Proc. Natl. Acad. Sci. USA
Vol. 93, pp. 5090–5093, May 1996
Evolution

Distribution of spontaneous plant hybrids

NORMAN C. ELLSTRAND*†, RICHARD WHITKUS*, AND LOREN H. RIESEBERG‡

*Department of Botany and Plant Sciences and Program in Genetics, University of California, Riverside, CA 92521-0124; and ‡Rancho Santa Ana Botanic Gardens, 1500 North College Avenue, Claremont, CA 91711

Communicated by Wyatt W. Anderson, University of Georgia, Athens, GA, December 22, 1995

ABSTRACT **Natural hybridization is a relatively common feature of vascular plant species and has been demonstrated to have played an important role in their evolution. Nonetheless, it is not clear whether spontaneous hybridization occurs as a general feature of all plant families and genera or whether certain groups are especially prone to spontaneous hybridization. Therefore, we inspected five modern biosystematic floras to survey the frequency and taxonomic distribution of spontaneous hybrids. We found spontaneous hybridization to be nonrandomly distributed among taxa, concentrated in certain families and certain genera, often at a frequency out of proportion to the size of the family or genus. Most of these groups were primarily outcrossing perennials with reproductive modes that stabilized hybridity such as agamospermy, vegetative spread, or permanent odd polyploidy. These data suggest that certain phylogenetic groups are biologically predisposed for the formation and maintenance of hybrids.**

The importance of interspecific hybridization as a feature of the micro- and macroevolutionary patterns of vascular plants is well known (1–6). Often the impression is that hybridization is ubiquitous and uniform among the higher plants. For example, Stebbins (3) wrote, "Occasional hybridization between recognizable species . . . is the rule in flowering plants," and "hybridization between previously isolated populations of plants is frequent in nearly every group which has been studied." Also, Raven (7) stated, "The formation of hybrids is a consistent feature of the adaptive system in many, if not most, groups of plants." More recently, Whitham *et al.* (8) asserted that "hybridization is common in all major plant taxonomic groups."

However, this prevailing view is controversial. Grant (4) pointed out that the frequency of natural hybridization in plants apparently varies with life history, pollination syndrome, breeding system, environmental disturbance, and genetic predisposition. For example, in a detailed analysis of the Concord flora, Mayr (9) found hybridization to be infrequent and restricted to a small number of genera. Recently, Arnold (10) has used the case history of introgression in Louisiana *Iris* to illustrate the variety of factors that may limit plant hybridization.

These conflicting views have lead us to the question of whether hybridization is a general feature of vascular plants, varying mostly with opportunity (i.e., the number of coexisting species) or whether certain groups are predisposed to hybridization. With the appearance of modern biosystematic floras, it is now possible to address the question quantitatively. Therefore, we surveyed five major biosystematic floras to assess the frequency and distribution of spontaneous (i.e., natural) hybridization among plant taxonomic groups.

MATERIALS AND METHODS

We chose five biosystematic floras that include information on spontaneous hybrids. We chose regions that have received intensive botanical scrutiny and cover at least 16,500 km^2 of land area. The floras represent two areas of Europe, the British Isles (11) and Scandinavia (12); two areas of North America, the Great Plains (13) and the Intermountain West (14); and one tropical region, the Hawaiian Islands (15). None of these floras include nonvascular plants. The flora from the Intermountain West region (14) is complete for only 64 families (about 40% of the total); we report only on the families presented.

For each flora, we counted all native and naturalized species, all genera, and all families. We also counted all spontaneous interspecific hybrids and hybrid species (including allopolyploids) that arose within the region represented by the flora. We did not count hybrids among subspecies, cases deemed doubtful by the flora, or probable primary intergradation as suggested by the flora. If a hybrid or hybrid species arose outside of the region of concern and was subsequently introduced into the region, it was not counted. If evidence that the same two species had hybridized more than once was presented, the combination was only counted once. For a few genera, a flora indicated multiple known hybrids, but without quantitative detail (for the British Isles: *Rubus*; for Scandinavia: *Agrostis* and *Euphrasia*; for the Great Plains: *Solidago*). We treated these cases conservatively, assigning four hybrids to each genus. Likewise, we treated apomictic microspecies complexes conservatively, counting only those hybrids specifically listed in the flora; thus, the number of hybrids for genera like *Taraxacum, Hieracium*, and *Rubus* are underestimated. The likely number of interspecific hybrids in these agamospermous groups would only exaggerate the nonrandom taxonomic distribution of hybridity reported below. We did not make any other judgments to modify our lists.

We recognize that all floras may have certain biases—that reporting of hybrids may vary with the systematic attention given to a region or taxon. With the exception of the flora of the British Isles, we acknowledge that our database represents a substantial underestimate of the total number of spontaneous hybrids. Nonetheless, the reporting of hybrids has been a common activity for well over 100 years. Thus, floras from botanically well-studied regions should give at least a crude "first-approximation" of the phylogenetic distribution of hybridization. Our data set is available on request.

RESULTS AND DISCUSSION

All five floras reported a substantial number of hybrids (Table 1). Spontaneous hybridization is not ubiquitous among plant families; in each flora, between 16 and 34% of the families have at least one reported hybrid (Table 1). Hybridization is further restricted to a much smaller fraction of genera; in each flora, only 6–16% of the genera have one or more reported hybrids (Table 1). Of those families with at least one hybrid, only about 8–15% of the families accounted for more than half of the hybrids in each flora (Table 2). Likewise, only a small subset of the genera with one or more hybrids, 5–21%,

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

†To whom reprint requests should be addressed.

Table 1. Number of taxa and hybrids in five biosystematic floras

Flora	Families*	Genera*	Species	Hybrids
British Isles	164	918	2950	642
Taxa with hybrids (%)	56 (34)	143 (16)		
Scandinavia	134	661	2172	207
Taxa with hybrids (%)	42 (31)	91 (14)		
Great Plains	171	855	2778	168
Taxa with hybrids (%)	36 (21)	72 (8)		
Intermountain*	64	492	2316	134
Taxa with hybrids (%)	20 (31)	57 (12)		
Hawaii	146	650	1817	169
Taxa with hybrids (%)	23 (16)	37 (6)		

Values in parentheses indicate percent of taxa with hybrids.
*See text.

Table 2. Taxonomic distribution of hybrids in five biosystematic floras

		Percent taxa accounting for >50% hybrids			
Flora	Hybrids	All families	Families with hybrids	All genera	Genera with hybrids
British Isles	642	3.7	10.7	1.0	6.3
Scandinavia	207	4.5	14.3	2.4	17.6
Great Plains	171	2.5	11.1	1.4	16.7
Intermountain*	134	4.7	15.0	2.4	21.1
Hawaii	169	1.4	8.7	0.3	5.4

*See text.

accounted for more than half of a flora's reported hybrids (Table 2).

Table 3 lists the six families and four genera with the most hybrids in each flora, what we designate as "important" families with hybrids and genera with hybrids. We did not list more because, with the exception of the British Flora (see Table 4), the number of hybrids per family and genus drops off so rapidly, the large number of "ties" would render the table meaningless. Many of the families occur as important families in more than one flora. Most are dicot families, but the Poaceae and Cyperaceae are important families with hybrids in multiple floras. Family size plays only a partial role in whether a large number of hybrids occur in it. A comparison of the two lists reveals that the most important genera often account for half or more of the hybrids in the most important families. Generally, the genera with the most hybrids occur in the families with the most hybrids; only one of the 20 important genera listed in Table 3 occurs in a family not listed. Clearly, the contributions of a family are often due to one or two genera with very large numbers of known hybrids.

In fact, many substantial families have no hybrids reported in the floras analyzed. The five largest for each flora are listed in Table 4. We do not claim that these groups are absolutely free of hybridization in a particular flora; rather, our point is that some large and well-studied families have a low incidence of reported hybridization relative to their size. Interestingly, a few families listed (Solanaceae, Brassicaceae, and Apiaceae) have no reported hybrids for more than one of the floras. Few other generalizations are apparent for the families in Table 4, except that almost all are insect-pollinated.

Given that families have some known hybridization, does the incidence of hybridization increase with the number of species in that family? To address this question, we ranked the top 10 families with hybrids in all five floras (9 families in the case of the Great Plains and Hawaii because of many ties in the 10th

Table 3. Six families and four genera with the most hybrids in five biosystematic floras

Flora	Families (rank)*	Hybrids	Genera (Family)	Hybrids
British Isles	Scrophulariaceae (6)	88	*Euphrasia* (Schrophulariaceae)	71
	Salicaceae (20)	55	*Salix* (Salicaceae)	55
	Rosaceae (3)	53	*Epilobium* (Onagraceae)	43
	Onagraceae (25)	46	*Rosa* (Rosaceae)	36
	Poaceae (2)	45		
	Asteraceae (1)	41		
Scandinavia	Cyperaceae (4)	30	*Carex* (Cyperaceae)	25
	Poaceae (2)	25	*Salix* (Salicaceae)	15
	Asteraceae (1)	18	*Viola* (Violaceae)	7
	Salicaceae (17)	15	*Calamagrostis* (Poaceae)	5
	Rosaceae (3)	13		
	Dryopteridaceae (31)	9		
Great Plains	Asteraceae (1)	29	*Amaranthus* (Amaranthaceae)	12
	Poaceae (2)	20	*Aster* (Asteraceae)	10
	Rosaceae (7)	15	*Rosa* (Rosaceae)	9
	Fabaceae (3)	14	*Verbena* (Verbenaceae)	8
	Amaranthaceae (31)	13		
	Verbenaceae (34)	8		
Intermountain†	Asteraceae (1)	43	*Penstemon* (Scrophulariaceae)	10
	Scrophulariaceae (3)	19	*Carex* (Cyperaceae)	9
	Poaceae (1)	19	*Castilleja* (Scrophulariaceae)	7
	Cyperaceae (4)	11	*Oryzopsis* (Poaceae)	7
	Boraginaceae (5)	7	*Stipa* (Poaceae)	7
	Orchidaceae (15)	6		
Hawaii	Gesneriaceae (9)	67	*Cyrtandra* (Gesneriaceae)	67
	Asteraceae (1)	49	*Dubautia* (Asteraceae)	24
	Campanulaceae (4)	12	*Bidens* (Asteraceae)	10
	Rubiaceae (7)	9	*Clermontia* (Campanulaceae)	8
	Euphorbiaceae (12)	4		
	Lamiaceae (5)	4		

*In terms of species number.
†See text.

Table 4. Five largest families with no reported hybrids in the flora consulted

Flora	Families	Genera	Species
British Isles	Solanaceae	12	29
	Campanulaceae	9	27
	Crassulaceae	5	26
	Caprifoliaceae	6	21
	Oxalidaceae	1	14
Scandinavia	Apiaceae	40	52
	Chenopodiaceae	10	39
	Geraniaceae	2	16
	Solanaceae	8	14
	Gentianaceae	5	14
Great Plains	Cyperaceae	13	113
	Brassicaceae	36	99
	Ranunculaceae	12	53
	Apiaceae	31	52
	Caryophyllaceae	17	50
Intermountain	Liliaceae	23	60
	Lamiaceae	24	45
	Solanaceae	9	32
	Asclepiadaceae	4	21
	Rubiaceae	4	14
Hawaii	Rutaceae	3	55
	Solanaceae	12	35
	Piperaceae	2	27
	Brassicaceae	10	23
	Scrophulariaceae	15	22

rank) and used Spearman's rank correlation to compare with their relative size. We analyzed only the 10 largest families with hybrids because these few families always contain the bulk of the hybrids (at least 72%). In all five cases, the correlation was positive, indicating a relationship between number of hybrids and family size. However, the relationship was strong and significant for only two of the floras (Great Plains, $r = 0.73$, $P = 0.02$; Intermountain, $r = 0.73$, $P = 0.02$), marginally significant for one (Scandinavia, $r = 0.59$, $P = 0.0599$), and weak and not significant for the other two (British Isles, $r = 0.21$, $P = 0.54$; Hawaii, $r = 0.36$, $P = 0.31$).

Do these trends reflect biology, taxonomic uncertainty, or biases of the authors of the floras surveyed? Artificial heterogeneity would be an outcome of the latter two factors. For example, the genus *Euphrasia* has been interpreted as a series of narrowly delimited species with intermediates reflective of hybridization (16) or of a smaller number of more broadly defined species based on how readily taxa hybridize (17). In the genera *Salix* and *Carex*, many hybrids have been proposed in the literature, leading to an attitude that hybrids are common, but more critical studies have shown that reevaluation of claims of widespread hybridization are necessary (18–20). We accept that taxonomic revisions will be required in many groups and treat this factor as a random variable. Indeed, genera that are well understood in certain floras also occur in Table 4 (e.g., *Epilobium, Penstemon, Dubautia*, Hawaiian *Bidens*). One way of testing for authors' biases is to contrast our geographically and floristically similar floras (written by different authors). We compared our lists of families with hybrids for the two Palearctic floras: the British flora (11) and the Scandinavian flora (12). The two lists show high concordance. Most (86%) families with hybrids in the Scandinavian flora also have at least one listed hybrid in the British flora, but those with no known British hybrid have only a single hybrid known in Scandinavia. Similarly, most (68%) British families with hybrids also have at least one listed Scandinavian hybrid; two-thirds (12 of 18) of those with no hybrids in the Scandinavian flora only have a single hybrid known in the British Isles. Therefore, the major difference between the hybrid lists for these floras lies in families with a single hybrid, those that least influence our trends.

A comparison of our Great Plains data with our Intermountain data shows a similar trend. Most (75%) families with hybrids in the Intermountain flora also have one or more listed hybrids in the Great Plains flora; in the opposite situation, 79% of the appropriate Great Plains families have at least one listed hybrid in the Intermountain flora.

The hybrid flora of the British Isles is by far the most extensively studied (21). Thus, we used this sample for closer scrutiny of genera with large numbers of spontaneous hybrids. In Table 5, we list the 10 most important genera with hybrids and some of their characteristics. These genera contain well over half of the spontaneous hybrids of the British Isles.

Certain trends are obvious in Table 5. With the exception of *Euphrasia*, all of the genera are typically perennials. All genera are typically outcrossing, often with enforced outcrossing (e.g., dioecy in the case of *Salix*, self-incompatibility in the sexual species of *Taraxacum* and *Rubus*). Pollen vectors, however, are varied, including wind, water, and insects. Finally, again with the exception of *Euphrasia*, all of the genera have mechanisms for clonal reproduction, mostly by vegetative spread, but also by agamospermy and permanent odd polyploidy. These trends are also present in the genera listed in Table 3.

These trends make sense. Outcrossing species are more likely to have the opportunity to hybridize. Perennial hybrids are more likely to be found and identified. Clonal reproduction, regardless of mechanism, will stabilize hybridity (cf. ref. 4). However, while outcrossing may foster hybridization and clonal reproduction may stabilize hybrids, they are not necessarily sufficient to allow a genus to engage in frequent, spontaneous hybridization. For example, many large, characteristically perennial, outcrossing, clonal genera in the British Isles flora (e.g., *Allium, Epipactis*, and *Trifolium*) have little or no record of hybridization.

Our results demonstrate that hybrids occur nonrandomly over families and genera. However, we were limited to the

Table 5. Ten genera with the most reported hybrids in the British flora

Genus	Hybrids	Habit	Pollen vector	Breeding system	Opportunity for clonal reproduction
Euphrasia	71	Annual herb	Insect	Outcross, self	None
Salix	55	Tree shrub	Insect	Outcross	Vegetative spread
Epilobium	43	Annual-perennial herb	Insect	Outcross, self	Vegetative spread
Rosa	36	Shrub	Insect	Outcross, self	Vegetative spread, permanent odd polyploidy
Carex	34	Perennial herb	Wind	Outcross, self	Vegetative spread
Rumex	29	Annual-perennial herb	Wind	Outcross	Vegetative spread
Potamogeton	25	Perennial herb	Wind, water	Outcross	Vegetative spread
Dactylorhiza	19	Perennial herb	Insect	Outcross	Vegetative spread
Taraxacum	13	Perennial herb	Insect	Apomict, outcross	Agamospermy
Rubus	'many'	Perennial herb, shrub	Insect	Apomict, outcross	Agamospermy, vegetative spread

information that is readily obtainable. For example, we were surprised to find that few modern floras contain the biosystematic information necessary to conduct our survey. Modern floras must meet the trade-off of utility for field use versus a repository of information for evolutionary and ecological biologists. The major current floras of the British Isles (11, 22) are a good example of providing ecological, evolutionary, and genetic information. Even in the floras we surveyed, we were unable to assess whether ecological factors such as disturbance or ecotones were correlated with the occurrence or hybrids. Also, we note that our only tropical flora, that of Hawaii, has the lowest frequency of hybrids. While this might be a function of this particular flora or of tropical floras in general, it is more likely a function of the fact that tropical floras have received less biosystematic attention than temperate floras.

CONCLUSIONS

We found spontaneous hybridization to be common in five major biosystematic floras. However, it is clear that the occurrence of spontaneous hybridization is not universal, but concentrated in a small fraction of families and an even smaller fraction of genera. These genera may be viewed as potential "hot spots" of contemporary hybridization (but we concede that a few may simply represent cases of taxonomic uncertainty). These genera are generally characterized by perennial habit, outcrossing breeding system, and reproductive modes that are able to stabilize hybridity.

The taxonomic distribution of spontaneous hybridization leads us to certain conclusions. It is not as ubiquitous as frequently believed. Therefore, hybridization is not likely to be a common adaptive mechanism. We recognize that hybridization is an important factor in plant evolution; many plant species apparently have hybrid ancestry. However, hybridization need not be ubiquitous or adaptive to be evolutionarily important. A single, partially fertile, hybrid individual can suffice as progenitor of a new species. Several species or even genera may evolve from the resulting hybrid lineage. At any given time, only a tiny fraction of hybrids may give rise to new lineages. Still, that tiny fraction, summed over thousands of generations, can make a considerable impact in evolutionary time.

Likewise, it is not hybridization *per se* that is necessarily adaptive. Adaptive or not, evolution following hybridization will occur most frequently in those groups in which hybridization is most common, that is, groups characterized by (*i*) outcrossing and incomplete reproductive isolation so that hybridization occurs among species, (*ii*) sufficient developmental and ecological flexibility so that hybrids develop to maturity, and (*iii*) perennial habit and apomictic or vegetative reproduction so that hybrids, even if partially sterile, have a long time for some reproductive success. The higher frequency of hybrid ancestry in plant species compared with that in animal species may have more to do with fundamental differences between animals and plants—types of reproductive isolation, developmental flexibility, and opportunities for vegetative reproduction—than the adaptive nature of the plant hybrid genome.

We thank S. Hegde, D. Elam, P. Arriola, J. Clegg, and two reviewers for their comments that improved an earlier draft of this article. This research was supported, in part, by National Science Foundation Mid-Career Fellowship DEB-92022581 (to N.C.E.) and National Science Foundation Grants BSR-9019872 (to L.H.R.) and DEB-9204261 (to R.W.).

1. Lotsy, J. P. (1916) *Evolution by Means of Hybridization* (Nijhoff, Dordrecht, The Netherlands).
2. Anderson, E. (1949) *Introgressive Hybridization* (Wiley, New York).
3. Stebbins, G. L. (1959) *Proc. Am. Philos. Soc.* **103,** 231–251.
4. Grant, V. (1981) *Plant Speciation* (Columbia Univ. Press, New York), 2nd Ed.
5. Arnold, M. L. (1992) *Annu. Rev. Ecol. Syst.* **23,** 237–261.
6. Rieseberg, L. H. & Ellstrand, N. C. (1993) *Crit. Rev. Plant Sci.* **12,** 213–241.
7. Raven, P. H. (1976) *Syst. Bot.* **1,** 284–316.
8. Whitham, T. G., Morrow, P. A. & Potts, B. M. (1991) *Science* **254,** 779–780.
9. Mayr, E. (1992) *Am. J. Bot.* **79,** 222–238.
10. Arnold, M. L. (1993) *Plant Genet. Newsl.* **9** (2), 14–17.
11. Stace, C. A. (1991) *New Flora of the British Isles* (Cambridge Univ. Press, Cambridge, U.K.).
12. Mossberg, B., Stenberg, L. & Ericsson, S. (1992) *Den Nordiska Floran* (Wahlström & Widstrand, Solna, Sweden).
13. Great Plains Flora Association (1986) *Flora of the Great Plains* (Univ. of Kansas Press, Lawrence.
14. Cronquist, A., Holmgren, S. H., Holmgren, N. H., Reveal, J. L. & Holmgren, P. K. (1972–1974) *Intermountain Flora* (Hafner, New York), Vols. 1 and 3, Parts B, 4, 5, and 6.
15. Wagner, W. L. (1990) *Manual of the Flowering Plants of Hawaii* (Univ. of Hawaii Press, Honolulu).
16. Snell, P. D. & Yeo, P. F. (1970) *Bot. J. Linn. Soc.* **63,** 189–234.
17. Karlsson, T. (1976) *Bot. Not.* **129,** 49–60.
18. Argus, G. W. (1986) *Syst. Bot. Monogr.* **9,** 1–170.
19. Meikle, R. D. (1992) *Proc. R. Soc. Edinburgh B* **98,** 13–20.
20. Cayouette, J. & Catling, P. M. (1992) *Bot. Rev.* **58,** 351–438.
21. Stace, C. A. (1975) *Hybridization and the Flora of the British Isles* (Academic, London).
22. Clapham, A. R., Tutin, T. G. & Moore, D. M. (1987) *Flora of the British Isles* (Cambridge Univ. Press, Cambridge, U.K.), 3rd Ed.