Effects of Life History Traits on Genetic Diversity in Plant Species

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SUMMARY

Seven two-trait combinations (e.g. breeding system and seed dispersal mechanism) of five life history characteristics were used to analyse interspecific variation in the level and distribution of allozyme genetic diversity in seed plants. Highly significant differences were seen among categories for all seven comparisons. Life form and breeding system had highly significant influences on genetic diversity and its distribution. Regardless of other traits, outcrossing species tended to be more genetically diverse and had less genetic differentiation among their populations. Similarly, woody plants have less among population differentiation and somewhat more genetic diversity than non-woody species with similar life history traits. An analysis of twelve plant families indicated that species within families with predominately outcrossing, woody species had more genetic diversity and less interpopulation differentiation than species within families with predominately herbaceous species.

1. INTRODUCTION

The availability of biochemical and molecular techniques to identify single-gene markers has made it possible to estimate genetic diversity for a wide array of organisms. In particular, the use of electrophoretic techniques to estimate genetic diversity at allozyme loci has produced a rich source of comparative data on the genetic diversity contained within plant and animal species. Currently more than 2200 studies have reported allozyme variation for seed plants. Allozyme loci are particularly valuable for comparative population genetic studies as they are fairly numerous and are codominant. Moreover, the same enzyme systems can usually be resolved in different plant taxa.

Within ten years of the first plant allozyme studies, plant population geneticists began to summarize the data available for seed plants to determine whether generalizations could be made concerning genetic diversity and its distribution. These early reviews revealed that plant species with different breeding systems, seed dispersal mechanisms, geographic ranges and life forms tended to maintain different mean levels of genetic diversity within their populations (Gottlieb 1977; Hamrick 1978; Brown 1979; Hamrick *et al.* 1979). Subsequent reviews compared levels of genetic diversity among populations within species and among related species. Interspecific comparisons demonstrated that genetic distance statistics were generally predictive of phylogenetic relationships. For example, progenitor-derived species pairs tended to be more genetically distinct than populations within species but less genetically distinct than well-defined congeners (Gottlieb 1977; Crawford 1983). Hamrick (1983) and Loveless & Hamrick (1984) used several life history and ecological traits to determine whether interpopulation genetic heterogeneity was related to the species' characteristics. They found that life form, geographic range, breeding system and taxonomic status had significant effects on the partitioning of genetic diversity within and among plant populations.

The most comprehensive review of plant allozyme diversity is that of Hamrick & Godt (1989). This review was the first to simultaneously calculate genetic diversity parameters within *and* among populations. Parameters were also introduced to describe genetic diversity within species (typically only within-population parameters had been reported). These analyses indicated that significant differences in genetic diversity existed between species with different life history traits. An additional observation was that the majority ($\approx 75\%$) of the variation in genetic diversity among species was not explained by the eight life history traits. However, these traits explained nearly 50% of the interspecific variation in among-population genetic diversity.

One shortcoming of the previous reviews was that comparisons between species categorized for combinations of several life history traits were precluded by the limited number of entries in the database. For example, it was not possible to determine directly whether outcrossing species with large geographic ranges had more genetic diversity than selfing, endemic species.

Since our last review (prepared in 1988) the number of plant allozyme studies has increased by approximately 250 per year. The number of studies in our database now permits analyses of two-trait combinations of the life history traits. In this paper we examine genetic diversity in seven two-trait combi-

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nations that earlier analyses indicated are most likely to influence genetic diversity and its distribution. Among groups, we highlight traits that are associated with extremes of genetic variation and its distribution. By examining relationships between two life history traits and genetic diversity and its distribution, we hoped to identify significant biological patterns. The current size of our database also allowed us to compare genetic diversity parameters for several plant families.

2. METHODS

The data utilized in this review are an updated (to autumn 1992) version of the data used by Hamrick & Godt (1989). Only those studies with genetic interpretations of electrophoretic banding patterns were included in the analyses. For each paper and species (= an entry) we extracted or calculated three parameters used to measure genetic diversity within species and among the species' populations. To be included, studies were required to report data from polymorphic and monomorphic loci or report data of polymorphic loci from at least two populations. Deficiencies in the data for a relatively high proportion of the papers precluded the calculation of all genetic diversity parameters from many studies. Taxa that were the focus of more than one study (e.g. *Pinus sylvestris*) are represented more than once in the data. We chose this approach rather than calculating a mean value for each species represented by multiple entries because different entries often contain unique information. For example, different entries often represent population samples from different sections of the species' range and/or have utilized different loci. Due to the overall size of the database the redundancy caused by including multiple entries per species has little effect on the mean values for any group. There were 1491 entries considered for this review; on average 735 entries supplied useful data.

(*a*) *Genetic diversity parameters*

Three genetic diversity parameters were calculated: the percentage of loci polymorphic within the species (P_S), genetic diversity within species (H_{es} = Hardy-Weinberg expected heterozygosity; Weir 1990), and the proportion of total genetic diversity residing among populations (G_{ST}). The proportion of polymorphic loci was calculated by dividing the number of loci polymorphic within the species (i.e. entry) as a whole by the total number of loci analysed. Genetic diversity was calculated for each locus (including monomorphic and polymorphic loci) by:

$$H_{es} = 1-\Sigma\bar{p}_i^2,$$

where $\bar{p}_i$ is the frequency of the i th allele pooled across all populations analysed for the species. Mean genetic diversity at the species level was obtained by averaging H_{es} over all loci. Variation among populations was estimated with Nei's genetic diversity statistics (Nei 1973). Total genetic diversity for the species (H_T) and mean diversity within populations ($\bar{H}_S$) were estimated for each polymorphic locus using the equation given above. The proportion of genetic diversity residing among populations (G_{ST}) was determined for each polymorphic locus by:

$$G_{ST} = (H_T - \bar{H}_S)/H_T$$

Mean H_T, $\bar{H}_S$ and G_{ST} values were calculated by averaging values obtained for each polymorphic locus.

We have chosen to report genetic diversity statistics calculated for the species rather than the more commonly used within-population values. Our rationale is that the measurement of genetic diversity within species is more biologically meaningful than mean population genetic diversity. Moreover, as species with the same overall genetic variation may have quite different mean within-population genetic diversities (depending on the distribution of genetic diversity among populations), we conclude that species values of P_s and H_{es} coupled with estimates of G_{ST} provide the most succinct and informative descriptors of genetic diversity.

(*b*) *Combinations of life-history traits*

In our earlier review (Hamrick & Godt 1989) we classified each species using categorical variables for each of eight life history traits: taxonomic status, life form, geographic range, regional distribution, breeding system, seed dispersal, mode of reproduction and successional status. The classification of each species for these eight traits was determined from descriptions in the original papers or from floras. Based on the results of our previous analyses, we limited the current analysis to the five traits that had the greatest influence on the levels and distribution of genetic diversity. These were: (1) breeding system, (2) seed dispersal mechanism, (3) life form, (4) geographic range and (5) taxonomic status (table 1). All six combinations of traits 1–4 were

Table 1. *Categories of each of the five life history traits used to produce the two-trait combinations*

(See Hamrick & Godt 1989 for more complete explanation of the traits.)

categories for each trait				
breeding system	seed dispersal mechanism	life form	geographic range	taxonomic status
outcrossing	attached	annual	endemic	gymnosperm
mixed mating	gravity	short-lived perennial	narrow	dicotyledon
selfing	ingested	long-lived perennial	regional	monocotyledon
	wind		widespread	

Table 2. *Proportion of variation among species (R^2) explained by each combination of traits*

trait combination	R^2		
	P_s (%)	H_{es}	G_{ST}
breeding system/seed dispersal mechanism	0.159	0.110	0.392
breeding system/taxonomic status	0.130	0.069	0.390
breeding system/geographic range	0.112	0.087	0.370
life form/breeding system	0.148	0.089	0.396
life form/seed dispersal mechanism	0.145	0.087	0.222
life form/geographic range	0.121	0.101	0.264
seed dispersal mechanism/ geographic range	0.120	0.107	0.126

analysed, plus breeding system × taxonomic status (see table 2 for the complete list). When fewer than 15 entries provided useful data for a two-trait category, the category was excluded from the analyses. A slightly lower cutoff ($n > 13$) was used for the comparison of genetic diversity among plant families.

(*c*) *Statistical analyses*

The statistical analyses employed generally followed procedures utilized by our earlier review (i.e. Hamrick & Godt 1989). Means and standard errors of genetic diversity parameters were calculated for each two-trait category. Differences among categories of the seven combinations were analysed by performing separate one-way ANOVAS using the GLM procedures of SAS (SAS Institute, Inc. 1988) with trait categories treated as class variables. A least squares means procedure (SAS Institute, Inc. 1988) was employed in a pairwise fashion to determine significant differences among categories.

3. RESULTS AND DISCUSSION

The ANOVAS performed on the three genetic diversity parameters revealed highly significant differences ($p < 0.0001$) among categories of the seven two-trait combinations. However, the proportion of interspecific variation (R^2) in P_s and H_{es} explained by the analysis was quite low (table 2). The R^2 values for P_s ranged from 0.112 to 0.159, while R^2 values for H_{es} were lower (0.069–0.110). Thus, most of the variation in genetic diversity among species was not explained by the two-trait combinations. This was not surprising as only 24% of the interspecific variation in H_{es} was accounted for by a multiple regression model that incorporated eight life history traits (Hamrick & Godt 1989). In the 1989 analysis, geographic range accounted for 32% of the explained variation while life form, breeding system and seed dispersal also explained significant proportions (25%, 17% and 17%, respectively).

A much higher proportion of the overall interspecific variation for G_{ST} was explained by the two-trait categories (table 2), with R^2 values for G_{ST} ranging from 0.126 to 0.396. Trait combinations that involved the breeding system explained a relatively high proportion of the variation (mean $R^2 = 39\%$). Trait combinations involving life form, seed dispersal and geographic range had moderate R^2 values (mean R^2 = 28%, 25% and 25%, respectively). In our earlier analyses the eight life history traits accounted for 47% of the heterogeneity in G_{ST} values (Hamrick & Godt 1989). Breeding system and life form were most closely associated with the among species variation in G_{ST} and together accounted for 84% of the variation explained (Hamrick & Godt 1989). We have argued previously (Hamrick & Godt 1989, 1996*a*) that the genetic diversity maintained by a species is a function not only of its life history traits but also depends heavily on the species' ecological and evolutionary history. Fluctuations in the number and size of populations, biogeography and the speciation process itself may have played critical roles in determining the current genetic composition of species.

Table 3. *Mean levels of genetic variation within species and its distribution among populations for combined categories of breeding system and seed dispersal mechanism*

(N = mean number of entries, P_s = percentage of loci polymorphic within species, H_{es} = genetic diversity within species, G_{ST} = proportion of total genetic diversity at polymorphic loci found among populations. See the text for an explanation of these parameters. Values that do not share a letter are significantly different at $p < 0.05$.)

trait combination	n	P_s (%)	H_{es}	G_{ST}
outcrossing				
attached	63	67.9^a	0.188^b	0.114^d
gravity	178	50.2^b	0.152^{cde}	0.189^c
ingested	54	52.4^b	0.200^{ab}	0.223^c
wind	186	62.4^a	0.157^{cd}	0.101^d
mixed-mating				
gravity	63	52.7^b	0.174^{bc}	0.248^c
ingested	17	34.1^c	0.108^{ef}	0.269^c
wind	62	42.0^{bc}	0.118^{ef}	0.175^{cd}
selfing				
attached	29	64.7^a	0.236^a	0.426^b
gravity	94	34.5^c	0.097^f	0.533^a

(*a*) *Analyses of two-trait combinations*

(i) *Breeding system and seed dispersal*

The trait combinations involving breeding systems and seed dispersal mechanisms explained relatively high proportions of the interspecific variation in P_s, H_{es} and G_{ST} (table 2). For the per cent of polymorphic loci (P_s) three combinations (outcrossing/attached, outcrossing/wind and selfing/attached) had significantly higher values (table 3). Selfing, gravity-dispersed species had the lowest mean values. A similar result was seen for H_{es}; selfing species with animal-attached seeds had the highest genetic diversity and selfing, gravity-dispersed species had the lowest H_{es} values. Species with different life history traits had markedly different G_{ST} values. On average, selfing species with gravity-dispersed seeds exhibited five-fold more differentiation than outcrossing, wind-dispersed species.

When seed dispersal mechanism was held constant and breeding system categories were varied we found only a weak pattern for P_s and H_{es}. Although comparisons were difficult due to missing categories, it

Table 4. *Mean levels of genetic variation within species and its distribution among populations for combined categories of breeding system and taxonomic status*

(See table 3 for definitions of the symbols used.)

trait combination	n	P_s (%)	H_{es}	G_{ST}
outcrossing				
gymnosperm	115	70.8^{a}	0.169^{ab}	0.073^{e}
monocot	78	52.5^{b}	0.158^{ab}	0.157^{d}
dicot	286	54.0^{b}	0.165^{ab}	0.184^{d}
mixed-mating				
monocot	20	53.1^{b}	0.183^{ab}	0.212^{cd}
dicot	94	46.6^{b}	0.143^{ab}	0.240^{c}
selfing				
monocot	40	55.4^{b}	0.195^{a}	0.412^{b}
dicot	98	32.6^{c}	0.091^{c}	0.587^{a}

Table 5. *Mean levels of genetic variation within species and its distribution among populations for combined categories of breeding system and geographic range*

(See table 3 for definitions of the symbols used.)

trait combination	n	P_s (%)	H_{es}	G_{ST}
outcrossing				
endemic	57	54.4^{ab}	0.142^{cdef}	0.179^{de}
narrow	131	55.8^{ab}	0.155^{bcd}	0.169^{de}
regional	211	59.9^{a}	0.171^{abc}	0.120^{e}
widespread	79	55.3^{ab}	0.183^{ab}	0.170^{de}
mixed-mating				
endemic	24	40.5^{cd}	0.100^{ef}	0.174^{de}
narrow	33	40.5^{cd}	0.123^{def}	0.326^{e}
regional	30	49.3^{abc}	0.164^{abcd}	0.272^{cd}
widespread	27	60.1^{a}	0.206^{a}	0.169^{de}
selfing				
endemic	16	13.5^{e}	0.034^{g}	0.591^{a}
narrow	19	28.7^{de}	0.093^{fg}	0.512^{ab}
regional	68	45.1^{c}	0.121^{def}	0.572^{a}
widespread	38	47.2^{bc}	0.165^{abcd}	0.446^{b}

appears that for gravity-dispersed species, P_s and H_{es} were significantly lower in selfing species. Breeding system categories had a much more pronounced effect on G_{ST}. Gravity-dispersed, outcrossing species had significantly lower G_{ST} values than either mixed-mating or selfing species with gravity-dispersed seeds. Species with attached-or wind-dispersed seeds show a similar pattern across breeding system classes.

When species with the same breeding system but different seed dispersal mechanisms were considered, we found that outcrossing species with attached or wind-dispersed seeds had lower mean G_{ST} values than outcrossing species with gravity or ingested seed dispersal mechanisms. Within mixed-mating species, wind-dispersed species also had a somewhat lower G_{ST} value, while species with gravity and ingested seed dispersal mechanisms had similar values. Among selfers, gravity-dispersed species had significantly higher G_{ST} values than species that disperse seeds via attachment. Thus, species that we perceive to have limited pollen and seed dispersal tend to have more genetic differentiation among populations than species with more potential for gene movement. No such patterns were seen for genetic diversity within species.

(ii) *Breeding system and taxonomic status*

Comparisons between breeding system and the taxonomic status of species explained relatively little of the interspecific variation for P_s and H_{es} but explained a relatively high proportion of the variation for G_{ST} (table 2). Selfing dicots had the lowest P_s and H_{es} values and the highest G_{ST} value, while outcrossing gymnosperms had the highest P_s value and a G_{ST} value that was eight-fold lower than that for selfing dicots (table 4). Selfing monocots had the highest H_{es} value. The high H_{es} values seen for selfing monocots may be due to the relatively high number of crop species (24%) represented in this category. A recent review of the crop allozyme literature indicated that monocot crops have elevated levels of genetic diversity while dicot crops have values that are equivalent to non-crop dicots (Hamrick & Godt 1996*b*). Within outcrossing species, gymnosperms had significantly lower G_{ST} values than the angiosperms. There were no significant differences for H_{es} among the outcrossing taxa. There was a weak trend in the data indicating that mixed-mating or selfing monocots may have more genetic diversity than dicots with the same breeding systems. Monocots had lower G_{ST} values than dicots. The high proportion of wind-pollinated species within the monocots (91 of 138 monocot taxa are grasses) may have influenced this result.

Within taxonomic categories the various breeding systems produced a predictable pattern. As expected both outcrossing monocots and dicots had lower G_{ST} values than monocots or dicots that self or have a mixed-mating system. Outcrossing dicots generally had more genetic diversity than dicots with mixed-mating or selfing mating systems. This trend is reversed in the monocots, with selfing monocots having somewhat higher H_{es} values than either mixed-mating or outcrossing species. The different patterns seen for the monocots and dicots may be due to the fact that many outcrossing dicots are woody plants while outcrossing monocots are typically herbaceous. Hamrick & Godt (1989) and Hamrick *et al.* (1992) have shown that, regardless of their taxonomic status, woody plants have significantly higher P_s and H_{es} values than either annuals or perennial herbaceous species.

(iii) *Breeding system and geographic range*

The combination of breeding system and geographic range explained little of the variation in genetic diversity within species (H_{es}) but a relatively high proportion of the variation among species for G_{ST} (table 2). The highest P_s values were found for outcrossing, regionally distributed species and mixed-mating widespread species (table 5). Widespread, mixed-mating species also had the highest H_{es} value. The lowest H_{es} and P_s values were for endemic selfing species. The lowest G_{ST} value was found for outcrossing, regionally distributed species, while the highest G_{ST} value was for endemic, selfing species. Selfing endemic species had the lowest P_s and H_{es} and the highest G_{ST} values for any two-trait category in our overall analysis.

Table 6. *Mean levels of genetic variation within species and its distribution among populations for combined categories of life form and breeding system*

(See table 3 for definitions of the symbols used.)

trait combination	n	P_s (%)	H_{es}	G_{ST}
annual				
outcrossing	98	59.1^{b}	0.186^{a}	0.191^{cd}
mixed-mating	29	40.3^{ef}	0.115^{cd}	0.343^{b}
selfing	102	43.2^{de}	0.131^{c}	0.553^{a}
short-lived perennial				
outcrossing	140	43.7^{cd}	0.123^{c}	0.218^{cd}
mixed-mating	48	53.6^{bc}	0.172^{ab}	0.238^{c}
selfing	32	29.9^{f}	0.081^{d}	0.442^{b}
long-lived perennial				
outcrossing	241	65.5^{a}	0.180^{ab}	0.094^{e}
mixed-mating	24	42.5^{ef}	0.135^{bc}	0.145^{de}

Within a breeding system category endemic and narrowly-distributed species tended to have lower P_s and H_{es} values than species with more extensive geographic ranges. There was, however, no such pattern for G_{ST}. Endemic and narrowly distributed species have G_{ST} values that were equivalent or smaller than those of more widely distributed species.

Within each geographic distribution category outcrossing species tended to have lower G_{ST} values than either mixed-mating or selfing species. However, the difference in G_{ST} seems to be greatest between mixed-mating and selfing species. For endemic and narrowly distributed species there was a gradual decrease in H_{es} values with increased inbreeding. No distinct trend was seen, however, for widespread species. By our definition, widespread species occur on two or more continents. This group is generally biased towards weedy species whose human-oriented ecology may influence genetic diversity and its distribution.

(iv) *Life form and breeding system*

The combination of life form and breeding system also explained low proportions of the variation found among species for P_s and H_{es} but had the highest R^2 value for G_{ST} (table 2). Long-lived perennials with an outcrossing breeding system had the highest P_s value, while annual outcrossing species had the highest H_{es} values (table 6). Short-lived perennial species with selfing breeding systems had the lowest P_s and H_{es} values. The range in G_{ST} values was portrayed by the five-fold difference in G_{ST} between annual selfing species and long-lived, outcrossing species.

Within the life form categories there was a decrease in genetic diversity and an increase in G_{ST} with increased selfing. Within the breeding system categories there was a significant decrease in G_{ST} values with increasing longevity. For each of the three breeding system categories G_{ST} was highest for annual plants, intermediate for short-lived perennials and lowest for long-lived perennials. No general pattern was apparent for P_s and H_{es}. The effect of life form on G_{ST} was probably due to differences in the pollen and seed dispersal abilities between herbaceous and woody plants. The larger stature and relatively lower population densities characteristic of trees should result in more gene dispersal (and, thus, lower G_{ST} values).

Table 7. *Mean levels of genetic variation within species and its distribution among populations for combined categories of life form and seed dispersal mechanism*

(See table 3 for definitions of the symbols used.)

trait combination	n	P_s (%)	H_{es}	G_{ST}
annual				
attached	42	74.2^{a}	0.227^{a}	0.277^{bc}
gravity	141	44.9^{c}	0.132^{de}	0.380^{ab}
ingested	26	34.8^{d}	0.138^{cde}	0.406^{a}
wind	21	51.8^{bc}	0.156^{cbd}	0.392^{ab}
short-lived perennial				
attached	26	55.7^{b}	0.165^{cbd}	0.230^{cd}
gravity	144	43.8^{cd}	0.133^{de}	0.233^{cd}
ingested	21	38.3^{cd}	0.128^{cde}	0.321^{abc}
wind	43	40.7^{cd}	0.100^{e}	0.266^{cd}
long-lived perennial				
attached	33	63.8^{ab}	0.185^{ab}	0.094^{ef}
gravity	50	58.0^{b}	0.178^{c}	0.177^{de}
ingested	28	64.8^{ab}	0.225^{a}	0.099^{def}
wind	159	63.8^{b}	0.159^{cbd}	0.086^{f}

(v) *Life form and seed dispersal*

Combinations of life forms and seed dispersal mechanisms explained relatively low proportions of interspecific variation in P_s and H_{es} and a lower proportion of variation in G_{ST} than did combinations that included the breeding system (table 2). Annual species with attached dispersal mechanisms have the highest values of P_s and H_{es}, while annual plants with ingested seeds have the lowest P_s value and short-lived perennial species with wind-dispersed seeds have the lowest H_{es} value (table 7). The highest G_{ST} values were found for annual plants with ingested seeds, while the lowest G_{ST} values were produced by long-lived perennials with wind-dispersed seeds.

Within the life form categories, species that disperse seeds by animal-attachment had higher P_s and H_{es} values than species with other seed dispersal mechanisms, although the differences were not large. For G_{ST} there was no discernable pattern between seed dispersal mechanisms. Within seed dispersal categories there was no recognizable pattern for P_s across life forms but there is a weak pattern for H_{es}. Longer-lived plants tended to have higher H_{es} values than either annual or short-lived species regardless of their seed dispersal mechanisms. This trend was particularly marked for species with gravity and ingested seed dispersal mechanisms. In contrast, G_{ST} values were strongly influenced by life form. For all seed dispersal categories annual plants had approximately three-fold higher G_{ST} values than long-lived perennials. Long-lived perennials also had significantly lower G_{ST} values than short-lived perennials. This pattern was probably due to the higher proportion of tree species in the long-lived perennial category.

Table 8. *Mean levels of genetic variation within species and its distribution among populations for combined categories of life form and geographic range*

(See table 3 for definitions of the symbols used.)

trait combination	n	P_s (%)	H_{es}	G_{ST}
annual				
endemic	35	50.1^{bcd}	0.149^{cde}	0.223^{cd}
narrow	60	39.6^{ef}	0.113^{ef}	0.352^{b}
regional	65	49.8^{cd}	0.143^{cde}	0.499^{a}
widespread	70	56.5^{bcd}	0.200^{a}	0.296^{bc}
short-lived perennial				
endemic	30	32.1^{f}	0.083^{f}	0.325^{bd}
narrow	52	49.8^{cd}	0.148^{cde}	0.216^{cd}
regional	93	42.2^{def}	0.123^{def}	0.280^{bc}
widespread	59	48.2^{cd}	0.154^{cd}	0.194^{de}
long-lived perennial				
endemic	32	48.1^{cde}	0.105^{ef}	0.150^{def}
narrow	70	59.5^{ab}	0.163^{bc}	0.132^{ef}
regional	151	67.0^{a}	0.190^{ab}	0.086^{f}

(vi) *Life form and geographic range*

The combination of life form and geographic range explained a low proportion of the among-species variation in P_s and H_{es} and only moderate amounts of variation in G_{ST} values (table 2). The highest values of P_s were associated with long-lived perennial species with regional geographic ranges, while widespread annual species had the highest H_{es} values (table 8). Short-lived, endemic perennials had the lowest P_s and H_{es} values. Annual species with regional distributions had the highest G_{ST} values and long-lived perennials with regional distributions had the lowest G_{ST} values.

Within annual and short-lived perennial life forms geographic range had no discernable effects on P_s, H_{es} and G_{ST} (table 8). However, within the long-lived perennial category both P_s and H_{es} increased and G_{ST} decreased significantly with more widely distributed species. Variation in life form had little effect on the levels of genetic diversity contained within endemic species. However, for narrowly and regionally distributed species genetic diversity was significantly higher in long-lived perennial species. Widespread annual species had more genetic diversity than widespread short-lived perennials. Endemic species with different life forms had different, but non-significant, G_{ST} values due to the low number of entries in these categories. In contrast, for narrow and regionally distributed species, annuals had higher G_{ST} values than short-lived and long-lived perennials. As most long-lived perennials in the database are trees, we conclude that tree species have less genetic differentiation among their populations than other plant species with similar geographic distributions.

(vii) *Seed dispersal and geographic range*

This combination of traits explained a much lower proportion of the variation in G_{ST} and approximately the same levels of variation in P_s and H_{es} as the other combinations (table 2). Widespread species with animal-attached seeds had the highest P_s and H_{es} values, while species with ingested seeds and narrow distributions had the lowest H_{es} and P_s values (table 9). Wind-dispersed species with endemic distributions also had low genetic diversity. Wind-dispersed species with regional distributions had the lowest G_{ST} values, while widespread species with ingested seeds had the highest G_{ST} values.

Table 9. *Mean levels of genetic variation within species and its distribution among populations for combined categories of seed dispersal mechanisms and geographic range*

(See table 3 for definitions of the symbols used.)

trait combination	n	P_s (%)	H_{es}	G_{ST}
attached				
narrow	17	68.3^{a}	0.214^{ab}	0.215^{cdef}
regional	45	64.3^{ab}	0.192^{abc}	0.245^{cd}
widespread	31	72.4^{a}	0.221^{a}	0.201^{def}
gravity				
endemic	53	46.2^{d}	0.130^{def}	0.198^{def}
narrow	85	46.3^{d}	0.136^{def}	0.291^{bc}
regional	126	44.6^{d}	0.128^{ef}	0.336^{ab}
widespread	70	47.8^{d}	0.174^{bc}	0.247^{cd}
ingested				
narrow	22	32.3^{e}	0.097^{f}	0.254^{bcd}
regional	33	60.1^{abc}	0.213^{ab}	0.216^{cde}
widespread	18	48.6^{cd}	0.201^{abc}	0.441^{a}
wind				
endemic	34	43.4^{de}	0.107^{f}	0.259^{bcd}
narrow	59	57.2^{bc}	0.148^{cde}	0.123^{ef}
regional	106	63.6^{ab}	0.163^{bcd}	0.104^{f}
widespread	25	55.1^{bcd}	0.144^{cdef}	0.156^{def}

Within a seed dispersal category, the species' geographic range had little predictable effect on measures of genetic diversity. Species with ingested and wind-dispersed seeds tended to have significantly more genetic diversity in more widely distributed species, but species with gravity and attached dispersal mechanisms did not demonstrate this pattern. Within the wind-dispersed category endemic species had significantly higher G_{ST} values than either narrow or regionally distributed species, but this pattern was not repeated for the other seed dispersal categories. Within geographic range categories there was no pattern with the seed dispersal mechanisms for P_s. For H_{es}, however, species with attached seed dispersal generally had higher values than species with other seed dispersal mechanisms. Regardless of the geographic range of the species, species with wind-dispersed seeds tended to have lower G_{ST} values than species with other seed dispersal mechanisms. A curious observation is that species with attached seeds generally had high levels of genetic diversity in all of the analyses. This unexpected result may be due to the high number of monocots in this category.

(*b*) *Plant families*

The analysis of genetic diversity within plant families indicated that, in general, families with predominantly herbaceous species had less genetic diversity and higher genetic differentiation among their populations than families with predominantly long-lived woody peren-

Table 10. *Mean levels of genetic variation within species and its distribution among populations for several plant families*

(See table 3 for definitions of the symbols used.)

family	n	P_s (%)	H_{es}	G_{ST}
Asteraceae	101	45.3	0.127	0.204
Chenopodiaceae	22	40.6	0.099	0.540
Cucurbitaceae	23	40.4	0.168	0.397
Onagraceae	23	34.4	0.106	0.338
Orchidaceae	16	44.8	0.137	0.087
Schrophulariaceae	16	37.2	0.123	0.372
Solanaceae	23	32.0	0.094	0.426
Poaceae	91	62.7	0.201	0.284
Fabaceae	48	59.6	0.184	0.277
Myrtaceae[a]	14	81.8	0.222	0.134
Fagaceae[a]	27	65.3	0.198	0.085
Pinaceae[a]	103	73.0	0.176	0.073

[a] Families with predominantly woody taxa.

nials (table 10). There were, however, a few interesting exceptions. In particular, the Orchidaceae had levels of genetic diversity typical of other predominantly herbaceous families but had an exceptionally low mean G_{ST} (table 10). This result was perhaps due to the species-specific pollinators characteristic of orchids, and to their tiny wind-borne seeds. Both of these traits could produce high rates of gene flow among populations. The Poaceae was also atypical for a herbaceous family as its species have high genetic diversity and comparatively less genetic heterogeneity among populations. Families with predominantly woody species (ie. Fagaceae, Pinaceae and Myrtaceae (= *Eualyptus* in our data)) all had high genetic diversity values and exhibited little differentiation among populations. The only family analysed with a significant mixture of herbaceous and woody taxa was the Fabaceae. Interestingly, its mean genetic diversity parameters were intermediate between the predominantly herbaceous and the predominantly woody families. Comparisons of genetic diversity parameters within the Fabaceae demonstrated that herbaceous legumes ($n = 32$) had mean P_s, H_{es} and G_{ST} values of 53%, 0.160, 0.352 respectively, while values for the woody legumes ($n = 18$) were 76%, 0.229, and 0.124. These results suggest that genetic diversity and its distribution are more closely associated with these individual species' life history traits than with their phylogenetic status.

4. CONCLUSIONS

These results reinforce the conclusions of earlier reviews by demonstrating the influence of life history traits on levels and distribution of genetic diversity in seed plants. All traits examined had significant effects on the three genetic diversity parameters considered. Life form and breeding system in particular had significant influences on genetic diversity and its distribution. More specifically, outcrossing species have significantly less genetic diversity among their populations, regardless of their other traits. Species with low interpopulation genetic differentiation also tend to have more overall genetic diversity. The most interesting insight arising from the two-trait analyses is the observation that woody plants have lower G_{ST} values than herbaceous plants with the same combinations of life history traits, regardless of their phylogenetic relationship. Earlier reviews (Loveless & Hamrick 1984; Hamrick & Godt 1989) speculated that woody plants had lower G_{ST} values because trees have certain life history traits in common. The present analysis, however, indicates that woody plants have lower G_{ST} values and somewhat higher P_s and H_{es} values than non-woody species that share the same breeding systems, geographic ranges and seed dispersal mechanisms. As discussed earlier, the tall stature and comparatively low population densities of trees should result in greater dispersal distances for pollen and seeds than would occur in populations of shorter, more dense herbaceous species.

The greater potential for gene movement of trees should also affect their ability to maintain genetic diversity (Hamrick & Nason 1996). New alleles arising in populations of outcrossing tree species should have a higher probability of being dispersed into other populations than novel genes introduced into populations of herbaceous species with limited gene dispersal potential. Due to their greater dispersal potential, novel alleles are less likely to be lost to tree species through drift or population extinction. In contrast, novel alleles are more likely to be lost in species that experience less gene flow. These species should, as a result, have fewer polymorphic loci and less overall genetic diversity.

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