

## THE "HYBRID BRIDGE" HYPOTHESIS: HOST SHIFTING VIA PLANT HYBRID SWARMS

The mechanisms by which herbivorous insects acquire or shift to new host varieties or species are basic to understanding the evolution of plant-herbivore interactions. These mechanisms should also apply to plant parasites, pathogens, and perhaps even pollinators. Presently, host shifting is explained by either preadaptation or mutation hypotheses that require herbivores to make a single jump in shifting from one host species to another. Preadaptation hypotheses suggest that herbivores are preadapted to shift onto new host species but are prevented from doing so by the absence of these host species. When the barrier to shifting is removed following changes in either the herbivore's or the host's distribution (Tabashnik 1983; Thomas et al. 1987), a shift may result. In contrast, when herbivores are not preadapted to a host, one or more key mutations must occur to allow the herbivore to recognize and survive on the new host species (Bush 1974, 1975; Futuyma 1983; Jermy 1984).

These hypotheses do not consider the potential importance of naturally occurring hybrid plants that morphologically, genetically, and spatially bridge gaps between parental species and may allow herbivores to shift in a series of gradual steps. Based on our studies of insect distributions on cottonwood trees, we propose the "hybrid bridge hypothesis," which argues that the presence of plant hybrid intermediates facilitates host shifting by herbivores such that host shifting is more likely to occur in their presence than in their absence. Although we limit the present discussion to plant hybrids, a recent study by Le Brun et al. (1992) suggests that *Barbus meridionalis* × *barbus* fish hybrids may play a similar role in facilitating host shifting by gill parasites between the parental species.

The hybrid bridge hypothesis is not mutually exclusive of either preadaptation or mutation hypotheses and likely enhances both. For example, when allopatric distribution of plant species is the only barrier to host shifting, preadaptation hypotheses predict that herbivorous insects are stymied in shifting from one species to another unless their distributions become sympatric. However, if these plants hybridize such that the gap between their distributions is "spatially bridged" by hybrid intermediates (see, e.g., Potts 1986; DePamphilis and Wyatt 1989; Keim et al. 1989), herbivores could shift onto the new host species via these intermediates even though the plant species remain allopatric.

Similarly, hybrids may bridge the "morphological and/or genetic gaps" between plant species so that herbivores experience novel morphologies and genomes in a series of gradual steps. Because hybrid swarms may include individual plants with all possible combinations of the parental genomes (i.e., pure parentals,

F<sub>1</sub>'s, and complex backcrosses with varying proportions of each genome), herbivores colonizing these hybrids encounter various levels of the novel host's genome without having to shift directly onto the novel host species. This may be particularly important where the factors controlling successful host shifts are polygenic; hybrid plants can permit a gradual shift toward the new host as the necessary mutations accumulate.

To understand how plant hybrid intermediates may facilitate a host shift, consider a hypothetical situation in which host shifting requires a single mutation in an insect coupled with its previous exposure to the new host. This situation is not implausible as there is evidence to suggest that survival on new hosts is under the control of one or a few genes (Hatchett and Gallun 1970) and that previous exposure to a host species induces a preference for that host (Jermy et al. 1968; Jaenike 1982; Boer and Hanson 1984; Papaj and Prokopy 1988). In our example, insects on the old host that acquire the mutation to survive on the new host do not recognize it as "food," having never encountered it before, and the host shift is thwarted. However, if hybridization occurs between old and new host species, hybrid intermediates may have the recognition cues and survival factors for both plant species. Thus, when the mutation enabling survival on the new host arises, either before or after hybrids are colonized, insects on hybrid hosts gain the necessary exposure to recognition cues of the new host and can subsequently shift to the new host species.

If hybridization were rare, its potential role in host shifting would be greatly diminished; however, hybridization between plant species is common and well documented. For example, *Betula* species hybridize widely in Europe (Lotsy 1925, 1931), as do species of *Geum* and *Salix*; *Melandrium* in Sweden; *Nothofagus* in New Zealand; and *Pinus*, *Quercus*, *Gilia*, *Iris*, and *Diplacus* in western North America (see Grant 1981). *Eucalyptus* hybridize in Australia (Griffin et al. 1988), and *Crataegus* (Phipps 1984) and *Populus* (Eckenwalder 1984) hybridize extensively in North America. Past hybridization events are thought to account for 30%–80% of extant plant species (Stace 1987; see references in Wendel et al. 1991).

We predict that host shifting will be affected by the pattern of plant hybridization as this determines the degree to which hybrid genotypes span the genetic gap between plant species. For example, in the progression from F<sub>1</sub> sterility, to unidirectional introgression, to bidirectional introgression, the genetic gaps between parental species diminish to form a continuum of intermediates. This point is illustrated in figure 1, beginning with a hypothetical system of nonhybridizing plant species A and B (fig. 1A). If these species hybridize to produce sterile F<sub>1</sub> offspring, all hybrids contain 50% of the genomes of the parental species (fig. 1B) (see, e.g., Ownbey 1950; Cook 1979; Weber and Campbell 1989). The production of sterile F<sub>1</sub> hybrids should facilitate host shifting, but two large genetic gaps remain. An intermediate form of hybridization known as unidirectional introgression occurs when fertile F<sub>1</sub>'s backcross only to one of the parental species to produce a continuum of hybrid genotypes from that parent to F<sub>1</sub>'s, but a large genetic gap remains between F<sub>1</sub>'s and the other parental species (fig. 1C) (see, e.g., Crawford 1974; Jones 1978; Keim et al. 1989). This pattern should

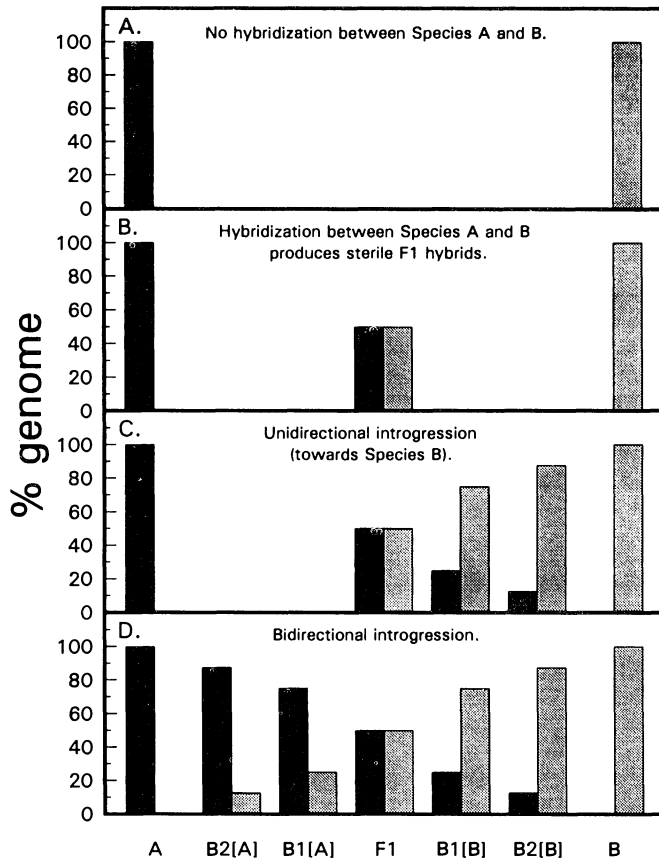


FIG. 1.—The various patterns of hybridization that result in different morphological and genetic gaps between species. *A*, In the absence of hybridization the gap between species *A* and *B* is greatest, and current models of host shifting assume this is the general pattern. *B*, When hybridization between species *A* and *B* produces sterile  $F_1$ 's, the gap between species is reduced to two smaller gaps. *C*, Unidirectional hybridization to *B* produces a continuum of hybrid genotypes between *B* and  $F_1$  hybrids, but a large gap remains between  $F_1$ 's and *A*. *D*, Bidirectional introgression produces a complete morphological and genetic continuum of hybrids from *A* to *B* with no gaps.

facilitate host shifting halfway between the two species, but the remaining gap still represents a barrier to host shifting in gradual steps. Last,  $F_1$  hybrids may backcross to both of the parental species in a pattern of bidirectional introgression resulting in a complete continuum of hybrid genotypes (fig. 1*D*) (see, e.g., Potts and Reid 1985; Potts 1986; Warwick et al. 1989). A genetic continuum with no gaps should be most likely to facilitate host shifting.

As hybrids also typically have intermediate morphologies, the above arguments, based on hybrids bridging genetic gaps, should also apply to hybrids

bridging morphological gaps (see, e.g., Potts and Reid 1985, 1988; Keim et al. 1989). This should be especially true when the morphologies of the hybridizing species are as different as cottonwoods (Keim et al. 1989) or the more extreme *Eucalyptus* described by Potts and Reid (1985, 1988).

#### TESTING THE HYBRID BRIDGE HYPOTHESIS

Existing studies do not show an overall pattern of herbivore distribution in hybrid zones. Insect species and their densities have been reported as being greater on hybrid plants than on the parental plant species (Drake 1981; Whitham 1989; Whitham et al. 1991). Similar reports occur for parasites of animal hybrids (Sage et al. 1986; Dupont and Crivelli 1988). However, other studies have found that herbivore densities may be the same or lower on hybrids than on the parental species (McClure 1985; Boecklen and Spellenberg 1990). In other cases, herbivore species and numbers on hybrid hosts reflect the degree to which hybrids resemble the parental species (Manley and Fowler 1969; Roskam and van Uffelen 1981).

These mixed results can be partially attributed to a lack of specific knowledge in these diverse systems. Studies do not always compare the performance and distribution of herbivores on hybrid hosts relative to their pure hosts (Caldbeck et al. 1978; Burkot and Benjamin 1979; Abrahamson et al. 1990). Furthermore, different categories of hybrids are not usually distinguished even though their susceptibilities to herbivores may be very different. For example,  $F_1$  hybrids may be highly resistant while backcross hybrids may be susceptible (Paige et al. 1990), so valid comparisons between different hybrid systems need to consider hybrid category. For these reasons, all we can clearly conclude from the current literature is that insect herbivores can incorporate hybrid plants into their host range. Consequently, our development and discussion of the hybrid bridge hypothesis are restricted primarily to the galling insects of cottonwoods for which the pattern of hybridization is known.

#### *Galling Arthropods on Cottonwoods*

Along the drainage of the Weber River in northern Utah, Fremont cottonwood, *Populus fremontii*, grows at elevations of about 1,300–1,500 m, and narrowleaf cottonwood, *Populus angustifolia*, grows at elevations of about 1,400–2,300 m. Between the communities of Riverdale and Mountain Green, there is a 13-km zone where these species overlap in distribution and hybridize. In this hybrid swarm DNA analyses of trees have identified the pattern of hybridization as unidirectional;  $F_1$  individuals are produced that, in turn, backcross only to narrowleaf cottonwood (Keim et al. 1989). Thus, the form of this swarm is similar to that shown in figure 1C, where species A and B correspond to Fremont and narrowleaf cottonwood, respectively.

This system provides a critical test of the hybrid bridge hypothesis because the unidirectional pattern of introgression generates both a distinct genetic and morphological gap and also a continuum of genotypes and morphologies at the same site. The hypothesis predicts that host shifting is more likely to occur between narrowleaf cottonwood and  $F_1$  hybrids because of the presence of a contin-

uum of intermediates. However, the lack of intermediates between  $F_1$  hybrids and Fremont cottonwood leaves a large gap that could represent a barrier to host shifting. Thus, our a priori prediction was that hybrid intermediates would facilitate host shifting from narrowleaf to  $F_1$ 's but the gap between  $F_1$ 's and Fremont would inhibit shifting between these latter two groups.

Data on herbivore distributions were collected using timed censuses on 30 trees in each of four morphological categories: Fremont,  $F_1$ 's, backcross hybrids, and narrowleaf. Trees were categorized based on a combination of plant traits that had been identified using DNA analyses and experimental crosses between known parents (Keim et al. 1989). Because these categories are not equally distributed in the hybrid zone, sampling was designed to reduce potential site effects. For example, approximately equal numbers of trees from the center and either end of the 13-km hybrid zone were sampled for each category. Reproductively mature trees were surveyed for 2 min for each herbivore species. Since trees ranged in height from 5 to 30 m, the portion surveyed for each tree was standardized by examining only the lowest 3 m of foliage on all sides of the tree.

Gall-forming herbivores were surveyed because they are typically host-specific and were not likely to be found on both cottonwood species, their distinct galls allowed accurate censusing, and their galls were a long-term record of their presence even after the herbivore was gone. Surveys were conducted in late July and early August, when gall formers had produced their galls yet before leaf abscission occurred. The eight species censused were not select examples from our survey; they represented all of the galling herbivores surveyed indigenous to either Fremont or narrowleaf.

The distribution of galling herbivores supports three distinct predictions of the hybrid bridge hypothesis. First, the prediction that galling herbivores are unable to shift from Fremont onto  $F_1$  hybrids, because of the absence of backcross intermediates, is supported by the distributions of the galling species surveyed indigenous to Fremont. None of the leaf-galling aphids *Pachypappa pseudobursa*, *Pemphigus populicaulis*, *Pemphigus populitransversus*, and *Pemphigus* sp. had successfully shifted from Fremont to  $F_1$ 's or beyond to narrowleaf cottonwood (fig. 2). Although characteristic signs of their failed galls were found on  $F_1$ 's, which signified that these aphids naturally encounter and recognize hybrid trees as hosts, each species has thus far been unsuccessful in shifting from Fremont onto  $F_1$  hybrids.

The second prediction, that the presence of backcross intermediates enables herbivores to shift from narrowleaf onto  $F_1$  hybrids, is fulfilled by each of the galling species surveyed indigenous to narrowleaf. Three leaf-galling aphid species (*Pemphigus populiglobuli*, *Pemphigus betae*, and *Thecabius populimonilis*) and a bud-galling mite (*Aceria* sp.) have successfully shifted across backcross intermediates onto  $F_1$  hybrids (fig. 3).

The third prediction is that herbivores that have shifted from narrowleaf onto  $F_1$ 's via backcross intermediates are unable to shift further from  $F_1$ 's to Fremont because of the absence of intermediates between these two categories. Again, for the galling species indigenous to narrowleaf that have all shifted to  $F_1$ 's, none have shifted onto Fremont (fig. 3). Each of the three predictions tested in this

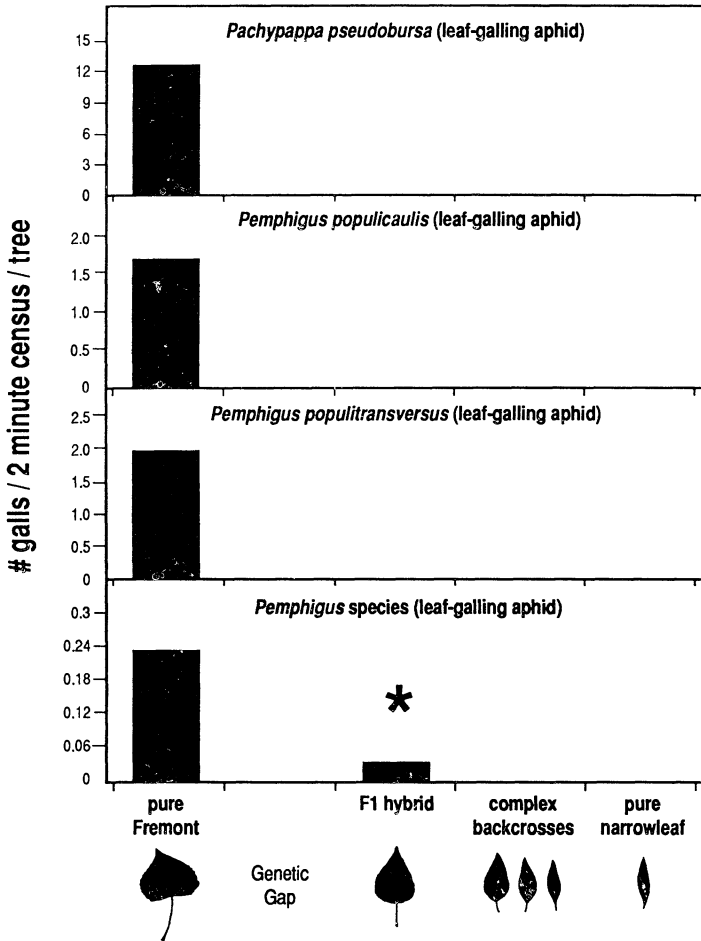


FIG. 2.—The distributions of four aphid species indigenous to Fremont cottonwood show that these species have not bridged the morphological and genetic gap to  $F_1$  hybrids. The sole exception to this pattern (*asterisk*) was a single *Pemphigus* sp. gall found on an  $F_1$  hybrid.

cottonwood system has been supported four times by different galling species, and the same patterns have been observed in a second year of censusing.

Although the above patterns support the hybrid bridge hypothesis, as an alternative hypothesis, dominance of narrowleaf genes affecting herbivore preference also could explain the observed distributions of galling insects (M. D. Rausher, personal communication). For example, if narrowleaf genes for these traits are dominant to those of Fremont, insects may perceive hybrids as “narrowleaf.” This alternative could explain why galling species native to narrowleaf trees occur

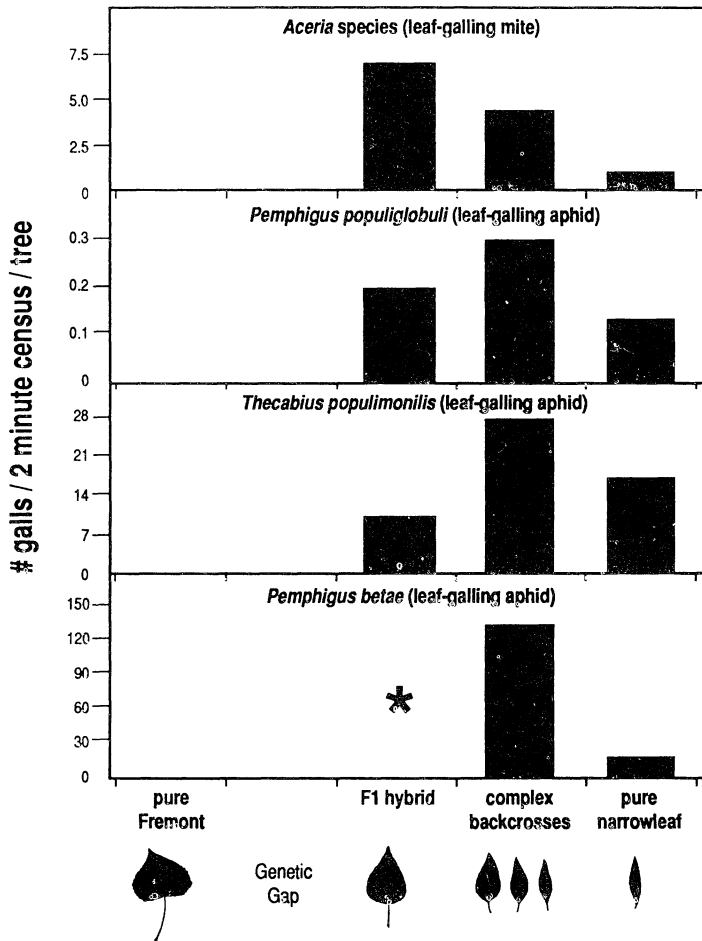


FIG. 3.—The distributions of four species (three aphids and one mite) indigenous to narrowleaf cottonwood show that these species have shifted to F<sub>1</sub> hybrids via hybrid intermediates, but they have not bridged the gap between F<sub>1</sub>'s and Fremont cottonwood where hybrid intermediates are absent. (The asterisk indicates low densities of only 17 galls on 30 surveyed trees.)

on hybrids but do not occur on Fremont. It might also explain why species native to Fremont are not observed on hybrids.

Two lines of evidence argue against this hypothesis. First, it is unlikely that the eight species studied (one mite and seven aphid species) use the same recognition cues to locate hosts and that all narrowleaf cues are dominant, although this has yet to be tested. Second, if insects perceive hybrid trees as "narrowleaf," colonization rates by these insects should be the same for the sympatric F<sub>1</sub>,

backcross, and narrowleaf trees that co-occur in the hybrid zone. However, Moran and Whitham (1990) showed that the fall migrants of *P. betae* heavily colonize backcross hybrids, whereas  $F_1$  hybrids are avoided.

#### DISCUSSION AND CONCLUSIONS

##### *Assumptions*

The hybrid bridge hypothesis has two basic assumptions. First, plants must hybridize, and hybridization must be common if this mechanism is more than just a rare occurrence. This assumption is met since hybridization is common to all major plant taxonomic groups (Grant 1971). Second, herbivores must have the capacity to shift onto hybrid hosts. This point is supported by our study and numerous others (e.g., Manley and Fowler 1969; Drake 1981; Roskam and van Uffelen 1981; McClure 1985; Whitham 1989; Boecklen and Spellenberg 1990; Whitham et al. 1991). Further, the use of hybrids by herbivores is not restricted to a single plant taxon but is widespread (e.g., the above citations include deciduous trees in North America, broadleaf evergreens in Australia, and conifers in Japan).

##### *Predictions*

Based on our initial tests of the hybrid bridge hypothesis, we make several predictions. First monophagous herbivores are more likely than polyphagous herbivores to benefit from the presence of a hybrid bridge for host shifting. These groups represent opposite ends of a gradient along which the value of hybrid intermediates in facilitating host shifts will change. Monophagous herbivores are best exemplified by gall formers, which are typically host-, organ-, and tissue-specific and are perhaps the most specialized guild of phytophagous insects (Shorthouse 1982). Because of the tight relationship necessary for the herbivore to elicit a galling response from its host plant, we predict that gall formers are the least likely of all feeding guilds to bridge the intervening genetic gap onto a new host species in the absence of hybrid intermediates. In contrast, polyphagous herbivores have already shown an ability to span genetic gaps between plant species by feeding on plants in different families, several genera, or distantly related species in the same genus.

Second, hybridizing plant species will share more herbivores than nonhybridizing species, for example, cynipid gall wasps on oaks (*Quercus* sp.). Oaks frequently hybridize within a subgenus but not between subgenera, which reflects the distribution of cynipid wasps that usually attack only one or a few closely related oak species, always within the same subgenus (Cornell and Washburn 1979). However, this pattern may merely reflect the genetic similarity of the hybridizing species and not the fact that they hybridize. To test the prediction critically, comparisons need to be made of the herbivores of two plant species at sites where they hybridize and at other sites where they do not.

Third, the pattern of hybridization allows for specific predictions. When the hybrid bridge is symmetrical (i.e., when  $F_1$  sterility or bidirectional introgression



occurs),  $F_1$ 's should have the same number of herbivore species in common with both of the parental species. When the bridge is asymmetrical (i.e., when unidirectional introgression occurs),  $F_1$ 's will share more herbivore species with the parent to which introgression occurs than with the parental species with which hybridization does not occur, which is supported by the present study.

### *Implications*

The hybrid bridge hypothesis may have important implications for the preservation of biodiversity. First, by bridging the spatial, morphological, and/or genetic gaps between parental species, hybrids could have a greater species richness than either of the parents because the hybrids can accumulate the fauna of both parents (e.g., hybrid fish, Dupont and Crivelli 1988; hybrid plants, Whitham et al. 1991; but see Boecklen and Spellenberg 1990). This fauna includes not only herbivores and pathogens but also their associated predators and parasites. Therefore, by conserving hybrid zones, it can be argued that we preserve both important centers of plant evolution and focus points of biodiversity (Whitham et al. 1991).

Second, by facilitating host shifting, hybrid zones may also promote speciation. Host shifting has been suggested as one way (Bush 1969, 1974, 1975) in which sympatric speciation could occur through habitat diversification (see also Maynard Smith 1966; Tauber and Tauber 1977; Felsenstein 1981; Rice 1987). Because the new host represents an environment distinct from the old host, herbivore populations on old and new hosts may be subject to divergent selection pressures that could then lead to reproductive isolation, race formation, and eventual speciation. Thus, if hybrid zones are centers of plant speciation, they may also be centers of insect speciation as well. For example, Moran and Whitham (1988) have suggested that race formation in the leaf-galling aphid *Pemphigus betae* may, in part, be a consequence of hybridization between Fremont and narrowleaf cottonwood. In the hybrid zone where susceptible hosts are common, this aphid annually alternates between cottonwoods and herbaceous plants. In the pure narrowleaf zone where trees are more resistant, *P. betae* remains almost solely on herbaceous plants. Reciprocal transfer experiments in the field and the performance of aphid clones in the lab argue that the differences in these life cycles are genetically based (Moran and Whitham 1988; Moran 1991). If hybrids facilitate host shifting and host shifting leads to genetic differentiation, then hybrid zones could also play a role in insect speciation.

### ACKNOWLEDGMENTS

We thank K. Christensen, N. Cobb, R. DeClerck-Floate, G. W. Fernandes, C. Gehring, J. Maschinski, S. Mopper, P. Price, M. Rausher, P. Service, D. Siemens, S. Stein, and three anonymous reviewers for their valued comments. We greatly appreciate the use of facilities provided by PacifiCorp during our field seasons. Financial support was provided by National Science Foundation (NSF) grants BSR-8906391, BSR-8918380, BSR-9107042, U.S. Department of Agriculture (USDA) grant 91-37302-6224, and a Sigma Xi Grant-in-Aid of Research.

## LITERATURE CITED

- Abrahamson, L. P., E. H. White, C. A. Nowak, R. D. Briggs, and D. J. Robison. 1990. Evaluating hybrid polar clonal growth potential in a three-year-old genetic selection field trial. *Biomass* 21:101–114.
- Boecklen, W. J., and R. Spellenberg. 1990. Structure of herbivore communities in two oak (*Quercus* spp.) hybrid zones. *Oecologia* (Berlin) 85:92–100.
- Boer, G. de, and F. E. Hanson. 1984. Food plant selection and induction of feeding preferences among host and non-host plants in larvae of the tobacco hornworm *Manduca sexta*. *Entomologica Experimentalis et Applicata* 35:177–193.
- Burkot, T. R., and D. M. Benjamin. 1979. The biology and ecology of the cottonwood leaf beetle, *Chrysomela scripta* (Coleoptera: Chrysomelidae), on tissue cultured hybrid *Aigeiros* (*Populus* × *Euramericana*) subclones in Wisconsin. *Canadian Entomologist* 111:551–556.
- Bush, G. L. 1969. Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). *Evolution* 23:237–251.
- . 1974. The mechanism of sympatric host race formation in the true fruit flies (Tephritidae). Pages 3–23 in M. J. D. White, ed. *Genetic mechanisms of speciation in insects*. Australian and New Zealand Book, Sydney.
- . 1975. Sympatric speciation in phytophagous parasitic insects. Pages 187–207 in P. W. Price, ed. *Evolutionary strategies of parasitic insects and mites*. Plenum, New York.
- Caldbeck, E. S., J. S. McNabb, Jr., and E. R. Hart. 1978. Poplar clonal preferences of the cottonwood leaf beetle. *Journal of Economic Entomology* 71:518–520.
- Cook, C. D. K. 1970. Hybridization in the evolution of *Batrachium*. *Taxon* 19:161–166.
- Cornell, H. V., and J. O. Washburn. 1979. Evolution of the richness-area correlation for cynipid gall wasps on oak trees: a comparison of two geographic areas. *Evolution* 33:257–274.
- Crawford, D. J. 1974. A morphological and chemical study of *Populus acuminata* Rydberg. *Brittonia* 26:79–89.
- DePamphilis, C. W., and R. Wyatt. 1989. Hybridization and introgression in buckeyes (*Aesculus*: Hippocastanaceae): a review of the evidence and a hypothesis to explain long-distance gene flow. *Systematic Botany* 14:593–611.
- Drake, D. W. 1981. Reproductive success of two *Eucalyptus* hybrid populations. I. Generalized seed output model and comparison of fruit parameters. *Australian Journal of Botany* 29:25–35.
- Dupont, F., and A. J. Crivelli. 1988. Do parasites confer a disadvantage to hybrids? a case study of *Alburnus alburnus* × *Rutilus rutilus*, a natural hybrid of Lake Mikri Prespa, northern Greece. *Oecologia* (Berlin) 75:587–592.
- Eckenwalder, J. E. 1984. Natural intersectional hybridization between North American species of *Populus* (Salicaceae) in sections *Aigeiros* and *Tacamahaca*. II. Taxonomy. *Canadian Journal of Botany* 62:325–335.
- Felsenstein, J. 1981. Skepticism towards Santa Rosalia, or why are there so few kinds of animals? *Evolution* 35:124–138.
- Futuyma, D. J. 1983. Selective factors in the evolution of host choice by phytophagous insects. Pages 227–244 in S. Ahmad, ed. *Herbivorous insects*. Academic Press, New York.
- Grant, V. 1971. *Plant speciation*. Columbia University Press, New York.
- . 1981. *Plant speciation*. 2d ed. Columbia University Press, New York.
- Griffin, A. R., I. P. Burgess, and L. Wolf. 1988. Patterns of natural and manipulated hybridisation in the genus *Eucalyptus* L'Hérit.—a review. *Australian Journal of Botany* 36:41–66.
- Hatchett, J. H., and R. L. Gallun. 1970. Genetics of the ability of the Hessian fly (*Mayetiola destructor*) to survive on wheats having different genes for resistance. *Annals of the Entomological Society of America* 63:1400–1407.
- Jaenike, J. 1982. Environmental modification of oviposition behavior in *Drosophila*. *American Naturalist* 119:784–802.
- Jermey, T. 1984. Evolution of insect/host plant relationships. *American Naturalist* 124:609–630.
- Jermey, T., F. E. Hanson, and V. G. Dethier. 1968. Induction of specific food preference in lepidopterous larvae. *Entomologica Experimentalis et Applicata* 11:211–230.
- Jones, C. E. 1978. Pollinator constancy as a pre-pollination isolating mechanism between sympatric species of *Cercidium*. *Evolution* 32:189–198.

- Keim, P., K. N. Paige, T. G. Whitham, and K. G. Lark. 1989. Genetic analysis of an interspecific hybrid swarm of *Populus*: occurrence of unidirectional introgression. *Genetics* 123:557–565.
- Le Brun, N., F. Renaud, P. Berrebi, and A. Lambert. 1992. Hybrid zones and host-parasite relationships: effect on the evolution of parasitic specificity. *Evolution* 46:56–61.
- Lotsy, J. P. 1925. Species or linneon. *Genetica* 7:487–506.
- . 1931. On the species of the taxonomist in its relation to evolution. *Genetica* 13:1–16.
- Manley, S. A. M., and D. P. Fowler. 1969. Spruce budworm defoliation in relation to introgression in red and black spruce. *Forest Science* 15:365–366.
- Maynard Smith, J. 1966. Sympatric speciation. *American Naturalist* 100:637–650.
- McClure, M. S. 1985. Susceptibility of pure and hybrid stands of *Pinus* to attack by *Matsucoccus matsumurae* in Japan (Homoptera: Coccoidea: Margarodidae). *Environmental Entomology* 14:535–538.
- Moran, N. A. 1991. Phenotype fixation and genotypic diversity in the complex life cycle of the aphid, *Pemphigus betae*. *Evolution* 45:957–970.
- Moran, N. A., and T. G. Whitham. 1988. Evolutionary reduction of complex life cycles: loss of host-alternation in *Pemphigus* (Homoptera: Aphididae). *Evolution* 42:717–728.
- . 1990. Differential colonization of resistant and susceptible host plants: *Pemphigus* and *Populus*. *Ecology* 71:1059–1067.
- Ownbey, M. 1950. Natural hybridization and amphiploidy in the genus *Tragopogon*. *American Journal of Botany* 37:487–499.
- Paige, K. N., P. Keim, T. G. Whitham, and K. G. Lark. 1990. The use of restriction fragment length polymorphisms to study the ecology and evolutionary biology of aphid-plant interactions. Pages 69–87 in R. K. Campbell and R. D. Eikenbary, eds. *Aphid-plant genotype interactions*. Elsevier, Amsterdam.
- Papaj, D. R., and R. J. Prokopy. 1988. The effect of prior adult experience on components of habitat preference in the apple maggot fly (*Rhagoletis pomonella*). *Oecologia* (Berlin) 76:538–543.
- Phipps, J. B. 1984. Problems of hybridity in the cladistics of *Crataegus*. Pages 417–438 in W. F. Grant, ed. *Plant biosystematics*. Academic Press, Toronto.
- Potts, B. M. 1986. Population dynamics and regeneration of a hybrid zone between *Eucalyptus risdonii* Hook. f. and *E. amygdalina* Labill. *Australian Journal of Botany* 34:305–329.
- Potts, B. M., and J. B. Reid. 1985. Analysis of a hybrid zone between *Eucalyptus risdonii* Hook. f. and *E. amygdalina* Labill. *Australian Journal of Botany* 33:543–562.
- . 1988. Hybridization as a dispersal mechanism. *Evolution* 42:1245–1255.
- Rice, W. R. 1987. Speciation via habitat specialization: the evolution of reproductive isolation as a correlated character. *Evolutionary Ecology* 1:301–314.
- Roskam, J. C., and G. A. van Uffelen. 1981. Biosystematics of insects living in female birch catkins. III. Plant-insect relation between white birches, *Betula* L., Section *Excelsae* (Koch) and gall midges of the genus *Semudobia* Kiefer (Diptera, Cecidomyiidae). *Netherlands Journal of Zoology* 31:533–553.
- Sage, R. D., D. Heyneman, K. Lim, and A. C. Wilson. 1986. Wormy mice in a hybrid zone. *Nature* (London) 324:60–63.
- Shorthouse, J. D. 1982. Resource exploitation by gall wasps of the genus *Diplolepis*. Pages 193–198 in J. H. Visser and A. K. Minks, eds. *Proceedings of the 5th International Symposium of Insect-Plant Relationships*. Wageningen. Pudoc, Wageningen.
- Stace, C. A. 1987. Hybridization and the plant species. Pages 115–127 in K. M. Urbanska, ed. *Differentiation patterns in higher plants*. Academic Press, New York.
- Tabashnik, B. E. 1983. Host range evolution: the shift from native legume hosts to alfalfa by the butterfly, *Colias philodice eriphyle*. *Evolution* 37:150–162.
- Tauber, C. A., and M. J. Tauber. 1977. A genetic model for sympatric speciation through habitat diversification and seasonal isolation. *Nature* (London) 268:702–705.
- Thomas, C. D., D. Ng, M. C. Singer, J. L. B. Mallet, C. Parmesan, and H. L. Billington. 1987. Incorporation of a European weed into the diet of a North American herbivore. *Evolution* 41:892–901.
- Warwick, S. I., J. F. Bain, R. Wheatcroft, and B. K. Thompson. 1989. Hybridization and introgression in *Carduus nutans* and *C. acanthoides* reexamined. *Systematic Botany* 14:476–494.
- Weber, J. E., and C. S. Campbell. 1989. Breeding systems of a hybrid between a sexual and an

- apomictic species of *Amelanchier*, shadbrush (Rosaceae, Maloideae). *American Journal of Botany* 76:341–347.
- Wendel, J. F., J. M. Stewart, and J. H. Rettig. 1991. Molecular evidence for homoploid reticulate evolution among Australian species of *Gossypium*. *Evolution* 45:694–711.
- Whitham, T. G. 1989. Plant hybrid zones as sinks for pests. *Science* (Washington, D.C.) 244:1490–1493.
- Whitham, T. G., P. A. Morrow, and B. M. Potts. 1991. The conservation of hybrid plants. *Science* (Washington, D.C.) 254:779–780.

KEVIN D. FLOATE\*  
THOMAS G. WHITHAM

DEPARTMENT OF BIOLOGICAL SCIENCES  
NORTHERN ARIZONA UNIVERSITY  
FLAGSTAFF, ARIZONA 86011-5640

*Submitted September 27, 1991; Revised April 13, 1992; Accepted April 23, 1992*

\* Present address: Agriculture Canada Research Station, PO Box 3000, Main, Lethbridge, Alberta T1J 4B1, Canada

*Editor: Mark D. Rausher*