DIFFERENTIAL COLONIZATION BY EPIPHYTES ON NATIVE (CIBOTIUM SPP.) AND ALIEN (CYATHEA COOPERI) TREE FERNS IN A HAWAIIAN RAIN FOREST

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In Hawaiian rain forests, many species grow as epiphytes either exclusively or in addition to a terrestrial habit. Two types of sites are favored by epiphytes: 1) the bryophyte mats that form on the branches and trunks of forest trees, and 2) trunks of tree ferns. The predominant group of native tree ferns is in the genus *Cibotium* (Dicksoniaceae), known in Hawai'i as *hapu'u*. Five endemic *Cibotium* species occur in the Hawaiian Islands (Wagner 1990), three within Haleakala National Park—*C. chamissoi* Kaulf., *C. glaucum* (J. E. Smith) Hook. & Arn., and *C. splendens* (Gaud.) Krajina *ex* Skottsb. (Medeiros and Loope unpubl. ms.).

An alien tree fern, Cyathea cooperi (Hooker ex F. von Mueller) Domin in the family Cyatheaceae, native to eastern Australia, has locally invaded native forests on the Hawaiian islands of Kaua'i, O'ahu, and Maui (Medeiros et al. 1992). In 1987, well established populations were discovered in the remote rain forests of Kipahulu Valley, within Haleakala National Park, probably originating through wind blown spores from plant nurseries on the coast near the settlements of Hana and Nahiku, 12 km distant. The largest population of Cyathea cooperi in the valley occurs in native Metrosideros polymorpha and Acacia koa rain forest at 730 m elevation and comprises over 800 individuals. Based on the height of the largest individuals (4 m) and the extent of the population, colonization probably began in the 1970's. Numerous smaller understory trees, shrubs, herbs, and pteridophytes at the site form a diverse assemblage of native species, including local endemics.

As biologists with Haleakala National Park, one of our major objectives is to detect newly invading species capable of damaging native plant and animal populations and/or ecosystem properties before they become widespread, so that chances for control are maximized. An expedition in April 1991 was devoted entirely to examining the status and impact of *C. cooperi* in Kipahulu Valley. In conjunction with an effort to assess the stand structure of the population of this Australian tree fern in fixed plots, we compared the epiphyte populations on native and alien tree fern species.

METHODS

The immediate vicinity of the main *Cyathea* cooperi population was chosen as the study area. All individuals of the two native tree ferns, *Cibotium chamissoi* and *C. glaucum*, that exceeded 1.5 m in height were located and sampled. *Cyathea cooperi* was much more common in the area and was sampled only within fixed study plots used in assessing stand structure. For all three species, only large individuals (>1.5 m height) were selected. For each tree fern, all vascular plant epiphyte species were listed and the number of individuals of each species recorded.

RESULTS

Eleven of 16 tree ferns (66%) of the native *Cibotium glaucum* surveyed had populations of epiphytes, all with native species and three (18%) with alien species. Nineteen of 21 (91%) tree ferns of the native *Cibotium chamissoi* had populations of epiphytes; all with native species, none with alien species. Twenty of 50 tree ferns (40%) of the alien *Cyathea cooperi* had populations of epiphytes, 12 with native species (24%) and 12 (24%) with alien species.

Thirty-four species of vascular plants were recorded as epiphytes on the three species of tree ferns at the study site (TABLE 1). Of these, 18 species were pteridophytes (in 13 families), three species were monocots (3 families), and 13 were dicots (11 families). Of these, 28 species (82%) were native and six were alien (18%). Of the native species, 10 species were indigenous (34%), 17 were endemic (60%), and one taxa unidentified to the species level (*Huperzia* sp.) was classified as native only.

Of the six non-native species, there were two ferns (*Athyriopsis japonica* and *Cyathea cooperi*), one grass (*Paspalum conjugatum*), one sedge, (*Rhynchospora caduca*) and two dicots (*Ageratina adenophora* and *Rubus rosifolius*). All are invasive species in Hawaiian rain forests, with *P. conjugatum* recognized as one of the worst weed species in native Hawaiian habitats (Smith 1985). All six alien species were classified as mostly terrestrial but also epiphytic. TABLE 1. List of vascular plant species recorded as epiphytes on *Cibotium chamissoi*, *C. glaucum*, and *Cyathea cooperi*, Kipahulu Valley, Hawaiian Islands. The rough categories of frequency are "rarely" (occurring on 1–2 tree ferns), "sparingly" (occurring on 3–4 tree ferns), and "commonly" (occurring on more than 4 tree ferns).

Pteridophytes

Aspleniaceae

Asplenium contiguum Kaulf.

Indigenous

Common both terrestrially and as epiphyte. Found sparingly on *Cyathea cooperi*, common on

Cibotium glaucum and Cibotium chamissoi. Athyriaceae

Amynaccac

Athyriopsis japonica (Thunb.) Ching Alien: native to Asia Found mostly terrestrially but also as an epiphyte.

Found sparingly on *Cyathea cooperi* only.

Cyatheaceae

Cyathea cooperi (Hook. ex F. Muell.) Dom. Alien: native to eastern Australia Found mostly terrestrially but also as an epiphyte. Found rarely on *Cyathea cooperi* only.

Dicksoniaceae

Cibotium glaucum (J. E. Smith) Hook. & Arn. Endemic to main Hawaiian Islands Found mostly terrestrially but also as an epiphyte. Found sparingly on Cibotium glaucum only.

Elaphoglossaceae

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

Indigenous: pantropical, variety endemic to Hawaiian Islands

Primarily found as epiphyte.

Found rarely on Cibotium glaucum only.

Gleicheniaceae

Dicranopteris linearis (Burm.) Underw. Indigenous: Japan, India, New Zealand to main Hawaiian Islands

Found mostly terrestrially but also as an epiphyte. Found rarely on *Cibotium glaucum* only.

Grammitaceae

Adenophorus hymenophylloides (Kaulf.) Hook. & Grev.

Endemic to main Hawaiian Islands Primarily found as epiphyte. Found rarely on *Cibotium chamissoi* only.

Adenophorus pinnatifidus Gaud. Endemic to main Hawaiian Islands Primarily found as epiphyte. Found rarely on *Cibotium glaucum* only.

Adenophorus tamariscinus (Kaulf.) Hook & Grev. Endemic to main Hawaiian Islands Primarily found as epiphyte. Found commonly on *Cibotium glaucum* and sparingly on *Cibotium chamissoi*.

Grammitis tenella Kaulf. Endemic to main Hawaiian Islands

TABLE 1. Continued.

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Primarily found as epiphyte.

Found rarely on Cibotium chamissoi only.

Hymenophyllaceae

Vandenboschia davallioides (Gaud.) Copel.

Endemic to main Hawaiian Islands

- Found mostly as an epiphyte, but also occurs terrestrially.
- Found rarely on Cibotium glaucum only.

Lycopodiaceae

Huperzia sp.

Native to the Hawaiian Islands

Found mostly as an epiphyte, but also occurs terrestrially.

Found sparingly on *Cyathea cooperi* and rarely on *Cibotium chamissoi.*

Lycopodium cernuum L.

Indigenous: pantropical Common both terrestrially and as epiphyte.

Found rarely on *Cibotium chamissoi* only.

Lycopodium phyllanthum Hook. & Arn.

Indigenous: India to main Hawaiian Islands Found mostly as an epiphyte, but also occurs terres-

trially. Found rarely on *Cibotium glaucum* and *Cibotium* chamissoi only.

Nephrolepidaceae

Nephrolepis cordifolia (L.) Presl.

Indigenous: pantropical

Found mostly as an epiphyte, but also occurs terrestrially.

Found rarely on Cibotium chamissoi only.

Ophioglossaceae

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

Indigenous: pantropical; subspecies found on Pacific islands

Primarily found as epiphyte.

Found sparingly on Cibotium chamissoi only.

Polypodiaceae

Pleopeltis thunbergiana Kaulf.

Indigenous

Found mostly as an epiphyte, but also occurs terrestrially.

Found rarely on Cyathea cooperi and Cibotium glaucum.

Psilotaceae

Psilotum nudum (L.) Beauv.

Indigenous: pantropical and subtropical

Found mostly as an epiphyte, but also occurs terrestrially.

Found sparingly on Cibotium glaucum and com-

monly on Cibotium chamissoi only.

Monocotyledons

Cyperaceae

Rhynchospora caduca Elliott

Alien: native to the southern U.S.

Found mostly terrestrially but also as an epiphyte. Found rarely on *Cibotium glaucum* only.

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TABLE 1. Continued.

Pandanaceae

Freycinetia arborea Gaud. Indigenous: Polynesia, Samoa, New Caledonia and

main Hawaiian Islands Found mostly as an epiphyte, but also occurs terres-

trially.

Found sparingly on Cibotium chamissoi only.

Poaceae

Paspalum conjugatum Berg.

Alien: native to tropical America

Found mostly terrestrially but also as an epiphyte.

Found commonly on *Cyathea cooperi* and rarely on *Cibotium glaucum*.

Dicotyledons

Araliaceae

Cheirodendron trigynum (Gaud.) Heller

Endemic to main Hawaiian Islands

Found mostly terrestrially but also as an epiphyte.

Found commonly on Cibotium glaucum and Cibotium chamissoi.

Asteraceae

Ageratina adenophora (Spreng.) King and Robinson Alien: native to Mexico

Found mostly terrestrially but also as an epiphyte. Found rarely on *Cyathea cooperi* only.

Campanulaceae

Clermontia arborescens (Mann) Hillebr.

Endemic to Hawaiian Islands of Moloka'i, Lana'i, and Maui

Common both terrestrially and as epiphyte.

Found sparingly on *Cibotium glaucum* and rarely on *Cibotium chamissoi*.

Ericaceae

Vaccinium calycinum Sm.

Endemic to main Hawaiian Islands

Common both terrestrially and as epiphyte.

Found sparingly on Cibotium glaucum and commonly on Cibotium chamissoi.

Fabaceae

Acacia koa Gray

Endemic to main Hawaiian Islands Found mostly terrestrially but also as an epiphyte.

Found rarely on Cibotium chamissoi only.

Hydrangeaceae

Broussaisia arguta Gaud.

Endemic to main Hawaiian Islands

Found mostly terrestrially but also as an epiphyte. Found rarely on *Cyathea cooperi* and on *Cibotium* chamissoi.

Myrtaceae

Metrosideros polymorpha Guad.

Endemic to main Hawaiian Islands

Found mostly terrestrially but also as an epiphyte. Found commonly on *Cibotium glaucum* and *Cibotium chamissoi.*

Syzygium sandwicensis (Gaud.) Nied.

TABLE 1. Continued.

Endemic to the Hawaiian Islands of Kaua'i, O'ahu, Moloka'i, Lana'i, and Maui

Found mostly terrestrially but also as an epiphyte. Found rarely on *Cibotium chamissoi* only.

Piperaceae

Peperomia cookiana C. DC. Endemic to the Hawaiian Islands of Kaua'i, Moloka'i, Maui, and Hawai'i

Common both terrestrially and as an epiphyte.

Found commonly on *Cyathea cooperi*, and sparingly on *Cibotium glaucum* and *Cibotium chamissoi*.

Rosaceae

Rubus rosifolius Sm.

Alien: native to Asia

Found mostly terrestrially but also as an epiphyte. Found commonly on *Cyathea cooperi* only.

Rubiaceae

Coprosma ochracea Oliver

Endemic to the Hawaiian Islands of O'ahu, Moloka'i, Lana'i, Maui, and Hawai'i

Found mostly terrestrially but also as an epiphyte. Found rarely on *Cibotium chamissoi* only.

Hedyotis affinis (Hook. & Arn.) Wagner and Herbst Endemic to main Hawaiian Islands

Common both terrestrially and as epiphyte.

Found rarely on Cibotium glaucum only.

Rutaceae

Pelea clusiifolia Gray

Endemic to main Hawaiian Islands

Found mostly terrestrially but also as an epiphyte.

Found commonly on Cibotium glaucum and Cibotium chamissoi.

The two native *Cibotium* species supported more individual epiphytes than did trunks of *Cyathea cooperi* of comparable size. On the 16 plants of *Cibotium glaucum*, there were an average of 20.2 individuals of native epiphyte species. On the 21 individuals of *Cibotium chamissoi*, there were 11.4, and on *Cyathea cooperi* (N = 50) an average of 1.1 individuals of native epiphyte species.

Four of the six alien epiphyte species were recorded only on the non-native *Cyathea* tree ferns. One alien species and 23 native species (82% of native species) were recorded only on native *Cibotium* tree ferns.

Of the 28 native epiphyte species, six (21%) are exclusively epiphytes, six (21%) are predominantly epiphytes but can be found terrestrially, six (21%) are common both epiphytically and terrestrially, and 10 species (36%) are mostly terrestrial species, but can occur epiphytically. The six species that were found only as epiphytes were all small-sized ferns and fern allies. Ten

TABLE 2. Average number of epiphytes of native and alien vascular plant species per trunk of native (*Cibotium* spp.) and alien (*Cyathea cooperi*) tree ferns. Means that do not differ at a 0.01 confidence level based on the *t*-test are indicated by a common superscript (A, B, C).

	Average no. of plants per trunk	
	Native	Alien
<i>Cibotium glaucum</i> ($N = 16$)	20.2^	0.25 ^c
Cibotium chamissoi $(N = 21)$	11.4^	0 ^c
Cibotium (both spp.) $(N = 37)$	15.84	0.1 ^c
Cyathea cooperi $(N = 50)$	1.1 ^B	0.5 ^c

native species could be classified as species that are normally large statured and whose growth as an epiphyte will result in long-term survival only if the roots eventually contact the soil.

Cyathea cooperi appears to support more individuals of the alien epiphyte species than do the native tree ferns. *Cibotium chamissoi* had no alien epiphyte species and *Cibotium glaucum* averaged 0.25 individuals of alien epiphyte species. However, *C. cooperi* averaged 0.5 individuals of alien epiphyte species per trunk. Compared to the total number of individuals on each plant, the percentage of alien species is 0% for *Cibotium glaucum*, 1.7% for *Cibotium chamissoi*, and 31.3% for *Cyathea cooperi* (TABLE 2).

DISCUSSION

Why should there be more epiphytes on Cibotium tree ferns than on Cyathea cooperi tree ferns? We could generate two possible reasons. First, Cyathea cooperi is much faster growing than Hawaiian tree ferns (Cibotium); therefore, large plants of Cyathea may be relatively young, while a comparable sized individual of Cibotium is likely to be of considerable age. A second reason may be that the trunks of *Cvathea cooperi* are in some fashion (mechanically or chemically) resistant to establishment of epiphytes. A horticulturist on Maui reported that, when orchids and other plants were attached to Cvathea trunks in cultivation trials, the epiphytes did very poorly and seemed to be harmed by the aerial roots of Cyathea (G. Westcott pers. comm.). In contrast, the broken fibers of the Hawaiian tree ferns Cibotium are widely used as planting media for orchids. It is likely that both factors are operative.

The tendency for many species of Hawaiian plants to occur both rooted in soil and as epiphytes is characteristic of island rain forests (Mueller-Dombois & Howarth 1981). In Kipahulu Valley, occurrence of primarily terrestrial plant species as epiphytes has been important in

CONCLUSIONS

maintaining biological diversity locally when there is substantial and frequent ground distur-

bance due to feral pig rooting.

Cyathea cooperi, though undocumented until recently as invasive, is an aggressive species that has established in native forests on several islands in the 1970's and is rapidly spreading (Medeiros *et al.* 1992). In addition to impacts such as aggressive competition for space and light, the evidence presented here demonstrates that the alien tree fern supports fewer epiphytes than the two native *Cibotium* tree ferns.

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