

FOREST PATHOLOGY IN HAWAII*

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ABSTRACT

Native Hawaiian forests are characterised by a high degree of endemism, including pathogens as well as their hosts. With the exceptions of koa (*Acacia koa* Gray), possibly maile (*Alyxia oliviformis* Gaud.), and, in the past, sandalwood (*Santalum* spp.), forest species are of little commercial value. On the other hand, these forests are immensely important from a cultural, ecological, and evolutionary standpoint. Forest disease research was lacking during the mid-twentieth century, but increased markedly with the recognition of ohia (*Metrosideros polymorpha* Gaud.) decline in the 1970s. Because many pathogens are themselves endemic, or are assumed to be, having evolved with their hosts, research emphasis in natural areas is on understanding host-parasite interactions and evolutionary influences, rather than disease control. Aside from management of native forests, attempts at establishing a commercial forest industry have included importation of several species of pine, *Araucaria*, and *Eucalyptus* as timber crops, and of numerous ornamentals. Diseases of these species have been introduced with their hosts. The attacking of native species by introduced pathogens is problematic — for example, *Armillaria mellea* (Vahl ex Fr.) Quél. on koa and mamane (*Sophora chrysophylla* (Salisb.) Seem.). Much work remains to be done in both native and commercial aspects of Hawaiian forest pathology.

Keywords: endemic species; indigenous species; introduced species; island ecology; ohia decline.

INTRODUCTION AND HISTORY

Forest pathology in Hawaii, as elsewhere, originated with casual observations of obvious disease and decline phenomena by amateur observers and general foresters. In earlier times, forest problems were not categorised into various fields of study as succinctly as at present from the standpoint of causative agents, whether insects, pathogens or abiotic influences. Nor were forest problems critically investigated to determine cause. They were reported in conjunction with observations of crop diseases and insect problems (*see* Lyon

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1909, 1918, 1919; Larsen 1910; Horner 1912; Forbes 1918). Early twentieth century mycologists and forest pathologists who examined material from Hawaii, or who personally visited the Islands, including E.A.Burt (1923) and, most importantly, F.L.Stevens (1925), were the first to categorise most pathogen-induced forest diseases as distinct phenomena. Although forestry considerations were prevalent during this time, much of the emphasis was in experimenting, under the direction of forest supervisor H.L.Lyon, with introduced species to find those that were better suited for watersheds and timber production than were native species. In particular, Lyon (1909, 1918) recommended planting introduced trees in wet sites with poor drainage. Two Australian species, *Eucalyptus robusta* Sm. and paperbark (*Melaleuca quinquenervia* (Cav.) Blake), planted at Lyon's recommendation, have thrived in Hawaiian forests (Hodges, Alvenas, & Ferreiro 1986).

Forest pathology received little emphasis in Hawaii following Stevens' 1925 publication "Hawaiian Fungi" until the ohia decline phenomenon, described in greater detail below, emerged as a major concern in the 1970s, and the United States Department of Agriculture Forest Service's Institute of Pacific Islands Forestry (IPIF) was established in 1967, headquartered in conjunction with the Hawaii Department of Land and Natural Resources (DLNR) in Honolulu. (Whereas Hawaii has no national forests, IPIF's function was to provide support to DLNR in addressing forest problems in the Islands.) IPIF brought together specialists in ecology, entomology, forest pathology, and supporting fields. With IPIF's impetus, several noted forest pathologists, either IPIF employees or collaborators from other agencies (including R.V.Bega, F.F.Laemmlen, W.T.Nishijima, E.E.Trujillo, J.T.Kliejunas, W.H.Ko, M.F.Stoner, and C.S.Hodges Jr) combined their research efforts on ohia decline. A similar group of entomologists also participated. As indicated by the work detailed below, studies other than those limited to ohia decline were also carried out by many of these researchers. D.E.Gardner of the National Park Service and later USGS-Biological Resources Division, U. S. Department of the Interior, was not directly involved with ohia decline but concentrated studies on a number of other native forest diseases.

Native Hawaiian forests are characterised by a high degree of endemism. They typically consist of two overstorey trees, the morphologically variable ohia-lehua (*Metrosideros polymorpha*) and koa (*Acacia koa*) predominating at higher elevations, with a larger number of subcanopy trees, shrubs, and herbaceous species. Ohia forests are the most extensive throughout the Islands, occupying an estimated 62% of total forest area, and occur in a variety of habitats (Hodges, Adee, Stein, & Doty 1986). In its current concept (Wagner *et al.* 1990), *A. koa* represents a complex including three formerly recognised species — *A. koa*, *A. koaia* Hbd., and *A. kauaiensis* Hbd. *Acacia koa* included three varieties — *A. koa* var. *koa* Gray, *A. koa* var. *latifolia* (Benth.) St John, and *A. koa* var. *waianaiensis* St John (St John 1979). Notwithstanding the current inclusion of these forms in a single species for taxonomic purposes, the previously recognised specific and varietal distinctions remain useful from the perspective of pathology. The previously recognised *A. koa* var. *latifolia*, the most robust of the forms and endemic to the island of Hawaii, is commercially valuable: the rich, intricately grained wood is desirable for furniture construction, panelling and veneers, and crafting of small wooden items. Apart from this, and the devastating sandalwood trade of the early 1800s (Degener 1973), current management concerns about native forests are directed primarily at understanding and preserving ecological processes and relationships rather than commercial exploitation. As with their hosts, most of the

pathogens of native Hawaiian forest species are themselves endemic or are presumed to be. Thus, particularly in preserves such as national parks, the objective of forest disease research is toward understanding the role pathogens play in the ecosystem rather than their control.

FOREST DISEASES

Ohia Decline

During the 1970s and 1980s, forest management and research attention was dominated by the widespread dieback of ohia-lehua, referred to as ohia decline, first recognised as such in the late 1960s. Earlier, Larsen (1910) reported large areas of dead and dying ohia on the island of Kauai. Later, Horner (1912) and Forbes (1918) noted widespread mortality of both koa and ohia on the islands of Hawaii and Maui, which was attributed to “bark beetles”. No known attempt was made to further investigate the problem. The bearing of these observations on ohia decline, as it was later defined, is not clear. Early projections in the ohia decline study predicted a rapid, cataclysmic demise of Hawaii’s ohia forests, prompting State and Federal agencies to fund studies into the cause and possible control of this phenomenon (Petteys *et al.* 1975). Entomologists investigated several insects, but concentrated on a native wood-boring cerambycid beetle, *Plagithmysus bilineatus* Sh., as the most probable cause of the decline (Burgan & Nelson 1972; Samuelson & Gressitt 1976; Papp *et al.* 1979; Nagata & Stein 1982). The clear association of this beetle with declining trees suggested a straightforward cause of decline, with the problem readily solved. However, investigation showed the beetles to be attracted to injured trees or those already in decline rather than to healthy controls (Burgan & Nelson 1972; Nagata & Stein 1982). Thus, the role of *P. bilineatus*, or of other insects investigated, as primary causes of decline could not be established, although their secondary role in exacerbating the phenomenon was possible.

Likewise, the effects of several pathogenic root-infecting fungi were considered, primarily *Pythium vexans* D. By. (Kliejunas & Ko 1975), *Armillaria mellea* (Laemmlein & Bega 1974; Burgan & Nelson 1972), and *Phytophthora cinnamomi* Rands. Of these, the *P. cinnamomi* showed early promise as the cause of the problem and was given by far the greatest research attention (Kliejunas 1979; Kliejunas & Ko 1973, 1975, 1976a, b; Kliejunas *et al.* 1977; Papp *et al.* 1979; Bega 1974; Hwang & Ko 1978). The fungus was usually found at sites of decline, and was isolated from roots of ohia — and of koa as well — but correlation between decline symptoms and presence of the pathogen was not sufficiently consistent to account for *P. cinnamomi* as the primary cause (Papp *et al.* 1979), although, as with *P. bilineatus*, it may contribute secondarily to the phenomenon in some localities (Hodges, Adee, Stein, & Doty 1986). In pathogenicity tests, Kliejunas (1979) found many native hosts to be tolerant of *P. cinnamomi* and interpreted this as evidence of a long-term host-pathogen association, suggesting that the fungus may be indigenous to Hawaii.

The role of forest soil nutrition in triggering the decline was also investigated (Kliejunas & Ko 1974; Gerrish & Bridges 1984). Whereas positive correlation was often found between addition of soil nutrients and tree vigour, the lack of nutrients could not be shown to result in onset of decline (Hodges, Adee, Stein, & Doty 1986).

Botanist F.R. Fosberg had earlier discovered an ascomycetous fungus — at first designated *Diaporthopsis metrosideri* Roane & Fosb. but later changed to *Endothia metrosideri* (Roane & Fosb.) Barr — fruiting on the bark of ohia in Hawaii Volcanoes National Park (Fosberg 1983; Barr 1983). He postulated that *E. metrosideri* might pose a serious threat to ohia, possibly as the cause of ohia decline. However, the pathogenicity of *E. metrosideri* has not been established, and because the rather conspicuous fruiting bodies have not been observed on dead or declining trees in major decline areas, the role of *E. metrosideri* in ohia decline is doubtful (Hodges, Adee, Stein, & Doty 1986).

Investigations from an ecological perspective by Mueller-Dombois and his associates (Mueller-Dombois 1980, 1982, 1986, 1987; Mueller-Dombois *et al.* 1981, 1983; Jacobi 1983; Evenson 1983) engendered the “synchronous cohort senescence” theory of decline. According to this theory, ohia decline is a complex natural phenomenon, involving both biotic and abiotic factors, with several types of site-related decline identified on the basis of forest structure, habitat and soil type, and regeneration pattern. In the absence of many of the predators and diseases that combine with senescence to cause the demise of old-growth forests elsewhere, cohort senescence serves as a mechanism whereby synchronously senescing even-aged stands give way to forest regeneration. A second disturbance is necessary after the onset of senescence — a storm, temporary flooding, or soil drought — which would not affect vigorous stands, but which might trigger decline in a senescing stand. Because of its temporary effect, the nature and occurrence of such an event might be difficult to ascertain during a later investigation. After the triggering event, more easily detected secondary pathogens and insects, such as those mentioned above, may attack the weakened trees (Hodges, Adee, Stein, & Doty 1986). Since the 1970s and 1980s when ohia decline received a great deal of attention, ohia regeneration, at least at certain decline sites, has allayed initial fears of total demise of the species in Hawaii. Emphasis on this phenomenon consequently has been de-intensified.

Koa Wilt

Gardner (1978a) reported a wilt disease of koa seedlings in Hawaii Volcanoes National Park. The disease was associated with a seed-borne virulent strain of the vascular wilt fungus *Fusarium oxysporum* (Schlecht.) Sny. & Hans., later designated as *F. oxysporum* f. sp. *koa* Gardner (Gardner 1980a). Gardner’s report coincided with observations of a general dieback among all age classes of koa, from saplings to mature but previously healthy trees, on the slopes of Mauna Loa (Gardner 1996a, 1997a; Anderson *et al.* 2002). Attack of vigorous trees indicates that the pathogen, like other vascular wilt fusaria, is sufficiently virulent to infect its host without requirement for predisposition. Koa wilt appears in centres of infection, where all or nearly all of the trees at infection sites become irreversibly symptomatic. Whereas infection centres are most readily observed on the slopes of Mauna Loa on Hawaii Island, where stands with yellowing and thinning crowns associated with tree death are conspicuous (Fig. 1), koa wilt may account for heretofore unexplained declining koa at other island sites as well. Little is known as to the ecology, and particularly the origin, of *F. oxysporum* f. sp. *koa*, although the pathogen appears to conform to the general infection pattern of other relatively well-understood vascular wilt fusaria (Beckman 1987). Accordingly, the pathogen resides saprophytically in the soil where it invades the root xylem and develops systemically throughout the vascular system

of susceptible plants. The internal presence of the fungus, together with lack of early symptoms such as root rot, allows extensive invasion before wilting symptoms, often rapidly developing, become visible. Stoner *et al.* (1975) found *F. oxysporum* in koa rhizosphere soils on Mauna Loa in the same regions where dieback now occurs, but these investigators did not attempt to determine pathogenicity of their isolates. Although koa dieback has been recognised as a disease for a relatively short time, evidence of dieback among older koa stands indicates that the pathogen, if in fact this was the cause, may have been active well before the disease was recognised as such. As indicated above, the origin of the pathogen is a matter of speculation. Other *F. oxysporum*-caused wilt diseases of leguminous trees are known elsewhere: *Pterocarpus* in Africa (Sanderson *et al.* 1996), *Acacia* in India (Bagchee 1945), and *Albizia* in the United States, Argentina, Puerto Rico, and Russia (Hepting 1971). Determination of possible conspecificity among these fungi with *F. oxysporum* f. sp. *koae* has not been attempted. However, the vascular wilt fusaria are characterised by their host specificity, suggesting that the pathogen is itself endemic, having evolved with its endemic host. Further study is needed to establish the distribution of the pathogen and its effect on koa populations throughout the islands (Anderson *et al.* 2002).

Ohia and Koa Forest Decline

Regarding early observations of large areas of dead and dying ohia and koa on Maui, Hawaii, and Kauai (Larsen 1910; Horner 1912; Forbes 1918), Laemmlen & Bega (1972) made similar observations based on 1954 aerial surveys. They reported approximately 67 000 acres (27 126 ha) of koa and ohia forest on the island of Hawaii to be in slight (<20% dead trees) to severe (60% or more) decline. In 1965, the affected areas had increased by 10 000 acres (4049 ha), with more-recent ground surveys indicating a steadily deteriorating situation. The decline was characterised as a rapid wilt causing a thinning of foliage with many dead twigs, followed eventually by complete defoliation and death. The most severely affected forest was on the slopes of Mauna Kea at elevations of 750–1700 m. The authors mentioned several possible causes or contributing biotic factors, including the fungi *Armillaria mellea*, *Phytophthora cinnamomi*, and *Diatrype princeps* Penz. & Sacc.; and the insects *Xylosandrus compactus* Eichhoff (black twig borer) and *Plagithmysus bilineatus*; together with the activities of wild pigs and other mammals (presumably rats). Abiotic factors, such as changes in soil drainage were also suggested as possible contributing factors. The above-described koa wilt disease, associated with *F. oxysporum*, had not been described at the time of Laemmlen & Bega's observations, and thus was not considered in their report. However, this disease is specific to koa and would not account for a general decline of mixed forests composed of koa, ohia, and possibly other species as well. At the time of their report, Laemmlen & Bega (1972) indicated that quantitative and qualitative studies of the decline were to be initiated, but the original scope of the work most likely became refocused on the emerging ohia decline phenomenon (Hodges, Adee, Stein, & Doty 1986), leaving the general decline of earlier concern unaddressed (Gardner 1996a, 1997a).

Koa Rusts

In the first comprehensive listing of plant diseases and their pathogens in Hawaii, F.L. Stevens (1925) described *Uromyces koae* Arth. ex Stevens as a new species of rust fungi (Uredinales) on koa, with uredinial witches' brooms and telial leaf pustules (Gardner

1978b, 1981). Gardner & Hodges later recognised *U. koae* as a complex of indigenous and endemic species with affinities to *Acacia* rusts in Australia, New Zealand, and Taiwan (Gardner 1991; Hodges & Gardner 1984; Gardner & Hodges 1985). The uredinial and telial spore states of Stevens' (1925) concept of *U. koae* were found to represent two distinct species (Hodges & Gardner 1984). Discovery of spermogonia on the fleshy witches' broom phyllodes of the original uredinial state (Gardner *et al.* 1979), followed by discovery of inconspicuous telia and uredinia on otherwise normal phyllodes (Hodges & Gardner 1984), led to recognition of this rust as *Uromyces digitatus* Wint., considered to be the same fungus as that described by McAlpine (1906) on *Acacia* hosts in Australia (Fig. 2). Hodges & Gardner (1984) thus considered this rust indigenous to Hawaii. The telial state of Stevens' concept (1925) was found to be a distinct endemic species with previously overlooked spermogonia, retaining the binomial *U. koae* (Fig. 3). This rust was morphologically demicyclic but functionally microcyclic, as the uredinoid aeciospores no longer function in the life cycle (Chen *et al.* 1996). Cummins & Hiratsuka (1983), noting that because of their several distinctive characteristics these *Acacia* rusts did not belong in the genus *Uromyces*, re-established the genus *Atelocauda* to accommodate these fungi.

Most recently, Walker (2001) in Australia created the genus *Racospermyces* as a more appropriate placement for these unique rusts. As suggested above, although the hosts of Hawaiian *Acacia* rusts are currently included in the single genus *A. koa*, recognition of the forms comprising this host complex remains useful in considerations of host/pathogen relationships. Thus, *A. angustiphylloda* Gardner (now *R. angustiphyllodius* (Gardner) J.Walker, a microcyclic derivative of *R. digitatus* (Wint.) J.Walker (Gardner 1991) (Fig. 4), is confined to the former *Acacia latifolia*, occurring only on the island of Hawaii. Furthermore, *Endoraecium hawaiiense* Hodges & Gardner (Fig. 5) is known only on the island of Oahu in two widely separated locations; at one site the rust occurs on the previous *Acacia koa* var. *koa*, whereas at the other it occurs on *A. koa* var. *waianaiensis* (Hodges & Gardner 1984).

The rusts of koa most frequently cause flagging of branches rather than death of the entire infected tree, but *Endoraecium acaciae* Hodges & Gardner (Fig. 6), the more prevalent of the two endocyclic forms described by Hodges & Gardner (1984), may cover susceptible trees with witches' brooms and cause severe damage to the host. *Racospermyces koae* (Arth. ex Stevens) J.Walker is limited to young shoots of its *Acacia latifolia* host (Fig. 3). Infection of apical meristems may cause stem deformation, which may detract from the quality of commercial timber (Gardner 1997a).

Other Rust Diseases

A number of other rust fungi occur on native forest species (Gardner 1994a). These include relatively recently described microcyclic rusts on hosts of the Rutaceae family — *Puccinia rugispora* Gardner on *Zanthoxylum dipetalum* Mann and *P. rutainsulara* Gardner on *Melicope* (= *Pelea*) spp. (Gardner 1990) (Fig. 7). As with other endemic fungi that have evolved with their endemic hosts, these rusts do not appear to pose a serious threat to their hosts, but are most interesting from the standpoint of their ecological relationships and unique developmental processes (Gardner 1994b, 1996b).

Hennen & Hodges (1981) described a complex of closely allied rust fungi — *Uredo stevensii* Arth. ex Stevens, *Puccinia levata* Hennen & Hodges, and *P. vitata* Hennen &

Hodges — on native *Chamaesyce* (= *Euphorbia*) hosts. Of these, the microcyclic *P. vitata*, on *C. olowaluana* (Sherff) Croizat & Degener, is perhaps the most conspicuous in the production of prominent, pendulous, spermogonial-telial witches' brooms up to 45 cm in diameter. As with *R. koeae*, described above, teliospore development is unique and of interest from an evolutionary standpoint (Gardner 1988b).

Uromyces alyxiae Arth. ex Stevens occurs on the endemic forest species *Alyxia oliviformis* (Apocynaceae). This vine, known as maile, was highly prized in ancient Hawaiian culture and remains so today for its attractive foliage and the fragrant scent of its stems and leaves. Lei (wreaths) of maile are used widely in festive and commemorative occasions. Consequently, the gathering of maile has resulted in its depletion from forests in some localities, with maile cultivation becoming attractive as a commercial industry. While maile rust does not usually cause the demise of its host, presence of the conspicuous raised brown pustules on the leaves detracts aesthetically from the usefulness of the plant. Like other endemic microcyclic rusts, *U. alyxiae* is of evolutionary and developmental interest (Gardner 1987), with obvious affinities to Australia (Gardner 1989; Tierney & Gardner 1992) and possibly other Pacific islands.

Mamane Witches' Broom

Sophora chrysophylla (mamane) is a subcanopy tree of the Fabaceae interspersed in mid-elevation koa-ohia forests. At higher elevations, mamane forms a dominant element of subalpine vegetation in dry to mesic shrub and forestland on most of the major islands. The immature seeds of this tree provide a critical food source for the palila (*Loxioides bailleui* Oustalet), an endangered bird of the honeycreeper group. A recently recognised witches' broom disease is associated with a new species of *Botryosphaeria* — *B. mamane* Gardner (Gardner 1997b). The brooms consist of abnormally thickened, roughened, upright twigs with shortened internodes and unsuppressed lateral buds. The brooms arise from contorted, spindle-shaped, or sometimes gall-like stem thickenings (Fig. 8). Numerous black, well-developed stromata, from which cirrhi of macroconidia are exuded, consistently appear erupting through split bark of dead brooms and branch swellings. The disease occurs as one-to-several isolated brooms among otherwise-normal growth or, more rarely, trees may be predominantly broomed, with little or no normal growth present. Affected tissue dies prematurely, leaving trees with dead broomed branches (Fig. 9). Heavily broomed trees may be completely killed. Apparent confinement of the morphologically distinct *B. mamane* to its endemic Hawaiian host suggests that the pathogen is itself endemic. Because of its recent discovery, nothing is known concerning the historical ecological role of mamane witches' broom among mamane populations in the Islands.

Armillaria Root Rot of Mamane

Root rot caused by *Armillaria mellea* is widespread throughout Hawaii's forests, attacking a variety of native and non-native woody hosts (Laemmlen & Bega 1974; Raabe & Trujillo 1963). This pathogen recently was found responsible for a widespread dieback occurring in mamane forests constituting upper elevation palila habitat on the slopes of Mauna Kea on the island of Hawaii (Gardner & Trujillo 2001) (Fig. 10). Characteristic mycelial fans of the fungus occur under the bark near the soil line of declining trees

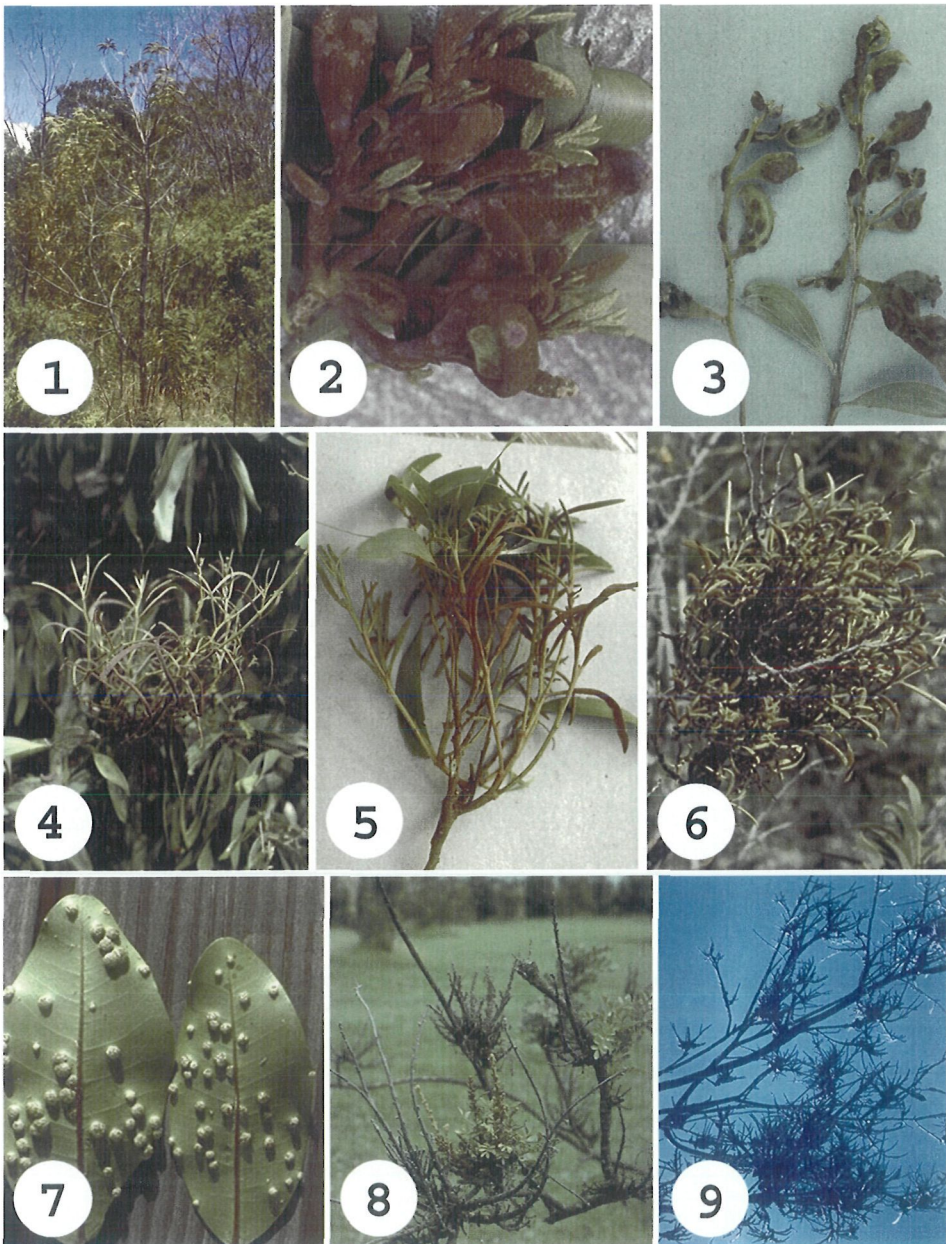


FIG. 1—Koa wilt, caused by *Fusarium oxysporum* f. sp. *koa*.

FIG. 2 to 6—Rusts on koa. (2) *Racospermyces digitatus* (= *Atelocaula digitata*) witches' broom.

(3) *R. koae* on young shoots. (4) *R. angustiphylloides* (= *A. angustiphylloides*) witches' broom.

(5) *Endoraecium hawaiiense* witches' broom. (6) *E. acaciae* witches' broom.

FIG. 7—Leaf rust pustules of *Puccinia rutainsulara* on mokihana (*Melicope* [= *Pelea*] *anisata* [Mann] Stone).

FIG. 8 and 9—Witches' brooms on mamane, caused by *Botryosphaeria mamane*. (8) Close-up of an infected branch. (9) Severely broomed dead tree.

(Fig. 11). *Armillaria* root rot of mamane is an example of an introduced pathogen devastating a native species. From a management standpoint, control of the disease is clearly indicated, but no practical approach is available.

Ohelo Red Leaf Disease

A branch and foliar disease of endemic *Vaccinium reticulatum* Sm. (ohelo) and *V. calycinum* Sm. (tree ohelo), both upper elevation forest shrubs, was long overlooked as an abnormality by forest managers who mistook the brilliant red foliage for the red coloration of normal new growth. However, close examination revealed witches' brooms with thickened twigs consistently associated with red foliage, and eventual death of infected tissue (Fig. 12). Gardner (1985) reported the condition as a fungal disease — "ohelo red leaf" — caused by *Exobasidium vaccinii* Wor. This pathogen, which produces prominent basidia on the undersurfaces of infected leaves, causes a similar disease on cranberry and blueberry crops in North America. Possibly because it has been recognised only recently as a disease, no information is available as to the introduction of the pathogen to the Islands, first appearance of symptoms, rate of spread, etc. A suggestion (unpubl. data) that the pathogen in Hawaii represents one, and possibly two, endemic derivatives of *E. vaccinii* has not been verified, but remains to be investigated. If this were the case, theoretical management action would be shifted from attempts at control to acceptance of the disease as a natural phenomenon. From a practical standpoint, the disease does not present a sufficient threat to ohelo to justify control.

Dodonaea Yellows

Dodonaea viscosa (L.) Jacq. (Sapindaceae) is known in Hawaii as a 'ali'i. In its current taxonomic concept (Wagner *et al.* 1990), this species is indigenous to Hawaii, being widely distributed throughout the Pacific, occurring also in Asian and South American countries. Because of its morphological variability, from low shrubs to tree-like forms, the current concept of *D. viscosa* encompasses several previously recognised species and varieties (Degener 1973). A 'ali'i occupies a variety of Hawaiian forest habitats, from near sea level to approximately 2333 m elevation. The species is ecologically significant as an early coloniser of new lava flows and similar disturbed sites, and occasionally is the dominant woody species in drier habitats (Mueller-Dombois *et al.* 1981). Because of its attractive foliage and yellow to bright red fruit capsules, a 'ali'i is important in native Hawaiian culture, being used for lei making and similar decorative applications.

Gardner (1980b) first reported a conspicuous and severe disease, referred to as "Dodonaea yellows," in Hawaii Volcanoes National Park on the island of Hawaii. Despite its prominence, no previously published reports of this disease could be located, nor were resource managers and other park personnel aware of it. Symptomatic plants later were found in other regions of the island and on other islands of Hawaii as well. Curiously, however, no evidence of Dodonaea yellows has been found in other world regions where the host occurs. Early in the investigation, Dodonaea yellows was considered to be a possible manifestation of sandalwood spike, a destructive phytoplasma-associated disease of sandalwood in India. Whereas sandalwood spp. are the primary hosts of sandalwood spike, occurrence of the disease also on *D. viscosa* in that country has been reported (Gardner & Kageler 1984; Gardner 1988a). Close comparison of the symptoms of

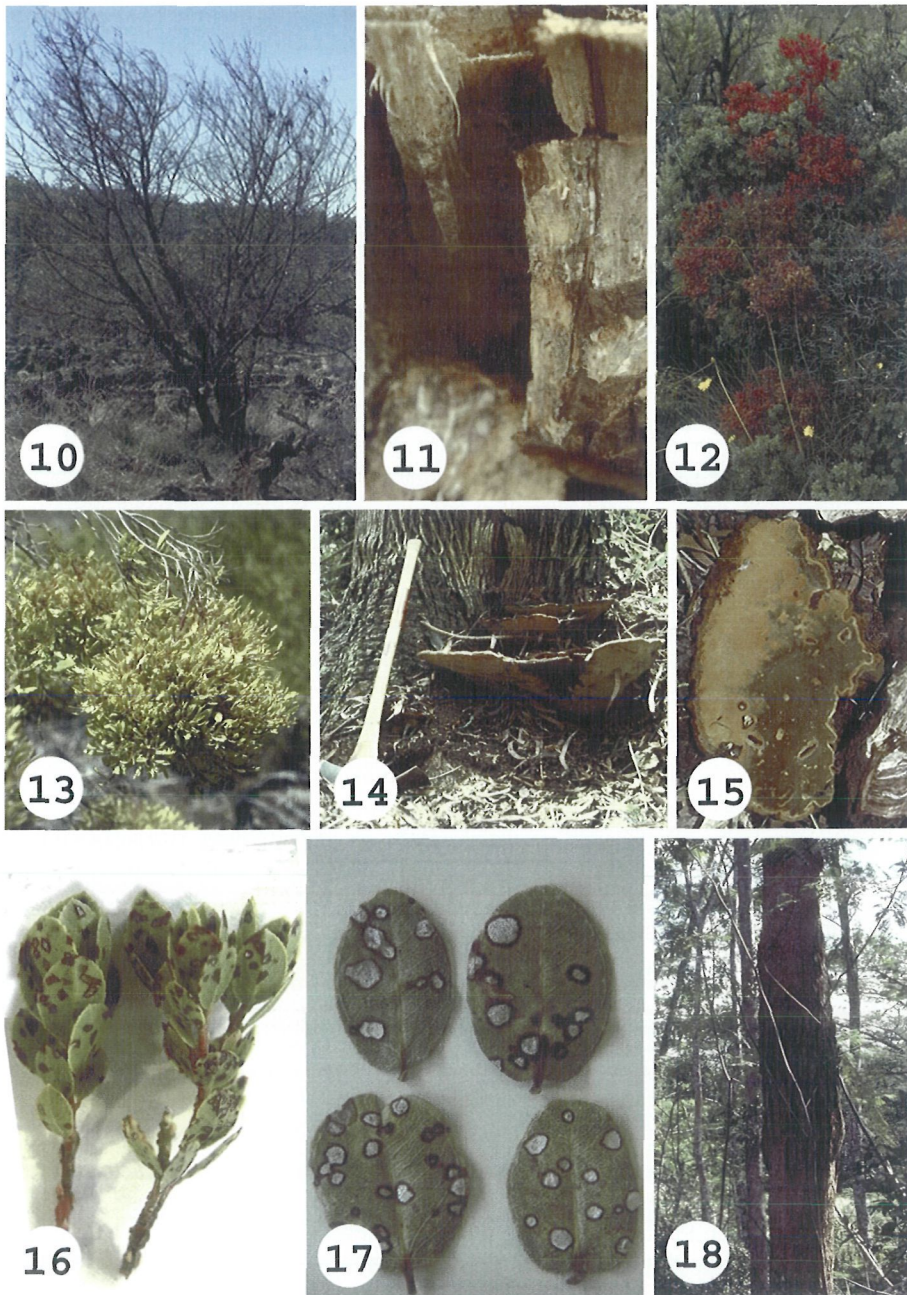


FIG. 10 and 11—Dieback of mamane, caused by *Armillaria mellea*. (10) Young dead tree. (11) Close-up of *A. mellea* mycelium in root crown sections.

FIG. 12—Red leaf disease of ohelo, caused by *Exobasidium vaccinii*.

FIG. 13—*Dodonaea* yellows witches' broom on a'ali'i, associated with a virus and a phytoplasma.

FIG. 14 and 15—Fruiting structures of *Phellinus kawakamii*, causing heartwood-decay on koa. (14) Large conks on the lower trunk. (15) Close-up of the undersurface. (to facing page)

Dodonaea yellows with published descriptions of sandalwood spike indicate that the two diseases are probably distinct from one another. On the other hand, much remains to be understood concerning both diseases. To date, no comparisons have been made using molecular analysis, which might significantly elucidate any possible relationship between the two diseases.

Dodonaea yellows is characterised by abnormally lengthened, stringy-appearing, young branches proliferating from axial buds and forming pendulous compact witches' brooms. Leaves on affected branches are stunted and exhibit a striking, often bright yellow, general chlorosis with red veins and petioles (Gardner 1988a) (Fig. 13). Affected plants gradually decline and die over a period of a few years; no recovery has been observed. Borth *et al.* (1988, 1990, 1995) found evidence of both viral and phytoplasma association with the disease. Although phytoplasma-caused crop diseases have been suspected in Hawaii, the evidence for phytoplasma bodies associated with Dodonaea yellows is considered the first positive documentation for such a disease in the Islands (Borth *et al.* 1995). As with other phytoplasma-caused diseases, leafhopper transmission of Dodonaea yellows is suspected, but attempts to confirm this with both native and introduced leafhopper species have not been successful (Gardner unpubl. data). Likewise, aside from a possible connection with sandalwood spike, no information is available as to the origin of Dodonaea yellows, whether introduced to Hawaii or endemic. Submission of photographs of Dodonaea yellows symptoms to forest pathologists and managers elsewhere in the range of Dodonaea has not yielded response that the disease is known elsewhere (Gardner unpubl. data).

Wood-rotting Higher Fungi

Burt (1923) and Petrak (1952, 1953), followed by Bega (1979), provided early documentation of forest diseases caused by wood-rotting basidiomycetes in Hawaii. These diseases are characterised by production of usually conspicuous fleshy or woody external fruiting structures, indicating the presence of already well-established internal infection. Bega (1979) reported the well-known forest pathogens *Phaeolus schweinitzii* (Fr.) Pat., *Laetiporus* (= *Polyporus*) *sulphureus* (Bull. ex Fr.) Bond. & Sing., and *Pleurotus ostreatus* (Jacq. ex Fr.) Kumm. as new records in Hawaii. These species, together with *Armillaria mellea* and *Ganoderma* sp., were associated with deteriorating old-growth stands of koa on several thousand acres of rangeland on the island of Hawaii at elevations of 1540–1840 m. Many wood-rotting fungi, while probably more prevalent than published reports indicate, occur typically in older senescent or presenescent trees, often hastening but not causing their decline. This is in contrast with virulent pathogens, such as rust fungi, or the vascular wilt *Fusarium oxysporum* of koa, described above, which are capable of attacking young vigorous forest trees. As mentioned above, *A. mellea*, a ubiquitous wood-rotting fungus with a wide host range, is also capable of attacking vigorous trees, as observed on mamane on Mauna Kea. This pathogen causes a stringy white root and butt rot of a number of woody hosts in Hawaii, including koa (Laemmlen & Bega 1974; Raabe & Trujillo 1963). Bega

Opposite page:

FIG. 16 and 17—Leaf spot diseases: (16) *Septoria* sp. on ohelo, (17) *Mycosphaerella* sp. on ohia.
FIG. 18—A large canker, caused by *Cryphonectria cubensis*, on *Eucalyptus robusta*.

(1979) reported that the honey-coloured mushrooms characteristic of *A. mellea* infection elsewhere were not known in Hawaii, but these have more recently been found to be common at certain sites (G. Wong pers. comm.).

A new species of *Phellinus*, described as *P. kawakamii* Larsen, Lombard & Hodges, was found on koa (i.e., the previously recognised *A. koa* var. *koa* and *A. koaia* — St John 1979) on the island of Kauai (Larsen *et al.* 1985). The same species also was found on introduced *Casuarina equisetifolia* L. on the islands of Hawaii and Oahu. This heartwood-decaying fungus produces white pocket-rot in its hosts and is characterised by a large fruiting body (to 70 cm wide, 20 cm thick) (Fig. 14 & 15). The conks are produced at, or near ground level and may be obscured by leaf litter and thus easily overlooked, possibly accounting for their relatively recent discovery. No fruiting bodies were found on koa during casual observations made in old-growth stands on the islands of Oahu, Maui, and Hawaii. However, internal decay typical of that produced by *P. kawakamii* was found in a substantial number of stumps of *A. koa* var. *koa* trees salvaged after a 1982 hurricane, indicating that the presence of fruiting bodies may not accurately indicate the incidence of disease (Larsen *et al.* 1985).

Aside from *P. kawakamii*, the above-mentioned wood-rotting fungi are introductions to Hawaii. Rather than killing their hosts directly, pathogenic heart and root-rotting fungi destroy timber usefulness and predispose trees to wind-throw and branch or stem breakage. Nelson & Wheeler (1963) reported that more than half of the large koa trees reported in a forest survey carried out in 1959–61 were considered unmerchantable because of excessive wood rot.

Although not classified among the basidiomycetes, wood-inhabiting fungi of the family Xylariaceae — *Hypoxyylon annulatum* (Schw.) Mont., *Nummularia guarantica* Speg., and *Xylaria rhopaliodes* Mont. — have been reported on koa (Stevens 1925). These genera produce dark, usually conspicuous stromata on the bark of infected trees. Most members of the Xylariaceae are saprophytic or weakly parasitic, which is probably true of the species occurring on koa.

Foliar and Shoot Diseases

Regarding foliar diseases, the number and variety of leaf-spotting diseases found in Hawaii's forests are such that only some of the most noteworthy are mentioned here. Sutton & Hodges (1983) described a new leaf-spotting fungus, *Gloeocoryneum hawaiiense* Sutton & Hodges, on *A. koa* var. *koa* on the island of Kauai. Although *G. hawaiiense* was found originally on only two trees, both were heavily infected. Leaves infected with this fungus have since been found on the island of Maui, indicating a wider distribution (Gardner unpubl. data). Stevens (1925) reported *Lophodermium intermissum* Starb. on presumably live koa on Oahu and Maui. *Lophodermium* spp. may occur either saprophytically or parasitically, causing leaf spots containing dark, erumpent fruiting bodies.

The Meliolales or "dark mildews", found primarily in tropical regions, are well represented in Hawaii, occurring on a wide range of endemic species. The members of this well-defined group are closely allied with one another and have characteristics in common with the powdery mildews (order Erysiphales) and the rust fungi. Thus, they are highly specialised, usually host-specific, and are obligate parasites. The dark mildews are

conspicuous as black, more or less circular spots or blotches on leaf surfaces, the fungal colonies often coalescing to cover much of the photosynthetic area. (In contrast to the sooty molds, the Capnodiales, with which they are sometimes confused, the dark mildews are not merely superficial saprophytes.) As mentioned, most of the dark mildews in Hawaii are known only from the endemic host on which each species occurs, and are themselves considered endemic (Stevens 1925; Goos & Anderson 1972).

Gardner & Hodges described leaf spot fungi on a number of endemic forest species, including *Elsinoe vaccinii* Gardner & Hodges on ohelo (Gardner & Hodges 1986) and *Botryosphaeria pipturi* Gardner & Hodges on *Pipturus hawaiiensis* Lévl. (mamaki), a common understorey shrub (Gardner & Hodges 1988). In addition, leaf spots were described on ohelo (Fig. 16) and tree ohelo, each caused by a different species of *Septoria*, on tree ohelo caused by *Mycosphaerella* sp., and on *Ilex anomala* H. & A. (native holly), also caused by a presumably host-specific species of *Mycosphaerella* (Gardner & Hodges 1988). Aside from the *Vaccinium* spp. hosts, *Septoria* spp. leaf spots occur on a number of Hawaiian plants (Gardner 1997c). A species of *Mycosphaerella* also causes a prominent leaf spot on ohia (Fig. 17).

A collar rot (Aragaki *et al.* 1972) and a shoot blight (Nishijima & Aragaki 1975) of koa seedlings were reported, caused by the fungi *Calonectria crotalariae* (Loos) Bell & Sobers and *C. theae* Loos, respectively. Incidence of collar rot appeared to be an isolated occurrence following the favourable effects of a forest fire in allowing dormant seeds to germinate and form an even-aged stand of seedlings. Fungal growth and red fruiting bodies were evident on infected plant stems above the soil line. Shoot blight on older shoots was characterised by brown-gray spots accompanied by leaf drop, but seedlings inoculated with the pathogen wilted quickly. The authors noted that shoot blights of ohia and koa have been encountered only infrequently in Hawaiian forests and do not seem to be of much consequence (Nishijima & Aragaki 1975).

Diseases of Commercial Introductions

Apart from the native forests discussed above, several tree species have been introduced to Hawaii, mostly for planting in small commercial timber or wood chip industries. The most common introductions include paperbark, a number of species of *Eucalyptus*, Norfolk and Cook Island pines (*Araucaria* spp.), and pine (*Pinus* spp.). (It is of interest here to note that Hawaii has no native gymnosperms, all having been introduced; hence, there are no native gymnosperm pathogens.)

Several leaf spot diseases of eucalypts occur in Hawaii, presumably having been introduced with their hosts. Among these, *Aulographina eucalypti* (Cooke & Masee) von Arx & Müller, reported from a large number of eucalypt hosts in Australia and New Zealand, is common on *E. globulus* Labill. in plantations on the islands of Maui and Hawaii. It also has been observed infrequently on *E. saligna* Sm. and *E. robusta*. On *E. globulus*, lesions may almost completely cover the leaves; however, even severe infection apparently causes only minor defoliation (Gardner & Hodges 1988). A eucalypt leaf spot disease caused by *Phaeoseptoria eucalypti* (Hansf.) Walker occurs commonly throughout the Islands in nurseries and young plantations on *E. saligna* and *E. grandis* Hill ex Maid. The disease is characterised by numerous angular to irregular purple leaf blotches, many of

which appear to never become necrotic, making pycnidia difficult to find (Gardner & Hodges 1988). Like its host genus, *P. eucalypti* is of Australian origin, where it occurs on several *Eucalyptus* spp. (Walker 1962).

Mid-elevation plantations of various species of pine, one of the more common being *Pinus radiata* D. Don, have been established on the major islands. Several apparent problems of disease and lack of vigour within these plantings probably result from inappropriate site selection for these introduced species rather than from specific virulent pathogens. A needle disease of *P. radiata*, caused by *Dothistroma septospora* (Dorog.) Morelet, occurs in plantations on Maui, and possibly on other islands. Infection produces red bands characteristic of the disease. Infected needles eventually die and are shed (Gardner & Hodges 1988). The fungus is thought to be native to Central America, but has been reported on numerous species of pines in North and South America, Africa, Asia, New Zealand, and Australia (Evans 1984).

Among diseases of introduced forest species, perhaps the most attention has been devoted to eucalypt canker caused by *Cryphonectria cubensis* (Bruner) Hodges, a fungus found to be conspecific with *Endothia eugeniae* (Nutman & Roberts) Reid & Booth, the pathogen that produces cankers on clove (*Syzygium aromaticum* (L.) Merr. in Indonesia (Hodges, Alvenas & Ferreiro 1986). On eucalypts, the disease is known primarily from the island of Kauai, where it causes large cankers in trunks of mature trees (Fig. 18). Data on mortality, rate of spread, and areas of forestland affected are lacking, however.

DISCUSSION

From a historical perspective, forest disease research in Hawaii is readily separated into two categories:

- (1) Having to do with the ohia decline phenomenon, particularly during the 1970s and early 1980s;
- (2) Studies of other disease situations.

By the mid-1980s, most leads as to a biotic etiology of ohia decline had been pursued and discarded as the "primary triggers" of the phenomenon. Research in the 1980s had less to do with forest pathology or entomology, but was directed to a greater extent toward elucidating the many facets of the complex "synchronous cohort senescence" theory of decline.

Aside from ohia decline, the relative dearth of forest disease research during the decades between Stevens' pre-1925 visit to Hawaii and the 1970s is evident in the scarcity of published information on forest diseases in the decades following Stevens' work. Stevens' 1925 publication must be cited in many current studies as the most recent contribution to the subject at hand, as illustrated by the work of Gardner and co-workers with koa rust. Because his stay in the Islands was only a few months' duration, Stevens was understandably not able to investigate the complex rust life-cycles in depth, but designated the spore states of koa rust that appeared reasonable based on cursory observation (1925). These concepts persisted until Gardner *et al.* (1979) found conspicuous spermogonia associated with the witches' brooms of the uredinial state of Stevens' description (Fig. 2). Because spermogonia cannot be associated with uredinia (Cummins 1959), this discovery necessitated the

redefinition of the brooms as the aecial state and initiated the search for the true telial and uredinial states. Although both telia and uredinia occur on koa, the obvious incongruity of telia being limited to young growth, well apart — usually on separate trees — from telial brooms led to Hodges & Gardner's (1984) discovery that the “telial state” represented a separate species.

The relatively recent discovery of *Dodonaea* yellows disease further illustrates the latent period of plant pathological activity in Hawaii. Despite its conspicuous symptoms and widespread distribution throughout the Islands, this condition had gone apparently undescribed, even having escaped Stevens' notice, until it was found in the late 1970s. Had this disease occurred elsewhere where forest pathologists had been active, a far greater understanding of it would have been expected by the 1970s.

From a managerial standpoint, understanding the ecological processes in native systems includes knowledge of the interactions between pathogens, both native and introduced, and their hosts. Many of these interactions, and the native pathogens themselves, provide intriguing examples of the evolutionary processes that have occurred in the extreme isolation of the Hawaiian Islands. The value of forest disease research to commercially oriented forestry requires little elaboration. Various avenues of investigation, particularly those involving modern molecular analysis approaches, remain open and challenging for forest pathology in Hawaii.

REFERENCES

- ANDERSON, R.C.; GARDNER, D.E.; DAEHLER, C.C.; MEINZER, F.C. 2002: Dieback of *Acacia koa* in Hawaii: Ecological and pathological characteristics of affected stands. *Forest Ecology and Management* 162: 273–286.
- ARAGAKI, M.; LAEMMLEN, F.F.; NISHIJIMA, W.T. 1972: Collar rot of koa caused by *Calonectria crotalariae*. *Plant Disease Reporter* 56: 73–74.
- BAGCHEE, K.D. 1945: Pathological notes: No. 2. Wilt and dieback of shisham, babul, and khair in the artificial regeneration under agriculture-cum-forestry management. *Indian Forestry* 71: 20–24.
- BARR, M.E. 1983: On *Diaporhopsis metrosideri*. *Mycologia* 75: 930–931.
- BECKMAN, C.H. 1987: “The Nature of Wilt Diseases of Plants”. APS Press, St. Paul, Minnesota.
- BEGA, R.V. 1974: *Phytophthora cinnamomi*: its distribution and possible role in ohia decline on the island of Hawaii. *Plant Disease Reporter* 58: 1069–1073.
- 1979: Heart and root rot fungi associated with deterioration of *Acacia koa* on the island of Hawai'i. *Plant Disease Reporter* 63: 682–684.
- BORTH, W.B.; GARDNER, D.E.; GERMAN, T.L. 1988. Closterovirus associated with *Dodonaea* yellows disease. (Abstract). *Phytopathology* 78: 1586.
- 1990: Association of double-stranded RNA and filamentous viruslike particles with *Dodonaea* yellows disease. *Plant Disease* 74: 434–437.
- BORTH, W.B.; HU, J.S.; KIRKPATRICK, B.C.; GARDNER, D.E.; GERMAN, T.L. 1995: Occurrence of phytoplasmas in Hawaii. *Plant Disease* 79: 1094–1097.
- BURGAN, R.E.; NELSON, R.E. 1972: Decline of ohia-lehua forests in Hawaii. *U.S.D.A. Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, General Technical Report PSW-3*. 4 p.
- BURT, E.A. 1923: Higher fungi of the Hawaiian Islands. *Annals of the Missouri Botanical Garden* 10: 179–189.

- CHEN, W.-Q.; GARDNER, D.E.; WEBB, D.T. 1996: Biology and life cycle of *Atelocauda koeae*, an unusual demicyclic rust. *Mycoscience* 37: 91–98.
- CUMMINS, G.B. 1959: "Illustrated Genera of the Rust Fungi". Burgess Publishing Co., Minneapolis, Minnesota. 131 p.
- CUMMINS, G.B.; HIRATSUKA, Y. 1983: "Illustrated Genera of the Rust Fungi". Revised edition. American Phytopathological Society, St. Paul, Minnesota. 152 p.
- DEGENER, O. 1973: Sandalwood or iliahi. Pp. 142–148 in "Plants of Hawaii National Parks. Illustrative of Plants and Customs of the South Seas". Braun-Brumfield Inc., Ann Arbor, Michigan.
- EVANS, H.C. 1984: The genus *Mycosphaerella* and its anamorphs *Cercoseptoria*, *Dothistroma* and *Lecanosticta* on pines. *Commonwealth Mycological Institute Mycological Paper, No. 153*. 102 p.
- EVENSON, W.E. 1983: Climate analysis in ohia dieback areas on the island of Hawaii. *Pacific Science* 37: 375–384.
- FORBES, D. 1918: Report of committee on forestry. *Hawaiian Planters' Record* 18: 202–205.
- FOSBERG, F.R. 1983: A possible new pathogen affecting *Metrosideros* in Hawaii. *Newsletter of the Hawaiian Botanical Society* 22: 13–16.
- GARDNER, D.E. 1978a: A seedling disease of koa caused by *Fusarium oxysporum*. (Abstract). *Phytopathology News* 12: 190–191.
- 1978b: Koa rust, caused by *Uromyces koeae*, in Hawaii Volcanoes National Park. *Plant Disease Reporter* 62: 957–961.
- 1980a: *Acacia koea* wilt caused by *Fusarium oxysporum* f. sp. *koeae*, f. sp. nov. *Phytopathology* 70: 594–597.
- 1980b: Apparent pathological conditions of *Vaccinium* spp. and *Dodonaea* sp. in Hawaii Volcanoes and Haleakala National Parks. Pp. 125–128 in Smith, C.W. (Ed.) "Proceedings of the 3rd Conference in Natural Sciences, Hawaii Volcanoes National Park". Cooperative Park Studies Unit, Department of Botany, University of Hawaii, Honolulu.
- 1981: Nuclear behavior and clarification of the spore stages of *Uromyces koeae*. *Canadian Journal of Botany* 59: 939–946.
- 1985: Red leaf disease of native Hawaiian *Vaccinium* species caused by *Exobasidium vaccinii*. *Plant Disease* 69: 805–806.
- 1987: Teliospore germination of *Uromyces alyxiae*, an endemic Hawaiian rust. *Mycologia* 79: 914–917.
- 1988a: The apparent yellows disease of *Dodonaea* spp. in Hawaii. Pp. 225–231 in Maramorosch, K.; Raychaudhuri, S.P. (Ed.) "Mycoplasma Diseases of Crops: Basic and Applied Aspects". Springer-Verlag, New York.
- 1988b: Teliospore germination of *Puccinia vitata*, an endemic Hawaiian rust. *Mycologia* 80: 590–593.
- 1989: Maile rust has a new cousin in Australia. *Newsletter of the Hawaiian Botanical Society* 28: 32–33.
- 1990: New rusts on endemic Hawaiian Rutaceae. *Mycologia* 83: 141–144.
- 1991: *Atelocauda angustiphylloida* n. sp., a microcyclic rust on *Acacia koea* in Hawaii. *Mycologia* 83: 650–653.
- 1994a: The native rust fungi of Hawaii. *Canadian Journal of Botany* 72: 976–989.
- 1994b: Teliospore germination and nuclear behavior of *Puccinia rutainsulara*, a microcyclic Hawaiian rust. *Mycologia* 86: 486–493.
- 1996a: Notes on the decline problem of koa. *Newsletter of the Hawaiian Botanical Society* 35: 27–31.

- 1996b: *Puccinia rugispora*: An unusual microcyclic rust endemic to Hawaii. *Mycologia* 88: 671–676.
- 1997a: *Acacia koa*: A review of its diseases and associated fungi. Pp. 56–63 in Ferentinos L.; Evans, D.O. (Ed.) “Koa: A Decade of Growth”, Proceedings of Symposium of The Hawaii Forest Industry Association, 18–19 November 1996, Honolulu, Hawaii.
- 1997b: *Botryosphaeria mamane* sp. nov. associated with witches’-brooms on the endemic forest tree *Sophora chrysophylla* in Hawaii. *Mycologia* 89: 298–303.
- 1997c: The genus *Septoria* (Fungi: Deuteromycetes) in Hawaii. *Bernice P. Bishop Museum Occasional Papers* 49: 3–9.
- GARDNER, D.E.; HODGES, C.S. Jr 1985: Spore surface morphology of Hawaiian *Acacia* rust fungi. *Mycologia* 77: 575–586.
- 1986: Hawaiian forest fungi. VII. A new species of *Elsinoe* on native *Vaccinium*. *Mycologia* 78: 506–508.
- 1988: Hawaiian forest fungi. IX. *Botryosphaeria pipturi* sp. nov. and miscellaneous records. *Mycologia* 80: 460–465.
- GARDNER, D.E.; KAGELER, V.A.D. 1984: The apparent yellows disease of *Dodonaea*: Symptomatology and considerations of the etiology. *Newsletter of the Hawaiian Botanical Society* 23: 7–16.
- GARDNER, D.E.; TRUJILLO, E.E. 2001: Association of *Armillaria mellea* with mamane decline at Pu’u La’au. *Newsletter of the Hawaiian Botanical Society* 40: 33–34.
- GARDNER, D.E.; MILLER, T.; KUHLMAN, E.G. 1979: *Tuberculina* and the life cycle of *Uromyces koeae*. *Mycologia* 71: 848–852.
- GERRISH, G.; BRIDGES, K.W. 1984: A thinning and fertilizing experiment in *Metrosideros* dieback stands in Hawaii. *University of Hawaii, Honolulu, Hawaii Botanical Science Paper* 43. 107 p.
- GOOS, R.D.; ANDERSON, J.H. 1972: The Meliolaceae of Hawai’i. *Sydowia, Annales Mycologici Series II* 26: 73–80.
- HENNEN, J.F.; HODGES, C.S. Jr 1981: Hawaiian forest fungi. II. Species of *Puccinia* and *Uredo* on *Euphorbia*. *Mycologia* 73: 1116–1122.
- HEPTING, G.H. 1971: Diseases of forest and shade trees of the United States. Pp. 64–67. *U.S. Department of Agriculture Handbook No. 386*.
- HODGES, C.S. Jr; GARDNER, D.E. 1984: Hawaiian forest fungi. IV. Rusts on endemic *Acacia* species. *Mycologia* 76: 332–349.
- HODGES, C.S. Jr; ALVENAS, A.C.; FERREIRO, F.A. 1986: The conspecificity of *Cryphonectria cubensis* and *Endothia eugeniae*. *Mycologia* 78: 343–350.
- HODGES, C.S. Jr; ADEE, K.T.; STEIN, J.D.; DOTY, R.D. 1986: Decline of ohia (*Metrosideros polymorpha*) in Hawaii: a review. *U.S.D.A. Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, General Technical Report PSW-86*. 22 p.
- HORNER, A. 1912: Report of the committee on forestry. *Hawaiian Planters’ Record* 6: 60–69.
- HWANG, S.C.; KO, W.H. 1978: Quantitative studies of *Phytophthora cinnamomi* in decline and healthy ohia forests. *Transactions of the British Mycological Society* 70: 312–315.
- JACOBI, J. 1983: *Metrosideros* dieback in Hawaii: a comparison of adjacent dieback and non-dieback rain forest stands. *New Zealand Journal of Ecology* 6: 79–97.
- KLIEJUNAS, J.T. 1979: Effects of *Phytophthora cinnamomi* on some endemic and exotic plant species in Hawaii in relation to soil type. *Plant Disease Reporter* 63: 602–606.
- KLIEJUNAS, J.T.; KO, W.H. 1973: Root rot of ohia (*Metrosideros collina* subsp. *polymorpha*) caused by *Phytophthora cinnamomi*. *Plant Disease Reporter* 57: 383–384.
- 1974: Deficiency of inorganic nutrients as a contributing factor to ohia decline. *Phytopathology* 64: 891–896.

- 1975: The occurrence of *Pythium vexans* in Hawaii and its relation to ohia decline. *Plant Disease Reporter* 59: 392–395.
- 1976a: Association of *Phytophthora cinnamomi* with ohia decline on the island of Hawaii. *Phytopathology* 66: 116–121.
- 1976b: Dispersal of *Phytophthora cinnamomi* on the island of Hawaii. *Phytopathology* 66: 457–460.
- KLIEJUNAS, J.T.; SCHARPF, R.F.; SMITH R.S., JR. 1977: The occurrence of *Phytophthora cinnamomi* in Hawaii in relation to ohia forest site and edaphic factors. *Plant Disease Reporter* 61: 290–293.
- LAEMMLEN, F.F.; BEGA, R.V. 1972: Decline of ohia and koa forests in Hawaii. (Abstract). *Phytopathology* 62: 770.
- 1974: Hosts of *Armillaria mellea* in Hawai'i. *Plant Disease Reporter* 58: 101–103.
- LARSEN, L.D. 1910: Pathological inspection on Kauai. *Hawaiian Planters' Record* 3: 68–71.
- LARSEN, M.J.; LOMBARD, F.F.; HODGES, C.S. Jr 1985: Hawaiian forest fungi. V. A new species of *Phellinus* (Hymenochaetaceae) causing decay of *Casuarina* and *Acacia*. *Mycologia* 77: 345–352.
- LYON, H.L. 1909: The forest disease on Maui. *Hawaiian Planters' Record* 1: 151–159.
- 1918: The forests of Hawaii. *Hawaiian Planters' Record* 18: 276–281.
- 1919: Some observations on the forest problems of Hawaii. *Hawaiian Planters' Record* 21: 289–300.
- McALPINE, D. 1906: "The Rusts of Australia". Government Printer, Melbourne.
- MUELLER-DOMBOIS, D. 1980: The ohia dieback phenomenon in the Hawaiian rain forest. Pp. 153–161 in Cairns, J.J. (Ed.) "The Recovery Process in Damaged Ecosystems". Ann Arbor Scientific Publication, Ann Arbor, Michigan.
- 1982: Island ecosystem stability and *Metrosideros* dieback. Pp. 138–146 in Proceedings of the Fourth Conference in Natural Science, June 2-4, 1982. Hawaii Volcanoes National Park. Cooperative Park Resources Studies Unit, University of Hawaii, Honolulu.
- 1986: Perspectives for an etiology of stand-level dieback. *Annual Review of Ecological Systems* 17: 221–243.
- 1987: Natural dieback in forests. *BioScience* 37: 575–583.
- MUELLER-DOMBOIS, D.; BRIDGES, K.W.; CARSON, H.L. 1981: "Island Ecosystems". Hutchinson Ross Publishing Co., Woods Hole, Massachusetts.
- MUELLER-DOMBOIS, D.; CANFIELD, J.E.; HOLT, R.A.; BUELOW, G.P. 1983: Tree-group death in North American and Hawaiian forests: a pathological problem or a new problem for vegetation ecology? *Phytocoenologia* 11: 117–137.
- NAGATA, R.; STEIN, J.D. 1982: Attraction of the two-lined ohia borer, *Plagithmysus bilineatus* (Coleoptera: Cerambycidae), to stressed ohia trees. Abstract. P. 251 in Proceedings of the Fourth Conference in Natural Science, June 2-4, 1982. Hawaii Volcanoes National Park. Cooperative Park Resources Studies Unit, University of Hawaii, Honolulu.
- NELSON, R.E.; WHEELER, P.R. 1963: "Forest Resources in Hawai'i". Hawaii Department of Land and Natural Resources, Honolulu.
- NISHIJIMA, W.T.; ARAGAKI, M. 1975: Shoot blights of 'ohi'a and koa caused by *Calonectria theae*. *Plant Disease Reporter* 59: 883–885.
- PAPP, R.P.; KLIEJUNAS, J.T.; SMITH, R.S. Jr; SCHARPF, R.F. 1979: Association of *Plagithmysus bilineatus* (Coleoptera: Cerambycidae) and *Phytophthora cinnamomi* with the decline of ohia-lehua forests on the island of Hawaii. *Forest Science* 25: 187–196.
- PETRAK, F. 1952: Ein Beitrag zur Pilzflora von Hawai. *Sydowia, Annales Mycologici* 6: 363–371.
- 1953: Beiträge zur Pilzflora von Hawai'i. *Sydowia, Annales Mycologici* 7: 381–409.

- PETTEYS, E.Q.P.; BURGAN, R.E.; NELSON, R.E. 1975: Ohia forest decline: its spread and severity in Hawaii. *U.S.D.A. Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, Research Paper PSW-105*. 11 p.
- RAABE, R.D.; TRUJILLO, E.E. 1963: *Armillaria mellea* in Hawai'i. *Plant Disease Reporter* 47: 776.
- ST JOHN, H. 1979: Classification of *Acacia koa* and relatives (Leguminosae). *Hawaiian Plant Studies* 93. *Pacific Science* 33: 357–367.
- SAMUELSON, G.A.; GRESSITT, J.L. 1976: A study of *Plagithmysus* and *Xyleborus* borers in relation to ohia decline. Final report of results, U.S.D.A., Forest Service PSW, Grant 11 to Bernice P. Bishop Museum, Honolulu, Hawaii. 15 p.
- SANDERSON, F.R.; KING, Y.K.; SAIFUL, A.; PHENG, Y.C.; HO, O.K. 1996: A *Fusarium* wilt (*Fusarium oxysporum*) of Angsana (*Pterocarpus indicus*) in Singapore. *Gardens' Bulletin of Singapore No. 48*: 89–127.
- STEVENS, F.L. 1925: Hawaiian Fungi. *Honolulu, Hawaii, Bernice P. Bishop Museum Bulletin* 19. 189 p.
- STONER, M.F.; STONER, D.K.; BAKER, G.E. 1975: Ecology of fungi in wildland soils along the Mauna Loa transect. *Department of Botany, University of Hawaii, Honolulu, US/IBP Island Ecosystems IRP, Technical Report* 75.
- SUTTON, B.C.; HODGES, C.S. Jr 1983: Hawaiian forest fungi. III. A new species, *Gloeocoryneum hawaiiense*, on *Acacia koa*. *Mycologia* 75: 280–284.
- TIERNEY, J.W.; GARDNER, D.E. 1992: A new rust on *Alyxia ruscifolia* in Queensland. *Australasian Plant Pathology* 21: 37–38.
- WAGNER, W.L.; HERBST, D.R.; SOHMER, S.H. 1990: "Manual of the Flowering Plants of Hawaii", Volumes 1 & 2. Bernice P. Bishop Museum Special Publications. University of Hawaii Press and Bishop Museum Press, Honolulu.
- WALKER, J. 1962: Notes on plant parasitic fungi. I. *Proceedings of the Linnean Society NSW* 87: 162–176.
- 2001: A revision of the genus *Atelocaula* (Uredinales) and description of *Racospermyces* gen. nov. for some rusts of *Acacia*. *Australasian Mycologist* 20: 3–28.