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Genetic diversity, mating systems, and interpopulation gene flow in neotropical *Hemionitis palmata* L. (Adiantaceae)

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Molecular data from isozyme analyses were used to characterize levels and patterns of genetic diversity in populations of the neotropical cheilanthoid fern *Hemionitis palmata*. All populations exhibited lower levels of genetic diversity than most other fern species previously studied. Variability in fixation indices and estimated intragametophytic selfing rates suggest that the predominant mating system varies from outcrossing to moderate levels of selfing among populations. Populations were significantly genetically differentiated from each other and estimated levels of interpopulation gene flow were generally low (i.e. $Nm < 1.0$). The wide geographical distribution of *H. palmata* may be accounted for by the ability of founding individuals to inbreed. Such an ability, along with founder effects, may explain the observed high levels of genetic differentiation among populations.

Keywords: gene flow, genetic diversity, *Hemionitis*, mating systems.

Introduction

Among studies of vascular plants, considerable experimental and theoretical work has been conducted on the population genetics of angiosperms and gymnosperms (see Hamrick & Godt, 1990), but only recently have there been similar studies of pteridophytes (e.g. Haufler, 1987; Peck *et al.*, 1990; Soltis & Soltis, 1987a, 1990). Empirical studies of primarily north temperate, homosporous ferns have demonstrated that most species are either primarily outcrossing, with relatively high levels of genetic variability (Gastony & Gottlieb, 1985; Haufler, 1985; Soltis & Soltis, 1987a and references therein, 1990; Wolf *et al.*, 1988), or primarily selfing, with consequent lower levels of variability (McCauley *et al.*, 1985; Soltis & Soltis, 1986). These results are similar to those from studies of angiosperms (see Barrett & Eckert, 1990; Schemske & Lande, 1985) and generally support the theoretical model of Lande & Schemske (1985) which predicts a bimodal distribution of outcrossing rates among species as alternative, evolutionarily stable, reproductive modes. Evidence for mixed mating systems has been reported for only two species of homosporous ferns, *Blechnum spicant* (Soltis & Soltis, 1988) and *Dryopteris expansa* (Soltis & Soltis, 1987b), although it is not known if these represent equilibrium states.

In addition to their capacity for outcrossing and *inter*gametophytic selfing (i.e. the union of gametes from separate gametophytes, both derived from the same parent, as with selfing in angiosperms and gymnosperms), homosporous ferns are capable of *intra*gametophytic selfing, the result of the fusion of gametes derived from a single, bisexual gametophyte. Spores are the individual products of meiosis in homosporous ferns and germinate to produce free-living, multicellular gametophytes, each of which possesses the ability to become bisexual. Because both male and female gametes derived from such a gametophyte will be genetically identical at every locus (barring mutation) (e.g. Wilkie, 1963), the occurrence of intragametophytic self-fertilization will have a profound impact on the patterns and levels of genetic variability within and among conspecific populations. For example, high levels of intragametophytic selfing seem to account for the large inbreeding coefficients (F_{IS}) estimated in species of *Botrychium*; *B. dissectum* has a mean F_{IS} of 0.951 (McCauley *et al.*, 1985) and *B. virginianum* has a mean F_{IS} of 0.957 (Soltis & Soltis, 1986). The ability or inability to undergo intragametophytic selfing may also affect a variety of life-history attributes of a species (Crist & Farrar, 1983; Peck *et al.* 1990), including colonization ability and ecological amplitude. The ability to self may also affect the genetic

divergence of populations, modes of speciation, and the evolutionary potential of a phylogenetic lineage (e.g. Clegg, 1990). Although all homosporous fern gametophytes theoretically have the capacity for bisexuality and intragametophytic selfing, in many species effective or actual unisexuality and outcrossing are promoted by a variety of mechanisms (Klekowski, 1969; Näf, 1979; Peck *et al.*, 1990; Schneller *et al.*, 1990).

Recent studies of a variety of organisms have provided direct or indirect estimates of gene flow within and among natural populations (see Hamrick, 1987; Slatkin, 1987; and references therein). Several studies have demonstrated relationships between gene flow and various factors including dispersal ability (e.g. Waples, 1987), pollinator activity (e.g. Handel, 1983; Schaal, 1980), and mating systems (Hamrick, 1987 and references therein). Specific predictions can be made about the probability of genetic divergence of populations over time, given various levels of gene flow, when simplifying assumptions are made in theoretical models. These models typically assume random mating and no mutation or natural selection (Slatkin, 1985; Wright, 1931, 1943, 1951); however, Slatkin & Barton (1989) recently demonstrated that even these assumptions can be relaxed. Wright (1931) demonstrated that, in the absence of natural selection, two populations are expected to diverge genetically as a result of genetic drift, if levels of gene flow are sufficiently low. Specifically, if a proportion m of a population of effective size N is replaced each generation by migrants from a source population, the two populations will diverge genetically if $Nm < 1.0$. Values of Nm greater than 1.0 will tend to maintain genetic homogeneity between populations at selectively neutral loci.

Studies of interpopulational gene flow have been conducted on only a few species of homosporous ferns. These studies have estimated relatively high levels of gene flow among populations of outcrossing species and lower levels among those of inbreeders (Soltis *et al.*, 1988; Wolf *et al.*, 1991). Of the two species with mixed mating systems, *Blechum spicant* showed relatively high levels of gene flow ($Nm = 2.95$), whereas *Dryopteris expansa* exhibited much lower levels ($Nm = 0.83$; Soltis *et al.*, 1988). Much more empirical evidence must be obtained on pteridophyte populations to test the generality of these early findings, incorporating data from a greater taxonomic, ecological, and geographical array of species.

The present study employed enzyme electrophoretic surveys of natural populations of the homosporous fern *Hemionitis palmata* L. (Adiantaceae) to assay levels of genetic diversity. Predominant mating systems operating within populations were inferred and levels of interpopulational gene flow were estimated.

Hemionitis palmata occurs from central Mexico to southern South America and variously in the West Indies; populations occur in a variety of mesic to seasonally dry habitats, ranging from rain forests and riparian communities to open, rocky hillsides.

Materials and methods

Whole plants were collected from sampled populations from Mexico, Jamaica, and Costa Rica and returned to the University of Kansas greenhouse for cultivation. Leaf material was collected from these living specimens for genetic analyses employing starch-gel electrophoresis. Electrophoretic conditions and locality information (see Table 1) are described in Ranker *et al.* (1989).

Several measures were calculated for each population to estimate overall levels of genetic diversity, including P, proportion of loci surveyed that were polymorphic, A, average number of alleles per locus (across all loci), and H_o and H_e, average observed and expected heterozygosities (across all loci). Genetic differentiation of conspecific populations was estimated with Wright's standardized variance in allele frequencies, F_{ST} (Nei, 1977; Wright, 1965, 1978) and Nei's unbiased genetic identity, I (Nei, 1978), as calculated by BIOSYS-1 (Release 1.7; Swofford & Selander, 1989). Because F_{ST}, as calculated by BIOSYS-1, is a weighted average for all alleles at a locus, it is equivalent to G_{ST}, the gene diversity among populations (Nei, 1973, 1977; Swofford & Selander, 1989; Wright, 1978). The null hypothesis, $F_{ST} = 0$, was tested using the chi-square test of Workman & Niswander (1970):

$$\chi^2 = 2N_t F_{ST}(k-1); \text{d.f.} = (k-1)(s-1);$$

where N_t is the total sample size at a locus, k is the number of alleles, and s is the number of populations.

Levels of inbreeding were estimated for each polymorphic locus, within populations, by the fixation index

$$F = 1 - [H_o/H_e],$$

and summarized as weighted averages across populations by F_{IS} (see Weir & Cockerham, 1984). If F is primarily determined by mating behaviour, it can be equated with an inbreeding coefficient (Wright, 1969). The significance of F at each polymorphic locus in each population was calculated using a chi-square test of H_o versus H_e. The null hypothesis, $F_{IS} = 0$, was tested with the chi-square test of Li & Horvitz (1953):

$$\chi^2 = F_{IS}^2 N_t(k-1); \text{d.f.} = [k(k-1)]/2$$

Table 1 Allele frequencies at polymorphic loci

Locus	Allele	Population*								
		SANG	*J845*	*J849*	*J852*	*J853*	*J861*	*J862*	*LS*	*PARG*
Pgi-2	6	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	
	9									1.00
	N	29	50	39	23	26	17	18	81	49
Hk	8		0.33	0.95	0.96	0.94	1.00	0.28	0.02	1.00
	12	1.00	0.67	0.05	0.04	0.06		0.72	0.98	
	N	18	24	21	23	26	17	18	81	49
Idh	13	0.86	1.00	0.23	0.20	0.40	1.00	1.00	1.00	1.00
	17	0.14		0.77	0.80	0.60				
	N	29	50	39	23	26	17	18	81	49
Lap	4	0.96	0.98	0.58	0.50	0.23	0.97	1.00		
	11	0.04	0.02	0.42	0.50	0.77	0.03		1.00	0.14
	15									0.86
	N	27	50	20	23	26	17	18	5	7

*Localities of populations: *SANG* — Oaxaca, Mexico; *J845* thru *J862* — Jamaica; *PARG* & *LS* — Costa Rica (see Ranker *et al.*, 1989).
N = sample size/population/locus.

with N_t and k defined as above. Estimates of intragametophytic selfing rates were obtained with the maximum likelihood, bootstrap-*t* algorithm and computer program of Holsinger (1987), using $t = 100$ resamplings for each population.

Values of *Nm* were calculated as estimates of interpopulational gene flow by the relationship:

$$F_{ST} \approx 1/[4Nm + 1]$$

(Dobzhansky & Wright, 1941; Wright, 1931, 1943, 1951), which assumes an island model of population structure. Slatkin & Barton (1989) recently demonstrated, however, that the relationship provides reasonable estimates of *Nm* under a wide variety of population structures, in addition to the island model. They also demonstrated that by using G_{ST} as an approximation of F_{ST}, as was done in the present study, reliable estimates of *Nm* could be obtained (Slatkin & Barton, 1989), similar to those derived from the private-allele method of Slatkin (1985). In addition, they suggested that employing the F_{ST} method might actually be preferred over the private-allele method for electrophoretic data, given the intrinsic limitations of these data and potential problems due to sampling and gel-scoring errors involving the detection of rare, private alleles.

Results

Electrophoretic results were obtained from nine enzyme systems and for 10 putative loci: aspartate aminotransferase (*Aat*), aldolase (*Ald-2*), hexokinase (*Hk*), isocitrate dehydrogenase (*Idh*), leucine aminopeptidase (*Lap*), phosphoglucomutase (*Pgm-2*), phosphoglucose isomerase (*Pgi-2*), shikimate dehydrogenase (*Skdh*) and triosephosphate isomerase (*Tpi-1* and *Tpi-2*). Allele frequencies are listed for all populations at the four polymorphic loci, *Pgi-2, Idh, Hk* and *Lap* (Table 1). All other loci were monomorphic within and among populations.

Population genetic diversity

Relative to other fern species, populations of *H. palmata* exhibited low levels of genetic diversity (Table 2), similar to the inbreeder *Botrychium virginianum* (Soltis & Soltis, 1986).

Genetic differentiation of populations

The sampled populations were generally highly divergent, with highly significant F_{ST} values at all four polymorphic loci (Table 3). Of the 36 possible comparisons between pairs of *H. palmata* populations, all but two produced highly significant F_{ST} values (Table 4). Jamaican populations *J845* and *J862* were genetically identical, as was the pair *J849* and *J852*, with F_{ST} values of 0.000.

Pair-wise comparisons of populations produced genetic identities ranging from 0.71 to 1.00, with a mean of 0.87 (Tables 4 and 5). The population from southern Costa Rica (*PARG*) was much more divergent from all other populations than were any of the

Table 2 Population-level genetic diversity statistics. P = Proportion of loci examined that were polymorphic at the 1% level; A = number of alleles per locus (averaged across all loci); H_o = average observed heterozygosity (across all loci); H_e = average expected heterozygosity under Hardy–Weinberg equilibrium (across all loci); n = sample size; means are given because data were not obtained from all individuals for all loci. Standard error in parentheses

Population*	Mean n per locus	P	A	H_o	H_e
SANG	25.4 (2.0)	0.20	1.20 (0.13)	0.020 (0.020)	0.032 (0.025)
J845	47.4 (2.6)	0.20	1.20 (0.13)	0.062 (0.058)	0.049 (0.045)
J849	33.2 (3.0)	0.30	1.30 (0.15)	0.056 (0.039)	0.095 (0.058)
J852	20.8 (2.2)	0.30	1.30 (0.15)	0.070 (0.042)	0.092 (0.057)
J853	26.0 (0)	0.30	1.30 (0.15)	0.077 (0.043)	0.096 (0.057)
J861	17.0 (0)	0.10	1.10 (0.10)	0.006 (0.006)	0.006 (0.006)
J862	18.0 (0)	0.10	1.10 (0.10)	0.022 (0.022)	0.041 (0.041)
PARG	40.6 (5.6)	0.10	1.10 (0.10)	0.000 (0.000)	0.026 (0.026)
LS	65.8 (10.1)	0.10	1.10 (0.10)	0.000 (0.000)	0.005 (0.005)
Mean		0.19	1.19	0.035	0.049
Population-level means for 11 species of outcrossing ferns†					
		0.36	1.67	—§	0.113
Population-level for inbreeding *Botrychium virginianum*‡					
		0.22	1.25	—§	0.035

Abbreviations as in Table 1.
†Averaged from values reported in Gastony & Gottlieb (1985), Haufler (1985), Soltis & Soltis (1987c), Soltis *et al.* (1990), and Wolf *et al.* (1988).
‡From Soltis & Soltis (1986).
§Not available for all species.

Table 3 F_{ST} and Nm at polymorphic loci

Locus	F_{ST}	N_m
Pgi-2	0.998***	0.001
Hk	0.723***	0.096
Idh	0.593***	0.172
Lap	0.642***	0.139
Mean	0.698***	0.102

***$P < 0.001$.

other populations from each other (Tables 4 and 5). This was true even when *PARG* was compared to *LS*, the northern Costa Rican population. *PARG* was as equally divergent from *LS* ($I = 0.73$) as it was from the Mexican population *SANG* ($I = 0.71$), and slightly more divergent from *LS* than it was from the Jamaican populations (mean $I = 0.78$). Concordantly, *LS* was similar to populations from Mexico ($I = 0.90$) and Jamaica (mean $I = 0.85$) more so than it was to *PARG*. The low genetic identities between *PARG* and other populations were primarily due to the fixation of a unique allele in this population at *Pgi-2* and the high frequency (0.86) of another unique allele at *Lap*.

Estimates of inbreeding

Values of F and their degrees of statistical significance varied among loci and populations (Table 6). None of the fixation indices calculated for populations *J845*, *J853*, *J861*, and *J862*, were statistically different from zero.

Intragametophytic selfing

Estimated rates of intragametophytic selfing varied among populations (Table 7), ranging from 0.0000 to 0.5242. Only two of the selfing estimates, *J849* (0.4181) and *J853* (0.1760), had 95 per cent confidence intervals that did not include zero; hence, it is only in those two populations that significant levels of selfing can be hypothesized to have occurred. However, because the lower boundary of the selfing-rate confidence interval for population *J853* was very near zero (i.e. 0.0026), and none of the per locus fixation indices for that population were significantly different from zero (Table 6), selfing may not have occurred to a significant degree in that population. Due to the total absence of heterozygotes in populations from Costa Rica (*PARG* and *LS*), it was not possible to calculate selfing rates with the algorithm employed.

Table 4 Genetic differentiation of *H. palmata* populations and estimates of gene flow. Above diagonal: pairwise F_{ST} values (top) and Nei's genetic identities (bottom). Below diagonal: estimates of *Nm* 'nd' indicates cases where populations were not differentiated (i.e $F_{ST}=0$; $I=1.00$), thus calculations of *Nm* were not possible using F_{ST}

	SANG	*J845*	*J849*	*J852*	*J853*	*J861*	*J862*	*LS*	*PARG*
SANG	—	0.133***	0.528***	0.554***	0.555***	0.722***	0.109***	0.720***	0.829***
		0.99	0.85	0.83	0.83	0.90	0.99	0.91	0.71
J845	1.63	—	0.438***	0.470***	0.467***	0.442***	0.000	0.659***	0.752***
			0.88	0.87	0.86	0.96	1.00	0.89	0.76
J849	0.22	0.32	—	0.000	0.064**	0.420***	0.468***	0.639***	0.641***
				1.00	0.99	0.92	0.87	0.81	0.77
J852	0.20	0.28	nd	—	0.049**	0.465***	0.499***	0.645***	0.651***
					0.99	0.91	0.86	0.82	0.77
J853	0.20	0.29	3.66	4.85	—	0.463***	0.497***	0.551***	0.613***
						0.91	0.85	0.87	0.80
J861	0.10	0.32	0.35	0.29	0.29	—	0.519***	0.939***	0.848***
							0.95	0.81	0.81
J862	2.04	nd	0.28	0.25	0.25	0.23	—	0.695***	0.779***
								0.89	0.75
LS	0.10	0.13	0.14	0.14	0.20	0.02	0.11	—	0.896***
									0.73
PARG	0.05	0.08	0.14	0.13	0.16	0.04	0.07	0.03	—

**$P<0.01$; ***$P<0.001$.

Interpopulation gene flow

All per-locus estimates of *Nm* across all populations were well below 1.00 with a mean of 0.102 (Table 3). The generally low values across all polymorphic loci were consistent with the significant heterogeneities observed at those loci. Estimates of *Nm* between pairs of populations, however, revealed some variability (Table 4). The Mexican population, *SANG*, was nearly genetically identical to the Jamaican populations *J845* and *J862* (pairwise $I=0.99$ in both cases), and estimates of *Nm* were both above 1.00 (1.63 and 2.04, respectively). Similarly, gene flow between the latter two populations was effectively infinite due to complete genetic identity (i.e. $I=1.00$) at the loci examined. Pairwise estimates of *Nm* among *J849, J852* and *J853* were all greater than 1.00 or, as above, effectively infinite due to complete genetic identity between *J849* and *J852*. (Note that when $F_{ST}=0.0$, an exact value for *Nm* cannot be estimated because of 0.0 in the denominator of the expression relating F_{ST} to *Nm*.)

Discussion

Population genetic diversity and mating systems

Variance in both intragametophytic selfing estimates (Table 7) and fixation indices (Table 6) among populations of *H. palmata* suggest that this tropical species has a mixed mating system similar to those reported for the north temperate taxa, *Blechnum spicant* (Soltis & Soltis, 1988) and *Dryopteris expansa* (Soltis & Soltis, 1987b). Although *H. palmata* is often found in seemingly stable, climax communities (Stoltze, 1981), it also invades disturbed sites such as river banks, road cuts, and banana or coffee plantations (T. A. Ranker personal observations; Tryon & Tryon, 1982). The apparent variability in mating system of this species may both reflect and allow its wide ecological amplitude and its great geographical range from central Mexico and the Caribbean to southern South America.

Variability in mating system among populations could be influenced by a variety of mechanisms affecting sexual expression in gametophytic populations. These include, but are not limited to, sexual ontogeny (Klekowski, 1969; Lloyd, 1974) and the action of male-inducing pheromones called antheridiogens (Haufler & Ranker, 1985; Näf, 1979; Schneller *et al.*, 1990; Scott & Hickok; 1987). Antheridiogens are produced by maturing gametophytes of some species and released into the surrounding substrate. Newly germinating gametophytes exposed to an antheridiogen-enriched substrate will become male only, whereas the more mature gametophytes become female, thus promoting intergametophytic crossing. Scott & Hickok (1987) discovered variability in antheridiogen sensitivity in different natural strains of *Ceratopteris richardii*, as did Kirkpatrick (1988) among individuals within populations of *Gymnocarpium dryopteris* subsp. *disjunctum*, which suggests that such variability may

Table 5 Genetic identities between conspecific populations. Mean pairwise values are given for *H. palmata* populations for comparisons involving more than two populations (ranges in parentheses)

Populations compared	*I*	Source
All populations	0.87 (0.71,1.00)	
All but *PARG*	0.90 (0.81,1.00)	
Jamaican populations	0.92 (0.85,1.00)	
Costa Rican populations	0.73	
Mexico vs. Jamaica	0.90 (0.83,0.99)	
Jamaica vs.		
LS, Costa Rica	0.85 (0.81,0.89)	
PARG, Costa Rica	0.78 (0.75, 0.81)	
Mexico vs.		
LS, Costa Rica	0.90	
PARG, Costa Rica	0.71	
Blechnum spicant	0.996	P. Soltis & D. Soltis (1988)
Bommeria elegans	0.790	Ranker (1987)
Bommeria hispida	0.879	Haufler (1985)
Cheilanthes subcordata	0.900	Ranker (1987)
Cystopteris bulbifera	0.826	Haufler *et al.* (1990)
Cystopteris protrusa	0.834	Haufler *et al.* (1990)
Pellaea andromedifolia	0.943	Gastony & Gottlieb (1985)
Polystichum munitum	0.997	Soltis *et al.* (1990)
P. acrostichoides	0.998	Soltis *et al.* (1990)
P. dudleyi	0.969	Soltis *et al.* (1990)
P. imbricans	0.974	Soltis *et al.* (1990)
P. lemmonii	0.989	Soltis *et al.* (1990)
P. lonchitis	0.966	Soltis *et al.* (1990)
Pteridium aquilinum		Wolf *et al.* (1991)
British populations	0.995	
Majorca vs. Britain	0.989	
N. America vs. Europe	0.681	

Table 6 Fixation indices (F) at individual polymorphic loci and values across populations within species (F_{IS}). Blanks indicate monomorphic loci

Locus	*SANG*	*J845*	*J849*	*J852*	*J853*	*J861*	*J862*	*LS*	*PARG*	F_{IS}
Hk	—	−0.312	1.000***	−0.045	−0.061	—	0.446	1.000***	—	0.143*
Idh	0.169	—	0.422*	−0.243	0.281	—	—	—	—	0.179***
Lap	1.000*	−0.020	0.284	0.565**	0.133	0.016	—	—	1.000**	0.445***

*$P < 0.05$; ***$P < 0.001$.

not be uncommon in fern species. Schneller *et al.* (1990) have also presented preliminary evidence which demonstrates that individuals and populations of *H. palmata* differ in their sensitivity to antheridiogen.

Geographically widespread plant species typically show the highest levels of genetic variability (Hamrick & Godt, 1990; Karron, 1987). The extremely low levels of genetic variability observed within populations of the widespread species *H. palmata*, however, are similar to those of the highly inbred species of *Botrychium* (McCauley, *et al.*, 1985; Soltis & Soltis, 1986; Table 2). Features of the mating system of *H. palmata* may increase its ability to colonize new habitats, and, therefore, be important in determining genetic diversity within and among populations. Recurring colonization events, spatially and temporally, would produce frequent genetic bottlenecks and could account for the extremely low levels of genetic

Table 7 Estimates of intragametophytic selfing

Population	Selfing rate	95% confidence interval	Loci employed
*SANG**	0.1526	(0.0000,0.3663)	*Idh*
J845	0.0000	(0.0000,0.0649)	*Hk, Lap*
J849	0.4181	(0.1035,0.6890)	*Hk, Idh, Lap*
*J852**	0.0000	(0.0000,0.0555)	*Hk, Idh*
J853	0.1760	(0.0026,0.2992)	*Hk, Idh, Lap*
J861	0.0000	(0.0000,0.0101)	*Lap*
J862	0.5242	(0.0000,0.6666)	*Hk*

*Values represent estimates calculated after removing information from *Lap* which had statistically significant fixation indices in the two populations noted; inclusion of *Lap* caused significant departures from parameter estimates based on *G* goodness-of-fit tests (see Holsinger, 1987; Soltis *et al.*, 1988).

variation in both inbreeding and outcrossing populations of this species.

Colonization history and gene flow among Jamaican populations

A detailed analysis of the distribution of allele frequencies among Jamaican populations (Table 1) revealed spatial patterns that may reflect the colonization history of this species both onto Jamaica and among sites within Jamaica. The populations fall into two distinct groups of three each, based on allele frequencies at *Lap* and *Idh*, which suggests that the members of each trio share a more recent common ancestor than do the two trios (Table 1). The three populations from St Andrew Parish (*J849, J852*, and *J853*) all had high frequencies of Idh^{17} and Lap^{11} (superscripts refer to allelic designations), whereas the remaining three populations from Portland Parish to the north and Clarendon Parish to the west were fixed, or nearly so, for Idh^{13} and Lap^{4}. The high genetic identities between the Mexican population of *H. palmata* (*SANG*) and two Jamaican populations from the latter trio (*J845* and *J862*; $I = 0.99$ for both; Table 4) may indicate a relatively recent, long-distance dispersal event from one area to the other. The distributions of allele frequencies at *Idh* and *Lap* imply that the ancestral populations of each trio resulted from separate colonization events. This could have occurred via two distinct colonizations from mainland sources or, alternatively, via one colonization onto Jamaica giving rise to a single founding population with subsequent dispersal producing a second genetically distinct population as a result of a sampling or founder effect. Under the latter scenario, additional populations would have been established from each distinct population via either recent spore dispersal and colonization or by more ancient dispersal followed by continued migration between populations. Either situation would prevent genetic divergence of populations within trios, as observed at *Idh* and *Lap*.

Evidence from a third polymorphic locus (*Hk*; Table 1) supports a close genetic relationship among the three populations from St Andrew Parish, with high frequencies of Hk^{8}, and between two (*J845* and *J862*) of the other three populations, with high frequencies of Hk^{12}. The third population from the latter trio (*J861*) was fixed for Hk^{8}, which could be accounted for by dispersal from *J845* or *J862* (or a different, but genetically similar, population) with a loss of Hk^{12} via a founder effect. Founder effects may also explain the observed genetic differentiation of the two populations sampled from Costa Rica (Tables 1 and 5).

In conclusion, the data support the hypothesis that mating behaviour and founder effects appear to be the primary factors controlling levels and patterns of genetic diversity within and among populations, as well as the colonization and migration ability of *H. palmata*.

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