POPULATION BIOLOGY OF GRASSES

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Contents

1

Allozyme diversity in the grasses

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Since Lewontin & Hubby (1966) and Harris (1966) independently discovered allozyme polymorphisms within populations of *Drosophila* and humans, allozymes have provided the most widely used descriptors of genetic diversity in natural plant and animal populations. Their usefulness can be ascribed to several features, including codominant expression, apparent neutrality, and ease and cost of detection. Today allozymes are utilized in studies of plant populations to determine breeding systems, describe mating systems, determine paternity, estimate gene flow via seed and pollen, examine clonal structure, and determine systematic relationships (Soltis & Soltis, 1989). In conservation biology and crop science, the description of genetic structure provides sampling guidelines for the *ex situ* and *in situ* preservation of genetic diversity (e.g. Marshall & Brown, 1975; Brown & Briggs, 1991; Godt, Hamrick & Bratton, 1995; Swenson *et al.*, 1995; Godt & Hamrick, 1996). Furthermore, allozymes have been utilized to study the evolution of crop species and to identify cultivars (Doebley, 1989; Torres, 1989).

Although allozyme diversity does not necessarily reflect variation in quantitative traits, it provides a handy yardstick for comparisons of diversity within populations and across species. Over 1000 published studies report allozyme variation in seed plants. These represent a wide cross-section of the plant world, although commercially valuable species (i.e. trees and crops) and temperate species have received the most attention. As the number of allozyme studies has grown, several reviewers have described patterns in allozyme diversity and its distribution (Gottlieb, 1977; Brown, 1979; Hamrick, Linhart & Mitton, 1979; Crawford, 1983; Hamrick & Godt, 1989). Notably, these reviews have consistently shown that the distribution of genetic diversity is strongly associated with a plant's breeding system, with most of the genetic diversity in outbreeding species found

within populations, while nearly half of the genetic diversity of selfing species is found among populations. Woody species tend to maintain more genetic diversity, whereas species with restricted geographic distributions harbour the least. Moreover, although patterns emerge when plant species are considered in their entirety, the ability to predict genetic diversity and its distribution in particular species remains somewhat elusive. One can only conclude that the evolutionary and ecological history of each species uniquely determines its genetic composition and structure.

The number of published allozyme studies now permits examinations of patterns of genetic diversity within several plant groups. In particular, some of the larger plant families (i.e. Asteraceae, Fabaceae and Poaceae) can be examined in some detail. This could provide further insights into genetic diversity patterns since the effects of phylogeny can be partially controlled. In this study we examine allozyme diversity within the grasses.

Materials and methods

Studies considered

In 1989, we surveyed the vascular plant literature and constructed a data base of allozyme studies that incorporated 653 studies of seed plants (Hamrick & Godt, 1989). These data form the foundation for the current review. Because we have since updated the data base for several groups of plants, the overall data are more comprehensive for some groups than for others. Specifically, the data base was updated and reviewed in 1990 for all plants (Hamrick, Godt & Sherman-Broyles, 1992), for tropical trees in 1993 (Hamrick, 1994) and for crop species in 1996 (Hamrick & Godt, 1997). For this review we updated the data base with respect to the grasses by adding studies published between 1990 and mid-1996. Although the inclusion of more studies from particular groups might be perceived to have biased the overall data set, the summary statistics for all plant species changed very little with the inclusion of additional information.

All studies that reported allozyme variation were considered for the data base. However, studies that reported electrophoretic phenotypes without genetic interpretation of the data could not be used. Some taxa have been analysed more than once; these studies are not complete duplications because they often represent studies by different labs, or by the same lab studying populations in different portions of the species' range or assessing different loci. Such species are represented in the data base more than once.

Genetic parameters

Genetic diversity statistics were extracted from or calculated for each study. These statistics describe genetic diversity within each species, within populations, and among populations within species. Within-population genetic diversity statistics represent population means, and thus are influenced by the distribution of genetic diversity among populations. (For example, within-population values will be relatively lower for species whose genetic diversity is distributed among, rather than within, populations.) For this reason, we introduced calculations that describe species' genetic diversity (Hamrick & Godt, 1989). Efforts have been made to standardize genetic statistics throughout the data base (i.e. parameters were re-calculated if we concluded the authors had used different criteria or equations). In addition, we calculated as many genetic statistics as possible from the data reported (e.g. tables of genotypes or allele frequencies were sometimes available even though the complete array of genetic statistics was not reported). Nonetheless, data were not available in every study to permit calculation of all genetic parameters; hence the number of studies utilized varied among parameters.

For the species and population means, we calculated (as shown in Table 1.1) percentage polymorphic loci (P), mean number of alleles per locus (A), effective number of alleles per locus (A_e), and genetic diversity (H_e; expected heterozygosity given Hardy–Weinberg assumptions). Parameters that are subscripted with an s indicate species values, whereas those subscripted with a p represent population means. Total genetic diversity (H_T) was calculated at polymorphic loci and partitioned into that found within populations (H_S) and among populations (D_{ST}). The proportion of total genetic diversity found among populations (G_{ST}) was then calculated. We also estimated gene flow (as measured by Nm, the number of migrants per generation) based on genetic structure (Table 1.1).

Species traits

Each species was categorized for the following traits: regional distribution (boreal-temperate, temperate or tropical), geographic range (widespread, regional, narrow or endemic), life form (annual or perennial), mode of reproduction (sexual or a mixture of asexual and sexual), breeding system (outcrossed, mixed-mating or selfed); seed dispersal mechanism (wind, explosive, animal-ingested or animal-attached, gravity or a mixture of gravity and animal-attachment), and successional status (early, mid or late). Information on the species' traits was obtained from the original

Table 1.1. *Calculations of genetic parameters*

The subscripts *s* and *p* indicate species level and population parameters respectively.

A. Percentage polymorphic loci
P_s=the number of loci that exhibit two or more alleles in the study, divided by the number of loci examined
P_p=the proportion of loci that exhibit two or more alleles within each population, averaged across populations

B. Mean number of alleles per locus
A_s=the total number of alleles observed in the study, divided by the number of loci examined
A_p=the number of alleles observed per locus within populations, averaged over loci within populations, and averaged across populations

C. Effective number of alleles per locus
$A_{es}=1/(1-H_{es})$, where H_{es} is as defined below
$A_{ep}=1/\Sigma p_i^2$ where p_i is the frequency of the *i*th allele at a locus. Calculated for every locus, averaged over loci and over populations

D. Genetic diversity
$H_{es}=1-\Sigma \bar{p}_i^2$ where $\bar{p}_i$ is the mean frequency of the *i*th allele, calculated for each locus, and then averaged over loci
$H_{ep}=1-\Sigma p_i^2$ where p_i is the frequency of the *i*th allele in each population

E. Among population diversity
$H_T=1-\Sigma \bar{p}_i^2$, a measure of total genetic diversity, where $\bar{p}_i$ is the mean frequency of the *i*th allele across all populations. H_T is calculated for each polymorphic locus and averaged across these loci
$H_S=1-\Sigma p_i^2$, a measure of within-population genetic diversity, calculated for each population where p_i is the frequency of the *i*th allele
$D_{ST}=H_T-H_S$, calculated for each polymorphic locus
$G_{ST}=D_{ST}/H_T$, calculated for each polymorphic locus, and averaged over loci

F. Gene flow (assessed as Nm, the number of migrants per generation)
$Nm=(1-G_{ST})/4G_{ST}$

study or from floras. When detailed trait information was unavailable, educated guesses were made based on such characteristics as seed shape, floral morphology, or characteristics of closely related taxa. Some categories within traits represent arbitrary divisions of a continuum (e.g. geographic range) and thus placement of species into particular categories has been in part subjective. For geographic range, we considered a species to be widespread if it occurred on more than one continent, regional if it occupied a large area within a continent (e.g. the eastern US), narrow if it was found in a more restricted area (e.g. the southeastern US) and endemic if it was extremely localized (e.g. found only in the Florida panhandle). Species that

propagated themselves clonally by such means as rhizomes, stolons, or by agamospermy were categorized as having a mixed mode of reproduction.

Statistical analyses

The statistical analyses used paralleled those of Hamrick & Godt (1989) and Hamrick *et al.* (1992). For each species trait, means and standard errors were calculated. The analytical procedures of SAS (SAS Institute, Inc., 1987) were employed to analyse differences between categories of trait variables. Specifically, differences between categories were analysed using the general linear model (GLM) procedures of SAS coupled with a least squares means procedure (LSM/PDIFF) to test for pair-wise differences.

Results and discussion

Many allozyme studies of the Poaceae have been published but only a fraction of these provided data that could be used to describe allozyme diversity. Of 415 studies, about 57% or 237 studies contained data appropriate for this review. Forty-three genera and 143 species were represented in this data set. Not surprisingly, crop species and their close relatives were the focus of many studies.

Genetic diversity in grasses compared with other plants

In the data set, 16 or 17 allozyme loci were analysed per study for grasses as well as for other plant species (Table 1.2). The mean number of populations studied was higher for the grasses than for other plants (21 vs 12), most likely reflecting that studies of commercially valuable Poaceae often incorporate numerous accessions.

Within species and populations, a higher proportion of loci are polymorphic within the grasses and these loci have more alleles per locus with frequencies that are similar to those found in other plants (Table 1.2). Thus, overall genetic diversity is higher for grass species (H_{es}) and within grass populations (H_{ep}). However, grasses exhibit somewhat more genetic differentiation among populations (G_{ST}) than other species. About 27% of total genetic diversity is found among grass populations compared with 22% for other plant species.

Table 1.2. *Allozyme diversity in the grasses compared with other plants*

See Table 1.1 for description and calculation of genetic parameters. N is the mean number of studies contributing to the calculation of the genetic parameters.

A. Species

Group	N	Mean no. populations	Mean no. loci	P_s	A_s	A_{es}	H_{es}
Grasses	161	21	16	60.0	2.38	1.27	0.191
Other plants	666	12	17	50.8	1.92	1.20	0.146

B. Within population

Group	N	Mean no. populations	Mean no. loci	P_p	A_p	A_{ep}	H_{ep}
Grasses	135	21	16	40.8	1.66	1.19	0.138
Other plants	684	12	17	34.1	1.52	1.15	0.112

C. Among populations

Group	N	Mean no. populations	Mean no. loci	H_T	H_S	G_{ST}
Grasses	140	21	16	0.340	0.243	0.272
Other plants	576	12	17	0.295	0.225	0.216

Associations between life history traits and genetic diversity

Life form

The effect of generation length on genetic diversity in plants is difficult to predict. On one hand, mutations may accumulate at a faster rate within populations of annuals because they cycle more rapidly than perennials. On the other hand, long-lived perennials may experience more environmental variation within their life spans and may face selective pressures by herbivores and other organisms whose populations are frequently evolving at a more rapid rate. These potentially frequency-dependent selective pressures could lead to the maintenance of higher levels of genetic diversity within populations of perennials.

Within the grasses, annual species have a significantly higher proportion of polymorphic loci (65% vs 55%) and more alleles per locus (2.65 vs 2.12) than perennials (Table 1.3). However, annual and perennial grasses do not differ significantly in overall genetic diversity (H_{es}). Thus, the higher

Table 1.3. *Within-species allozyme diversity for grasses with different attributes.*

See Table 1.1 for description and calculation of genetic diversity parameters. N is the mean number of values contributing to P_s, A_s, A_{es} and H_{es}. (NS indicates non-significant differences; * indicates $P \leq 0.05$; ** indicates $P \leq 0.01$ and *** indicates $P \leq 0.001$). Values within a category followed by the same letter are not significantly different. The mean numbers of populations and loci analysed are given in Table 1.5. (Note that only two categories were statistically analysed under seed dispersal because of the small sample size for wind-dispersed seeds.)

Classification	N	P_s	A_s	A_{es}	H_{es}
Life form					
		*	**	NS	NS
Annual	80	65.0a	2.65a	1.28a	0.193a
Perennial	80	55.2b	2.12b	1.26a	0.190a
Geographic range					
		*	*	NS	NS
Endemic or narrow	36	56.9ab	2.16a	1.28a	0.204a
Regional	60	54.2a	2.13a	1.21a	0.165a
Widespread	65	66.8b	2.72b	1.32a	0.209a
Regional distribution					
		**	***	NS	NS
Boreal or temperate	128	56.6a	2.16a	1.27a	0.187a
Tropical or tropical-temperate	33	73.4b	3.14b	1.29a	0.208a
Breeding system					
		**	*	NS	**
Selfing	79	51.4a	2.11a	1.24a	0.162a
Mixed-mating	14	66.7b	2.15ab	1.36a	0.256b
Outcrossing	69	69.1b	2.69b	1.29a	0.212b
Seed dispersal					
		**	***	NS	NS
Gravity	84	54.5a	1.99a	1.25a	0.176a
Attached or gravity-attached	73	67.1b	2.88b	1.30a	0.211a
Wind	4	42.0	1.69	1.19	0.156
Mode of reproduction					
		**	**	NS	NS
Sexual	104	64.5a	2.57a	1.28a	0.196a
Sexual and asexual	57	51.7b	2.03b	1.26a	0.182a
Successional status					
		***	*	**	**
Early	131	64.7a	2.48a	1.30a	0.207a
Mid	30	40.3b	1.96b	1.15b	0.118b

number of alleles per locus within annual species must be due to more low frequency alleles. The occurrence of these rare alleles could be due in part to the electrophoretic analysis of many accessions and landraces of annual crop species (Hamrick & Godt, 1997). It could also reflect the more complete reporting of allelic diversity in species such as annual crops where there is concern for germplasm conservation (alleles found at frequencies of less than 0.01 are often not reported). Similar trends in genetic diversity appear comparing within-population diversity of annual and perennial grasses, although the differences are not significant (Table 1.4). These results do not differ substantially from patterns found when all seed plant species are considered. Within species and populations annual herbs have a higher proportion of variable loci and more genetic diversity than perennial herbs (Hamrick & Godt, 1989).

Geographic range

Species with large geographic ranges may experience a broader range of biotic and abiotic conditions that could impose varied selective pressures on populations and lead to higher genetic diversity within species. In addition, species with widespread distributions often (but not always) consist of more individuals than species with more restricted distributions. Thus overall effective population sizes of such species may be higher, leading to predictions of more genetic diversity within widespread species.

In the data set, only four grass species were categorized as 'endemics'; we pooled these species with narrowly distributed species. Most grasses had regional or widespread distributions. Genetic diversity at the species level (H_{es}) did not differ significantly among geographic range categories, although widespread species had a significantly higher number of alleles per locus and regional species had a significantly lower proportion of polymorphic loci (Table 1.3). Within populations, however, significant differences were observed among species with different geographic ranges, with widespread species having a higher proportion of polymorphic loci that resulted in higher overall genetic diversity (Table 1.4). The lack of differences between geographic range categories at the species level and the occurrence of significantly higher levels of genetic diversity within populations of widespread species indicate that widespread species exhibit less genetic divergence among their populations.

Differences between species with different geographic ranges were more striking when all plants were considered (Hamrick & Godt, 1989). In this case, widespread species had nearly twice the genetic diversity of endemics,

Table 1.4. *Within-population allozyme diversity for grasses with different attributes*

See Table 1.1 for description and calculation of genetic diversity parameters. N is the mean number of values contributing to P_p, A_p, A_{ep} and H_{ep}. (NS indicates non-significant differences; * indicates $P \leq 0.05$; ** indicates $P \leq 0.01$ and *** indicates $P \leq 0.001$). Values within a category followed by the same letter are not significantly different. The mean numbers of populations and loci analysed are given in Table 1.5. (Note that only two categories were statistically analysed under seed dispersal because of the small sample sizes for wind-dispersed seeds.)

Classification	N	P_p	A_p	A_{ep}	H_{ep}
Life form					
		NS	NS	NS	NS
Annual	80	44.2a	1.73a	1.21a	0.147a
Perennial	56	36.1a	1.56a	1.16a	0.125a
Geographic range					
		**	***	NS	**
Endemic or narrow	23	38.3a	1.44a	1.15a	0.122a
Regional	53	31.8a	1.45a	1.14a	0.104a
Widespread	59	50.6b	1.92b	1.24a	0.174b
Regional distribution					
		NS	NS	NS	NS
Boreal or temperate	114	40.0a	1.65a	1.18a	0.134a
Tropical or tropical-temperate	22	44.8a	1.74a	1.20a	0.162a
Breeding system					
		***	**	NS	***
Selfing	80	33.4a	1.51a	1.15a	0.109a
Mixed-mating	9	54.2b	2.03b	1.30a	0.218b
Outcrossing	47	51.0b	1.83b	1.23a	0.175b
Seed dispersal					
		*	NS	NS	*
Gravity	67	36.3a	1.60a	1.15a	0.117a
Attached or gravity-attached	66	45.5b	1.72a	1.22a	0.160b
Wind	3	34.9	1.05	1.16	0.131
Mode of reproduction					
		**	NS	NS	*
Sexual	96	44.7a	1.72a	1.20a	0.150a
Sexual and asexual	40	31.5b	1.52a	1.14a	0.108b
Successional status					
		**	**	*	**
Early	115	44.1a	1.74a	1.21a	0.150a
Mid	21	22.9b	1.28a	1.07a	0.066b

and 130% to 150% the mean genetic diversity of regional and narrowly distributed species, respectively (Hamrick & Godt, 1989).

Regional distribution

Terrestrial plant and animal species diversity tends to increase as one moves towards the Equator. Thus, terrestrial tropical species may experience a more biotically diverse environment compared with temperate species. This observation leads to the question of whether an increase in biotic diversity is accompanied by more genetic diversity within tropical species or their populations.

For this analysis, we pooled the nine boreal grasses analysed with the temperate species. Only 16 grass species were classified as strictly tropical; these were pooled with species whose ranges spanned temperate and tropical regions. Although cold temperate species had a lower percentage polymorphic loci and fewer alleles per locus, this difference did not translate into significantly lower genetic diversity at the species level (Table 1.3). Within populations no trends in genetic diversity were apparent between the two groups (Table 1.4). In contrast, when all plants were considered, species in boreal-temperate regions had significantly higher genetic diversity than those in other regions (Hamrick & Godt, 1989). This observation was probably due to the large number of woody species in the north temperate data set. Woody species tend to maintain high levels of genetic diversity (Hamrick *et al.*, 1992). Because relatively few tropical trees have been analysed, the overall data set is somewhat biased with regard to species composition in temperate vs tropical regions.

Breeding system

Marked differences were found between species with different breeding systems in earlier reviews of the allozyme literature (Hamrick *et al.*, 1979; Hamrick & Godt, 1989). However, these comparisons incorporated a wide range of taxa. Inherent biases in the data could have led to these results. For example, tree species have high levels of genetic diversity, yet there are very few (if any) predominantly selfing trees. This data set may present the most balanced comparison of species with different breeding systems to date because the number of selfers and outcrossers analysed is fairly equal. More importantly, in this study we partially control for phylogeny.

Within the grasses analysed, 17 species were classified as having mixed-mating systems; most were classified as selfers or outcrossers. Selfing

species were genetically depauperate relative to mixed-mating and outcrossing species, both within species and populations. For selfers, genetic diversity at the species level (H_{es}) was 76% of the mean value found for outcrossers (Table 1.3) and 62% of the within population genetic diversity (H_{ep}) of outcrossers (Table 1.4). Selfing grasses typically had fewer polymorphic loci and fewer alleles at those loci than species with more open breeding systems. The concordance of these observations within a taxonomic family indicates that the general observation of less genetic diversity within all selfing plant species is robust.

One explanation for diminished levels of genetic diversity within selfing grasses is the occurrence of coadapted gene complexes associated with different environmental conditions (Clegg & Allard, 1972; Hamrick & Allard, 1972; Hamrick & Holden, 1979). The selection of such gene complexes could lead to diminished levels of within-population diversity but cannot account for diminished genetic diversity at the species level.

A more comprehensive explanation for the occurrence of lower levels of genetic diversity in selfing species is as follows. Novel mutations are less likely to spread among populations of selfers compared with outcrossers since the genes of outcrossers are routinely spread via pollen and seed whereas selfers must rely primarily on seed movement. Furthermore, most selfing species are annuals, whose population sizes often fluctuate. Thus, the low likelihood of gene flow and the increased possibility of population extinction may lead to less frequent incorporation of new mutations into the overall gene pool of selfing species (Hamrick & Nason, 1996). An additional factor is that individuals within even highly polymorphic selfing species are largely homozygous; thus, new populations may be founded by individuals carrying little genetic diversity. An alternative explanation for low genetic diversity within selfers is that many selfing species may be derived from outcrossing relatives. Because the initial number of individuals developing reproductive isolation from the parental outcrossers may be low (e.g. one selfing individual can self-perpetuate), selfing species may acquire only a fraction of the genetic diversity present in their progenitors.

Seed dispersal

Grasses do not have the variety of seed dispersal mechanisms found in plants at large (but see Cheplick, this volume). To our knowledge, none of the grasses included in this study is adapted for dispersal by ingestion nor do any have explosive seed dispersal mechanisms. In this data set, four species were categorized as wind-dispersed and 11 as being dispersed both

by attachment to animals and by gravity. Means for the wind-dispersed species were calculated, but these species were not included in statistical analyses of seed dispersal (e.g. Tables 1.3 and 1.4). The grasses dispersed by a combination of animal attachment and gravity were arbitrarily pooled with the species that were primarily dispersed via animal attachment. The result was fairly equitable numbers for species that were dispersed by some form of attachment, and those that had no specialized means of dispersal (gravity-dispersed). Species with the potential for higher gene flow via attachment tended to maintain more genetic diversity, and this was significant for the percentage polymorphic loci (P_s and P_p), the species' mean number of alleles per locus (A_s) and mean population genetic diversity (H_{ep}; Tables 1.3 and 1.4). This trend is consistent with observations made over all plant species (Hamrick & Godt, 1989).

Mode of reproduction

Nearly all vegetatively reproducing species also reproduce sexually, although sexual reproduction may be infrequent. The question we addressed was whether species with the capacity for clonal spread differ genetically from those that spread primarily through seed production. In the most comprehensive review of the plant allozyme literature, no significant differences in overall genetic diversity were found between taxa with these traits (Hamrick & Godt, 1989). Using a carefully selected but limited data set Ellstrand & Roose (1987) also suggested that clonally spreading species maintain as much genetic diversity as sexually reproducing species. This question is probably best addressed by controlling for phylogeny, which this data set accomplishes, at least partially.

Sexually-reproducing grasses had a higher percentage polymorphic loci and mean number of alleles per locus within species but did not differ in genetic diversity (H_{es}) from species that reproduced both sexually and asexually (Table 1.3). However, sexually reproducing grasses did have higher within-population diversity (H_{ep}=0.150 vs 0.108; Table 1.4). This could be due to lower effective population sizes within clonally reproducing species. Little or no sexual reproduction or recruitment within established stands of clonally reproducing species is a common observation (Eriksson, 1993).

Successional status

All the grass taxa were classified as early or mid-successional (four late-successional species were pooled with the mid-successional species). Early suc-

cessional species had a higher percentage polymorphic loci, more alleles per locus and higher effective numbers of alleles per locus within their species and populations (Tables 1.3 and 1.4). This resulted in about a two-fold difference in genetic diversity (H_{es} and H_{ep}) between early colonizing grasses and mid-successional grasses. These differences could be due to the high number of crop species (considered early successional) in the data (Hamrick & Godt, 1997).

Species vs population genetic diversity

For the species analyses, significant differences in P_s and A_s were found among all seven life history traits whereas only one trait exhibited differences for A_{es} and two for H_{es}. Thus, differences in the percentage polymorphic loci and mean number of alleles per locus frequently did not translate into greater mean effective number of alleles per locus, or more genetic diversity (H_{es}). In contrast, mean population differences in the percentage polymorphic loci and mean number of alleles per locus frequently translated into significant differences in mean population diversity (H_{ep}). These differences between species and mean population analyses reflect in part the fact that rare alleles can have a large influence on P and A at the species level without corresponding changes in genetic diversity (H_{es}). While this is true for population analyses also, within-population measures represent means, and rare alleles will have less influence on the overall P and A values. Thus, it is more generally true that differences in P and A within-populations result in differences in genetic diversity (H_{ep}).

Genetic structure

Only two traits (geographic range and breeding system) had significant influences on the partitioning of genetic diversity within and among grass populations (Table 1.5). Grasses that occur on more than one continent and endemics or narrowly distributed species had less genetic divergence among their populations than species with regional distributions. *A priori*, we expect more divergence among populations of widespread species compared with species having small distributions, unless the ability of species to exchange genes among their populations is positively correlated with their geographic ranges. Thus, the occurrence of less divergence among populations of grasses with endemic or narrow ranges compared with regionally distributed species is consistent with predictions. In contrast, the low level of divergence among widespread species is contrary to expecta-

Table 1.5. *Distribution of genetic diversity among populations for grasses with different attributes*

NS indicates non-significant differences; * indicates $P \leq 0.05$; ** indicates $P \leq 0.01$ and *** indicates $P \leq 0.001$). Values within a category followed by the same letter are not significantly different.

Classification	N	Mean no. populations	Mean no. loci	H_T	H_S	G_{ST}
Life form						
				NS	NS	NS
Annual	83	34	18	0.327a	0.236a	0.290a
Perennial	58	7	13	0.355a	0.249a	0.252a
Geographic range						
				NS	**	***
Endemic or narrow	19	8	15	0.325a	0.242ab	0.231a
Regional	52	11	17	0.345a	0.183a	0.398b
Widespread	69	35	15	0.337a	0.285b	0.190a
Regional distribution						
				NS	NS	NS
Boreal-temperate	112	19	15	0.348a	0.245a	0.275a
Tropical or temperate-tropical	28	32	21	0.300a	0.228a	0.270a
Breeding system						
				NS	***	***
Selfing	73	35	18	0.329a	0.192a	0.415a
Mixed-mating	13	7	10	0.406a	0.355b	0.156b
Outcrossing	53	10	14	0.329a	0.286b	0.112b
Seed dispersal						
				NS	NS	NS
Gravity	64	11	16	0.336a	0.218a	0.315
Attached or gravity-attached	73	32	15	0.341a	0.262a	0.239
Mode of reproduction						
				NS	NS	NS
Sexual	107	28	17	0.332a	0.248a	0.269a
Sexual and asexual	33	6	14	0.360a	0.223a	0.291a
Successional status						
				NS	NS	NS
Early	123	23	16	0.340a	0.247a	0.275a
Mid	17	8	15	0.331a	0.201a	0.264a

tions. The lower level of divergence among widespread grass species may reflect the fact that many grasses in this category are crops (Hamrick & Godt, 1997). The distribution of genetic diversity within such species could be highly influenced by the world-wide transfer of germplasm. Differences in genetic structure among species with different geographic ranges is reflected in nearly significant differences ($P=0.06$) in estimated gene flow between these groups. Mean *Nm* values (calculated by averaging *Nm* values

Table 1.6. *Allozyme diversity in several grass genera*

See Table 1.1 for description and calculation of genetic diversity parameters. Values in parentheses indicate the number of studies contributing to the mean.

Genus	H_{es}	H_{ep}	G_{ST}
Avena	0.314 (5)	0.180 (7)	0.571 (5)
Bromus	0.109 (7)	0.099 (7)	0.268 (9)
Festuca	0.246 (6)	0.140 (3)	0.158 (2)
Hordeum	0.238 (15)	0.166 (21)	0.301 (18)
Lolium	0.201 (12)	0.168 (20)	0.286 (12)
Oryza	0.289 (4)	0.268 (2)	0.330 (4)
Panicum	0.216 (4)	0.258 (2)	0.058 (2)
Secale	0.161 (9)	0.157 (10)	0.052 (11)
Sorghum	0.112 (5)	0.036 (4)	0.725 (3)
Triticum	0.131 (9)	0.073 (11)	0.482 (11)
Zea	0.264 (16)	0.204 (14)	0.156 (15)
Zizanium	0.083 (5)	0.096 (7)	0.390 (5)

across species rather than from the overall mean G_{ST}) were 1.44 for endemic or narrowly distributed species, 1.56 for regionally distributed species and 3.06 for widespread species.

The genetic structure of grasses differed significantly among species with different breeding systems. For outcrossing grasses, about 11% of total genetic diversity was found among their populations. Mixed-mating species exhibited similar genetic structure, with 16% of the total genetic diversity found among populations. In contrast, about 42% of the genetic diversity within selfers was found among populations. These differences in genetic structure among species with different mating systems is a consistent finding of reviews of the plant allozyme literature (Loveless & Hamrick, 1984; Hamrick & Godt, 1989). Indirect estimates of gene flow were lowest for selfing species (Nm=0.96) and highest for outcrossers (Nm=3.52) with mixed-mating species having an intermediate value (Nm=2.43). These differences in gene flow were highly significant ($P \leq 0.0001$).

Genetic diversity and structure within grass genera

Genetic diversity statistics were calculated for 12 grass genera (Table 1.6). These genera reflect nearly the entire range of genetic diversity found among all plant species. For example, *Avena* and *Oryza* have quite high levels of genetic diversity at the species level (H_{es}=0.314 and 0.289, respec-