

Herbivory in Plant Hybrid Zones

STUDIES & EXPERIMENTAL ARTICLES

Drake, DW. (1981) Reproductive success of 2 eucalyptus hybrid populations II: comparison of pre-dispersal seed parameters. *Australian Journal of Botany* 29 (1): 37-48.

Eucalyptus meanophloia × *E. crebra* & *E. populnea* × *E. crebra* : seed consumers.

This is the first study in this area of research. Unlike nearly all of the subsequent papers, this research was performed from the botanical point of view. This is the second of a pair of papers investigating the differential reproductive success of two eucalyptus species pairs and their hybrids. Drake was primarily interested in the structure of hybrid zones and how they form and persist. Findings included one hybrid with diminished fertility and heightened susceptibility to seed loss and the other with fertility and seed loss intermediate to the parental types. As were most of the early studies, this was entirely a field study with no manipulations of any sort.

Whitham TG. (1989) Plant hybrid zones as sinks for pests. *Science* 244 (4911): 1490-1493.

Populus angustifolia × *P. fremontii* : *Pempigus betae*.

Whitham has a history of studying the leaf-galling aphid *Pempigus betae*, a pest species on *Populus angustifolia*. It seems likely that this paper was the direct result of his having noted a peculiar distribution pattern in the region studied. Whitham found that aphid populations were much denser on hybrids of *Populus fremontii* and *P. angustifolia* than they were on either pure parental type. Aphid survival trials using clones of trees from the hybrid zone suggested a strong genetic component to the “susceptibility” of these trees. Whitham proffered the theory that pest species might be drawn into hybrid zones in which their survival is generally higher and, over time, lose the traits which allowed them to exploit the original host species. He coined this phenomenon a “hybrid sink” (which should not be confused with a sink in the “source-sink” sense) and likened it to the agricultural use of “trap crops”. He suggested that this phenomenon might be widespread in hybrid zones.

Boecklen WJ, Spellenberg R. (1990) Structure of herbivore communities in 2 oak (*Quercus* spp.) hybrid zones. *Oecologia* 85 (1): 92-100.

Quercus depressipes × *Q. rugosa* & *Q. emoryi* × *Q. coccolobifolia* : miners & gallers.

This study examined density and species diversity of leaf-mining Lepidopterans and gall-forming Hymenopterans in two oak hybrid zones. Found that both densities and diversities were significantly lower in both hybrid zones, contrary to Whitham's hypothesis. This seemed a more convincing test of the hybrid sink hypothesis than Whitham's, since it examined many species in two hybridization complexes in separate geographical regions. The only disappointment was that, unlike Whitham's system, I found no subsequent papers exploring the genetic makeup of the hybrid zone (degree of introgression/backcrossing).

Whitham TG, Morrow PA, Potts BM. (1991) Conservation of hybrid plants. *Science* 254 (5033): 779-780.

With this letter Whitham became a proponent for reform to conservation policies which treat hybrid plants (hybrids in general) as valueless entities. He argued that hybrid zones should be focal points of conservation since many herbivore/parasite species might be found exclusively in such zones, as he had shown in his 1989 study.

Aguilar JM, Boecklen WJ. (1992) Patterns of herbivory in the *Quercus-grisea* × *Quercus-gambelii* species complex. *Oikos* 64 (3): 498-504.

Quercus grisea × *Q. gambelii* : miners & galls.

This study is very similar to the previous Boecklen study. A third hybrid zone was examined. Hybrids in this complex had parasite infestations intermediate to the two parental types. The authors included some thoughts on the need to consider host characteristics such as architecture, leaf morphology, and geographic range in addition to hybrid/non-hybrid classification.

Floate KD, Kearsley MJC, Whitham TG. (1993) Elevated herbivory in plant hybrid zones: *Chrysomela confuens*, *Populus* and phenological sinks. *Ecology* 74(7):2056-2065.

Populus angustiolia × *P. fremontii* : *Chrysomela confuens*.

This paper took the “sink” concept a bit off the deep end. Having found that the beetles studied spent most of their time in the hybrid zone, the authors further noted that the beetles were following the flush of new leaves—early in the narrowleaf (*P. angustiolia*), later in the Fremont and intermediate in the hybrids. The beetles in the hybrid zone thus had greater reproductive success and so the hybrid zone maintained a greater abundance of these *Chrysomelids*. I wasn’t at all convinced that “sink” was proper nomenclature for this phenomenon. However, this study did demonstrate that the reasons for differences in the hybrid zone need not be subtle.

Paige KN, Capman WC. (1993) The effects of host-plant genotype, hybridization, and environment on gall-aphid attack and survival in cottonwood: the importance of genetic studies and the utility of RFLPs. *Evolution* 47(1):36-45.

Populus angustiolia × *P. fremontii* : *Pempigus betae*.

This study revisited Whitham’s original 1989 work. Genetic analysis on the trees examined in Whitham’s study showed a remarkable pattern: F1 hybrids and first backcrosses with narrowleaf were highly resistant, but successive backcrosses became increasingly susceptible. Sheds much light on Whitham’s 1989 study and highlights the utility of genetic work in this field of study. The authors’ correlation of aphid density with altitude was not entirely convincing—they did not reference any information on aphid distribution and altitude outside of a hybrid zone.

Floate KD, Whitham TG. (1993) The hybrid bridge hypothesis - host shifting via plant hybrid swarms. *American Naturalist* 141 (4): 651-662.

Populus angustifolia × *P. fremontii* : various single species from other studies.

Using prior cottonwood system studies as evidence, the authors proposed that parasite species might change their host species along hybridization gradients (created by backcrossing)—an extension and a relaxation of the “hybrid sink” concept. The theory is engaging, but the cited evidence is not convincing. The word “sink” does not appear in this paper, nor does the concept of “hybrid sinks” receive much attention in subsequent papers. Instead, Whitham begins to focus on conservation/biodiversity concepts as developed in Whitham, et al 1994. (see also Pilson 1999)

Fritz RS, Nichols-Orians CM, Brunfeldt SJ. (1994) Interspecific hybridization of plants and resistance to herbivores - hypotheses, genetics, and variable responses in a diverse herbivore community. *Oecologia* 97 (1): 106-117.

Salix sericea × *S. eriocephala* : 11 herbivores and one pathogen.

Similar to Boecklen 1990. Genetic analysis was used to confirm the categorization of individual willows as parental or hybrid types. The authors also established terminology by which hybrid effects on pest species could be categorized relative to its parental species: “susceptible”, “resistant”, “additive” (intermediate to the two parental types), “dominant” (equal to one parent), and “no difference” (equal to both parents). These terms are widely adopted in subsequent literature. Six of the herbivore species indicated hybrid susceptibility and therefore lent some support to Whitham’s hybrid sink theory. The rest were split between additive and dominance.

Whitham TG, Morrow PA, Potts BM. (1994) Plant hybrid zones as centers of biodiversity—the herbivore community of 2 endemic Tasmanian eucalypts. *Oecologia* 97 (4): 481-490.

Eucalyptus amygdalina × *Eucalyptus risdonii* : insect & fungal spp.

This descriptive study is the centerpiece in the argument to reform the conservation attitude towards hybrid plants. The authors found that nearly 75% of the 40 parasitic taxa identified were significantly more abundant in the hybrid zones than in the pure parental zones. Some rare species were almost entirely restricted to the hybrid zone. As the number of hybrid systems in which there are significantly more herbivore species and individuals grows, the more credence this theory will gain.

Martinsen GD, Whitham TG. (1994) More birds nest in hybrid cottonwood trees. *Wilson Bulletin* 106 (3): 474-481.

Populus angustifolia × *P. fremontii* : birds.

I found this to be a rather flat and unconvincing study. A general survey revealed equal presence of bird species in the hybrid and two parental zones. A nest survey revealed a preponderance of nests in the hybrid zone. The authors suggest that this is a result of the hybrids’ possession of an appealing architecture. I was unconvinced that this should lend any support to the authors’ claims that the hybrid zone will tend to support a greater density and diversity of birds.

Floate KD, Whitham TG. (1995) Insects as traits in plant systematics—their use in discriminating between hybrid cottonwoods. *Canadian Journal of Botany* 73 (1): 1-13.

Populus angustifolia × *P. fremontii* : arthropod community.

I found this to be a very intriguing study, but I was not wholly convinced about its utility. The authors evaluated the potential of arthropod bioassays to determine the genetic makeup of individual trees in the hybrid zone (narrowleaf, Fremont, F1 or B1 hybrid, or B2+ hybrid). Using 50 insect and spider species, the bioassay results agreed with the results of a genetic analysis 98% of the time. They made a convincing case that at least some of the arthropods in this hybrid zone community are very discriminating in their choice of host plant.

Orians CM, Fritz RS. (1995) Secondary chemistry of hybrid and parental willows - phenolic glycosides and condensed tannins in *Salix sericea*, *S. eriocephala*, and their hybrids. *Journal Of Chemical Ecology* 21 (9): 1245-1253.

Salix sericea × *S. eriocephala*.

This is a fine paper, but the treatment of this topic is better in Orians, et al 2000.

Fritz RS, Roche BM, Brunfeldt SJ, Orians CM. (1996) Interspecific and temporal variation in herbivore responses to hybrid willows. *Oecologia* 108 (1): 121-129.

Salix sericea × *S. eriocephala* : 12 insect herbivores.

The authors tested 12 herbivore species in each of 4 consecutive years, determining the interaction category (Fritz, et al 1994) for the hybrid plants (48 total categorizations). They also developed an algorithm by which these hybrid-herbivore statistics could be classified with a minimum number of statistical tests. They continued to use this algorithm in the future (with some changes), but it was never not adopted by others. There were two surprises in this study: 1. the algorithm seemed to misclassify a fair number of relationships, 2. several species had three different classifications across the four years. The results emphasized the need for multiyear field studies in order to find the dominant paradigms.

Orians CM, Huang CH, Wild A, Dorfman KA, Zee P, Dao MTT, Fritz RS. (1997) Willow hybridization differentially affects preference and performance of herbivorous beetles. *Entomologia Experimentalis et Applicata* 83(3): 285-294.

Salix sericea × *S. eriocephala* : 5 beetle species.

Studies from this group (Fritz & Orians) are hereafter characterized by experiments performed in the lab using hybrids grown from seed created with known parentage. This particular study was a preference/performance lab study on 5 beetle species. The study demonstrated high variability across the beetle species. Further tests suggested that willow specialists may take host identification cues from the presence/absence of defensive chemicals generated by many willows (which *eriocephala* lack). Performance's correlation with preference was about what one would expect for chance. The results were not generally statistically significant, but were qualitatively suggestive.

Fritz RS, McDonough SE, Rhoads AG. (1997) Effects of plant hybridization on herbivore-parasitoid interactions. *Oecologia* 110 (3): 360-367.

Salix sericea × *S. eriocephala* : *Phyllonorycter salicifoliella*.

This is one of a very small number of papers looking at tritrophic interactions in hybrid zones. The technique—constructing mortality tables for each host type (*sericea*, *eriocephala*, and F1 hybrid)—was compelling, although the analysis was less so. The discussion of the biology of this particular willow hybridization complex was excellent.

Floate KD, Martinsen GD, Whitham TG. (1997) Cottonwood hybrid zones as centres of abundance for gall aphids in western North America: Importance of relative habitat size. *Journal of Animal Ecology* 66 (2): 179-188.

Populus angustifolia × *P. various* : *Pempigus betae*.

A repeat of the field study part of Whitham 1989 in multiple locations. A pattern was established across all locations: the leaf-galling aphids were always concentrated in the hybrid zone. The sink hypothesis was brought up one last time as well as two other possibilities: hybrid zones as aphid sources (in the source-sink sense) and disruptive introgression (breaking down pure-narrowleaf resistance). The authors also included a pitch for the conservation of plant hybrid zones based on this data.

Kokkonen K. (2000) Mixed significance of plant vigor: two species of galling *Pontania* in a hybridizing willow complex. *Oikos* 90:97-106.

Salix caprea × *S. starkeana* : *Pontania* spp.

This was a preference/performance field study in which physical characteristics of the host plants were found to be most important to preference. Performance was correlated with preference for one species, but not the other. Sample sizes were much too small to obtain significant effects, but the trends and technique seemed promising. This study was rather similar to Orians, et al 1997.

Orians CM, Griffiths ME , Roche BM, Fritz RS. (2000) Phenolic glycosides and condensed tannins in *Salix sericea*, *S. eriocephala* and their F1 hybrids: not all hybrids are created equal. *Biochemical Systematics and Ecology* 28 619-632.

Salix sericea × *S. eriocephala*.

This was a detailed treatment of the interaction between hybridization and the production of defensive chemicals. This experiment established that not all hybrids are equal *and* served as a reminder that not all parental types are equal either. Results showed that tannins were produced at about the midpoint between the parental types, but phenolic glycosides were generally below the midpoint between the parental types.

Fritz, RS, CG Hochwender, DA Lewkiewicz, S Bothwell, CM Orians (2001) Seedling herbivory by slugs in a willow hybrid system: developmental changes in damage, chemical defense, and plant performance. *Oecologia* 129(1):87-97

Salix sericea × *S. eriocephala* : *Arion subfuscus*.

This was a detailed examination of patterns of preference and performance of slugs consuming hybrid and pure-species willows and the development of chemical defenses in

willow seedlings. With a few exceptions, this was a well designed experimental study. The common garden component may have suffered from pseudoreplication and/or edge effects. The lack of correspondence between preference and performance found here is apparently widespread in preference/performance literature.

REVIEW ARTICLES

Strauss SY. (1994) Levels of herbivory and parasitism in host hybrid zones. *Trends in Ecology & Evolution* 9(6):209-214.

This was a nice introduction to the early years of investigation. It stepped through some of the early hypotheses, discussed mechanisms, and contained a table summarizing the results of 19 studies, some of which involved animal hybrids and their parasites.

Fritz RS. (1999) Resistance of hybrid plants to herbivores: genes, environment, or both? *Ecology* 80(2):382–391.

In 1999, Robert Fritz was the editor of a special feature on hybridization and resistance to parasites in the journal *Ecology*. This and the following three review articles are from that special feature.

This review focused exclusively on hybrid plants, probing into various ways that researchers had tried to tease apart the effects of genetics and the environment. Fritz emphasized the need to know the genetic background of the hybrids under examination (F1, F2, or various kinds of back-crosses). He also made an excellent case for the need for manipulation experiments using both common garden and reciprocal transplant techniques to complement the growing number of observational studies. Several recent papers from himself and Orians were examples of such research.

Mouliá C (1999) Parasitism of plant and animal hybrids: are facts and fates the same? *Ecology* 80(2):392–406.

This review compared results from animal and plant studies, including especially the difference in the influence of environmental factors. The author was primarily interested in the use of hybrid zones as windows into the evolutionary process. She suggested that examining a more diverse suite of hybrid complexes would most assist evolutionary studies.

Pilson D (1999) Plant hybrid zones and insect host range expansion. *Ecology* 80(2):407–415.

This paper explores the hybrid bridge hypothesis, elucidating some of its implicit assumptions. The author suggested ways to update the theory so it might fit with the current body of work on host range in herbivorous insects. He further discussed how such an updated theory might be tested. I found it interesting reading, but very tightly focused on a small part of the overall hybrid plant-animal interaction picture.

Whitham TG, Martinsen GD, Floate KD, Dungey HS, Potts BM, Keim P. 1999. Plant hybrid zones affect biodiversity: tools for a genetic-based understanding of community structure. *Ecology* 80(2):416–428.

This was a sweeping review of the observational literature, with the most time spent elucidating the examples which best support the view that plant hybrid can be essential elements of biodiversity conservation. 152 case studies are cited—a small number of these were included in a summarizing table similar to that in Strauss 1994. The authors made a forceful argument for their cause, somewhat marred by the presence of several less-than-satisfying papers referenced in key parts of their narrative.

Fritz RS, Moulia C, Newcombe G. 1999. Resistance of hybrid plants and animals to herbivores, pathogens, and parasites. *Annual Review of Ecology & Systematics* 30:565–91

This article was similar to, but better and less constrained than Fritz 1999.