CBM:s Skriftserie 3: 7–24. Uppsala 2001.

Population status of five Hawaiian endemic fern taxa within the genus *Diellia* (Aspleniaceae)

Ruth Aguraiuja

Aguraiuja, R. 2001. Population status of five Hawaiian endemic fern taxa within the genus Diellia *(Aspleniaceae). – CBM:s Skriftserie 3: 7–24.*

The life-stage and size structure of 10 populations of five endemic fern taxa was studied (*Diellia erecta* Brack; *D. falcata* Brack; *D. pallida* W.H. Wagner; *D. unisora* W.H. Wagner and *D.* x *lauii* (*D. falcata* x *D. unisora*) W.H. Wagner), with the aim of assessing the overall condition of the populations. During the study, populations were defined as spatially distinct assemblages of plants at certain sites, with no consideration of the genetic structure of the populations. Spatial patchiness of habitat, clumped distribution patterns, life-stage specific survival and slow establishment of gametophytes are characteristic of all taxa of the genus *Diellia.* Data from field observations of *D. falcata* over three months lead to the assumption that *Diellia* ferns show a continuous growth pattern with irregular periods of dormancy and spore release with defined peaks. The proportion of vegetative premature and reproductively mature sporophytes could be one possible variable for use in the assessment of the population status of *Diellia* ferns in short-term studies. The single population of *D. pallida* in Mahanaloa Valley, Kauai, is in critical condition with only 31 individuals of different life stages found in heavily disturbed habitat. The process of hybridisation between *D. falcata* and *D. unisora* requires further study, which may contribute to our understanding of the hybridisation of rare species and/or speciation.

Ruth Aguraiuja, Tallinn Botanic Garden, Kloostrimetsa tee 52, Tallinn EE-11913, ESTONIA.
Fax: +372-6005529. E-mail: ruth@tba.ee

Diellia pallida

Diellia x *lauii*

Introduction

The fern genus *Diellia* Brack. (*Aspleniaceae*) is endemic to the Hawaiian Islands, comprising six species and a single hybrid (Wagner 1994): *Diellia erecta* Brack.; *D. falcata* Brack.; *D. leucostegioides* (Baker) W. H. Wagner; *D. mannii* (D.C. Eaton) W. Robinson; *D. pallida* W.H. Wagner; *D. unisora* W.H. Wagner and *D.* x *lauii* (*D. falcata* x *D. unisora*) W.H. Wagner.

Diellia ferns are small to medium-sized ferns found on steep slopes in dry and mesic lowland and montane forests (Wagner 1951). They differ from *Asplenium* species by their short or fused submarginal sori, which open outwards and the areolate venation pattern. One exception is *D. leucostegioides,* which shares most of its morphological features with the other *Diellia* species, but has free venation and medial linear sori along the veins which is typical of *Asplenium* species (Wagner 1953).

The taxonomy of the genus and its species has undergone many changes through its history, being related to various genera and families by different authorities (Brackenridge 1854, Hillebrand 1888, Christensen 1925, Wagner 1952). The fact that these ferns are so rare and variable has meant that there is still no clear agreement about the taxonomic status of the genus *Diellia*. Recently, it has been reduced to a synonym under the genus *Asplenium* L. by R. Viane (Kramer & Viane 1990, Viane & Reichstein 1992).

Diellia is a monophyletic genus evolved from *Asplenium* ancestory (Wagner 1952, Wagner 1953), which has radiated out over the Hawaiian Islands. In his monographic study, Wagner suggested an origin from the *Asplenium trichomanes* group. Later, he suggested a more specific prototype in the form of *Asplenium leucostegioides* Baker (Wagner 1953), now recognised as *Diellia leucostegioides* (Baker) W.H. Wagner comb. nov. (Wagner et al. 1995).

D. erecta, and its associated forms, is the only *Diellia* species which was originally found on all of the bigger islands, though it is now only found on Hawaii, Maui, Molokai and Oahu. The five other *Diellia* species are all single island endemics. The type specimens of *D. leucostegioides* were collected on East-Maui sometime before 1879 and identified as *Asplenium normale* Don, only being described as a separate species some years later (Wagner 1953). Since that time, this species has not been relocated. *D. mannii,* originally collected from Kauai, has also not been found for 100 years (Anon. 1999). *D. pallida* is endemic to Kauai, found only in the western part of the Kokee Mountains. Three taxa are then endemic to the island of Oahu. *D. falcata,* the only locally common species of the genus, occurs over the whole of the Waianae Mountains. *Diellia unisora* was discovered at Pohakea Pass in the Waianae Mountains on Oahu in 1932. It is now rare with a localised distribution (Wagner 1951). *Diellia* x *lauii* is a recently discovered endemic hybrid (Wagner et al. 1999). It was mentioned as locally common when found by J. Lau in 1991. All three endemic taxa occur together in the Pualii-Palawai region in the southern Waianae Mountains. According to Wagner (1999), the hybrid establishes dense colonies in the vicinity of parental species.

The restricted distribution of the *Diellia* species is mentioned in several published studies (Hillebrand 1888, Smith 1934, Degener 1950, Wagner 1952, Fosberg & Herbst 1975, Wagner 1952). All species have always been considered very rare and local, on the verge of extinction, or decreasing. According to Wagner, these species have always been rare and localised because of the restricted area of suitable habitat. The major threats to their survival are habitat degradation by feral ungulates and competition with naturalised, introduced plant species (Anon. 1995, Anon. 1996, Anon. 1998, Anon. 1999). The first assessment of the status of the populations was given by Fosberg & Herbst (1975). Their work was based mainly on their lengthy personal experiences of Hawaiian flora and almost without quantitative data and ecological information. The current status of the taxa is given in Table 1.

According to Menges and Gordon (1996), the status and trends of populations of rare plants may be studied on three levels: population distribution; quantitative monitoring (study) of population size/condition; and demo-

Table 1. Status and distribution of the *Diellia* taxa

Taxon	IUCN 1997*	USFWS 1999**	Distribution
Diellia erecta	Endangered	13 pop. 63 ind.	Hawaii, Maui, Molokai, Oahu. Extinct Lanai and Kauai.
Diellia falcata	Endangered	22 pop. > 6000 ind.	Oahu
Diellia x *lauii*	–	–	Oahu
Diellia leucostegioides	–	0	Maui, not found
Diellia mannii	Extinct/Endangered	0	Kauai, not found
Diellia pallida	Endangered	3 pop. 23 ind.	Kauai
Diellia unisora	Endangered	4 pop. 700 ind.	Oahu

* IUCN Red List of Threatened Plants 1997, IUCN The World Conservation Union:5
** U.S. Fish & Wildlife Service Species List.
– not listed

graphic study of the population. The first level, including an inventory, distribution mapping and presence/absence and spatial extent of the populations, has been the base for the present status assessment of the populations of *Diellia* (Anon. 1996).

Long-term studies of demography, together with life-cycle studies, give useful information for conservation management concerning critical stages and specific biological requirements of rare plants. Another method for describing population status/condition in a single census may be to study the population structure and determine the relative proportions of individuals in different life-cycle stages (van't Veer & den Nijs 1994). Monitoring the demographics of populations of rare plant species allows us to follow population trends and hypothesize about the demographic mechanisms driving them (Menges & Gordon 1996).

This paper describes the population size and life-stage structure of 10 populations of *D. erecta*, *D. pallida*, *D. falcata*, *D.* x *lauii* and *D. unisora*. For this study, populations were defined as spatially distinct assemblages of plants at certain sites, without considering the genetic structure of the populations. The aim of the study was to assess the status (condition) of the populations of the taxa within the endemic genus *Diellia*, on the basis of population structure and life cycle characteristics.

Methods

Over the period 13 February to 16 July 1999, field surveys were conducted to determine the current population status of four species and one hybrid within the genus *Diellia* at 13 sites on the islands of Kauai, Oahu, Molokai and Hawaii (Fig. 1). For all sites, general community and habitat descriptions were made and for all observed populations, the number of individuals and their life stage structure were assessed.

To describe the relevant plant communities, lists of associated species were compiled (Appendices 1 and 2). To describe the habitats at each locality, variables recorded included elevation (altitudinal range), aspect, slope, substrate, soil pH, soil moisture and canopy closure (Table 2).

Assessments of population size were derived mainly from direct counting of individuals, while sample estimates were made for the more abundant *Diellia falcata* at Kahanahaiki.

To record the stage structure of the populations, the following stages were differentiated: prothallium; sporeling; premature (pre-reproductive adult); mature (reproductive adult); dormant/dead (Figure 2). As prothalli were difficult to find and identify, during analyses of stage structure the prothalli and sporelings were pooled together. To identify the spore release period, the frond phases were described as follows: vegetative; sori developing; sori opened;

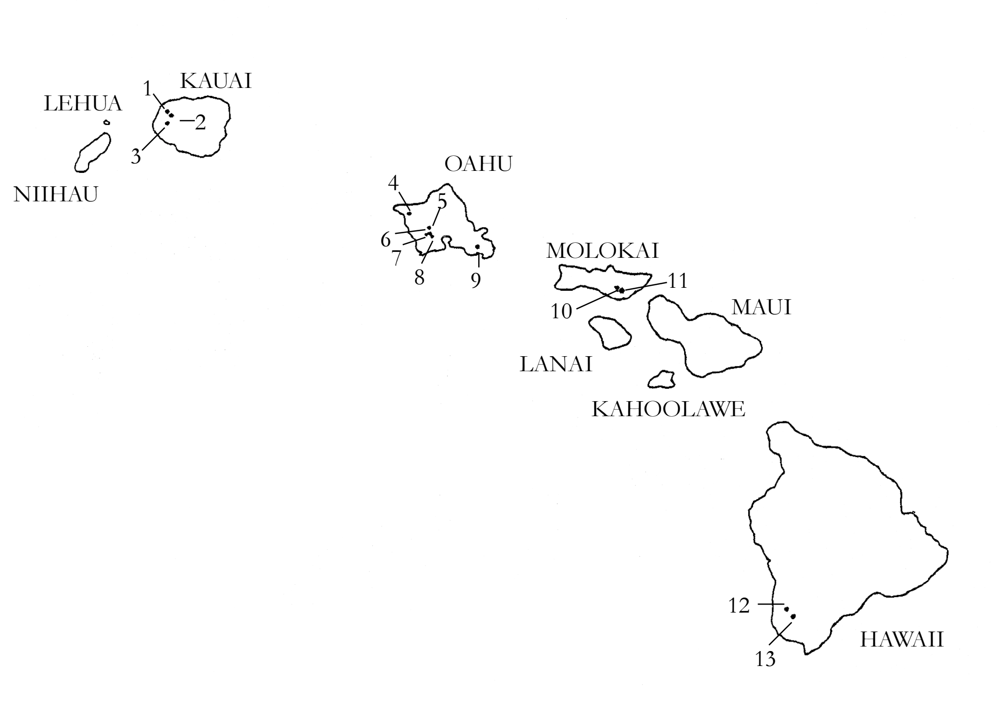

Figure 1. Study sites of the genus *Diellia* in Hawaii: 1– Mahanaloa (*D. pallida*); 2– Makaha (*D. pallida*); 3– Puu Ka Pele (*D. pallida*); 4 – Kahanahaiki (*D. falcata*); 5 – Pualii (*D. unisora*); 6 – South-Palawai (*D. unisora*); 7 – South-Palawai (*D.* x *lauii*); 8 – South-Palawai (*D. falcata*); 9 – Hawaii Loa (*D. erecta*); 10 – Onini Gulch (*D. erecta*); 11 – Puu Kolekole (*D. erecta*); 12 – Honomalino (*D. erecta*); 13 – Manuka (*D. erecta*).

sporangia dehisced. Where possible, the diameter and height of the plants and the length of the fronds were also measured. For each individual, the number of old stipes and vegetative and generative fronds was counted. At Kahanahaiki, a permanent plot of 6 x 10m was established and the population of *D. falcata* censused three times (March, April and June).

Voucher specimens (fronds and pinnae) are preserved in the herbarium at the National Tropical Botanical Gardens on Kauai. All statistical analyses were made using StatView for Windows, Version 5.0, SAS Institute Inc. 1992–1998.

Results

I found different taxa of the genus *Diellia* growing on nine sites (Table 2). For all observed populations, the number of individuals and their life stage structure was assessed. Measurements of individuals were made for four populations: at Hawaii Loa (*D. erecta*); Mahanaloa (*D. pallida*); Pualii (*D. unisora*) and Kahanahaiki (*D. falcata*).

Habitat and community

Diellia ferns are restricted to a particular spatially fragmented habitat type on the steep sides of gulches. Usually, they occur on northern slopes at an altitude of 300–1100 m a.s.l. Slope angle varied among sites from gentle to steep, nearly vertical, cliff faces. *D. falcata*, *D.* x *lauii*, *D. pallida* and *D. unisora* are usually terrestrial ferns, whilst *D. erecta* occurs on soil as well as on old lava blocks and cliffs. Sparse ground cover and a bare soil surface appear to be essential for the persistence of these populations. Typically, plants were found on soil that was rocky, granular and usually dry, with some leaf litter and mosses. Soil pH varied

Table 2. Checked sites with previous and current data.

Taxon	Island	Locality	Previous data (no. of ind.)	Source	Current data (1999) (no. of ind.)
D. erecta					
	Hawaii	Honomalino	20	Lau 1991	–
	Hawaii	Manuka	1	Lau 1992	205
	Oahu	Hawaii Loa	c. 40	Anon. 1998b	212
	Molokai	Onini Gulch	1	Wood 1997	1
	Molokai	Puu Kolekole	few	Anon. 1996	–
D. falcata					
	Oahu	Kahanahaiki	c. 40–2000	Anon. 1998b	c. 1000
	Oahu	S-Palawi	c. 10	Anon. 1998b	18
D. x lauii					
	Ohau	Pualii	few	Anon. 1998b	30
	Ohau	S-Palawii	hundreds	Lau 1991	141
D. pallida					
	Kauai	Puu Ka Pele	2	Flynn 1998	–
	Kauai	Makaha	6	Wood 1998	–
	Kauai	E-Mahanaloa	c. 10	Perlman 1991	4
	Kauai	W-Mahanaloa	c. 10	Wood 1996	31
D. unisora					
	Oahu	Pualii	c. 600	Anon. 1998b	153
	Oahu	S-Palawai	90	Anon. 1998b	112

– not found

from slightly acidic (sites on Oahu) to neutral and basic (Kauai, Mahanaloa) (Table 3).

The surrounding natural community was usually mesic lowland or mountain forest where *Metrosideros polymorpha* Gaud. is dominant. The communities at Pualii, South-Palawai in the Waianae Mts. and Hawaii Loa in the Koolau Mts. were dominated by naturalised *Psidium cattleianum* Sabine and *Schinus therebinthifolius* Raddi (Table 3).

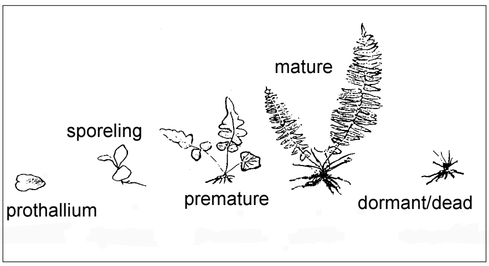

Figure 2. Schematic drawing of the life cycle stages of taxa in the genus *Diellia*: prothallium; sporeling; premature (pre-reproductive adult); mature (reproductive adult); dormant/dead.

Diellia erecta

A total of five sites on three islands were searched for populations of *D. erecta* (Table 2). On Molokai, only a single mature individual was found growing on a steep slope at Onini Gulch in mesic mixed forest. At the end of March, this individual plant had five fronds from its last growing period and one young generative frond. A few unopened sporangia were found between older, dehisced sporangia. This individual differed morphologically from ferns in other populations of *D. erecta* by its narrower pinnae, simple venation and distinct auricles, which diagonally overlapped the stipe and next pinna on the abaxial side of the frond.

In Manuka Natural Area Reserve, *D. erecta* was found growing along a loop trail in dry forest dominated by *Nestegis sandwicensis* (A. Gray)

Table 3. Habitat characteristics for the *Diellia* ferns

Taxa, site	Island	Alt (m)	Aspect	Slope	Moisture	Canopy
D. erecta						
Onini Gulch	Molokai	894	N	Steep, ca 45°	Mesic	Closed
Puu Kolekole	Molokai	920	N	Steep, ca 45°	Dry	Closed
Honomalino	Hawaii	586	S W	Gentle	Mesic	Closed
Manuka	Hawaii	625	S W	Moderate	Dry	Closed
Hawaii Loa	Oahu	360	S E	Steep, nearly vertical	Dry	Closed
D. falcata						
Kahanahaiki	Oahu	555–645	NW	Moderate	Mesic	Closed
S-Palawai	Ohau	670–730	N	Moderate	Mesic	Closed to semi-closed
D. x lauii	Ohau	670–730	N	Steep	Mesic	Closed to
S-Palawai	Kauai	670–730	N	Steep	Mesic	semi-closed
D. pallida						
Mahanaloa	Kauai	580–690	N	Steep	Mesic per. dry	Closed to semi-closed
Makaha	Kauai	915	N	Steep, nearly vertical	Dry	Closed to semi-closed
Puu Ka Pele	Kauai	1010	SE	Steep	Dry	Open to semi-closed
D. unisora						Open
Pualii	Oahu	670–750	N	Steep	Mesic	Closed to semi-closed
S-Palawai	Ohau	671–732	N	Steep	Mesic	Closed to semi-closed

Table 3. continues on next page

Degener, I. Degener & L. Johnson. Most of these individuals were found on moss covered lava blocks, with only a few growing on soil. Altogether, 151 individuals in various life cycle stages were recorded in this population (Figure 3). At the beginning of April, 61% of this population was in the reproductive stage. Fronds of all different phases were found on mature plants. The whole area was very dry and the ferns were wilting, with many of the wilted plants having young fronds with inconspicuous developing sori.

On Oahu, *D. erecta* was found on the southeastern slope of the Hawaii Loa Ridge. The slope was covered with non-native secondary forest, where *Psidium cattleianum* was dominant. All individuals were found on nearly vertical old lava cliffs. Altogether, 212 individuals in different life stages were recorded (Figure 3), with a single mature individual growing on a separate cliff 30m from the main population. In June, 13% of the population was in the reproductive phase and nearly half of the population (48.3%) consisted of prothallia and sporelings. Fronds of all phases were found on mature plants. Mean values of the measurements of individuals in different lifestages are given in Table 4.

Diellia falcata

Two sites with populations of *D. falcata* were visited in the Waianae Mts. on Oahu (Table 2). The entire population at Kahanahaiki Valley

Table 3. continued. Habitat characteristics for the *Diellia* ferns

Taxa, site	Substrate	Soil pH	Ground-cover	Natural community	Dominant species
D. erecta					
Onini Gulch	Brown soil with moss and leaf litter	–	20%	Mixed mesic forest	*Metr poly*
Puu Kolekole	Brown soil with leaf litter	–	10%	Mixed mesic forest	*Metr poly*
Honomalino	Old aa lava blocks and clinker	–	20%	Mesic Metr. forest	*Metr poly, Nest sand*
Manuka	Soil, old aa lava blocks and clinker	–	10%	Nest dry forest	*Nest sand*
Hawaii Loa	Old pahoehoe cliff	–	5%	Sec. forest of alien trees	*Psid catt, Schi tereb*
D. falcata					
Kahanahaiki	Heavy granular soil	5.7	30%	Lowland mesic forest	*Diosp hilleb*
	Brown-black granular soil	–	60%	Lowland mesic forest	*Cenchr agri*
S-Palawai	Rocky soil	5.0	20%	Relic mesic forest with sec. succession of weeds	*Psid catt*
D. × lauii					
S-Palawai	Rocky soil	5.0	20%	Relic mesic forest with sec. succession of weeds	*Psid catt*
D. pallida					
Mahanaloa	Pure native soil with leaf litter	6.9–7.7	<10%	Kauai diverse mesic forest	*Metr poly, Ptera kaua*
Makaha	Brown granular rocky soil	–	75%	Aca-Metr montane mesic forest	*Metr poly, Aca koa*
Puu Ka Pele	Brown granular rocky soil	–	30%	Remnants of dry mixed mesophytic forest	*Crypt mannii*
D. unisora					
Pualii	Granular rocky soil	–	<10%	Relic mesic forest with sec. succession of weeds	*Psid catt, Schin tereb*
S-Palawai	Granular rocky soil	–	20%		*Psid catt, Schin tereb*

consisted of 1000 or more individuals, growing in small and large groups on the north-western side of moderately steep slopes above the gulch bottom. The natural community at this site was *Diospyros hillebrandii* (Seem.) Fosb. mesic lowland forest. This area is owned by the Army Ecosystem Management Region and is fenced for protection from trampling by feral animals.

The 60 m^2 sample plot of *D. falcata* at Kahanahaiki was censused on three occassions (in March, April and June). In this population, the mature stage of sporophytes was more prevalent than stages of prothallia and sporelings (Figure 4). The number of individuals varied between months (Table 5), mainly because of the establishment and death of individuals during

Figure 3. Life stage structure of populations of *Diellia* taxa. *Census in April.

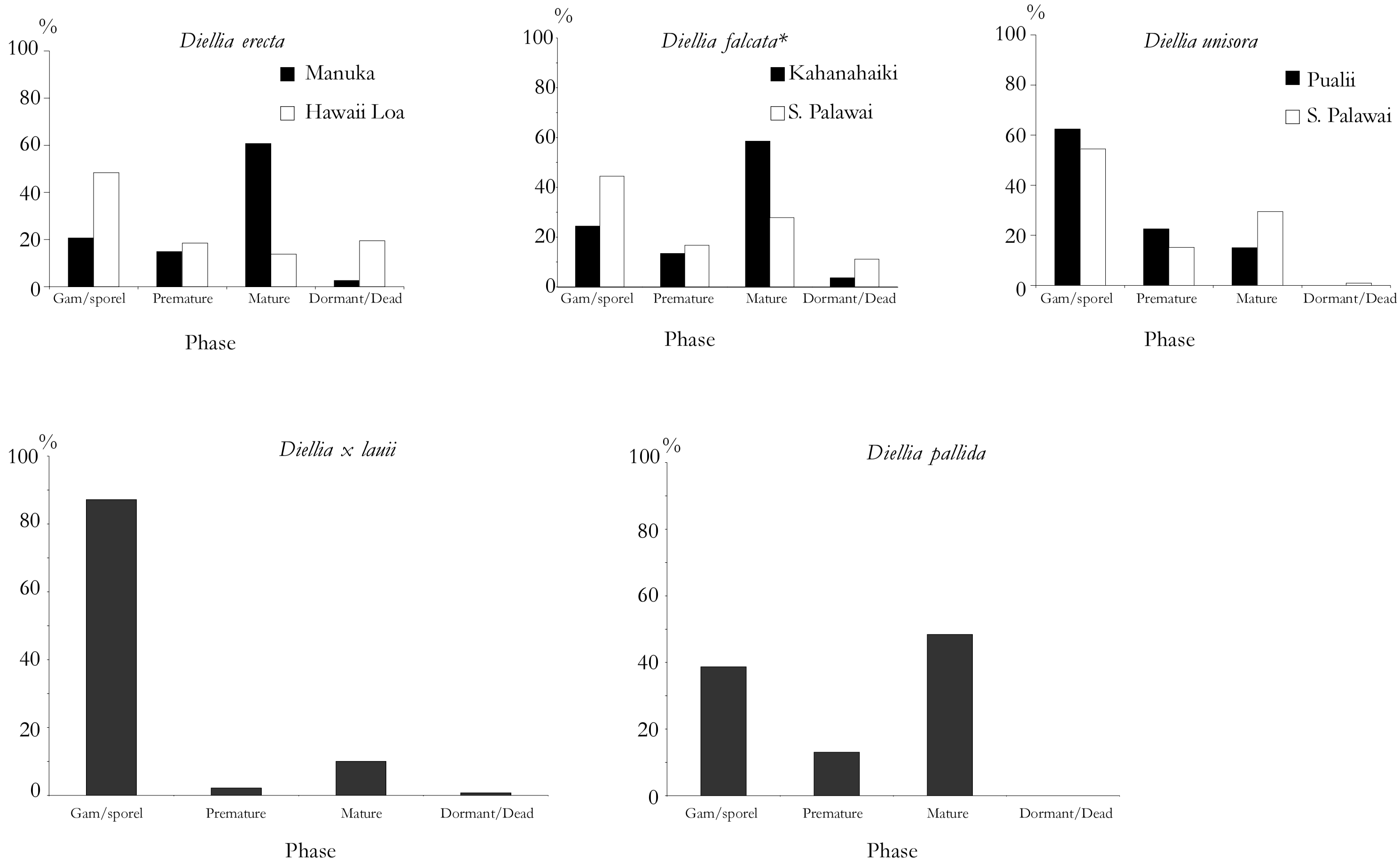

Table 4. Mean values (± SE) of measurements of the plants of *D.erecta*, *D. pallida*, *D. unisora* and *D. falcata* in different life stages.

Species	Site	Plant heigth (cm)	Frond length (cm)	Fronds per rhizome (no.)	Reproductive fronds per rhizome (no.)
Sporelings					
D. erecta	Hawaii Loa	0.5±0.1	0.7±0.1	2.7±0.2	–
D. pallida	Mahanaloa	0.4±0.1	0.5±0.1	2.0±0.3	–
D. unisora	Pualii	0.6±0.1	0.6±0.1	1.2±0.1	–
D. falcata M	Kahanahaiki	0.7±0.2	0.7±0.3	2.0±0.4	–
D. falcata A	Kahanahaiki	0.7±0.2	1.0±0.4	3.0±0.4	–
D. falcata J	Kahanahaiki	1.0±0.2	1.3±0.3	3.3±0.3	–
Premature					
D. erecta	Hawaii Loa	2.3±0.3	3.8±0.3	3.1±0.4	–
D. pallida	Mahanaloa	5.0±0.6	5.8±0.7	3.3±0.8	–
D. falcata	Pualii	3.4±0.7	4.2±0.9	4.0±0.4	–
D. falcata M	Khanakahaiki	5.5±0.5	7.2±0.8	3.8±0.5	–
D. falcata A	Khanakahaiki	4.7±0.5	7.0±0.8	3.2±0.4	–
D. falcata J	Kahanahaiki	5.1±0.9	7.8±0.9	3.0±0.3	–
Mature					
D. erecta	Hawaii Loa	6.0±0.7	9.2±0.8	3.4±0.5	1.8±0.3
D. pallida	Mahanaloa	14.0±1.2	19.6±2.8	2.1±0.2	1.4±0.2
D. unisora	Pualii	9.0±1.5	13.1±2.1	7.5±1.4	4.0±1.1
D. falcata M	Kahanahaiki	16.7±0.8	22.1±1.0	4.1±0.2	2.0±0.2
D. falcata A	Kahanahaiki	14.9±0.8	22.9±0.9	3.8±0.2	1.2±0.2
D. falcata J	Kahanahaiki	13.3±0.8	20.4±0.9	3.0±0.2	1.8±0.2

M– March
A – April
J– June

the prothallia and sporeling stages. The peak for gametophyte establishment and vegetative growth was in April. The formation and maturation of new reproductive fronds was also highest in April (Figure 5), whilst the total number of mature reproductive sporophytes was highest in June (52%). The total number of fronds (vegetative and reproductive) per individual differed significantly between March and June (ANOVA, $F = 5,234$, $p < 0.005$). The mean number of vegetative and reproductive fronds per rhizome was highest in March (Table 4).

During observations, the spread of an infestation of *D. falcata* by the greenhouse thrips *Heliothrips haemorrhoidalis* (Bouché) was discovered. Approximately 10% of the plants in the plot were damaged.

In the South-Palawai drainage, *D. falcata* occurred in small groups in the vicinity of *D. unisora* and *D.* x *lauii*. On the northern slope of the drainage, 18 individuals of different stages were observed (Figure 3). These ferns were growing in a mesic relic forest with a secondary succession of weeds, where *Psidium cattleianum* Sabine was dominant. Premature stages formed ca. 60% of the population.

%

Diellia falcata, Kahanahaiki

☐ March
■ April
■ June

Stage

Figure 4. Life stage structure of *D. falcata* at Kahanahaiki.

Diellia x *lauii*

In South-Palawai, *D.* x *lauii* was found in scattered groups over an area of ca. 1000 m^2 at an elevation of 670–730 m. In total, 140 plants in various life-stages were recorded in April (Figure 3). In this population, the prothallia and sporelings stages were more prevalent than premature and mature sporophytes. The prothallia and sporelings around premature and mature plants of the hybrid were counted as individuals of *D.* x *lauii*. At these stages, it is impossible to identify the species without damaging them, and they may actually belong to the parental species, hybrids or backcrossings. All mature individuals had new fronds with developing or already opened sori.

Individuals of the hybrid *D.* x *lauii* were very variable, with some of the intermediates similar to *D. falcata* and others to *D. unisora*. Spores of the hybrids appeared to be normal, except for a few individuals that showed irregular and poorly developed sori.

Diellia pallida

All previously known localities, except Koaie Canyon, were searched for *D. pallida*. Individuals were only found in Mahanaloa Valley in the Kokee Mountains, where two groups were found growing. In the eastern part of the population, only four separate individuals were found, whilst in the western part, 31 individuals in different life stages were recorded (Figure 2). Of these, 15 were mature with only four in the premature stage. For *D. pallida*, the mean number of vegetative and reproductive fronds per rhizome was the lowest (Table 4).

The whole area was heavily influenced by ungulates and *D. pallida* was only found in sites protected by stones or tree roots. Disturbed patches of forest with an open canopy were densely covered with introduced species.

Diellia unisora

D. unisora was studied at two sites, Pualii and

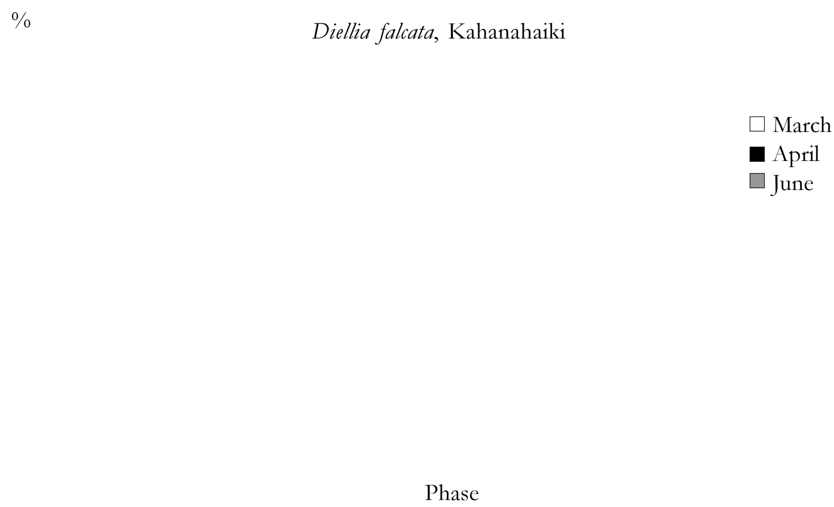

Figure 5. Phenology of *D. falcata* at Kahanahaiki during March, April and June. Proth – prothallium; veg – vegetative; dev– developing sori; deh– dehisced sori; dorm– dormant.

South-Palawai, in the Waianae Mts. (Table 2). At Pualii, *D. unisora* was growing in *Metrosideros-Acacia* lowland mesic relic forest with secondary succession of weeds. Dominant species found here were *Schinus terebinthifolius* and *Psidium cattleianum*.

This population held 183 plants growing in five groups (11, 20, 30, 40 and 82 individuals in each), with an approximate distance between groups of 60–100 m. The median-sized group of the population (30 individuals) proved to be hybrid *D.* x *lauii*. In March, two groups at the upper part of the population showed the prothallia and sporeling stages prevailing (Figure 3). Also, most of the mature plants had young generative leaves with developing or recently opened sori. The mean number of vegetative and reproductive fronds per rhizome was highest for *D. unisora* (Table 3). About 11% of the population were in the reproductive phase (Table 5).

In South-Palawai, *D. unisora* was only found in localized groups on very steep, rocky slopes in relic mesic forest with secondary succession of weeds. The dominant species here was *Psidium cattleianum*. In total, 112 plants in different life stages were counted (Figure 3). In April, 70% of this population were in the reproductive phase (Table 5).

Discussion

The populations of *Diellia* ferns are very localised and small, with plants usually growing in big or small clumps, or even solitary and scattered. Usually, *Diellia* ferns are very inconspicuous (except *D. falcata*) and their relative abundance can vary between years. In unfavourable years, or during long-lasting dry periods, the plants may not be apparent at all, and searching for these species may require more than one season to locate populations (Wood pers. comm.). At only four of 13 sites checked during this research were any plants found. The habitat at Puu Ka Pele on Kauai (*D. pallida*) seems to be irreversibly degraded, whilst the sites at Makaha on Kauai (*D. pallida*), Puu Kolekole on Molokai (*D. erecta*) and Honomalino on Hawaii (*D. erecta*) need repeated checking.

Diellia ferns seem to grow most vigorously in the shade, in areas of sparse ground cover and under a closed canopy. Occasional occurrences under shrubs or more open areas may be only

Table 5. Percentage of plants in different phenological phases at the time of observation of the populations of *Diellia.*

Taxa	Site	Time	Individuals (no.)	Veg (%)	Reprod (%)	Dormant/ dead (%)
D. erecta	H, Manuka	April	151	36	61	3
D. erecta	O, Hawaii Loa	June	212	68	13	19
D. falcata	O, S-Palawai	April	18	72	17	11
D. pallida	K, W-Mahanaloa	June	31	55	45	0
D. unisora	O, Pualii	March	93	89	11	0
D. unisora	O, S-Palawai	April	112	70	29	1
D. x lauii	O, S-Palawai	April	141	89	10	1
D. falcata	O, Kahanahaiki	March	128	47	48	5
D. falcata	O, Kahanahaiki	April	164	54	41	5
D. falcata	O, Kahanahaiki	June	140	37	52	11

temporary or due to the changes in the community. Furthermore, not all patches of suitable habitat are colonised.

According to Wagner (1952), the habitat of *Diellia* is transitory and depends to a certain degree on disturbance, which creates safe sites with bare soil for gametophyte establishement. However, all *Diellia* species have a short rhizome and very fragile stipes, which makes them particularly vulnerable to trampling, and during the present study, most of the sites visited were too heavily disturbed by feral ungulates. Most critical is that the single viable population of *D. pallida* at Mahanaloa, where prothallia, sporelings, premature sporophytes and mature individuals were found, only grows in places protected by stones or roots of the trees.

The occurrence of a natural spore bank of *Diellia* species and spore viability have not been studied. According to Dyer (1994), the regular turning of the upper layer of the soil may cause the depletion of a natural spore bank and prevent spontaneous re-establishment of a population. Considering that fern spore banks have been found in very different habitats at the study sites, experimental re-establishment of a population of *D. pallida* by natural soil spore bank could be possible at Makaha , where the habitat is overgrown with an introduced species (*Erigeron karvinskianus* DC).

The peculiarity of the pteridophytes is that the mature sporophyte, which is vascular, leafy and relatively large, is limited to establishment in a habitat that has proved to be suitable for the independent survival of its small thalloid nonvascular gametophyte. Environmental changes and periodic fluctuations in conditions must then be withstood through all following life cycle stages (Page 1979).

Water deficiency is the key limiting factor for pteridophytes in seasonally dry tropical areas, which determines their adaptations in relation to specific habitat use and seasonal periodicity of growth and dormancy (Kornaš 1985). As *Diellia* ferns grow in dry and mesic forests with occasional dry periods, they exhibit certain periodicity in their growth with alternate active and dormant periods. However, analyses of frond length and number of generative fronds over a three month period did not indicate any significant differences. It must then be assumed that *Diellia* ferns exhibit mainly continuous growth with only irregular dormant periods. Additional long-term studies could add more detailed information.

Observations made over the period of spore maturation and release indicate that most of the spores of the studied species are released during a peak period. For *D. falcata*, *D.* x *lauii* and *D. unisora* in Waianae Mts. on Oahu, this peak appears to be in April. As the growth of new fertile fronds, the development of sori on the fronds and the maturing of sporangia all take place gradually, the total period of spore dispersal is probably much longer, lasting for several months. Fronds from the last growing period had certain quantities of unopened sporangia together with older, dehisced sporangia. Unspread spores of *D. pallida*, collected from the fronds from the last growing period, were viable and germinated (Sugii 1999, pers. comm.).

The formation of new generations of ferns begins with the dispersal of spores to safe sites for germination and gametophyte establishment. Given the normal production of spores, it may be hypothesized that the occurrence of individual species of *Diellia* is limited only by the scarcity of safe sites rather than by spore dispersal.

The growth process from spore germination to establishment of prothallia and sporelings comprises two sensitive life stages. These stages are most vulnerable depending on microedaphic and microclimatic conditions (Peck et al. 1990), with mortality of individuals during these stages being the highest. Therefore, the proportion of individuals in the youngest and oldest life stages does not appear to adequately reflect the condition of the population. On the basis of life-stage structure analysis, the ratio of premature sporophytes to reproductively mature sporophytes appears to be one possible attribute for the assessment of the condition and status of populations of *Diellia* ferns in the short-term. The number of premature individuals, as an indicator of possible recruitment as reproductive individuals, appears to be a better indicator of the condition of the population than the most sensitive stages of prothallia and sporelings. Populations would seem to be in good condition where the number of premature individuals is equal to, or higher than, 2/3 of the number of mature individuals and sporelings (*D. erecta* in Hawaii Loa, *D. unisora* in South-Palawai). Populations where the number of premature individuals is significantly lower than the number of reproductive individuals may be experiencing population fluctuation or be disturbed by some other factor (*Diellia erecta* in Manuka, *Diellia falcata* in Kahanahaiki). In the case of a very small population combined with a low number of individuals in the premature stage, the population must be considered in critical condition (*Diellia pallida* in Mahanaloa). Further long-term demographic studies are required to check this hypothesis.

All the studied populations, except for *D. falcata* at Kahanahaiki and *D. erecta* at Manuka, had a higher proportion of plants in the gametophyte and sporeling stages than in more mature stages. The low proportion of these premature stages at Manuka may have been caused by a lengthy dry period and at Kahanahaiki by reduced shelter from a closed canopy. At Manuka, it was probable that in a lasting drought, the wilted fronds with very young sori would dry out and never reach the spore release phase. A consequent reduction in spore production, and thus establishment of new gametophytes and sporelings, may result in decreased recruitment in the population during the following years, allowing for fluctuations in population size.

For all *Diellia* species, there was a significant difference between the frond size of the plants at different life stages (Kruskal-Wallis, $H = 121.967$, $p < 0.001$). The number of fronds of *Diellia* ferns was not correlated with the life stage, and this is probably indicative of the soil and moisture conditions of the habitat. The significant difference between the number of fronds of *D. falcata* in March and June was probably caused by a dry period in May and June, which also increased the number of dormant and dead individuals.

Occasional reverting of mature plants to a vegetative stage (of only one or two short vegetative fronds) was observed at Kahanahaiki. This may have been as a result of ageing, or as a response to some unrecognised environmental stress in combination with a drought.

Though *Diellia* ferns have adequately adapted to tolerate drought, a peak in mortality for all stages possibly still occurs during the dry season. By comparing the species and populations at different sites on different islands, it was shown that there are seasonal variations in mortality depending on local differences in dry and wet periods. The periods of active growth, peak of spore release and germination timing are probably not only species specific, but also population specific. However, the limited period of observation made it difficult to evaluate the status of the different populations in relation to within-year climatic variation.

D. x *lauii* (*D. falcata* x *D. unisora*)
The actual distribution of these hybrids is not known, as observations from different sites on Pualii, South Palawai, inferred that these plants can represent many separate, independent parental hybridisations, rather than spreads from a single source. It is possible then, that the distribution of hybrids is wider than recorded in this study.

Hybrids are very variable, being intermediates between the parental species with mostly fertile fronds and normal spores. The normal appearance of the spores and the whole spectrum of intermediate forms suggests that the parent species and the intermediate forms are capable of interbreeding (Wagner et al. 1999). In hybrid swarms where one species predominates, the minor species often declines over time, whereas if both species contribute similarly to such a swarm, the integrity of both species may be lost. Thus, generations of hybridisation and backcrossing may erode the genetic integrity of a rare species (Levin et al. 1996).

Unfortunately, there is still insufficient information on the breeding systems, breeding barriers and hybridisation processes of *Diellia* species. For hybridisation to occur in the *Diellia*, there should be mixed populations of parental gametophytes, though such mixed populations of mature plants of different species were not found in this study. Hybrids and parental species did occur in a patchy pattern, but without direct contact between the parental species.

On the basis of current information, it is difficult to predict whether ongoing hybridisation, spreading of the hybrid, unstable hybrid formation or genetic assimilation of the rare parental species will prevail. Hybridisation of the rare and localized *D. unisora* with the locally common *D. falcata*, and possible growth of a hybrid population, may push *D. unisora* to extinction through genetic assimilation, while the process of natural hybridization may produce genotypes that establish new evolutionary lineages (Arnold & Hodges 1995). Further study is required to determine the actual distribution of hybrids and to monitor the status of the various species. Genetic studies of the populations, hybridisation experiments and an assessment of the fitness of hybrid classes and parental species could add a lot of relevant information.

Acknowledgements – I gratefully acknowledge the help of my supervisors Karin Bengtsson (Department of Conservation Biology, SLU) and Ken Wood (National Tropical Botanical Garden on Kauai) during this study. The research was funded by the Swedish Biodiversity Centre.

References

Anon. 1995. Recovery Plan for Waianae Plant Cluster (*D. falcata*, *D. unisora*). – U.S. Fish and Wildlife Service, Portland, Oregon: 38–43.

Anon. 1996. Draft Recovery Plan for the Multi-Island Plants (*Diellia erecta)* – U. S. Fish & Wildlife Service, Portland, Oregon: 30–33.

Anon. 1998a. IUCN Red List of Threatened Plants 1997. – IUCN The World Conservation Union: 5.

Anon. 1998b. Technical/Agency Draft Recovery Plan for Oahu Plants. 1998. – U.S. Fish and Wildlife Service, Portland, Oregon: 38–43.

Anon. 1999. U.S. Fish & Wildlife Service Species List.

Arnold, M. L. and Hodges, S. A. 1995. Are natural hybrids fit or unfit relative to their parents? – Trends in Ecology and Evolution Vol. 10, No 2: 67–71.

Brackenridge, W. D. 1854. United States Exploring Expedition. During the years 1838, 1840, 1841, 1842. Under the commend of Charles Wilkes – U. S. N. Vol. XVI. Botany, Cryptogamia. Filices including Lycopodiaceae and Hydropterides. By W. D. Brackenridge. With a Folio Atlas of Forty-six Plates. Philadelphia.

Christensen, C. 1925. Revised list of Hawaiian pteridophytes. – Bernice P. Bishop Museum Bulletin 25: 11–28.

Degener, O. and Greenwell A. B. 1950. Fl. Hawaiiensis, fam. 17d. *Aspleniaceae. Diellia erecta.*

Dyer, A. F. 1994. Natural soil spore banks – can they be used to retrieve lost ferns? – Biodiversity and Conservation 3: 160–175.

Farrar, D. R. 1976. Spore retension and release from overwintering fern fronds. – American Fern Journal Vol. 66, No 2: 49–52.

Fosberg, F. R. and Herbst, D. 1975. Rare and Endangered Species of Hawaiian Vascular Plants. – Allertonia 1(1).

Hillebrand, W. M. D. 1888. Flora of Hawaiian Islands. A description of their phanerogams and insular cryptogams. – London, New York, Heidelberg, pp. 619–624.

Kornaš, J. 1985. Adaptive strategies of African pteridophytes to extreme environments. – Proceedings of the Royal Society of Edinburgh 86B: 391–396.

Kramer, K. U. and Viane, R. 1990. *Aspleniaceae*. – In: Kubitzki, K. The Families and Genera of Vascular Plants. Vol. 1. Pteridophytes and Gymnosperms, pp. 52–57.

Levin, D. A., Francisco–Ortega, J. and Jansen, R. K. 1996. Hybridization and the Extinction of Rare Plant Species. – Conservation Biology 10(1): 10–16.

Menges, E. S. and Gordon, D. R. 1996. Three Levels of Monitoring Intensity for Rare Plant Species. – Natural Areas Journal 16: 227–237.

Page, C. N. 1979. Experimental Aspects of Fern Ecology. In: Dyer, A. F. The Experimental Biology of Ferns. Academic Press, London, pp. 550–589.

Peck, J. H., Peck, C. J. and Farrar, D. R. 1990. Influences of Life History Attributes on Formation of Local and Distant Fern Populations. – American Fern Journal 80(4): 126–142.

Smith, F. G. 1934. *Diellia* and its variations. – Bishop Museum Occasional Papers 10(16): 3–22.

van't Veer, R and den Nijs, C. M. 1994. Population structure of the rare, long–lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in The Netherlands. – Journal of Applied Ecology 31: 428–438.

Viane, L. L. R. and Reichstein, T. 1991. Notes about *Asplenium*: Some new names and combinations in *Asplenium* L. (*Aspleniaceae, Pteridophyta*). – Biol. Jb. Dodonaea 59: 157–165.

Wagner, W. H., Jr. 1951. The habitat of *Diellia.* – American Fern Journal 40: 21–32.

Wagner, W. H. Jr. 1951. A new species of *Diellia* from Oahu. – American Fern Journal 41: 9–13.

Wagner, W. H. Jr. 1952. The Fern Genus *Diellia.* Its Structure, Affinities and Taxonomy. – University of California Press.

Wagner, W. H Jr. 1953. An *Asplenium* protoype of the genus *Diellia.* – Bulletin of the Torrey Botanical Club, Vol. 80, No.1: 76 – 94.

Wagner, W. H. Jr. 1993. New species of Hawaiian pteridophytes. – Contr. Univ. Mich. Herb. 19: 66–68.

Wagner, W. H. and F. S. Wagner.1994. Revised checklist of Hawaiian Pteridophytes.

Wagner, W. H. Jr., Wagner, S. F. and Flynn, T. 1995. Taxonomic notes on the pteridophytes of Hawaii. – Contr. Univ. Michigan Herb. 20: 248.

Wagner, W. H. Jr., Wagner, F. S., Palmer, D. D. and R. W. Hobdy 1999. *Diellia* – Taxonomic notes on the pteridophytes of Hawaii. – Contr. Univ. Michigan Herb. 22: 168, 171.

Werth, C. R. and Cousens, M. I. 1990. Summary: The Contributions of Population Studies on ferns. – American Fern Journal 80(4): 183–190.

Appendix 1. Plant species commonly associated with *Diellia* taxa.

Site		Onini Gulch	Puu Kolekole	Honomalino	Manuka	Hawaii Loa	Kahanahaiki		S-Palawai		Mahanaloa	Makaha	Puu Ka Pele	Pualii
Diellia species		*D. erecta*						*D. f.*	*D.x l.*	*D. u.*	*D. pallida*			*D. u.*
1 *Acacia koa*	E									x		x	x	x
2 *Ageratina adenophora*	N	x	x					x	x	x				x
3 *Ageratina riparia*	N						x							x
4 *Aleurites moluccana*	Pol			x							x			
5 *Alphitonia ponderosa*	E		x	x								x		
6 *Alyxia oliviformis*	E						x	x	x	x	x			
7 *Antidesma p.* var. *platyphyllum*	E			x			x				x			
8 *Antidesma pulvinatum*	E			x										
9 *Bidens torta*	E								x	x				
10 *Broussaisia arguta*	E			x										
11 *Canthium odoratum*	I			x	x	x					x			
12 *Carex meniae*	E													x
13 *Carex meyenii*	I				x						x			
14 *Carex oahuensis*	E													x
15 *Carex wahuensis*	E										x			
16 *Cenchrus a.* ssp. *agrimonoides*	E						x							
17 *Chamaesyce multiformis*	E					x	x							
18 *Charpentiera elliptica*	E												x	
19 *Charpentiera tomentosa*	E						x							
20 *Clidemia hirta* var. *hirta*	N						x							
21 *Cocculus tribulus*	I				x									
22 *Coprosma foliosa*	E	x	x											
23 *Cordyline fruticosa*	Pol					x								
24 *Cryptocarya mannii*	E												x	
25 *Cyperus hillebrandii*	E													x
26 *Dianella sandwicensis*	I								x	x				
27 *Diospyros hillebrandii*	E						x				x			x
28 *Diospyros sandwicensis*	E			x	x						x			
29 *Dissochondrus biflorus*	E		x											
30 *Dodonea viscosa*	I	x	x								x	x		
31 *Dubautia linearis* ssp. *opposita*	E	x	x											
32 *Erigeron karvinskianus*	N											x		
33 *Fraxinus uhdei*	N	x	x											
34 *Hedyotis foggiana*	E										x			
35 *Hedyotis knudseni*	E										x			
36 *Hedyotis terminalis*	E						x							
37 *Hibiscus arnottianus*	E						x							
38 *Kalanchoe pinnata*	N										x	x	x	
39 *Lantana camara*	N												x	
40 *Lipochaeta rockii*	E		x											
41 *Luzula hawaiiensis*	E													x
42 *Melicope peduncularis*	E													x

Appendix 1. continued

Site		Onini Gulch	Puu Kolekole	Honomalino	Manuka	Hawaii Loa	Kahanahaiki		S-Palawai		Mahanaloa	Makaha	Puu Ka Pele	Pualii
Diellia species		*D. erecta*						*D. f.*	*D.* x *l.*	*D. u.*	*D. pallida*			*D. u.*
43 *Melinus minutiflora*	N	x	x											
44 *Metrosideros polymorpha*	E	x	x	x	x		x	x	x	x	x	x	x	x
45 *Morinda trimera*	E						x							
46 *Myrsine kauaiensis*	E												x	
47 *Myrsine lanaiensis*	E										x			
48 *Myrsine lessertiana*	E			x										
49 *Neraudia melastomifolia*	E													x
50 *Neraudia sericea*	E		x											
51 *Nestegis sandwicensis*	E	x		x	x		x				x			
52 *Ochrosia compta*	E	x	x											
53 *Oxalis corniculata*	N						x						x	
54 *Panicum nephelophilum*	E							x	x	x				
55 *Passiflora molissima*	N												x	
56 *Passiflora suberosa*	N							x	x	x				x
57 *Pisonia sandwicensis*	E			x	x	x								
58 *Pittosporum flocculosum*	E					x								
59 *Pleomele aurea*	E										x		x	
60 *Pouteria sandwicensis*	E		x				x							x
61 *Psidium cattleianum*	N					x	x	x	x	x				x
62 *Psychotria greenwelliae*	E												x	
63 *Psychotria hawaiiensis*	E				x									
64 *Psychotria mariniana*	E											x		
65 *Pteralyxia kauaiensis*	E										x			
66 *Ricinus communis*	N	x	x											
67 *Rubus argutus*	N											x		
68 *Rubus rosifolius*	N	x												
69 *Schinus terebinthifolius*	N			x		x	x	x	x	x				x
70 *Styphelia tameiameiae*	I	x	x									x		
71 *Tetraplasandra kavaiensis*	E											x		
72 *Wilkesia gymnoxiphium*	E											x		
73 *Xylosma hawaiiense*	E						x							
74 *Zanthoxylum dipetalum*	E											x		

Notes:
I – Indigenous
E – Endemic
Pol – Polynesian introduction
N– Naturalised

Appendix 2. Pteridophyte species commonly associated with the taxa of *Diellia*.

	Site		Onini Gulch	Puu Kolekole	Honomalino	Manuka	Hawaii Loa	Kahanahaiki		S-Palawai		Mahanaloa	Makaha	Puu Ka Pele	Pualii
	Diellia species		*D. erecta*						*D. f.*	*D.* x *l.*	*D. u.*	*D. pallida*			*D. u.*
1	*Adianthum hispidulum*	N			x							x		x	
2	*Asplenium kaulfussi*	E						x		x					
3	*Asplenium macraei*	E						x	x		x				x
4	*Asplenium nidus*	I			x		x								
5	*Blechnum occidentale*	N	x		x	x					x	x	x	x	x
6	*Cyrtomium falcatum*	N			x										
7	*Doodia kunthiana*	E	x	x					x	x	x	x	x	x	x
8	*Doryopteris decipiens*	E		x									x		
9	*Doryopteris decora*	E												x	
10	*Dryopteris fusco-atra*	E										x			
11	*Dryopteris hawaiiensis*	E												x	
12	*Dryopteris unidentata*	E			x			x							
13	*Lepisorus thunbergianus*	I								x					x
14	*Microlepia strigosa*	I	x	x			x	x				x		x	x
15	*Nephrolepis multiflora*	N		x	x	x									
16	*Odontosoria chinensis*	I								x					
17	*Phymatosorus scolopendria*	N					x								
18	*Psilotum nudum*	I			x				x	x				x	
19	*Pteridium decompositum*	E												x	
20	*Pteris cretica*	I												x	
21	*Pteris* x *hillebrandii*	E												x	
22	*Pteris irregularis*	E										x		x	
23	*Thelypteris dentata*	N										x			

Notes:
I – Indigenous
E – Endemic
N – Naturalised