. Silva. 1993. The insect fauna associated with *Myrica faya* in the Atlantic islands and on mainland Portugal. Abstracts of the First Symposium "Fauna and Flora of the Atlantic Islands," October 4-9, 1993, Funchal, Madeira, Portugal. p. 38.

In 1987, an intensive survey was conducted in the native habitats of fayatree for potential biocontrol insects. Populations of insects in the field were consistently found to be very small and to have only a minimal impact on the plant. Of the more than 20 insect species found associated with fayatree, most are general feeders, with only three thought to be specific. Only one insect species is found on all three island groups, with half of the insects found on any two groups. A totally different insect fauna was found on fayatree where it has been introduced, presumably, along the north coast of Portugal.

Markin, G. P., and E. Yoshioka. 1992. Evaluating proposed biological control programs for introduced plants. Pp. 757-778 In: C. P. Stone, C. W. Smith, and J. T. Tunison, eds. Alien plant invasions in native ecosystems of Hawai'i: Management and research. University of Hawai'i Press, Honolulu.

A rating system, by which numerical scores were given to indicate the predicted success of biocontrol efforts against particular weeds, was developed. To demonstrate the scoring system, three weeds which pose major threats to native Hawaiian ecosystems were chosen, including fayatree. A score of 80 was given for fayatree, indicating it was predicted to be more amenable to biocontrol than was banana poka, with a score of 65, but less amenable than gorse (90).

Markin, G. P., P.-Y. Lai, and G. Y. Funasaki. 1992. Status of biological control of weeds in Hawai'i and implications for managing native ecosystems. Pp. 466-482 In: C. P. Stone, C. W. Smith, and J. T. Tunison, eds., Alien plant invasions in native ecosystems of Hawai'i: Management and research. University of Hawai'i Press, Honolulu.

Whereas Hawai'i has been a leader in biocontrol, these efforts in the past have been concentrated on pests of agricultural lands. Recently, however, invasive alien woody species, including fayatree, in native Hawaiian forests have been targeted in biocontrol programs. This has constituted a new application for biocontrol. The newly initiated biocontrol program for forest weeds in Hawai'i was evaluated from the standpoint of potential of success.

Marler, P., and D. J. Boatman. 1952. An analysis of the vegetation of the northern slopes of Pico - the Azores. *Journal of Ecology* 40:143-155.

"The vegetation of the northern slopes of Pico has been affected by the recently assumed dominance of an introduced tree *Pittosporum undulatum*. This change has resulted in a complex of vegetation which has not been described in other accounts of Azores vegetation."

"There is a distinct sequence of vegetation starting from sea level. Woodland becomes the dominant vegetation from about 100-1200 m. A mixed consociation of *Persea azorica* and *M. faya* is dominant at about 500-1000 m. *Pittosporum undulatum* is dominant just below this zone from 200-500 m...The *Myrica-Persea* woodland is a more open forest with a well-developed ground flora" (than is the *Pittosporum* forest.)

At higher elevations, a cyclic series of stages was proposed in which a chain of continuous phases occurred rather than a stable community. Sheep grazing was considered an important factor in the cycle, in which domination rotated among *Rubus* sp., *Persea azorica*, *Erica azorica*, *Pteridium* sp., and fayatree. Grazing was suggested as the factor preventing extension of *Pittosporum* into the upper zone.

Martin, F. W., C. W. Campbell, and R. M. Ruberte. 1987. Perennial edible fruits of the tropics: An inventory. Agricultural Handbook No. 642. U. S. Department of Agriculture, Washington, D. C. 252 pp.

Numerous edible fruits of major and minor importance to the cultures of tropical and subtropical America, Africa, Asia, India, and the Pacific Ocean were described. Fayatree berries were listed as a minor fruit in the Canary Islands, but the specific use was not described. The berries of other species of *Myrica* were reported to be consumed as minor dietary components in southern Africa (*M. cordifolia*), Indonesia (*M. javanica*), tropical Asia and India (*M. sapida*), and Indochina (*M. integrifolia*).

McDermott, J. F., Jr., W. S. Tseng, and T. W. Maretzki. 1980. People and cultures of Hawai'i: A psychocultural profile. John A. Burns School of Medicine and University of Hawai'i Press, Honolulu.

Between 1876 and 1886 many families of Portuguese settlers from the Azores and Madeira immigrated to Hawai'i as farmers or plantation workers. Although the exact time of fayatree's introduction to Hawai'i is not known, it was probably introduced during this period of immigration.

Metcalf, C. R., and L. Chalk. 1950. Myricaceae. Pp. 1291-1294, *In*: Anatomy of the dicotyledons. Clarendon Press, Oxford.

A comprehensive treatment of the anatomy of the Myricaceae was provided. Whereas most of the work supporting the descriptions was based on species of *Myrica* other than fayatree, fayatree was cited as an example of a species with vessel perforation plates all scalariform and typically with fewer than 15 cross bars. Of particular note was a description of the anatomy of nodulation in the genus *Myrica* based largely on observations of *M. gale* by Bottomley, and on certain North American species of by Youngken.

Mian, S., G. Bond, and C. Rodriguez-Barrueco. 1976. Effective and ineffective root nodules in *Myrica faya*. Proceedings of the Royal Society of London B. 194:285-295.

The authors reported observations of inoculation trials where greenhouse-grown *M. cerifera*, *M. cordifolia*, *M. gale*, *M. pilulifera* and fayatree nodule endophytes were applied to the roots of greenhouse-grown fayatree seedlings. All but the inoculant from *M. gale* induced nitrogen-fixation ability in the seedlings. Sections of the ineffective nodules revealed that the endophyte failed to produce vesicles, the suspected site of nitrogen-fixation in nodules of non-legume hosts.

Miguel, C., and C. Rodriguez-Barrueco. 1974. Acetylene-reducing activity of detached root nodules of *Myrica faya* Ait. Plant and Soil 41:521-526.

Investigations were reported of the ability of fayatree to fix atmospheric nitrogen. Greenhouse-grown seedlings inoculated with root nodule preparations produced nitrogen-fixing root nodules and experienced vigorous growth. Non-inoculated seedlings were not vigorous.

Mildenhall, D. C. 1980. New Zealand Late Cretaceous and Cenozoic plant biogeography: A contribution. Palaeogeography, Palaeoclimatology, Palaeoecology 31:197-233.

Whereas the genus *Canacomyrica* is now restricted to New Caledonia, its fossils were identified in Eocene sediments in New Zealand. It became extinct there in the Miocene.

Millsbaugh, C. F. 1975. American medicinal plants. Dover Publications, Inc., New York.

The palmitate, myristicin, and palmitic acid which comprise the wax of *Myrica* impart an astringent taste to the fruit.

Moerman, D. E. 1986. Medicinal plants of native America, Vol. 1. Research Reports in Ethnobotany, Contribution 2, Technical Reports No. 19. University of Michigan Museum of Anthropology, Ann Arbor.

Bark, roots, leaves, branches, and twigs of *Myrica* spp., *M. cerifera*, and *M. gale* were listed in various preparations as useful for a number of folk medicine remedies.

Moncada, M. 1985. Pollen morphology in the genus *Myrica* (Dicotyledoneae: Myricaceae). Acta Botanica Cubana 0:1-4.

The pollen morphology of four species of *Myrica* from Cuba was described: *M. cerifera*, *M. punctata*, *M. shaferi*, and *M. cacuminis*. The latter three species were reported as endemic. The greatest affinity of pollen morphology was found between *M. cerifera* and *M. shaferi*, and between *M. punctata* and *M. cacuminis*. (In Spanish; original reference not seen, information from Biological Abstracts.)

Monz, C. A., and C. R. Schwintzer. 1989. The physiology of spore-negative and spore-positive nodules of *Myrica gale*. Plant and Soil 118:75-87.

The physiology of spore-negative and spore-positive nodules of *Myrica gale* was investigated by inoculating seedlings with strains of *Frankia*. Compared to spore-negative nodules, spore-positive nodules showed greater nitrogenase activity (indicating a higher rate of nitrogen-fixation) and less biomass investment by the host plant. Additionally, greater host plant biomass production was supported in plants inoculated with spore-positive strains. The authors concluded that spore-positive *Frankia* strains are more advantageous than spore-negative strains to the host plant.

Morris, M., D. E. Eveleigh, S. C. Riggs, and W. N. Tiffney, Jr. 1974. Nitrogen fixation in the bayberry (*Myrica pensylvanica*) and its role in coastal succession. American Journal of Botany 61(8):867-870.

Through the use of the acetylene reduction technique, the root nodules of *Myrica pensylvanica* (bayberry) were found to be capable of fixing nitrogen. Nodulation was plentiful and fixation was vigorous, indicating that the success of bayberry as an early successional species of dunes and impoverished coastal soils was due in part to this nitrogen-fixing capacity.

Motooka, P. S. 1981. Chemical weed control in pastures and ranges of Hawaii. College of Tropical Agriculture and Human Resources, University of Hawaii. Research Extension Series 005. 12 pp.

Fayatree was listed among weedy species in Hawai'i for which herbicidal treatment was recommended. The recommendation for fayatree was Picloram, 1:10 in water, frilled or stump application.

Motooka, P. S., D. L. Plucknett, and D. F. Saiki. 1969. Weed problems of pastures and ranges in Hawaii. Pp. 95-98 In: Proceedings of the First Asian-Pacific weed control interchange, June 12-22, 1967, University of Hawaii, Honolulu.

Fayatee was listed and described among other range and pasture weeds of Hawai'i, with the background of its origin and introduction, and its distribution in Hawai'i.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John Wiley and Sons, New York.

Periodic volcanic activity in the Hawaiian Islands produces sterile ash soils upon which primary succession occurs, that is, the formation of a community on a substrate which has not previously supported vegetation.

Mueller-Dombois, D., and L. L. Loope. 1990. Some unique ecological aspects of oceanic island ecosystems. Monographs in Systematic Botany from the Missouri Botanical Garden 32:21-27.

The authors summarized the vulnerability of native Hawaiian biota and ecosystems to alien plants and the implications of this knowledge for native ecosystem management and restoration. Fayatee was discussed in this context as one of the five most aggressive alien plant species in Hawai'i.

Mueller-Dombois, D., and L. D. Whiteaker. 1990. Plants associated with *Myrica faya* and two other pioneer trees on a recent volcanic surface in Hawai'i Volcanoes National Park. Phytocoenologia 19(1):29-41.

The authors investigated the effects of an increase in biologically available soil nitrogen caused by the fixation of nitrogen by fayatee, and associated weed invasion. No direct relationship was measured. Fayatee was observed as a pioneer species on old lava flows occurring in association with *Buddleja asiatica*, another invasive alien species. The authors hypothesized that fayatee is a secondary invader, sprouting and surviving in a favorable microhabitat produced by *Buddleja* under or near *Metrosideros polymorpha*.

Muller, J. 1981. Fossil pollen records of extant angiosperms. Botanical Review 47:1-142.

Fossilized pollen records were used to trace the origins of angiosperm families, including that of Myricaceae. Pollen of *Myrica* was found to be continuously present within the geographic range presently occupied by members of the family.

Nakamura, M. 1990. How to identify Hawaiian earthworms. Central University research note 11:101-110. Tokyo, Japan.

Alien earthworms prefer nutrient rich organic litter for food. This information is applicable to the ability of fayatee to enrich soil by the fixation of nitrogen, encouraging abnormally high populations of introduced earthworms which in turn further alter fayatee rhizosphere communities.

Neal, M. C. 1965. In gardens of Hawai'i. Second Printing. Special publication 50, Bishop Museum Press, Honolulu.

Fayatee, a shrub or small tree to about 20 feet high, was used for reforestation in Hawai'i. By 1944 its success of establishment led to measures by the Territorial Board of Agriculture and Forestry to attempt to eradicate it.

Ogimi, C., and H. Higuchi. 1981. Bacterial gall of yamamomo (*Myrica rubra*) caused by *Pseudomonas syringae* var. *myricae*, var. nov. *Annals of the Phytopathological Society of Japan* 47:443-448.

A new bacterial disease was found on *M. rubra* in several locations in Japan. Symptoms included galls 1-several centimeters in diameter on trunks and twigs. Small galls also occurred on leaf petioles. No actual mortality of host plants was reported. The causal bacterium was pathogenic only to *M. rubra* when tested on plants belonging to 35 families and 69 species. (In Japanese; original reference not seen, information from Biological Abstracts.)

Ohsawa, M. 1991. Montane evergreen broad-leaved forests of the Bhutan Himalaya. Pp. 89-156
In: M. Ohsawa, ed., *Life zone ecology on the Bhutan Himalaya II*. Chiba University, Chiba, Japan.

Myrica esculenta was reported as one of the three tree species dominating the second level canopy at a Bhutan Himalayan forest site at 2,270 m. *Rubus ellipticus*, a dry or open forest indicator, was noted as one of the understory shrubs. The upper canopy is exclusively dominated by *Quercus lanata*. *Myrica esculenta* was also one of many trees invading a site at 2,300 m of a *Q. lanata* forest.

Ohsawa, M., P. H. J. Nainggolan, N. Tanaka, and C. Anwar. 1985. Altitudinal zonation of forest vegetation on Mount Kerinci, Sumatra: With comparisons to zonation in the temperate region of east Asia. *Journal of Tropical Ecology* 1:193-216.

The uppermost forest at 2,900 m elevation of Mt. Kerinci was dominated by *Myrica javanica*, the only tree species at this altitude. Several ericaceous species formed the understory. *M. javanica* was reported as one of the well known early successional trees on Malaysian mountains.

Ohwi, J. 1965. *Flora of Japan*. English edition, F. G. Meyer and E. H. Walker, eds. Smithsonian Institution, Washington, D. C.

The author listed two species of *Myrica* from Japan, with their synonyms: *M. gale* var. *tomentosa* (= *M. tomentosa*, with the common name yachi-yanagi. *M. rubra* (= *M. nagi* and *Gale japonica*), common name yama-momo.

Palhinha, R. T. 1966. Catálogo das plantas vasculares dos Açores. Edição da Sociedade de Estudos Açorianos Afonso Chaves subsidiada pelas Juntas Gerais dos Distritos Autônomos de Ponta Delgada e Angra do Heroísmo, Lisboa.

Fayatree was listed, together with standard distribution and other voucher information, in a vascular flora of the Azores. (in Portuguese)

Pereira Coutinho, A. X. P. 1939. Flora de Portugal. Bertrand, Ltd., Lisbon.

The author considered fayatree, with the common names "samouco" or "faia das ilhas" a naturalized species in central and southern areas of the Portuguese mainland, having been introduced from Portuguese Macaronesia. This opinion contrasts with those of other botanists who consider fayatree native to mainland Portugal. (in Portuguese)

Pirone, P. P. 1978. *Diseases and pests of ornamental plants*. 5th Edition, John Wiley & Sons, New York.

Certain species of *Myrica* were listed among the ornamental trees and shrubs in the U. S. for which the author discussed diseases and pests. Diseases of *M. cerifera* (waxmyrtle) were reported to be black mildew, caused by *Irene calostroma* and *I. manca*. Black mildew was not considered sufficiently serious to require control measures. Leaf spots, were reportedly caused by the fungi *Phyllosticta myricae* and *Septoria myricae*. Rust, caused by the aecial state of *Gymnosporangium ellisii*, forms large numbers of bright orange pustules on the leaves, especially on the undersurfaces, in regions where white cedar, the telial host, also occurs. The was reported to be capable of causing considerable damage to *Myrica*, and to occasionally attack sweet fern (*Comptonia*).

Myrica gale (sweet gale) was reported to be subject to twig blight caused by *Diplodia* sp., leaf spots caused by *Ramularia moniloides* and *Septoria myricata*, and rusts caused by *Cronartium comptoniae* and *G. ellisii*.

Myrica pensylvanica (bayberry) was affected by bayberry yellows virus, which causes yellowing of leaves and stunting of plants, with few or no fruits being produced. The leaf spotting fungi *Mycosphaerella myricae* and *Phyllosticta myricae*, and the rust fungus *G. ellisii* also were reported to attack *M. pensylvanica*. The red-humped caterpillar (*Schizura concinna*) reportedly feeds on *M. pensylvanica* as well as on many other ornamental trees and shrubs.

Pittier, H, T. Lasser, L. Schnee, Z. L. deFelores, and V. Baldillioi. 1945. Catalogo de flora Venezolana. Lit. y Tip Vargas, Tomo 1. Caracas.

Myrica pubescens, *M. funckii*, *M. caracasana*, and *M. arguta* were listed for the family Myricaceae in Venezuela. (in Spanish)

Queiros, M. 1987. *Myrica faya* (Myricaceae). Pp. 17-24 In: A. Fernandes and R. B. Fernandes, eds., Iconographia selecta florae Azoricae. Vol. 2. A Secretaria Regionali Culturae Regionis Autonomae Azorensis Edita, Conimbriga.

A comprehensive list was compiled of early references to fayatree, some from the 17 and 1800s, most of which were not available for the present bibliography. A Latin description of fayatree was given, together with its synonyms and common Portuguese names, a discussion of its ecology in its native habitats, cultural uses, and distribution. The discussion of Daveau (in Bull. Soc. Bot. Fr. 67:364-365, 1920) was reviewed regarding the controversial question as to the possible origin of fayatree on the Portuguese mainland, as opposed to its introduction to this region. The discussion of Battandier (in Bull. Soc. Bot. Fr. 66: 278, 1919) was also reviewed regarding the possibility that fayatree occurred in northern Africa on the Atlantic coast of Morocco. (in Portuguese)

Quisumbing, E. 1951. Medicinal plants of the Philippines. Technical bulletin 16. Republic of the Philippines Department of Agriculture and Natural Resources, Manila.

Myrica rubra (= *M. nagi*) with the common names cham-poi, cham-pu, box myrtle, bayberry, or Chinese strawberry was reported in the Philippines.

Raabe, R. D., and E. E. Trujillo. 1963. *Armillaria mellea* in Hawai'i. Plant Disease Reporter 47:776.

The presence of *Armillaria mellea* in Hawai'i was documented. This fungus was found on fayatree in the Azores during exploration for potential biocontrol agents in Hawai'i. It was not reported to attack fayatree in Hawai'i, however.

Raven, P. H., and D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. Annals of the Missouri Botanical Garden 61:539-673.

In hypothesizing prehistoric biogeographical distribution of vegetation, the authors suggested that the Myricaceae could have migrated relatively recently to Africa and South America. *Canacomyrca* consists of a single New Caledonian species and may have no direct relationship to Myricaceae, but is at least a very distinct subfamily. Macrofossils of Myricaceae were reported from the Upper Cretaceous in South Africa.

Raven, P. H., R. F. Evert, and S. E. Eichorn. 1986. *Biology of plants*. Fourth edition. Worth Publishers, Inc., New York.

In a general discussion of the process of nitrogen fixation by higher terrestrial plants, the authors described the conversion of nitrogen gas into nitrate, which can be metabolized into amino acids and proteins by plants. The microsymbionts, in turn, use organic compounds supplied by the plant as an energy source. Although fayatree itself was not mentioned, the discussion is applicable to fayatree as a nitrogen fixer.

Reed, C. F. 1960. *Myrica pensylvanica*, a new host for *Phoradendron flavescens* in Virginia. *Castanea* 25(2):86.

Myrica pensylvanica was newly reported as a host, among a number of other woody species, for the mistletoe *Phoradendron flavescens* in Virginia.

Roivainen, H. 1947. Eriophyid news from Finland. *Acta Entomologica Fenici* 3:1-51.

The author examined a large collection of eriophyid, or gall-forming, mites from Finland and described a number of new species, including two free-living forms on *Myrica gale*. He named these *Eriophyes myricae* and *Phyllocoptes myricae*. (in Finnish (?); original reference not seen)

Rosa, M. A. P. 1961. A murchidão da *Myrica faya* Ait.: Sua caracterização pelo uso do fósforo P³². Publicações da Direcção Geral dos Serviços Florestais e Aquícolas, Vol. 28:135-190.

Experiments were undertaken to characterize a wilt of fayatree caused by the fungus *Dothiorella* sp. which was found in Madeira by exploratory entomologists from Hawai'i. Fungal infection induced the production of tyloses by the host plant which occluded vessel elements of the xylem tissue. These occlusions blocked water conduction and caused discoloration and wilting of surrounding tissues. (in Portuguese)

Ruehle, G. D. 1936. An epiphytotic of algal spot in South Florida. *Plant Disease Reporter* 20:221-222.

Fayatree, reported as *Myrica faya* Ait., was listed among several hosts of algal leaf spot in the Homestead area of southern Florida. The disease was caused by the semiparasitic alga *Cephaleuros mycoidea*. (Note: The host in question was probably misidentified as *M. faya*, since this species is not known to occur in the continental U. S., and its presence in Florida could not be confirmed (L. D. Whiteaker, personal communication).

St. Laurent, L., J. Bousquet, L. Simon, and M. Lalonde. 1987. Separation of various *Frankia* strains in the *Alnus* and *Elaeagnus* host specificity groups using sugar analysis. *Canadian Journal of Microbiology* 33:764-772.

To confirm the role of glycosides in the taxonomy of *Frankia*, 79 stains isolated from *Alnus* spp., *Comptonia* sp., spp., *Shepherdia* spp., *Hippophae* sp., *Myrica gale*, and *M. pensylvanica* were tested for sugar content and placed in host specificity groups using statistical analysis. The *M. gale* isolates were generally intermediate in their sugar content between the *Alnus* and *Elaeagnus* host specificity groups.

Sande, E., and D. R. Young. 1992. Effect of sodium chloride on growth and nitrogenase activity in seedlings of *Myrica cerifera* L. *New Phytologist* 120:345-350.

In growth chamber studies, 5-month-old seedlings of *Myrica cerifera* remained viable during exposure to 150 mM sodium chloride for 35 days, but concentrations above 50 mM significantly depressed plant and root nodule growth. Plants treated with 150 mM sodium chloride had a rate of nitrogen fixation 26% of that in control plants, indicating the possible effects of sea spray on nitrogen fixation.

Santos, G. L., L. W. Cuddihy, and C. P. Stone. 1989. Cut-stump and frill treatments on firetree in Hawai'i Volcanoes National Park. Pp. 135-136 In: 1989 Research Progress Report, Western Society of Weed Science, Honolulu, Hawai'i, March 14-16.

Research-in-progress was briefly reported testing the effectiveness of five herbicides for fayatree control. Herbicides were applied using the cut-stump or frill method. Round-up (glyphosate), which produced a 20 to 60% cambium mortality, was not considered effective for general application.

Schaede, R. 1938. Die Actinomyceten-Symbiose von *Myrica gale*. *Planta* 29:32-46.

The author provided an early account of the symbiosis of a root nodule forming actinomycete with *Myrica gale*. (in German)

Schwintzer, C. R. 1979. Nitrogen fixation by *Myrica gale* root nodules (in a) Massachusetts wetland. *Oecologia* 43:283-294.

Annual nitrogen fixation for *Myrica gale* was calculated from a seasonal nitrogenase activity curve. The rates were considered equivalent to the amount of nitrogen contained in bulk precipitation and are major components in the nitrogen budgets of the *M. gale* plants themselves, as well as the wetlands in which they grew.

Schwintzer, C. R. 1983. Primary productivity and nitrogen, carbon, and biomass distribution in a dense *Myrica gale* stand. *Canadian Journal of Botany* 61:2943-2948.

In a study of primary productivity in a dense stand of *Myrica gale*, Nitrogen fixation was found to provide 43% of the estimated annual nitrogen requirement.

Schwintzer, C. R. 1988. All field-collected actinorhizae examined on *Comptonia peregrina* and *Myrica pensylvanica* in Maine are spore negative. *Canadian Journal of Botany* 67:1460-1464.

Host-specificity for either spore-negative or spore-positive strains of *Frankia* by *Comptonia peregrina* and *Myrica pensylvanica* from a variety of field sites in Maine was investigated. All the nodules examined were spore-negative, that is, the strains of *Frankia* sp. infecting the nodules developed few spores. Spore-negative nodules may have greater nitrogenase activity and may be more effective in supporting host plant growth. Sporulation may be controlled by the strain of *Frankia* infecting the host or by the environment within the host plant nodule.

Schwintzer, C. R., and J. D. Tjepkema. 1983. Seasonal pattern of energy use, respiration, and nitrogenase activity in root nodules of *Myrica gale*. *Canadian Journal of Botany* 61:2937-2942.

The authors observed that nonnitrogen-fixing plants were more common than those that fix nitrogen, and are competitive with them in most ecosystems, suggesting that nitrogen fixation may have one or more costs which balance its obvious advantage. Annual nitrogen fixation was estimated to contribute about 33% of the annual nitrogen requirement. The study showed that the energy cost of nitrogen fixation by *Myrica gale*

was significant, but in a nitrogen-limited environment the added growth made possible by nitrogen fixation appeared to more than sufficient to make up for this cost. *Myrica gale* was shown to use nitrogen less economically than do peatland shrubs, further indicating that the cost of nitrogen fixation is not excessive.

Schwintzer, C. R., A. M. Berry, and L. D. Disney. 1982. Seasonal patterns of root nodule growth, endophyte morphology, nitrogenase activity, and shoot development of *Myrica gale*. *Canadian Journal of Botany* 60:746-757.

Myrica gale populations in central Massachusetts were observed throughout the ice-free season. Nitrogenase activity appeared in mid-May shortly after bud outbreak, was at its maximum between late June and mid-August, and disappeared in late October after all leaves had fallen. Most root nodules observed lived for 3 years or less. Colonizing hyphae of the *Frankia* endophyte were observed throughout the year in partially expanded cortical cells near the nodule lobe apex. Vesicles first appeared in mature cortical cells coincident with the onset of nitrogenase activity in mid-May, occupied most of infected tissue during the summer, and disappeared as nitrogenase activity stopped in late October. Evidence was presented that the vesicles were the site of nitrogenase activity.

Seubert, M., and C. Hochstetter. 1843. Übersicht der Flora der Azorischen Inseln. *Archiv für Naturgeschichte* 9.

The vegetation of the island of Pico (Azores) was first described, including fayatree. Five vegetation zones were recognized, but principal interest was in the altitudinal zonation of the plants on the volcanic cone of O Pico and comparatively little attention was given to the plant communities. (in German)

Shirakawa, T. 1967. Pasture weed and brush control guide. Unpublished mimeograph. University of Hawaii Cooperative Extension Series. 3 pp.

Picloram 1:10 in water, frilled or (cut) stump application was recommended for fayatree control in Hawai'i.

Silva, L. 1992. Contribuição para o estudo da Bioecologia de *Ascotis fortunata azorica* Pinker (Lep., Geometridae). Suplemento 3. *Boletim da Sociedade Portuguesa de Entomologia* 2:337-346.

Ascotis fortunata azorica is a defoliating insect of fayatree in the Azores. Studies carried out on the biology and ecology of this lepidopteran indicated this species to be polyphagous, that is, capable of feeding on a number of plants other than fayatree. This, and the fact that the insect is a member of a genus which includes pests already in Hawai'i, indicate that *A. fortunata azorica* would not be suitable as a biocontrol agent for fayatree in Hawai'i. (in Portuguese with English summary)

Silva, L., and J. Tavares. 1993. Phenological Cycles of *Myrica faya* Aiton (Myricaceae) in the Azores Islands. Preliminary results. Abstracts of the First Symposium "Fauna and Flora of the Atlantic Islands," October 4-9, 1993, Funchal, Madeira, Portugal. p. 59.

Weekly observations of phenological cycles of fayatree at two sites on São Miguel Island (Azores) indicated that flushing is not significant from December until April, average growth rate of shoots is about 7 cm/year, male flowering occurs from April to July, female flowering occurs from April to August. Immature fruit appears from May to September, while mature fruits are found from July to November. Fruit drop extends between September and November. Insect feeding, as indicated by leaf damage, peaks during summer and autumn. Leaf spots, fungal disease of meristems, and strong

winds near the coast may affect leaf longevity. Insects fed on male flowers in May, and on fruit between June and September.

Sjögren, E. 1973. Recent changes in the vascular flora of the Azores Islands. *Memorias da Sociedade Broteriana* 22:1-453.

Fayatree was listed as generally occurring from sea level to 800 m in the Azores.

Sjögren, E. 1984. Açores flores. *Editor e Distribuidor Direcção Regional de Turismo Horta Faial, Azores, Portugal.*

The author stated of fayatree: "A frequent member of the coastal endemic grass vegetation. *M. f.* is now threatened by the introduced *Pittosporum undulatum* ... On several lava-flows below 500 m *Myrica* has become totally expelled by the *Pittosporum*. The few remaining fairly pure stands of *Myrica* along the coasts ought to be protected." (in Spanish, Portuguese, German, and English).

This notation indicates that, although fayatree is considered an invasive, disruptive species in Hawai'i, in its native habitat this species is itself threatened by an introduced species to the extent that protection is recommended.

Skolmen, R. 1979. Plantings in the forest reserves of Hawai'i 1910-1960. Manuscript on file, Institute of Pacific Islands Forestry, Pacific Southwest Forest and Range Experiment Station, USDA Forest Service, Honolulu.

Fayatree was listed among the trees planted for reforestation in state forest reserves on the islands of Kaua'i, O'ahu, and Hawai'i. Most plantings were made in the 1920s.

Smathers, G. A., and D. E. Gardner. 1978. Stand analysis of an invading firetree (*Myrica faya* Aiton) population, Hawai'i; pp. 274-288 *In*: C. W. Smith, ed. *Proceedings, Second Conference in Natural Sciences, Hawai'i Volcanoes National Park, June 1-3.* University of Hawai'i Cooperative National Park Studies Unit, Honolulu.

The authors reported a study of vegetation recovery at Byron Ledge, near Kilauea Iki in Hawai'i Volcanoes National Park, a recent cinder deposit area of 'ohi'a forest which fayatree is rapidly invading. Whereas close association between fayatree and 'ohi'a was observed, fayatree did not appear to be replacing 'ohi'a, but showed a loss of vigor as tree size increased. Comparison of fayatree development in Hawai'i with that in its native habitats was considered imperative to better understand the potential ecological role of this species.

Smathers, G. A., and D. E. Gardner. 1979. Stand analysis of an invading firetree (*Myrica faya* Aiton) population, Hawai'i. *Pacific Science* 33:239-255.

The authors presented an expanded, more comprehensive report of the study published in 1978 (See above). A qualitative and quantitative assessment was made of stand structure and vigor, and fruiting characteristics of fayatree invading 'ohi'a habitat in the Kilauea Iki devastation area affected by a 1959 eruption of Kilauea Volcano. The primary dispersal mechanism of fayatree was suggested as nonnative fruit-eating birds. The ability of fayatree to sustain its aggressiveness indefinitely under the substrate conditions of the study site, and thus maintain its long-range threat to that habitat, was questioned.

Smathers, G. A., and D. E. Gardner. 1981. Stand analysis of an invading firetree (*Myrica faya* Aiton) population, Hawai'i. *Research and Resources Management Report 42, U. S.*

Department of the Interior, National Park Service, Southeast Regional Office, Natural Science and Research Division, Atlanta, Georgia. 20 pp.

A technical report on stand analysis of fayatree, mainly an edited version of the 1979 publication in Pacific Science (see above) was presented. A previous hypothesis that loss of stand vigor in trees greater than or equal to 4 cm basal diameter is a function of water stress was further developed.

Smith, C. W. 1985. Impact of alien plants in Hawai'i's native biota. Pp. 180-250 *In*: C. P. Stone and J. M. Scott, eds., Hawai'i's terrestrial ecosystems: Preservation and management. University of Hawai'i Cooperative National Park Studies Unit, Honolulu.

The author described 86 plants pests, including fayatree, in the Hawaiian Islands which have disruptive impacts on native ecosystems or that prevent reestablishment of natural communities following disruptive events. Distribution of the problematic species by island and by vegetation zones was also tabulated. Impacts of aggressive aliens in the Hawaiian ecosystem were discussed, along with suggestions for their management.

Smith, C. W. 1989. Non-native plants. Pp. 60-69 *In*: C. P. Stone and D. B. Stone, eds., Conservation biology in Hawai'i. University of Hawai'i Cooperative National Park Studies Unit, Honolulu.

Fayatree was listed along with koa haole (*Leucaena leucocephala*) and mesquite (*Prosopis pallida*) as examples of alien nitrogen-fixing species in Hawai'i. Such plants also enrich the soil as their litter decomposes, resulting in a medium in which other alien plants are encouraged to grow. Fayatree is found on all of the principal Hawaiian islands, but its greatest current impact is in the forest around Volcano on Hawai'i Island. Research on natural enemies from the native habitats, as well as on herbicidal and manual control of fayatree were reported to be in progress.

Smith, C. W. 1990. Weed management in Hawai'i's National Parks. 1990. Monographs in Systematic Botany from the Missouri Botanical Garden 32:223-234.

An overview was presented of the National Park Service weed management program in Hawai'i. Planning, mapping, and control strategies were discussed, including those for fayatree.

Smith, C. W., and C. Lutzow-Felling. 1993. *Myrica faya*: One man's meat is another man's poison. Abstracts of the First Symposium "Fauna and Flora of the Atlantic Islands," October 4-9, 1993, Funchal, Madeira, Portugal. p. 60.

Fayatree, introduced to Hawai'i by Portuguese immigrants in the late 1800s, now infests 40,000 ha. The cost for removal would exceed \$20 million, and maintaining control would cost \$2.5 million every year. Attempts to control fayatree with herbicides were successful on a limited scale but not cost effective. Control by grazing was not successful because goats and cattle demonstrate a distinct lack of preference for it. Exploration for biocontrol in the Azores, Madeira, and the Canary Islands is ongoing and has proved rewarding. A number of insects have been studied, some have been rejected, one has been released, and others are undergoing trial. Cooperators at the University of the Azores have been engaged to participate more detailed research.

Smith, C. W., and J. T. Tunison. 1992. Fire and alien plants in Hawai'i: Research and management implications for native ecosystems. Pp. 394-408 *In*: C. P. Stone, C. W. Smith, and J. T. Tunison, eds., Alien plant invasions in native ecosystems of Hawai'i: Management and research. University of Hawai'i Press, Honolulu.

Although woody alien plants usually invade burned areas only to a limited degree, fayatree was given as an example of a woody species which resprouts vigorously after a fire and thus presents the threat of reinvasion.

Smith, M. A. L., and D. Neely. 1981. Screening woody ornamental cuttings for propagation diseases. *Plant Disease* 65(11):893-995.

Myrica pensylvanica was included in a study of 16 woody ornamental species commonly propagated by cuttings, under a variety of mist and rooting medium treatments, for the effects of the root pathogens *Rhizoctonia*, *Phytophthora*, and *Pythium*. In three of the woody species, including *M. pensylvanica*, pathogenesis was reported to have virtually no effect, and roots developed successfully.

Spaulding, P., and J. R. Hansbrough. 1932. *Cronartium comptoniae*, the sweetfern blister rust of pitchpines. U. S. Department of Agriculture Circular 217.

The sweetfern blister rust fungus, *Cronartium comptoniae*, thought to be closely related to the fungus causing white pine blister rust, was reported to be highly destructive to several economically important species of pine, upon which it forms its spermatogonial and aecial states. Its alternate hosts, upon which uredinia and telia are formed, were reported as sweetfern (*Comptonia asplenifolia*) and sweet gale (*Myrica gale*). *Myrica carolinensis* was successfully inoculated experimentally, but had not been observed to become naturally infected. Inoculation attempts of *M. californica*, *M. cerfiera*, *M. pumila*, and *M. inodora* were not successful, indicating these as nonsusceptible species.

Sporne, K. R. 1975. The morphology of angiosperms. St. Martin's Press, New York.

The Myricaceae was considered an ancient family dating to the Tertiary Epoch of the Cretaceous Period with the living members representing relicts of once extensive tracts of subtropical forest that spread across the territory that is now central and southern Europe.

Sprent, J. I., and R. Scott. 1979. The nitrogen economy of *Myrica gale* and its possible significance for the afforestation of peat soils. Pp. 234-242, *In*: Gordon, J. C., C. T. Wheeler, and D. A. Perry, eds., Symbiotic nitrogen fixation in the management of temperate forests. Forest Research Laboratory, Oregon State University, Corvallis, Oregon.

The ability of *Myrica gale* to fix nitrogen was described as an important asset of the plant in colonizing peat soils. The performance of *M. gale* as a nitrogen fixer was found to vary significantly from site to site, with evidence that it preferred freely drained areas. When shed, its leaves contained just under 2% nitrogen. By the following summer, the nitrogen content of the litter was found to have dropped significantly, suggesting release into the ecosystem. This, together with *M. gale*'s ability to associate with planted conifers, suggested that the species should be further investigated as a source of nitrogen for forest trees in peat soils.

Sprent, J. I., R. Scott, and K. M. Perry. 1978. The nitrogen economy of *Myrica gale* in the field. *Journal of Ecology* 66:657-668.

Myrica gale is one of three non-leguminous, nitrogen-fixing woody angiosperms native to Britain. In view of the widespread occurrence of *M. gale* in Europe, field studies were undertaken to supplement the laboratory studies of Bond to assess the contribution of this species to the nitrogen economy of this species to the areas in which it grows. Data presented in this study were considered to support the suggestion by Bond (1951) that nitrogen fixation by *M. gale* is of considerable ecological importance in bog habitats.

Standley, P. C. 1920. Trees and shrubs of Mexico (Gleicheniaceae-Betulaceae). Contributions from the United States National Herbarium, Vol. 23, Part 1, Government Printing Office, Washington, D. C.

Myrica mexicana (= *M. xalapensis*; *M. lindenina*; *M. cerifera*) with the common names arbol de la cerra, luancanala, or chac all was reported from Mexico at Jalisco, Veracruz, from Yucatan and Chiapas, and from Guatemala. *Myrica pringlei* (= *M. parviflora confusa*), with the common name chilpanxohuilt, was reported from Hidalgo and Oaxaca, Mexico.

Stewart, D. P., and G. Bond. 1961. The effect of ammonium nitrogen on fixation of elemental nitrogen in *Alnus* and *Myrica*. Plant and Soil 14(4):347-359.

Experiments were conducted to determine the effects of combined nitrogen (as ammonium) on the ability of roots of *Alnus glutinosa* and *Myrica gale* to form nodules and fix atmospheric nitrogen. A significant nodule-forming ability was found on plants of these species grown in water culture with different levels of ammonium nitrogen labelled with N¹⁵ in the culture solution. The nodules continued to fix atmospheric nitrogen, although in a lesser amount, despite the presence of ammonium nitrogen in the rooting medium. In *Alnus*, but not in *Myrica*, fixation was considerably enhanced in the presence of a low level of ammonium nitrogen, owing to greater nodule development. Results suggested that under field conditions, some fixation of atmospheric nitrogen will always be associated with nodules present.

Steyermark, J. A., and B. Maguire. 1967. Botany of the Chimante Massif - II. Memoirs of the New York Botanical Garden 17:440-464.

Myrica rotundata was described as a new species from the sandstone table mountains of Guayana.

Stone, C. P. 1985. Alien animals in Hawai'i's native ecosystems: Toward controlling the adverse effects of introduced vertebrates. Pp. 251-297 In: C. P. Stone and J. M. Scott, eds., Hawai'i's terrestrial ecosystems: Preservation and management. University of Hawai'i Cooperative National Park Studies Unit, Honolulu.

Feral pigs exist in Hawai'i in a mutualistic relationship with certain dominant alien plants, including fayatree. Pigs were reported as distributors of fayatree, the berries of which averaged 12% of the total volume of food taken in the Puhimau Unit of Hawai'i Volcanoes National Park. The danger that aliens, such as fayatree, can, through nitrogen fixation, create their own favorable environment on Hawai'i's young and nitrogen-poor soils was emphasized. The study to determine the role of fayatree in altering primary succession in Hawai'i Volcanoes National Park was reportedly proposed and funded. Alien birds disperse, or are otherwise closely associated with alien plants. Fayatree was listed among the most important of these.

Stone, C. P., and D. Taylor. 1984. Status of feral pig management and research in Hawai'i Volcanoes National Park. Pp. 106-117 In: C. W. Smith, ed., Proceedings of the Fifth Conference in Natural Sciences, Hawai'i Volcanoes National Park. University of Hawai'i Cooperative National Park Studies Unit, Honolulu.

Feral pigs in Hawai'i Volcanoes National Park were reported to use certain food materials in greater abundance depending on the actual habitat of the park where pigs were located. Thus, pigs in the Puhimau area, a wet forest, used hapu'u (tree fern), fayatree berries, earthworms, and *Lycopodium* to a greater extent than did pigs in Kipuka Ki, a mesic forest.

Stone, C. P., L. W. Cuddihy, and J. T. Tunison. 1992. Responses of Hawaiian ecosystems to removal of feral pigs and goats. Pp. 666-704 In: C. P. Stone, C. W. Smith, and J. T.

Tunison, eds., Alien plant invasions in native ecosystems of Hawai'i: Management and research. University of Hawai'i Press, Honolulu.

Percent of alien plant cover and the number of alien species in plots in a pig-inhabited area near one of the experimental exclosures in the Thurston Lava tube area of Hawai'i Volcanoes National Park showed an increase in 1985 as compared to 1981. Fayatree was one of the new invaders in the plots over the 4-year period.

Strobel, G. A. 1991. Biological control of weeds. *Scientific American*, July, pp. 72-78.

The author presented a semipopular article outlining the theory, practices, and procedures of the biocontrol approach to weed control for a general readership. Fayatree, specifically, was not mentioned.

Sundberg, M. D. 1985. Pollen of the Myricaceae. *Pollen et Spores* 27(1):15-28.

Pollen of 30 species of *Myrica* and its close relatives was examined using light, scanning, and transmission electron microscopy. The results provided clarification for several taxonomic questions. Retention of the genus *Canacomyrica* in the Myricaceae was supported, although the author agreed with the suggestion of Leroy (1949) that a separate subfamily should perhaps be created for *Canacomyrica*, the Canacomyriceoideae. Pollen morphology did not support the generic status for *Gale* as defined by Chevalier (1901), but did support Chevalier's division of *Myrica* into the three sections Cerophora, Faya, and Morella. The use of pollen morphology in determining further taxonomic relationships within the family Myricaceae was reportedly limited due to intraspecific variation.

Sunding, P. 1979. Origins of the Macaronesian flora. Pp. 13-40 In: D. Bramwell, ed., Plants and islands. Academic Press. London.

Origins of vegetation of the Macaronesian islands was discussed from a biogeographical standpoint. It was hypothesized that during the Tertiary, the climate became cooler, the vegetation zones of Europe were pressed southward toward the Tethys, later the Mediterranean Sea, and further southward over land connections including the Strait of Gibraltar. Because of this displacement of vegetation zones and the drying of the climate, several plant species disappeared entirely, while others continued to exist in disjunct populations in favorable areas, including the Macaronesian islands, which were buffered by the ocean. Some species of the South European Tertiary flora, fayatree among others, besides occurring in Macaronesia, are still found in certain suitable places in the southwest of the Iberian peninsula.

The author provided information on the origin of the name "Macaronesia" which does not appear in ordinary maps or atlases but is frequently used among biologists to designate an area of natural biological delimitation. The concept of Macaronesia was reportedly introduced by the botanist Philip Baker Webb about 120 years ago. As well as the island groups, from a biogeographical standpoint, an area of southern Morocco on the African mainland has a natural affinity with Macaronesia and may be included in this grouping.

Takhtajan, A. 1969. Flowering plants: Origin and dispersal. Oliver and Boyd, Edinburgh. 310 pp.

In a classic text on the origin, dispersal, and biogeography of the angiosperms, the author attributed the origin of the Myricaceae to the Tertiary Period, approximately 60 million years before the present. The family was considered a relic of a once extensive subtropical Mediterranean flora.

Takhtajan, A. 1986. Floristic regions of the world. University of California Press, Berkeley and Los Angeles. 522 pp.

The author described 35 world floristic regions and listed the vascular plants which occupy a predominant position in each region. Fayatree was assigned to the Macaronesian floristic region, which includes the Azores, Madeira, Canary, Salvage, and Cape Verde Islands—Atlantic islands situated off the northwestern coast of the African continent. The most characteristic vegetative element of the region is forest dominated by evergreen members of the Lauraceae.

Tang, F. -T. 1974. A preliminary report on the Lacciferidae -- insect fauna with description of a new species. Acta Entomologica Sinica 17(2):205-209.

The author reviewed the Lacciferidae (Homoptera) of China, and described a new species, *Metatacharida myrica* from the branches of *Myrica rubra*. A detailed morphological description of the insect was provided. (in Chinese with English summary)

Tanimoto, V. M., and W. P. Char. 1992. Alien plant control on state lands including natural areas. Pp. 536-550 In: C. P. Stone, C. W. Smith, and J. T. Tunison, eds., Alien plant invasions in native ecosystems of Hawai'i: Management and research. University of Hawai'i Press, Honolulu.

Fayatree was designated for control by four State of Hawai'i Division of Forestry and Wildlife field offices, from 1975-time of publication, on the islands of Hawai'i, Maui, Kau'i, and O'ahu.

Taylor, D. 1992. Controlling weeds in natural areas in Hawai'i: A manager's perspective. Pp. 752-756 In: C. P. Stone, C. W. Smith, and J. T. Tunison, eds., Alien plant invasions in native ecosystems of Hawai'i: Management and research. University of Hawai'i Press, Honolulu.

Fifty-three species, from a list of 475 alien plants, have been identified by resource management of Hawai'i Volcanoes National Park as actually or potentially disruptive. Disruptive species were those threatening the integrity of native plant communities by displacing or hindering reproduction of native species, or altering community dynamics. Fayatree was given as an example of such a disruptive species.

Taylor, D., and G. P. Markin. 1992. Environmental assessment: Release of a defoliator moth as a biological control agent to control firetree in the park. Unpublished report, U. S. Department of the Interior, National Park Service, Hawai'i Volcanoes National Park.

The first proposal for release of an insect imported to Hawai'i from the natural habitats of fayatree and tested in the quarantine facility at Hawai'i Volcanoes National Park was the subject of an environmental assessment. The leaf-tip roller *Phyllonorycter myricae*, previously had been released on fayatree outside the park but near the park boundary.

The Nature Conservancy of Hawai'i/Natural Resources Defense Council. 1992. The alien pest species invasion in Hawai'i: Background study and recommendations for interagency planning. TNCH, Honolulu.

The "Firetree Control Committee (FCC)" was established in 1987 to develop and implement a long-term management plan to control fayatree. The plan was intended to guide both public and private actions for the next 20 years. The committee consisted of 25 members, representing: United States Department of Agriculture Soil Conservation Service, Resource Conservation and Development, Kau

Soil and Water District, National Park Service, State Department of Land and Natural Resources, U. S. Forest Service, University of Hawai'i Hilo Campus, Cooperative Park Studies Unit, Hawai'i Department of Agriculture, County of Hawai'i, and area ranchers. A list of immediate objectives of the FCC in controlling fayatree and educating the public as to the noxious nature of this weed was presented.

Thieret, J. W. 1966. Habitat variation in *Myrica pensylvanica* and *M. cerifera*. *Castanea* 31:183-185.

Two North American species of *Myrica*, *M. pensylvanica* and *M. cerifera*, were reported to be highly variable in habitat. Whereas *M. pensylvanica* is generally described as being without rhizomes, populations on Prince Edward Island were reported to have prominent rhizomes, causing it to key out to *M. pusilla*. For *M. cerifera*, this variability has resulted in the recognition and naming of two taxa when, in reality, only one was thought to exist. In various manuals, variations of *M. cerifera* are considered to be *M. pusilla*, *M. cerifera* var. *pumila*, or *M. pumila* where it occurs in Louisiana. Production of rhizomes may be a function of the xeric nature of the habitat rather than a consistent genetic factor useful in delimiting species. The author suggested that there was insufficient justification to recognize *M. pusilla* as a separate species from *M. cerifera*.

Thompson, R. 1989. Park Service battles alien tree from the Azores. Honolulu Star Bulletin, Feb. 27.

The invasiveness of fayatree in Hawai'i Volcanoes National Park and the need to fund biocontrol research to combat the problem was discussed in a newspaper article.

Thonner, F. 1962. The flowering plants of Africa. Reprint; (first published in 1915 by Dulau and Co., Ltd., London); Wheldon and Wesley, Ltd., and Hafner Publishing Co., New York.

In a flora of African genera, 25 species of *Myrica* were reported to occur in tropical and South Africa, the Canary Islands, and the Azores. The species were not listed, however.

Tiffney, B. H. 1986. Fruit and seed dispersal and the evolution of the Hamamelidae. *Annals of the Missouri Botanical Garden* 73:394-416.

The fruit of Myricaceae was described as drupaceous or almost a nutlet, sometimes enclosed by small bracteoles. The fruits were reportedly dispersed by birds, but water and wind dispersal were also considered possible. Geologically, the earliest report of the family was of *Comptonia octocostata* from the early Maastrichtian of Europe. This was followed by *C. goniocarpa* from the Early to Mid-Oligocene of (former) East Germany. *Myrica boveyana* appeared in the Early Eocene of southern England and was followed by a number of subsequent reports of other species.

Tjepkema, J. 1978. The role of oxygen diffusion from the shoots and nodule roots in nitrogen fixation by root nodules of *Myrica gale*. *Canadian Journal of Botany* 56:1365-1371.

Nitrogenase activity (acetylene reduction) and oxygen uptake by root nodules of *Myrica gale* were measured before and after removal of nodule roots. There was no significant effect of nodule root removal in respiration rate. The author concluded that only small amounts of oxygen were transported from the shoot to the nodules.

Torrey, J. G. 1978. Nitrogen fixation by actinomycete-nodulated angiosperms. *BioScience* 28:586-592.

The author reviewed published information on the structure and endophytic mechanism of the actinomycete microbe that symbiotically interacts with a variety of woody angiosperms. Attempts, mostly unsuccessful, to isolate the endophytes from root nodules and grow them in culture were described. The ecological importance of actinomycete-nodulated, nitrogen-fixing plants was also reviewed.

Torrey, J. G., and D. Callahan. 1978. Determinate development of nodule roots in actinomycete-induced root nodules of *Myrica gale*. *Canadian Journal of Botany* 56:1357-1364.

Young seedlings of *Myrica gale* were inoculated with the root nodule actinomycete (endophyte) to determine its effect on root development. Nodule root growth was found to be distinct in that it shows strong negative geotropism. The endophyte was restricted to cortical cells of the nodule lobe and was totally absent from tissues of the nodule root. A suggested probable role for nodule roots was to facilitate gas diffusion to the nitrogen-fixing endophyte site in the nodule lobe when nodules occur under conditions of low oxygen tension.

Torrey, J. G., and D. Callahan. 1979. Early nodule development in *Myrica gale*. *Botanical Gazette* 140 (Supplement):S10-S14.

Early development of root nodules in *M. gale* as seen in root tip sections was described. The route of actinomycete filament invasion into the root tip of *M. gale* and the early development of root nodules was traced.

Tulang, M. 1992. The U. S. Department of Agriculture's rural development approach to alien plant control in Hawai'i: A case study. Pp. 577-583 In: C. P. Stone, C. W. Smith, and J. T. Tunison, eds., Alien plant invasions in native ecosystems of Hawai'i: Management and research. University of Hawai'i Press, Honolulu.

The approach to fayatree control in Hawai'i was compared to that used for gorse (*Ulex europaeus*). The strategy involved interagency cooperation and the efforts of a task force and management team. Such an organization was reported to be in place at the time of writing, addressing the fayatree problem on several islands.

Tunison, T. J. 1992a. Fountain grass control in Hawai'i Volcanoes National Park: Management considerations and strategies. Pp. 376-393 In: C. P. Stone, C. W. Smith, and J. T. Tunison, eds., Alien plant invasions in native ecosystems of Hawai'i: Management and research. University of Hawai'i Press, Honolulu.

Management strategy for controlling fountain grass (*Pennisetum setaceum*) was the same as that used with fayatree and other aggressive alien plant species in Hawai'i Volcanoes National Park. That is, control efforts were not expended on a park-wide basis, in which the plant was considered not controllable. Control was concentrated in those areas of the most undisturbed and valuable habitat selected as representative of the park's resources.

Tunison, T. J. 1992b. Alien plant control strategies in Hawai'i Volcanoes National Park. Pp. 485-505 In: C. P. Stone, C. W. Smith, and J. T. Tunison, eds., Alien plant invasions in native ecosystems of Hawai'i: Management and research. University of Hawai'i Press, Honolulu.

Disruptive alien plants, i.e., those capable of replacing native vegetation, forming monospecific stands, and altering fire and nutrient cycling regimes were tabulated. Fayatree was among the most disruptive species which have expanded their ranges significantly and increased in density in the park

within the last 25 years. Widespread species such as fayatree were controlled in special ecological areas, and targeted for biocontrol as the only practical approaches available.

Tunison, J. T., and R. L. Loh. The invasion of faya tree in five plant communities, a baseline study, 1994. Technical report, University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu. In preparation.

Fayatree was described as successful invader because of prolific seed production, widespread dispersal by nonnative birds, rapid growth rate, and ability to grow under a wide range of light levels, including survival at low intensities. Fayatree is an actinorhizal nitrogen fixer, which also contributes to its rapid growth and success as an invader.

Tunison, J. T., and C. P. Stone. 1992. Special ecological areas: An approach to alien plant control in Hawai'i Volcanoes National Park. Pp. 781-798 *In*: C. P. Stone, C. W. Smith, and J. T. Tunison, eds., *Alien plant invasions in native ecosystems of Hawai'i: Management and research*. University of Hawai'i Press, Honolulu.

A Special Ecological Areas (SEA) approach was adopted in 1985 for control of widespread, disruptive alien plants in Hawai'i Volcanoes National Park. This approach involved the removal of all disruptive aliens in areas designated as representative of particular native habitats. Fayatree, considered beyond practical control through conventional methods in the park, was considered one of 11 particularly disruptive species targeted for intensive control in SEAs. Fayatree density was shown to decline significantly following four years of such control effort.

Tunison, J. T., S. Carlberg, and R. L. Loh. The effect of faya tree on understory vegetation in dry 'ohi'a woodland and scrub. Technical report, University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu. In preparation.

Data intended for publication as a technical report were gathered documenting the disruption of native woodland and scrub habitats of Hawai'i Volcanoes National Park by the invasion of fayatree.

Tunison, J. T., L. F. Castro, and R. L. Loh. Faya tree dieback: Distribution, demography, and associated ecological factors. Technical report, University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu. In preparation.

Data were gathered from field observations of an ongoing extensive, unexplained dieback of fayatree at Hawai'i Volcanoes National Park with the object of determining the cause (whether biotic or abiotic) and possible short and longterm effects of the phenomenon on fayatree populations. A concentric distribution of fayatree dieback pattern in Hawai'i Volcanoes National Park suggested that biotic agent(s) may be important in the etiology of this condition.

Tunison, J. T., C. W. Smith, and C. P. Stone. 1992. Alien plant management in Hawai'i: Conclusions. Pp. 821-833 *In*: C. P. Stone, C. W. Smith, and J. T. Tunison, eds., *Alien plant invasions in native ecosystems of Hawai'i: Management and research*. University of Hawai'i Press, Honolulu.

Approximately 90 of the 861 naturalized alien plant species in Hawai'i are significant threats to native ecosystems. Fayatree was included among those species which had not yet reached the natural limits of their ranges, nor probably also their densities, and thus pose an ever-increasing threat. Regional and statewide cooperation in management of weeds such as fayatree are demonstrated in organizations such as the multi-agency Firetree Committee, but much more could be done in regional and statewide management of widespread, disruptive species.

Tunison, J. T., C. P. Stone, and L. W. Cuddihy. 1986. SEAs provide ecosystem focus for management and research. *Park Science* 6:10-13.

Fayatree was listed among the most serious alien plant threats to Hawaiian ecosystems. The Special Ecological Area approach to managing such widespread and disruptive species in Hawai'i Volcanoes National Park involved concentrating intensive control effort in areas designated as representative of the park's native habitats. Control in the remainder of the park must await development of methods not currently available, such as biocontrol.

Turner, D. R., and P. M. Vitousek. 1987. Nodule biomass of the nitrogen-fixing alien *Myrica faya* Ait. in Hawai'i Volcanoes National Park. *Pacific Science* 41:186-190.

The association between canopy cover and basal area with root nodule biomass of fayatree, as measured at three sites in Hawai'i Volcanoes National Park, was discussed. In general, root nodule biomass was found to increase with an increase in basal area. The authors concluded that nitrogen fixation by invading fayatree was sufficient to alter patterns of succession in the park.

Tutin, T. G. 1953. The vegetation of the Azores. *Journal of Ecology* 41:53-61.

The previous observations of Seubert and Hochstetter (1843) and of Guppy (1917) were reviewed and summarized. The Azores were characterized as all of recent volcanic origin, with eruptions occurring on several islands within the last 400 years. (Note: since the time of this writing, the most recent eruption had occurred in 1958 on the island of Faial, DG.) Fayatree was dominant on a 1718 lava flow on the east end of the island of Pico. The "laurel forest," dominated by the broad-leaved evergreen trees *Persea azorica* and fayatree, appeared to be the climax type up to about 600 m elevation. These species grew to heights of 6-7 m in favorable localities.

Van Ryssen, F. W. J., and N. Grobbelaar. 1970. The nodulating and nitrogen fixing ability of South African *Myrica* species. *South African Journal of Science*. January:22-25.

The authors recognized nine valid species of *Myrica* in South Africa at the time of writing: *M. brevifolia*, *M. cordifolia*, *M. diversifolia*, *M. humilis*, *M. integra*, *M. kraussiana*, *M. pilulifera*, *M. quercifolia*, and *M. serrata*. Typical *Myrica* root nodules were found on specimens of all these species. Exposure of the root nodules and roots to a nitrogen-15 enriched atmosphere indicated that in all cases the nodules were capable of fixing nitrogen.

Viégas, A. P. 1944. Alguns fungos do Brazil. II. Ascomycetos. *Bragantia* 4(1/6):5-392.

Plyllachora myrica-rostratae was reported on *Myrica rostrata* among a large number of Ascomycetes reported, described, and illustrated from Brazil. (in Portuguese (?); original reference not seen)

Vitousek, P. M. 1986. Biological invasions and ecosystem properties: Can species make a difference? Pp. 163-176 In: H. A. Mooney and J. A. Drake, eds., *Ecology of biological invasions of North America and Hawai'i*. Springer-Verlag, New York.

Whereas most often relatively little is known of the nitrogen status of soil in areas invaded by nitrogen-fixing weed species, invasion by fayatree in Hawai'i is cited as an exception. The sites invaded are known to be extremely N-deficient, especially on young lava flows and ash deposits, and they contain no native N-fixers. Fayatree can form nearly monospecific stands in such areas. Since biological invasions by a wide variety of alien species in Hawai'i are most successful on more fertile sites, the addition of nitrogen fertility to soil may increase the probability of further invasions.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: Towards an integration of population biology and ecosystem studies. *Oikos* 57:7-13.

The author described how biological invaders can alter ecosystem-level properties, and conversely, how changes in ecosystem properties can alter population processes. *Faytree* was given as an example of an invasive species altering ecosystem-level properties in Hawai'i by increasing biologically available soil nitrogen as much as fourfold.

Vitousek, P. M. 1992. Effects of alien plants on native ecosystems. Pp. 29-41 *In*: C. P. Stone, C. W. Smith, and J. T. Tunison, eds., *Alien plant invasions in native ecosystems of Hawai'i: Management and research*. University of Hawai'i Press, Honolulu.

The author stated that nitrogen-fixing aliens occurred in many regions, including Pacific islands. Most often, relatively little has been known of the nitrogen content of the soil of the area invaded. The recent invasion of young volcanic substrates of Hawai'i Volcanoes National Park on the island of Hawai'i, the most recently formed of the archipelago, was an exception. The young ash deposits were extremely nitrogen-deficient and contained no nitrogen fixers. This setting therefore was ideal for evaluation of the rate and quantity of nitrogen contribution to the substrate. *Faytree* added three times more nitrogen to open-canopied 'ohi'a forests than did all natural sources combined, and thus appeared to be a significant factor in influencing rate and direction of primary succession.

Vitousek, P. M., and L. R. Walker. 1989. Biological invasion by *Myrica faya* in Hawai'i: Plant demography, nitrogen fixation, and ecosystem effects. *Ecological Monographs* 59:247-265.

Much of the work of Vitousek and his associates and others on the biology, history, and ecosystem effects of *faytree* in Hawai'i Volcanoes National Park was summarized in this paper. Vitousek and his associates investigated fruit production, dispersal and germination, seedling survival and growth rate of *faytree*. They have quantified nitrogen fixation by *faytree* and have projected the subsequent potential ecosystem-level effects of the introduced nitrogen.

Vitousek, P. M., L. L. Loope, and C. P. Stone. 1987. Introduced species in Hawai'i: Biological effects and opportunities for ecological research. *Trends in Ecology and Evolution* 2:224-227.

The authors discussed the contributions that the study of alien species in Hawai'i could have on the preservation of native ecosystems. The impacts of alien species on native species, on ecosystem level effects, and the interactions among alien species in Hawai'i were also discussed. *Faytree* was given as an example of an alien species which could alter ecosystem-level properties by altering nutrient circulation and soil characteristics.

Vitousek, P. M., L. R. Walker, L. D. Whiteaker, D. Mueller-Dombois, and P. A. Matson. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawai'i. *Science* 238:802-804.

The potential ecological effects of the net increase in nitrogen in poorly-formed soils of Hawai'i Volcanoes National Park were assessed. The authors concluded that *faytree* may alter ecosystem-level characteristics in the park. Although the longer term consequences of this alteration remain to be determined, even if *faytree* is eventually replaced by other species through ecological succession, it is unlikely that the effects of the nitrogen it fixes will disappear. Whereas the capacity to fix nitrogen was considered widespread in the Hawaiian flora, the ability of *faytree* to establish populations in young volcanic sites was considered unique.

Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1990. Manual of the flowering plants of Hawai'i. Vols. 1 & 2. University of Hawai'i Press and Bishop Museum Press, Honolulu.

The two volumes comprise a recent comprehensive flora of Hawai'i in which fayatree is described as a naturalized species, having been introduced by Portuguese laborers, who made wine from the fruit (from Little and Skolmen, 1989). Fayatree has become a serious pest in Hawai'i, occurring in mesic to wet forest and becoming dominant in many areas.

Wagner, W. L., D. R. Herbst, and R. S. N. Yee. 1985. Status of the native flowering plants of the Hawaiian Islands. Pp. 23-74 In: C. P. Stone and J. M. Scott, eds., Hawai'i's terrestrial ecosystems: Preservation and management. University of Hawai'i Cooperative National Park Studies Unit, Honolulu.

The authors presented a comprehensive discussion of the native flora of Hawai'i, and mentioned several introduced species as threats to native plants due to competition. Among these was fayatree, which, citing Neal (1965), was introduced to Hawai'i for use in reforestation.

Walker, E. H. 1976. Flora of Okinawa and the southern Ryukyu Islands. Smithsonian Institute Press, Washington, D. C.

Myrica rubra (= *M. nagi*), with the common name Yama-mono, was reported from Okinawa and the Ryukyu Islands, and *M. rubra* var. *alba*, common name shiro-mono, from Japan and Okinawa.

Walker, L. R. 1990. Germination of an invading tree species (*Myrica faya*) in Hawai'i. Biotropica 22:140-145.

The author reported greenhouse-conducted germination trials of fayatree. High (>80%) and low (<30%) shade conditions, and leaf litter reduced germination. Moderate shade (approximately 55-65%) and scarification enhanced germination.

Walker, L. R., and P. M. Vitousek. 1991. An invader alters germination and growth of a native dominant tree in Hawai'i. Ecology 72:1449-1455.

Evidence was presented that fayatree leaf litter inhibited germination of 'ohi'a, the most common overstory tree in native forests of Hawai'i Volcanoes National Park. The physical characteristics of the leaf litter were responsible for the inhibition, since germination occurred when litter was removed. No evidence of chemical leachate inhibition of 'ohi'a was found. Nitrogen-rich soils from fayatree sites increased 'ohi'a seedling growth, but young fayatrees growing in proximity to established 'ohi'a did not increase the growth of these trees. Whereas shading by fayatree improved 'ohi'a germination and seed survival, the net effect of faya on 'ohi'a was prevention of regeneration under a dense canopy of fayatree.

Walker, L. R., R. L. Loh, J. T. Tunison, and P. M. Vitousek. Population growth and nitrogen-fixation of faya tree (*Myrica faya*), 1986-1992. Technical report, University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu. In preparation.

This study was undertaken to document the growth of fayatree populations within infested areas of Hawai'i Volcanoes National Park, as distinct from the studies of range expansion of this tree since the time of its introduction to Hawai'i. The number of individual trees increased 2 to 18 fold. Populations increased more rapidly in recently invaded sites than in sites where fayatree was already well established. Rapid population growth occurred on both pahoehoe lava substrate with shallow ash and on deep cinder. Rapid population growth also occurred across a broad range of precipitation,

from 1,000 to 2,400 mm rain per year. Changes in nitrogen fixation were calculated that accompanied population growth. Nitrogen fixation by fayatree doubled the soil nitrogen input in sites where the invasion was in early stages and quadrupled input in more densely infested sites.

Walker, L. R., P. M. Vitousek, L. D. Whiteaker, and D. Mueller-Dombois. 1986. The effect of an introduced nitrogen-fixer (*Myrica faya*) on primary succession on volcanic cinder. (Abstr.) P. 98 In: C. W. Smith, ed., Proceedings of the Sixth Conference in Natural Sciences, Hawai'i Volcanoes National Park. University of Hawai'i Cooperative National Park Studies Unit, Honolulu.

The authors discussed the effects of increased available soil nitrogen, contributed by fayatree, on the natural succession cycle of typically poor volcanic soils on the island of Hawai'i. Interrelationships between fayatree and 'ohi'a were also considered. Fayatrees frequently become established under existing 'ohi'a trees. Fayatree seed rain was found exclusively under 'ohi'a canopies, and no seeds were found in the open, supporting the hypothesis of bird dispersal. On the other hand, fayatree seed germination was reduced by 50% in 'ohi'a leaf litter.

Wallace, A. R. 1881. Island life, or the phenomenon and causes of insular faunas and floras. Harper and Brothers, New York.

In discussing how the flora of the Azores may have been dispersed, the author noted that trees and shrubs with large and heavy fruits common on the European continent did not occur in the islands. Trees and shrubs indigenous to the islands, such as Portugal laurel, myrtle, laurestinus, elder, Canary laurel, and fayatree all bore small berries. He suggested that such small fruits were carried either externally or within the digestive tract of birds, the primary dispersal agents of plants among islands of the north Atlantic.

Walters, G. A. 1970. Selecting timber species to replace killed firetree in Hawai'i. USDA Forest Service Research Note PSW-211. Pacific Southwest Forest and Range Experiment Station, Berkeley, California. 4 pp.

Tests were reported of plantings of seven alien timber species and their potential to replace herbicide-killed fayatrees. The possible replacements were Australian toon, tropical ash, Queensland maple, blackwood, Moreton bay chestnut, and hoop pine. Australian toon showed the most promise as a reforestation tree on the basis of initial survival and growth potential.

Walters, G. A. 1972. Coppicing to convert small cull trees to growing stock. USDA Forest Service Research Note PSW-272. Pacific Southwest Forest and Range Experiment Station, Berkeley, California. 4 pp.

The effects of coppicing to convert damaged trees to growing stock trees were evaluated, and follow-up study on five tree species test-planted to replace fayatree killed by herbicidal application was reported. Many of the planted trees were damaged by falling detritus of fayatrees.

Walters, G. A. 1973. Tordon 212 ineffective in killing firetree in Hawai'i. USDA Forest Service Research Note PSW-284. Pacific Southwest Forest and Range Experiment Station, Berkeley, California. 3 pp.

A field trial to evaluate Tordon 212 for fayatree control was reported. The treatment was judged ineffective since an average of only 58% of treated trees was dead or dying two years following treatment.

Walters, G. A., and W. S. Null. 1970. Controlling firetree in Hawai'i by injection of Tordon 22K. USDA Forest Service Research Note PSW-217. Pacific Southwest Forest and Range Experiment Station, Berkeley, California. 3 pp.

U. S. Forest Service research was reported on fayatree control using Tordon 22K herbicide applied by injection into notches cut into the main stem. The herbicide was considered effective, with 100% canopy kill and 99% control of sprouting recorded one year after treatment.

Watt, J. M., and M. G. Breyer-Brandwijk. 1962. The medicinal and poisonous plants of southern and eastern Africa. Second edition, E. and S. Livingstone, Ltd., Edinburgh and London.

Myrica conifera, *M. brevifolia*, *M. burmanii*, *M. kilimondscharica*, *M. kraussiana*, *M. pilulifera* Rendle, *M. quercifolia*, and *M. cordifolia* all with the common names wasberry or washe, were reported in South Africa. *Myrica kandtiana* was reported in Zaire.

West, E. 1945. Notes on Florida fungi III. *Mycologia* 28(1):65-79.

The rust fungus *Gymnosporangium ellisii* was included among a list of 35 fungi which form witches' brooms in western Florida. These symptoms were observed on the telial host of the rust, white cedar (*Chamaecyparis thyoides*). An abundance of the aecial host, *Myrica cerifera*, occurred in the area and was reportedly "severely diseased", bearing large numbers of aecia on leaves and stems.

Wester, L. 1992. Origin and distribution of adventive alien flowering plants in Hawai'i. Pp. 99-154 In: C. P. Stone, C. W. Smith, and J. T. Tunison, eds., *Alien plant invasions in native ecosystems of Hawai'i: Management and research*. University of Hawai'i Press, Honolulu.

Fayatree was included in a comprehensive list of alien seed plants in Hawai'i, and information on its means and time of introduction, herbarium records, and distribution throughout the archipelago was given.

Wheeler, C. T. 1969. The diurnal fluctuation in nitrogen fixation in the nodules on *Alnus glutinosa* and *Myrica gale*. *New Phytologist* 68:675-682.

Maximum rates of nitrogen fixation in the root nodules of first-year plants of *Alnus glutinosa* and *Myrica gale* growing under natural illumination and constant temperatures were found by acetylene assay to be reached about midday. The rate of respiration in detached nodules was also highest near midday. These observations did not appear to be accounted for by ingress of photosynthates into the nodules at midday, as determined by analysis of gross carbohydrate levels in the nodules at different times of day.

White, F. 1993. African Myricaceae and the history of the Afromontane flora. *Opera Botanica* 121:173-188.

The author provided a comprehensive discussion of the Myricaceae of Africa and included fayatree which he stated was confined to Macaronesia, occurring in Madeira and the Azores and on all islands of the Canaries, but rare in the eastern ones. In Madeira the fruit is eaten by the endemic Madeira laurel pigeon and in the Canaries by the dark-tailed laurel pigeon. "It was introduced to several of the Hawaiian Islands and rapidly became an aggressive invader colonizing bare volcanic rock and recent ash deposits...Indigenous birds show little interest in its fruits but 5 species of exotic birds are known to ingest them. Among the birds, the Japanese white-eye...is the most frequent consumer, and seeds obtained from its faeces are viable..."

"Nearly every recent author has commented on the taxonomic difficulty of *Myrica*, and some have suggested that too many names are in current use." Whereas Killick had previously reduced the 19 species in South Africa to nine, White further reduced them to four, bringing the remaining species into synonymy: *M. humilis*, *M. quercifolia*, *M. cordifolia*, and *M. serrata*. Other African species were also discussed. The author cited a number of other papers discussing individual African species of *Myrica* providing a good reference source for this group, including the original reference to fayatree. He explained the justification for bringing many of the large number of African species into synonymy. Concerning the affinities of fayatree, White stated: "This species is currently placed in section Faya (Webb) A. Chev., which also includes two North American species *M. californica* Cham. and *M. inodora* W. Bartram. The section however is poorly defined and I know of no unequivocal evidence that *M. faya* is more closely related to the American than to the African species."

Whiteaker, L. D., and D. E. Gardner. 1985. The distribution of *Myrica faya* Ait. in the State of Hawai'i. Technical Report 55. University of Hawai'i Cooperative National Park Studies Unit, Honolulu. 31 pp.

A mapping survey was reported of the distribution of fayatree in the major Hawaiian Islands. Fayatree was reported on all the major islands, excluding Moloka'i and Kaho'olawe, in very diverse habitats. The common element in the wide environmental ranges was disturbance. No fayatree infestation was observed in mature, closed canopy native Hawaiian forest. The report concluded with possible control methods and anticipated results.

Whiteaker, L. D., and D. E. Gardner. 1987. The phenology and stand structure of *Myrica faya* Ait. in Hawai'i. Technical Report 62. University of Hawai'i Cooperative National Park Studies Unit, Honolulu. 20 pp.

Phenological data, collected during a 2-year study of 30 individual fayatrees at three sites on the island of Hawai'i, were reported. Minimum and maximum phenophase activity periods were observed; yet, at no time were any of the phenophases absent. Results indicate that low and high levels of precipitation and temperature extremes may represent environmental limits for fayatree.

Whiteaker, L. D., and D. E. Gardner. 1992. Firetree (*Myrica faya*) distribution in Hawai'i. Pp. 225-240 In: C. P. Stone, C. W. Smith, and J. T. Tunison, eds., Alien plant invasions in native ecosystems of Hawai'i: Management and research. University of Hawai'i Press, Honolulu.

Results of the mapping survey throughout the Hawaiian archipelago conducted in 1985 were updated and discussed, and distribution maps presented. Distribution patterns of fayatree indicate that this species had not yet reached the limits of its potential distribution in Hawai'i.

Whitten, H. 1984. Finding firetree enemies. Honolulu Star Bulletin, July 31, 1984, page A-20.

An expedition by C. S. Hodges and D. E. Gardner to the Azores, Madeira, and Canary Islands to identify potential biocontrol agents for possible introduction to Hawai'i for the control of fayatree was reported in a newspaper article.

Wilson, L. F. 1974. Life history and habits of a leaf tier, *Aroga argutiola* (Lepidoptera: Gelechiidae), on sweet fern in Michigan. The Canadian Entomologist 106(9):991-994.

The life history of the moth *Aroga argutiola* on *Myrica aspleniifolia* was described. Behavior of the insect was reported to involve tying leaves together to form a nest, from which the insect feeds on adjacent leaves.

Wilson, S. W., and A. G. Wheeler, Jr. 1984. *Pelitropis rotulata* (Homoptera: Tropiduchidae): Host plants and descriptions of nymphs. *Florida Entomologist* 67(1):164-168.

Nymphal stages of *Pelitropis rotulata* were described and illustrated. A list of 19 host plants, representing a wide range of families in North Carolina and Florida, was provided, including *Myrica cerifera*.

Woodward, S. A., P. M. Vitousek, K. Matson, F. Hughes, K. Benvenuto, and P. A. Matson. 1990. Use of the exotic tree *Myrica faya* by native and exotic birds in Hawai'i Volcanoes National Park. *Pacific Science* 44:88-93.

The significance of frugivory by native vs. alien birds and the subsequent contribution to dispersal of fayatree was investigated. The visitation and feeding habits of seven alien and four native avian species was observed at six sites in Hawai'i Volcanoes National Park. Results indicated that the alien Japanese white-eye (*Zosterops japonicus*) is a major dispersal agent for fayatree. These results contrast with those of LaRosa *et al.* (1985) in which Japanese white-eye was not indicated as a significant distributor of fayatree because it did not appear to ingest the seeds themselves, but removed the fleshy fruit from the seeds.

Yamayoshi, H. T. 1954. *Myrica faya* survey, District of Hamakua, Hawai'i. Unpublished report. Board of Commissioners of Agriculture and Forestry, Territory of Hawai'i, Hilo. 3 pp.

This report provides considerable specific information on the extent to which fayatree had become a problem in Hawai'i by 1954. The rapid spread of fayatree on the island of Hawai'i was noted, especially in the Hamakua District on the northeast side of the island, and plans to implement biocontrol were documented: "In connection with our proposed biological control of *Myrica faya* ... a reconnaissance trip was made to the Hamakua District in the vicinity of Paauilo and Kukaiau where this noxious pest has taken a firm foothold and has spread like 'wild fire' both into forest reserve and valuable ranch lands." The original site where fayatree was thought to have been introduced to the Hawaiian Islands was described: "The original source of infestation at Paauilo Homesteads, Lot 12, formerly owned by a Mr. Manuel De Lima, presently owned by Mr. Antone De Luz, Ranch foreman, Hamakua Mill Co., was visited. The writer had the privilege of seeing the last of the three original trees barely surviving among the thick *Eugenia jambos*, Linn., (rose apple) trees." Both mynah birds and Japanese white eye were recognized as important disseminators of fayatree, an assumption that was subject to experimental proof much later (see LaRosa *et al.* 1985, Woodward *et al.* 1990). The report also cited other areas of infestation on the island of Hawai'i, reported early chemical control methods by private landowners (e.g., Kukaiau Ranch). Chemicals used for control were sodium chlorate, 2-4-D, 2,4,5-T, and combinations of the latter two with both water and diesel fuel, which gave good results. Bulldozers, equipped with a pair of heavy rollers and cutting blades were used for mechanical control. Concern was also expressed regarding the occurrence in Hawai'i of *M. cerifera*, a species closely related to fayatree, which was reported to have been spreading in the Panaewa Forest Reserve in the land of Waiakea (island of Hawai'i). In retrospect, it is noteworthy that fayatree has continued to spread and is of increasing concern as a noxious weed in Hawai'i, whereas *M. cerifera* remains confined to its site of introduction and has not become a problem species.

Yang, P., and D. Foote. Demography and population dynamics of *Caloptilia schinella* (Lepidoptera: Gracilariidae), a biological control agent of fire tree, *Myrica faya*, in Hawaii Volcanoes National Park. Manuscript in preparation intended for publication in a professional journal.

The leaf roller, *Caloptilia schinella*, was introduced as a biological control agent of fayatree in Hawai'i. In an effort to evaluate the potential effectiveness of this insect, the population parameters

and characteristics were estimated by demographic analysis. Results reportedly showed that *C. schinella* had low fecundity (i.e., 74 eggs per female), longer mean generation time (66.9 days), and low intrinsic rate of increase (0.04 per day). Results also indicated that the insect reached the stage of stable age distribution very slowly. The insect was therefore not considered an ideal biocontrol agent for fayatree.

Yang, P., and D. Foote. Inventory of herbivorous insects on fire tree, *Myrica faya*, in Hawaii Volcanoes National Park and vicinity. Technical report, University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu. In preparation.

This report briefly recorded investigations of the authors on insects attacking fayatree in Hawai'i Volcanoes National Park and vicinity. Fifteen species of insects were found in the survey areas. These species represented six orders, but are mostly Lepidopteran and Homopteran. Most of the 15 species were reported to attack leaves, but insects were also found on other parts of fayatree including, twigs, stems, flowers, pollen, and fruit. The two-spotted leafhopper, an accidentally introduced insect, is the only species found to cause severe damage to fayatree. The released biocontrol agent *Caloptilia schinella* had reportedly spread to several areas of the park but with a very low population density and not causing any significant damage to fayatrees. The insect faunas on fayatree between its habitat in Hawai'i Volcanoes National Park and the places of its origin were compared. Some similarities were found between these locations, such as species number, orders, and damage site. The authors concluded that the native insect fauna in Hawai'i should be considered as an important factor in controlling invading pest plants.

Yang, P., D. Foote, V. P. Jones, and J. T. Tunison. A preliminary investigation of the effect of two-spotted leafhopper, *Sophonia rufofascia* (Kuoh & Kuoh), on fire tree, *Myrica faya* Aiton, in Hawaii Volcanoes National Park. Technical report, University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu. In preparation.

The authors investigated biotic factor which caused chlorosis, defoliation, and dieback of fayatree in Hawai'i Volcanoes National Park. The abundance of two-spotted leafhopper (*Sophonia rufofascia*), chlorosis rates, and defoliation rates of fayatree in three different types of geographic areas were surveyed and the relationships among them were analyzed. The direct damage on the leaves of fayatree by two-spotted leafhopper were assessed both in the laboratory and in the field. The results indicated strong relationships between chlorosis and defoliation rates and population levels of the two-spotted leafhopper. The "black spot" symptom appeared on the leaves within 24 hours after leafhopper feeding. In contrast, the yellowing symptom required more than 1 month to develop. The results indicated that a leafhopper-transmitted mycoplasma-like organism may not be involved in the decline syndrome as had been previously hypothesized.

Young, D. R. 1992. Photosynthetic characteristics and potential moisture stress for the actinorrhizal shrub, *Myrica cerifera* (Myricaceae), on a Virginia barrier island. *American Journal of Botany* 79(1):2-7.

Myrica cerifera was described as a common shrub in the marine coastal communities of the eastern U. S. This species is especially important because of its perceived influential role in ecological succession, owing at least in part to its nitrogen fixing ability resulting from an actinorrhizal association with *Frankia*. Other factors, notably moisture stress, also were considered important in community and ecosystem ecology on the barrier islands of Virginia. Aerial photographs indicated that, after establishment in island swales, *M. cerifera* quickly expanded to form extensive thickets. Its evergreen habit facilitated expansion by extending the growing season into the winter months. However, *M. cerifera* did not cover entire islands, but was restricted to well-defined patches, usually in swales, possibly limited by sensitivity to moisture stress.

These observations were contrasted with those of Vitousek and Walker on fayatree in Hawai'i, where porous volcanic soils were colonized, perhaps indicating less sensitivity to moisture stress in this species. References to other studies were given in which ecological effects of nitrogen fixation by other species of *Myrica* (i.e., *M. pennsylvanica* and *M. gale*) were assessed.

Young, D. R., E. Sande, and G. A. Peters. 1992. Spatial relationships of *Frankia* and *Myrica cerifera* on a Virginia, USA barrier island. *Symbiosis* 12:209-220.

Distribution of *Frankia* in soil of one of the barrier islands off the coast of Virginia was assessed by baiting this actinomycete with surface-sterilized seed of *Myrica cerifera* and correlating the distributions of both symbionts. Results indicated that distribution of *Frankia* in the relatively young, nitrogen poor soils of a barrier island exceeded that of the host, suggesting that *M. cerifera* had a potential to colonize sites where it did not currently occur. Edaphic factors and water availability also played a potential role in determining the distribution of *M. cerifera*.

Youngken, H. W. 1919. The comparative morphology, taxonomy and distribution of the Myricaceae of the eastern United States. *Contributions from the Botanical Laboratory, University of Pennsylvania* 4:339-400.

The author reviewed the family Myricaceae and provided a comprehensive treatment of the vegetative morphology and anatomy of the Myricaceae of the eastern U. S. (Original reference not seen; information from Macdonald (1977, 1989).

Zoerner, H. 1975. Studies of leaf-mining Lepidoptera, Coleoptera, and Hymenoptera: II. *Deutsche Entomologische Zeitschrift* 22(4/5):363-380.

Leaf mines were described in leaves of a number of forest trees and shrubs in the former East Germany, including *Myrica gale*. Most mines were made by Lepidopteran insects. Insects described included *Lithocolletis* sp., *Nepticula* sp., and *Bucculatrix* sp. (*B. myricae* (?)). (in German)