

PLANT GENOTYPE AFFECTS LONG-TERM HERBIVORE POPULATION DYNAMICS AND EXTINCTION: CONSERVATION IMPLICATIONS

PATRICK J. MCINTYRE¹ AND THOMAS G. WHITHAM

*Department of Biological Sciences and Merriam-Powell Center for Environmental Research,
Northern Arizona University, Flagstaff, Arizona 86011-5640 USA*

Abstract. Few studies have linked long-term herbivore population dynamics with plant genetics. In this study we present evidence that plant genotype and hybridization influence the population dynamics of the poplar bud gall mite, *Aceria parapopuli*. Using experimental transfers and a five-year data set on mite abundance on two cottonwood species (*Populus fremontii* and *P. angustifolia*) and their naturally occurring hybrids, we demonstrated that hybrid trees exhibiting an F₁ morphology were, on average, extremely susceptible to *A. parapopuli*. The susceptibility of these hybrids ranged several orders of magnitude and affected the population dynamics of *A. parapopuli* across the five years of study. Populations grew exponentially on susceptible hybrids in every year, eventually reaching a mean of ~140 galls per tree. In contrast, populations fluctuated around low densities (0.01–0.87 galls per tree) on their parental host species. Low gall densities on parental trees resulted in high annual extinction rates (mean = 62%) for mite populations on individual parental trees, in contrast to low annual extinction rates (mean = 7%) for mite populations on hybrid trees. We detected significant differences in gall population growth rates (intrinsic rate of increase, r) among hybrid genotypes across four years of study, ranging from $r = 0$ to $r = 1.5$, demonstrating that plant genotype influences a fundamental component of population dynamics. We argue that plant genotype should also impact metapopulation dynamics, because plant genotype affected the number of available colonists and directly affected mite extinction rates. If other arthropod species exhibit similar traits, these findings have important conservation implications. Because mite population growth and extinction are so closely tied to rare host genotypes, to conserve such species we must preserve rare host genotypes, which would represent a major challenge to current conservation practices that target species rather than genotypes.

Key words: *Aceria parapopuli*; arthropod galls; cottonwoods; Eriophyidae; hybridization; plant–herbivore interactions; plant resistance; population dynamics; *Populus*.

INTRODUCTION

Hybridization alters ecologically important traits by combining the genomes of different species (Rieseberg and Ellstrand 1993, Scribner 1993, Grant and Grant 1996, Wang et al. 1997). Among plants, hybridization influences herbivore resistance, thereby affecting the abundance and distribution of common herbivores. A recent review of 152 insect herbivores and pathogens associated with hybrid plants found that hybridization affected abundance in 79% of the cases (Whitham et al. 1999; see also Strauss 1994, Fritz et al. 1999). Consequences of plant hybridization range from increased susceptibility to herbivores (e.g., Whitham 1989, Graham et al. 1995), to cases of hybrid resistance (e.g., Boecklen and Larson 1994, Fritz et al. 1996). Although environmental factors may contribute to patterns of herbivore abundance in hybrid zones (Fritz 1999, Graham et al. 2001), common garden studies demonstrate

that hybrid susceptibility often has a strong genetic component (Messina et al. 1996, Fritz et al. 1998, Dungey et al. 2000). The genetic variation in herbivore resistance generated through hybridization makes hybrid zones powerful natural systems for studying the impacts of plant genetics on herbivore populations (Whitham et al. 1999).

Despite interest in how bottom-up factors such as plant quality impact herbivore population dynamics (Cappucino 1992, Hunter and Price 1992, Rossiter 1992, Price et al. 1995, Ylloja et al. 1999, Larsson 2000), few studies have linked genetic variation in host-plant quality to herbivore population dynamics (but see Schotzko and Bosque-Perez 2000, Underwood and Rausher 2000). However, several authors have proposed that the extreme variation in host-plant quality generated through plant hybridization influences herbivore population dynamics and evolution (Whitham 1989, Floate and Whitham 1993, Strauss 1994). Genetic influences on herbivores are of great potential importance in understanding the processes that regulate populations. In agricultural situations, the effects of plant genotype on herbivore population dynamics have

¹ Present address: Point Reyes National Seashore, One Bear Valley Road, Point Reyes Station, California 94956 USA. E-mail: Patrick_McIntyre@nps.gov

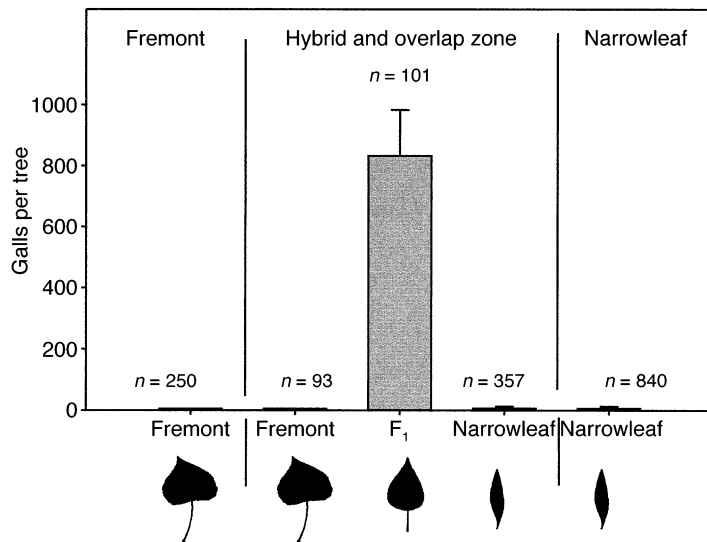


FIG. 1. *Aceria parapopuli* gall abundance (mean + 1 SE) by tree phenotype in the field. Gall abundance was measured as the total number of galls (both active and dead) per tree at a single census period and thus represents cumulative attack over several years (from Whitham et al. 1999). Sample sizes are the numbers of trees surveyed.

clear applied importance (e.g., controlling and predicting herbivore outbreaks). In the wild, genetic effects on population dynamics may be particularly important among clonal plants that cover large areas and are long lived. For example, a large clone on which herbivore populations grow rapidly could act as a source habitat (sensu Pulliam 1988), influencing herbivore populations on adjacent genotypes. Furthermore, consistent temporal impacts of plant genotype on herbivore populations may result in local adaptation to particular plant genotypes (e.g., Moran and Whitham 1988, Karban 1989, Mopper et al. 2000). If these adaptations to susceptible plant genotypes come at the expense of adaptations dealing with resistant plant genotypes, genotypes that are sources in ecological time may become sinks in evolutionary time as herbivores adapted to susceptible genotypes may lose the ability to survive on more resistant genotypes (Whitham 1989).

In this study we use the poplar bud gall mite (*Aceria parapopuli* Kieffer: Eriophyidae), which feeds on several cottonwood (*Populus*) species and their hybrids, to ask whether plant genotype and hybridization can influence long-term herbivore population dynamics. Underwood and Rausher (2000) used a modeling approach to demonstrate that empirical differences in herbivore growth rates and density-dependent mortality on different host genotypes were capable of influencing the long-term dynamics of herbivore populations. However, empirical examples of plant genotype influencing herbivore population dynamics over multiple years are lacking. We use experimental transfers and five years of population surveys on *A. parapopuli* in a common garden of replicated cottonwood genotypes to study the impact of plant genotype on herbivore population dynamics. Fig. 1 shows that *A. parapopuli* is nearly 800× more abundant on hybrid trees than pa-

rental trees in the wild. The enormous difference in apparent susceptibility to *A. parapopuli* between parental and hybrid types make this a good system in which to test for effects of host plant genotype on herbivore population dynamics. We address the following questions: (1) Is there genetic variation among and between hybrid and parental genotypes for resistance to *A. parapopuli*? (2) Does variation in plant resistance impact herbivore population extinction rates? (3) Does variation in plant resistance impact long-term herbivore population growth rates?

METHODS AND MATERIALS

Study sites.—Observational studies were conducted in a naturally occurring hybrid zone between Fremont cottonwood (*Populus fremontii*) and narrowleaf cottonwood (*P. angustifolia*). The hybrid zone is located along 13 km of the Weber River, near Ogden, Utah, USA, and is made up of F₁ and backcross hybrids and both parental species (Keim et al. 1989). Genetic analyses show that introgression is unidirectional, such that F₁ hybrids backcross only with *P. angustifolia* (Keim et al. 1989, Martinsen et al. 2001). F₁ hybrids are restricted to the 13-km hybrid zone, and the frequency of backcross hybrids drops off rapidly outside the hybrid zone (Martinsen et al. 2001).

Experimental studies using common garden trials were conducted at the Ogden Nature Center, located ~2 km from the current channel of the Weber River, within the lower elevational range of the hybrid zone. The garden was established in 1991 and is composed of 350 trees grown from cuttings of 81 naturally occurring parental and hybrid genotypes (six Fremont types, 16 F₁ types, 59 narrowleaf types). Each genotype was represented by 1–10 replicates (variation in clone numbers was primarily due to mortality after the initial planting). Trees were planted in a randomized-inter-

dispersed design. Prior to planting, cuttings were grown in the greenhouse for two years. All trees in the garden are clones of trees of known genotype (i.e., parental, F_1 , backcross hybrid), determined using 35 RFLP markers (methods described in Martinsen et al. [2001]). At the time the study began, most cuttings had matured into small trees (7–20 cm dbh).

Tree types.—Throughout this paper we refer to three tree types: (1) Fremont cottonwood, (2) F_1 morphotypes, and (3) narrowleaf morphotypes. These three classes are easily distinguished in ordinations, based on morphology (Floate and Whitham 1995), herbivore communities (Floate and Whitham 1995), and secondary plant chemistry (Crawford 1974), and appear to represent broad functional groups. However, based on molecular markers (G. Martinsen, *unpublished data*), trees in the F_1 morphotype category include some near F_1 hybrids that express the distinctive morphology of true F_1 's. Trees in the narrowleaf morphotype category include complex backcrosses to narrowleaf, as well as pure narrowleaf cottonwood. In contrast, all trees that express the Fremont morphology are true *Populus fremontii*, as backcrossing to *P. fremontii* does not occur naturally. These three morphotypes represent the functional tree types found in the hybrid zone. First and second generation backcrosses to narrowleaf, which would potentially represent a distinct “backcross” phenotype, are rare in the wild (Martinsen et al. 2001).

Herbivore natural history.—*Aceria parapopuli* induces galls on all species of *Populus* in western North America (Brown 1964, Drouin and Langor 1992). Female mites induce galls in axillary buds at the base of leaf petioles, during early spring as leaves are expanding. *A. parapopuli* is ~0.2 mm long and feeds by piercing individual plant cells with its stylets and sucking the cell contents (Drouin and Langor 1992, Lindquist and Oldfield 1996). Mites are haplodiploid with arrhenotokous parthenogenesis, and reproduce inside the galls throughout the summer at 2–3 wk intervals (Philip and Mengerson 1989, Sabelis and Bruin 1996). Mite populations can reach thousands per gall by the end of the summer (Cambell et al. 1969, Drouin and Langor 1992). Among eriophyid mites, dispersal within a host usually occurs through crawling, while dispersal among hosts occurs via the wind (Sabelis and Bruin 1996). Galls are typically active for a single season but can be active up to 15 years (Campbell et al. 1969).

Gall surveys.—We conducted annual surveys of gall abundance on trees in the common garden in 1998, 1999, and 2000. Surveys were conducted in late June, when newly initiated galls had reached maximum size and were easily spotted due to their red color. Each tree in the garden was visually scanned for 3 min to determine the presence or absence of galls. If galls were found, we counted all galls present on the tree. In addition to counting galls initiated during the study period, we were able to census galls initiated prior to our study. Galls induced by *A. parapopuli* are retained on

the host plant for several years after gall initiation. These older galls are easily aged by examining their position relative to terminal bud scars. In 1998, the first year of study, we counted and aged galls initiated in the years prior to our study, allowing us to reconstruct the history of colonization and population growth. We checked the accuracy of these prior-year censuses by examining the retention rate of newly initiated galls over the three years of our actual surveys. We adjusted these prior-year censuses upward to account for galls dropped from the trees (95% annual gall retention on F_1 type trees and 55% annual retention on narrowleaf types).

To test the hypothesis that patterns of mite abundance on hybrid and parental trees in the field are influenced by plant genotype, we compared patterns of gall abundance between hybrid and parental types in the common garden with the results of previously published field surveys (Whitham et al. 1999). For this comparison, we used the total number of galls (both old–retained and newly initiated galls) present on garden trees in the final study year (2000), because gall abundance on field trees was measured as the number of old–retained plus newly initiated galls on a tree at a single census period. Gall abundance was averaged across replicated clones to determine mean gall abundance per clone, and clone means were used to compare gall abundance among tree types. We tested for an effect of tree type on gall abundance with a Kruskal-Wallis (K-W) test followed by Fisher's LSD test on ranked data for pairwise comparisons (Conover 1999, Agresti 1996). These and all other statistical tests were performed on SPSS v. 10.0.7 (SPSS 1999).

In addition to testing for an effect of hybridization on gall abundance, within F_1 and narrowleaf types we tested for a clone effect. Fremont was not included because it was colonized at such low densities that a test of clone effects was not possible. To test for a clone effect on gall abundance, we selected all clones in the garden represented by at least three replicates. For both F_1 and narrowleaf type trees, we compared gall abundance among clones using a Kruskal-Wallis test followed by Fisher's LSD test on ranked data for pairwise comparisons.

We conducted experimental transfers of galls to trees in the common garden in mid April 2000. Transfers were made to four tree types: randomly chosen Fremont clones ($n = 5$ clones), randomly chosen narrowleaf type clones ($n = 6$ clones), deliberately chosen F_1 type “mite-susceptible” clones that naturally supported high gall densities ($n = 5$ clones), and deliberately chosen “mite-resistant” F_1 type clones that supported few or no galls ($n = 5$ clones). Transfers were conducted to four haphazardly chosen lower branches on each treatment tree. On each branch, we removed all naturally occurring galls and pruned back adjacent branches to reduce the likelihood of mites colonizing from elsewhere within the tree. Each of the four treat-

ment branches received a single "source twig," a 5–10 cm cottonwood twig with two to three active mite galls, which was tied to the treatment branch just below the terminal shoot. Source twigs were from a single F_1 hybrid in the field that supported high gall densities. Two branches on each tree were designated as controls, from which all galls were removed and nearby branches pruned back to prevent colonization. To test transfer success, we calculated a transfer success number (mean number of galls per transfer branch—mean number of galls per control branch) for each tree. We used a Kruskal-Wallis test to compare transfer success across the four tree types, followed by Fisher's LSD test on ranked data for pairwise comparisons.

To determine how mites performed within galls on the different tree types we compared mite population sizes from galls on F_1 and narrowleaf types. Fremont was not included because gall initiation was so rare on Fremont that we could not consistently find attacked trees. We conducted censuses in mid June, July, and August of 2000. At each census period, 10 galls were randomly chosen from three F_1 clones in the common garden. Due to the rarity of galls on narrowleaf types, we haphazardly collected two to three galls from each of six narrowleaf trees in the common garden, and used tree means for analysis in order to avoid pseudoreplication. We dissected galls into small (2–5 mm) pieces, which were placed in a 3.7-mL (1-dram) vial. The vial was filled with water and shaken vigorously by hand for 1 min. The contents of each vial were decanted into a small Petri plate and examined under a dissecting microscope to determine the number of mites present. We used a repeated-measures ANOVA to compare mite abundance between the groups, followed by Tukey's HSD tests for pairwise comparisons.

Mite population and colonization dynamics.—To test whether mite colonization dynamics differed among tree types, we compared the frequency of mite extinction between F_1 and narrowleaf type trees in the common garden. Fremont was not included in the analysis because mites rarely used it as a host. Extinction was defined as the absence of active galls on a tree that had supported at least one active gall the previous year. To avoid using data that included galls initiated before our study began, we calculated extinction frequencies only for 1999 and 2000. We used a chi-square test to compare extinction frequency between F_1 and narrowleaf type trees in both 1999 and 2000. In addition to comparing overall extinction rates between F_1 and narrowleaf type trees, we used logistic regression to model how gall population size in the previous year was related to the likelihood of gall extinction the following year. Because extinction events were rare on F_1 trees, and because few narrowleaf trees were attacked in either year, we combined extinction data from 1999 and 2000 for the logistic regression.

To test whether plant genotype influenced mite population dynamics, we tested for an effect of F_1 clone

on the intrinsic rate of increase of gall populations, r . We did not compare density dependence in growth rates because gall populations on F_1 type trees continued to exhibit exponential growth in the final year of our study. Rates of increase were not compared among narrowleaf types, because individual trees were not consistently attacked over the study period, preventing us from examining gall population growth rates on individual trees. We calculated a clone-specific rate of gall population increase for each replicated F_1 clone from 1997 to 2000 (1996 being excluded because mites were just beginning to colonize the garden at that time), by plotting natural log-transformed gall counts across time and running a linear regression to estimate the slope of the line fitted to the data. We calculated r separately for each individual of our replicated F_1 clones. We then tested for a clone effect on r with a Kruskal-Wallis test followed by Fisher's LSD test on ranked data for pairwise comparisons. Although we did not establish a direct link between gall population dynamics and the annual dynamics of mite populations within galls, gall populations are indicative of the year-to-year success and survival of groups of mites and should reflect the year-to-year dynamics of mite populations per tree.

RESULTS

Natural colonization of common garden trees.—The pattern of gall abundance across F_1 and parental types in the common garden closely mirrored the field pattern, demonstrating a strong plant-genetic component to the distribution of mites. In the field, gall abundance was 800× higher on F_1 types than parentals (Fig. 1) while in the common garden gall abundance was over 100× higher on F_1 types (Kruskal-Wallis $\chi^2 = 24.14$, $df = 2$, $P < 0.0001$, Fig. 2). Within the common garden, F_1 type clones supported 138 galls on average (range 0–1200 galls per clone), while Fremont and narrowleaf type clones supported less than a single gall on average (range 0–0.3 and 0–9.9 galls per type, respectively). Although mite densities in the common garden were lower than those observed in the wild, results described below show that garden populations were increasing exponentially, suggesting they may eventually reach the densities of wild populations.

In addition to a cross-type (i.e., F_1 , Fremont, narrowleaf types) effect on gall abundance, we detected a significant clone effect (i.e., different replicated genotypes) on gall abundance among F_1 types (Kruskal-Wallis test, $\chi^2 = 46.48$, $df = 9$, $P < 0.0001$), and narrowleaf types (Kruskal-Wallis test, $\chi^2 = 29.66$, $df = 14$, $P = 0.008$). Although we detected a significant clone effect within both types, the range of gall abundance was relatively small among narrowleaf types (0–9.87 galls per clone), but enormous among F_1 types (0–1200 galls per clone) (Fig. 3). Thus, in their apparent resistance, F_1 clones range from being completely resistant to exhibiting apparent breakdown in resistance. This is an important finding as it demon-

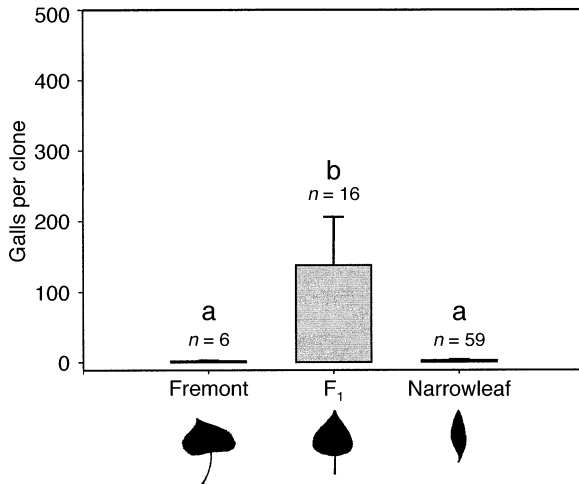


FIG. 2. *Aceria parapopuli* gall abundance (mean + 1 SE) by tree phenotype in the common garden. Gall abundance was measured as the total number of galls (both active and dead) per clone at the final census period (2000). Sample sizes are the numbers of different clones for each tree type. Statistically significant differences between means ($P < 0.05$) are indicated by different lowercase letters.

strates that the variation among hybrid types in mite responses is far greater than the sum of the variation among the parental tree types. Relative to the heavily attacked susceptible F₁ type clones, even those narrowleaf type clones that supported the most mites in their class appeared to be effectively resistant to mite attack.

Results of the gall transfer experiment support the hypothesis that hybrid susceptibility is genetically based, and also showed that F₁ type clones varied in resistance traits. Transfers to trees in the “susceptible” F₁ category resulted in four times as many galls as transfers to “resistant” F₁ types or parental types (Kruskal Wallis $\chi^2 = 14.61$, $df = 3$, $P = 0.002$; Fig. 4). These transfers rule out the possibility that trees without mites are suitable hosts but have not been colonized, and confirm the observational finding that F₁ type hybrids vary in susceptibility to *Aceria parapopuli*.

Surveys of naturally occurring galls in the common garden showed that F₁ type hybrids, in addition to supporting more galls than either parental tree species, supported larger mite populations per gall. By the final sampling period, mite abundance was 10–300× greater within galls from F₁ types than within galls from narrowleaf type trees ($F_{3,36} = 58.083$, $P < 0.001$; Fig. 5; note that galls on Fremont were too rare for analysis). There were 1–1021 mite individuals within galls from F₁ clones, while there were only 1–8 mite individuals within narrowleaf galls. Because narrowleaf galls supported very few mites (average = 1.54 mites per gall at final sampling period), we predicted that mite populations on narrowleaf trees are not large enough to sustain infestations from year to year in the absence of

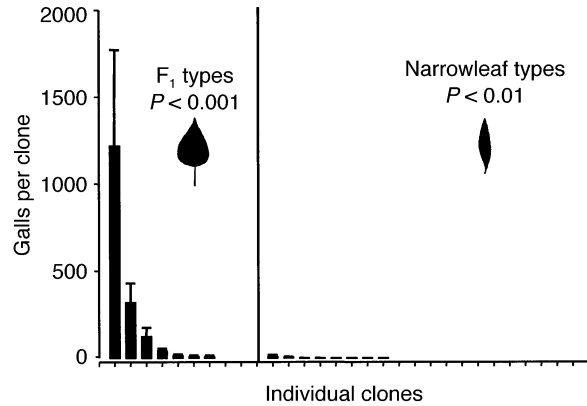


FIG. 3. *Aceria parapopuli* gall abundance (mean + 1 SE) on replicated F₁ and narrowleaf type clones in the common garden. Each tick mark on the x-axis represents a different clone. Sample size per clone ranged from 3 to 12 trees. Gall abundance is the cumulative number of galls observed over the five-year study period. Significance values represent a clone effect on gall abundance.

mites immigrating to narrowleaf hosts from F₁ trees with large mite populations.

By extrapolating the results of mites per gall to the tree level, our maximum estimates of mite abundance are 480 000 mites per F₁ type tree in the garden (based on 1600 active galls), and 1 500 000 mites per F₁ type tree in the field (based on a conservative estimate of 5000 active galls on heavily attacked trees in the wild) compared to a maximum of 54 mites/narrowleaf tree

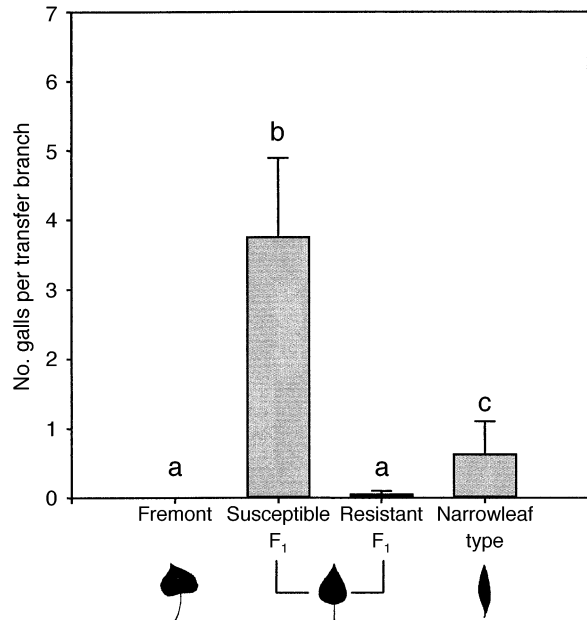


FIG. 4. Number of galls (mean + 1 SE) resulting from experimental transfers of *A. parapopuli* to four tree types (Fremont, resistant F₁, susceptible F₁, and narrowleaf). Statistically significant differences between means ($P < 0.05$) are indicated by different lowercase letters.

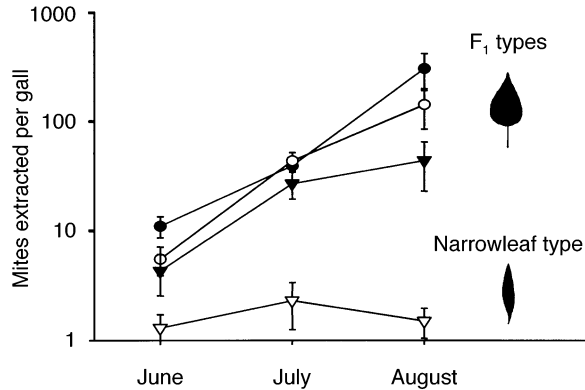


FIG. 5. Number of mites (mean \pm 1 SE) extracted from individual galls on three F_1 clones and a composite average of narrowleaf type trees at three census periods in 2000. Note the \log_{10} scale.

in either the field or garden (based on 33 active galls). These numbers are probably underestimates of maximum mite populations on F_1 trees, because mite populations within galls were still increasing at the final sample date.

Population dynamics: extinction and population growth rates.—Population trends for *A. parapopuli* differed dramatically between F_1 and parental tree types (Fig. 6). On F_1 types, gall populations increased exponentially from a few colonist galls in 1996 to total over 5800 active galls in our fifth study year. In contrast, gall populations on narrowleaf types remained at low densities across the study period (maximum annual abundance = 111 galls on narrowleaf type trees in the common garden compared to >6000 galls on F_1 types), and gall populations on these trees fluctuated from year to year.

After the common garden was first established in 1991, no mites were observed until 1996. The following three years were characterized by the rapid spread of mites among F_1 trees, but not on narrowleaf types. By 1998, mite colonization of F_1 's had increased from <10% to 70% of trees in the garden (Fig. 6A). Seventy percent colonization appeared to be an equilibrium value, as colonization remained at this level the following year, despite continued exponential growth of gall populations within already colonized trees (Fig. 6B). This rapid spread of mites throughout the common garden, followed by an apparent saturation of the proportion of attacked hosts, argues that mites had colonized all susceptible trees by the end of our study. Colonization rates on narrowleaf trees fluctuated in the last three years of observation, suggesting a stronger impact of the environment or other stochastic processes on mite populations that attacked narrowleaf types.

Extinction was more frequent on narrowleaf types than on F_1 types in 1999 ($\chi^2 = 39.3$, $df = 1$, $P < 0.001$) and in 2000 ($\chi^2 = 9.9$, $df = 1$, $P = 0.002$) (Fig. 7). In both years, extinction rates on narrowleaf types were

>50%. This high probability of going extinct from one year to the next, in conjunction with low rates of reproduction, (i.e., less than one mite extracted per gall), suggests that mite populations on narrowleaf type trees are not viable, because they would be unlikely to persist over time without a source of immigrants. In contrast, mite extinction rarely occurred on F_1 type hosts. Extinction was only 3% in 1999, and 11% in 2000. These low extinction rates, taken with large population sizes (i.e., hundreds of mites per gall), suggest that F_1 type trees represent stable host habitats. In combination, these population growth data argue that the relatively rare susceptible F_1 hybrid types represent sources of mites for colonizing trees throughout the Weber River, whereas common narrowleaf types represent unstable sinks where the probability of going locally extinct is very high.

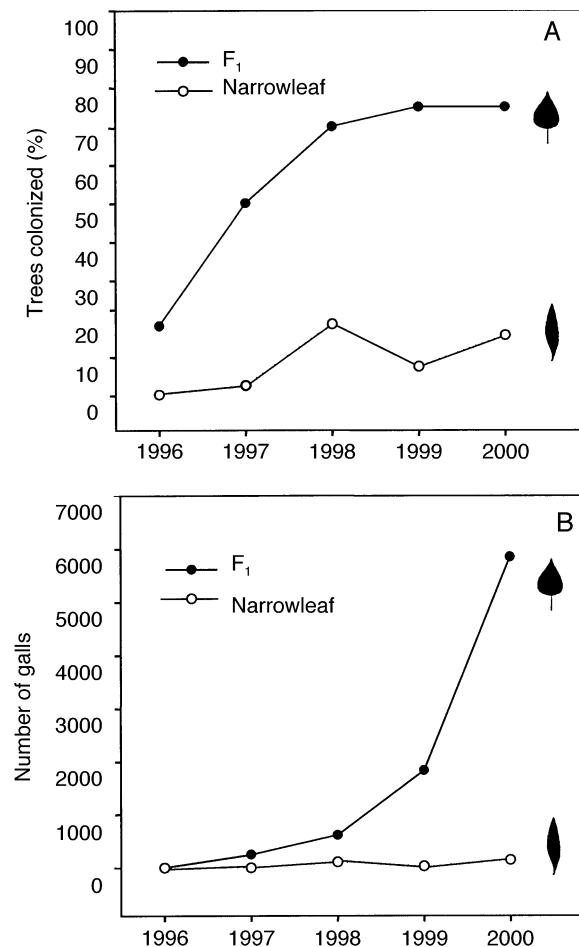


FIG. 6. *Aceria parapopuli* gall population and colonization dynamics across five years. The upper panel (A) depicts the percentage of F_1 and narrowleaf type trees that were colonized by at least one gall. The lower panel (B) depicts the censused population size of galls on all F_1 and narrowleaf type trees in the common garden. Error bars are not shown since points depict total gall counts across all trees in each category.

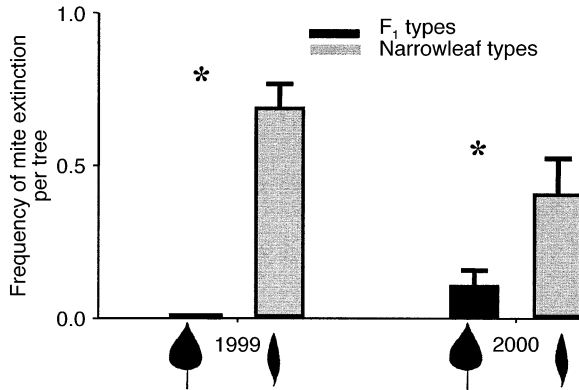


FIG. 7. Gall extinction frequencies in two years for F₁ type and narrowleaf type clones. Extinction was defined as absence of galls from a tree that had supported galls the previous year. Each asterisk represents a significant difference ($P < 0.05$) in extinction frequency as indicated by a chi-square test.

We detected a significant effect of gall population size from the previous year on the probability of gall extinction the following year for both F₁ (Wald $\chi^2 = 3.91$, $df = 1$, $P = 0.048$) and narrowleaf (Wald $\chi^2 = 4.8$, $df = 1$, $P = 0.039$) type trees. On both F₁ and narrowleaf type trees, extinction was more likely for trees with few galls (Fig. 8). However, the extinction probability showed a very low threshold on F₁ type trees, whereas the extinction probability declined linearly with population size on narrowleaf types. Extinction was never observed on F₁ hosts with more than two galls. F₁ type trees with one or two galls may represent normally resistant trees that are occasionally colonized by mites, while trees with more than two galls appear to represent suitable hosts on which populations have a high annual rate of persistence. In contrast to F₁ types, on narrowleaf types extinction of mites was commonly observed at all but the highest naturally occurring gall densities (27 galls/tree).

We detected significant variation in gall population growth rates across four years among F₁ clones (Kruskal-Wallis test, $\chi^2 = 45.713$, $df = 9$, $P < 0.001$). Mean intrinsic rates of increase (r), for gall populations varied from 0 to 1.5 among F₁ clones (Fig. 9). Thus, based upon four years of population growth data, gall populations remained at extremely low densities on some host genotypes, while other host genotypes supported phenomenal growth rates in which the population increased from a single colonizer to >1000 galls in four years. This finding demonstrates that there are genotype-specific gall population growth rates that have the potential to act as a major determinant of long-term herbivore population dynamics.

DISCUSSION

Genetically based hybrid susceptibility.—The results of this study demonstrate a clear and dramatic example of genetically based hybrid susceptibility to an herbi-

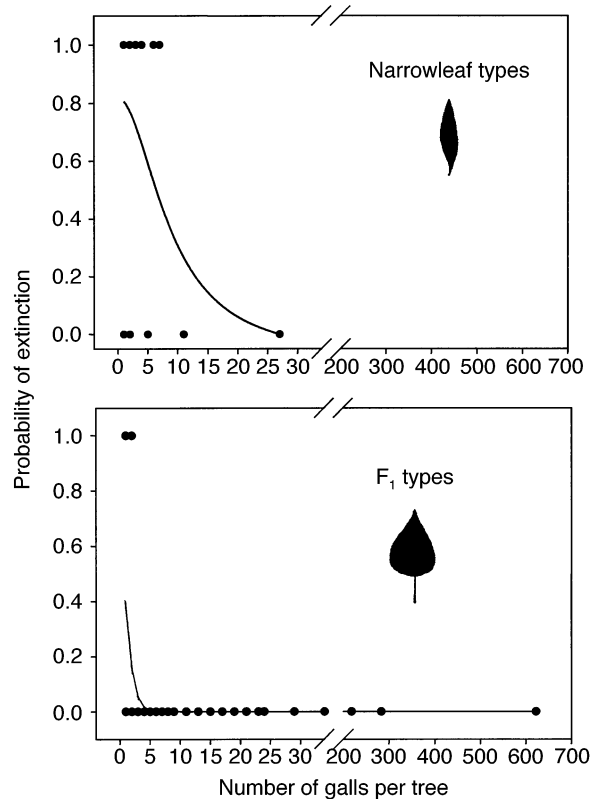


FIG. 8. Mites were less likely to go extinct on F₁ type hybrids than on narrowleaf type clones. Logistic curves show the probability of *Aceria parapopuli* extinction on an individual tree plotted against gall population size from the prior year, for F₁ and narrowleaf type trees. Note the break in the x-axis. Points show both extinction and persistence of populations.

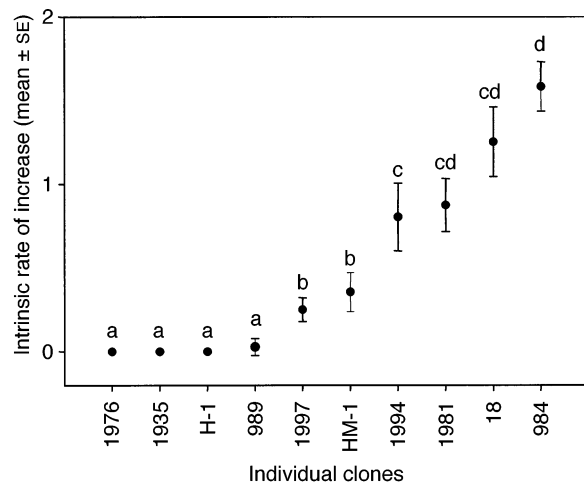


FIG. 9. Intrinsic rate of increase for *Aceria parapopuli* gall populations on individual F₁ type clones. Clone names are listed on the x-axis. Sample size per clone ranged from three to 10 galls. Clones sharing a lowercase letter were not statistically significantly different from each other ($P > 0.05$).

vore. Within a common garden, *Aceria parapopuli* galls were $>100\times$ more abundant on F_1 type trees than on parental types (Fig. 2). This corresponded closely with the distribution of galls in the field (Fig. 1). The increase in mean gall abundance on F_1 type clones was associated with an increase in variation in susceptibility. F_1 type clones ranged from completely resistant to exhibiting apparent breakdown in resistance (Figs. 3 and 4). Thus, F_1 types are not uniformly susceptible, but represent a heterogeneous group that includes individuals that are more susceptible than parental types and individuals with a level of resistance similar to that of parental types. This increased variation in a genetically based trait (i.e., herbivore resistance), generated through hybridization, is what makes hybrid zones powerful systems for exploring the ecological impacts of genetic variation among plants. These common garden studies demonstrate a strong genetic component to the distribution of *A. parapopuli*, and rule out the alternative hypothesis that, at a local level, hybrids are susceptible due to microsite differences in the locations of hybrid and parental trees. However, because our studies were not replicated in both pure and hybrid zones, we cannot rule out the possibility that parental and hybrid genotypes respond differently to environment (i.e., different $G \times E$ [genetic \times environmental] reaction norms), and that environment plays some role in producing the geographical patterns of *A. parapopuli* abundance.

Previous studies have found that *A. parapopuli* exhibits increased abundance on artificial hybrids (Campbell et al. 1969) and on native trees exhibiting hybrid morphology (Eckenwalder 1984, Kalischuck et al. 1997). However, our study is the first to use clones of native trees of known hybrid status in a common garden to experimentally demonstrate that plant genotype determines susceptibility to *A. parapopuli*. Because studies in other locations have observed high numbers of mites on hybrid morphotypes, we suggest that hybrid susceptibility to *A. parapopuli* may be a repeated biogeographic pattern: wherever cottonwoods hybridize, *A. parapopuli* is abundant. This type of repeated and consistent association between hybrid zones and herbivore abundance has been demonstrated for galling aphids over a 1500-km latitudinal gradient (Floate et al. 1997), although the role of hybrid genetics vs. environment in herbivore abundance is less clear in that system (Paige and Capman 1993). Because hybrid zones occur at multiple locations wherever parental species ranges overlap, they offer ecologists systems in which to test the repeatability of ecological patterns and evolutionary phenomena. In this sense, hybrid zones may be analogous to replicated habitats such as islands, lakes, and caves used to study the repeatability of evolution or ecology (e.g., Kane et al. 1992, Losos et al. 1998, Robinson and Schluter 2000).

Although we did not examine plant traits (e.g., growth rates, secondary chemistry) that may be directly

associated with susceptibility to *A. parapopuli*, and because our experiments utilized replicated hybrid and parental genotypes, we can broadly determine the pattern of genetic variation for resistance (e.g., resistance controlled by dominant or additive genes). The relatively continuous variation in gall abundance among hybrid and narrowleaf types (Fig. 3) suggests that resistance could be controlled by multiple genes of additive effect (Fritz et al. 1994). However, experimental crosses to reproduce F_1 and backcross genotypes, followed by resistance assays, are necessary to determine more about the underlying genetics of resistance (e.g., whether hybrid susceptibility is dependent on a threshold dose of genes' additive effect; Dungey et al. 2000). Plant resistance to eriophyid mites is thought to involve a hypersensitive response to gall initiation, similar to the hypersensitive response of plants to pathogens (Westphal 1992). The hypersensitive response is important in plant pathogen defense, and involves localized cell death in response to pathogen infection or cell-wall puncture (Dangl et al. 1996, Mittler and Lam 1996). In *Solanum dulcamara* attacked by the eriophyid mite *Aceria cladophthirus*, resistant plants exhibit a hypersensitive response resulting in localized necrotic lesions where mites pierce cells (Westphal et al. 1990, Bronner et al. 1991). Because the hypersensitive response is involved in gene-for-gene plant-pathogen interactions (De Wit 1997), variation in hypersensitive response alleles among hybrids and parentals may also explain variation in susceptibility. At least one plant—eriophyid system exhibits plant and herbivore strain compatibility similar to that known from plant-pathogen systems, suggesting complex genetic dynamics involving both plant and herbivore genotypes (Caresche and Wapshere 1974, Cullen and Moore 1983). It is possible that additive effects and gene-for-gene dynamics may operate in the same system, but differentially affect different stages of the herbivore life cycle. For example, the hypersensitive response could play a role in the success of gall initiation, while constitutive defenses controlled by many alleles could influence the success of feeding mites and the growth of mites within galls. Further experiments involving controlled crosses between resistant and susceptible plant genotypes and mite populations from multiple sources would be necessary to determine if both factors may be playing a role in plant susceptibility.

Host plant genotype, population dynamics, and metapopulation dynamics.—Plant genetics affected *A. parapopuli* gall population dynamics in three ways: (1) Across the five years of study, populations grew exponentially on F_1 types, while populations fluctuated on parental types, (2) Gall populations on individual narrowleaf trees exhibited annual extinction rates five times higher than rates on F_1 types, and (3) The intrinsic rate of increase of gall populations varied significantly among F_1 -type clones. Taken together, these results demonstrate that plant genotype and hybridization im-

pacted herbivore population dynamics over a five-year period. Furthermore, these results demonstrate that plant genotype is capable of impacting long-term population dynamics, because differences in r can impact the periodicity of population cycles and recovery from stochastic events (Renshaw 1991). However, detecting an effect of plant genotype on the rate of population increase is only a first step in understanding the role of host genetics in herbivore population dynamics, because density-dependent birth and death rates are crucial to understanding population regulation.

Studies that have detected an effect of plant genotype on the density-dependent birth or death rates of herbivores have been limited to a single season (e.g., Underwood and Rausher 2000, but see Schotzko and Bosque-Perez 2000). In order to clearly understand the role of plant genotype in long-term herbivore population dynamics, these types of studies need to be extended across multiple years to determine whether plant genotype influences long-term dynamics in a consistent fashion across temporal environmental variation. Stochastic environmental variation from year to year may override the effects of plant quality or genotype on population dynamics if populations are followed for more than a single season (e.g., Stiling and Rossi 1996). In addition, environmental factors may interact with plant genotype (e.g., Maddox and Cappuccino 1986) to influence population dynamics in complex fashions. Long-term studies, or studies that simulate temporal environmental variation (e.g., rainfall) are needed to determine if and how the effects of plant genotype on herbivore population dynamics vary temporally. An interesting possibility is that the impact of environmental variation on the expression of plant traits influencing herbivore population dynamics may vary among plant genotypes. Thus, the impact of environmental variation on long-term herbivore population dynamics could be mediated by plant genotype. Exploration of the consequences of variation in genotype \times environment interactions (i.e., different reaction norms among genotypes) on long-term herbivore population dynamics could be explored using a model-fitting approach similar to that of Underwood and Rausher (2000).

Our results suggest that plant genotype can also influence spatial population dynamics, such as metapopulation dynamics. From a metapopulation and epidemiological perspective, individual tree population growth rates can impact the rate of colonization of new hosts by influencing the abundance of emigrants. In combination with our results showing that hybridization affects individual tree extinction rates (Fig. 7), this demonstrates that plant genotype and hybridization may influence patch colonization and extinction rates, the central parameters of metapopulation and SIS epidemiological models (Levins 1969, Anderson and May 1991). Thus, plant genotype may affect the spread of mites among individual hosts at a site, and the persistence of mites as a metapopulation. Furthermore, the

genetics of individual clones may determine whether colonization of new host patches will be successful over the long term, because there may be a threshold number of susceptible host genotypes, or minimum amount of suitable habitat required for mites to persist in a population of host plants (cf. Kermack and McKendrick 1927, Lande 1988).

The impacts of plant genotype on herbivore population dynamics should be particularly important for long-lived plant species, and for clonal species that cover large areas. Clones that cover large areas may have strong effects on local dynamics if they act as a source habitat from which herbivores spread to colonize other host populations (cf. Pulliam 1988). Additionally, consistent effects of plant genotype on birth and death rates may impact the evolution of herbivore life history traits, resulting in local adaptation to individual plant genotypes (Karban 1989). Questions of spatial scale and host population genetic structure may be particularly important issues in understanding the impacts of plant genotype on herbivore populations. For example, effects of plant genotype on population dynamics may be stronger and easier to detect when single plant genotypes cover large areas of land, while the effects of plant genotype on population dynamics may be diffuse and difficult to detect when host stands are genetically diverse hosts.

Specialization on host genotype.—Several lines of evidence argue that *Aceria parapopuli* is locally (within the vicinity of the hybrid zone) specialized on F_1 type hybrids, and that narrowleaf trees represent marginal or sink habitat: (1) Annual tree-level extinction rates exceeded 50% on narrowleaf types, whereas on susceptible F_1 types the annual extinction rate was $<10\%$ and was restricted to trees with few galls, and (2) Galls on narrowleaf trees supported fewer than two mites on average, whereas galls on F_1 type clones supported nearly 100 mites on average. Furthermore, our extinction rates on narrowleaf types may actually be underestimates since we did not account for a potential rescue effect in which immigrants save a declining population from extinction (Brown and Kodrick-Brown 1977). Our observational and experimental results argue that if colonization from large mite populations on F_1 hosts were prevented, mite populations would be unlikely to persist on narrowleaf hosts where extinction rates are high and population sizes are low.

These patterns suggest that the functional resource of this herbivore population is not a particular plant species, but a relatively rare hybrid genotype. F_1 type hybrids comprise only $\sim 5\%$ of the trees in the Weber River hybrid zone. Because only $\sim 60\%$ of these F_1 types are susceptible (Fig. 3), the effective pool of viable hosts for *A. parapopuli* is further diminished. That viable populations of an herbivore may be restricted to relatively rare host genotypes or areas that support these genotypes has important conservation implications. In order to ensure the survival of arthro-

pod herbivores that are strongly impacted by plant genotype, we may need to conserve the genetic diversity of natural plant populations. It is particularly important that this herbivore may be restricted to hybrid genotypes, as naturally occurring and native hybrid plants such as cottonwoods receive little conservation attention, particularly in light of fears that native–exotic hybridization may lead to the extinction of native genotypes (e.g., Levin et al. 1995, Ayres et al. 1999, but see Whitham et al. 1991, 1999).

From a biogeographical perspective, restriction to F_1 types is a local phenomenon, because although F_1 type susceptibility is a repeated pattern (Eckenwalder 1984, Kalischuck et al. 1997) there are rivers on which large mite populations occur on parental host types (Drouin and Langor 1992; P. J. McIntyre, *personal observation*). However, in these rivers, mites may have genetically differentiated to successfully utilize the parental hosts and very little is known about the phylogeography of mites across North America. Furthermore, we do not know what is driving the apparent specialization on F_1 type hybrids in the Weber River and other rivers where mites are concentrated on F_1 type hybrids. F_1 types may be the only intrinsically susceptible hosts in the area, or there may be genotype \times environment interactions that result in parental hosts that are resistant in the environment of the hybrid zone. Alternatively, mites may be genetically adapted to F_1 types, with gene flow from large mite populations on F_1 hybrids preventing adaptation to more resistant narrowleaf types (e.g., hybrid sink hypothesis [Whitham 1989]). The apparent geographic variation in restriction to F_1 types could be utilized to determine the mechanisms underlying patterns of plant herbivore distribution and evolution on a geographic scale (cf. Thompson 1994).

In conclusion, this study provides the first empirical evidence that plant genotype and hybridization influence long-term (five-year) herbivore population dynamics and extinction. However, our study is only a first step in understanding the general importance of host plant genetic variation for herbivore populations, and we suggest that research in the following four areas is crucial for a more general understanding: (1) the effects of genetic variation among hosts and plants at the stand level (e.g., herbivore dynamics in monocultures vs. mixtures of host genotypes), (2) the spatial scales at which genetic variation impacts herbivore population dynamics (e.g., individual hosts or host patches), (3) how genetic variation among herbivore populations interacts with the genetic variation among host populations, and (4) how plant genetics interacts with environmental influences on herbivore populations to impact long-term dynamics. Finally, our results have important conservation implications. Because a rare class of hybrid tree supported >99% of the mite population, this implies that the conservation of genetic diversity in plants is not only important to the conservation of primary producers, but may also be crucial

for the survival of community members that are dependent on a small genetic subset of the host population for their survival.

ACKNOWLEDGMENTS

We thank Peter Price, Phil Service, and Greg Martinsen for comments on the manuscript, and Maggie Cross, Silas Page, Jen Schweitzer, and Gina Wimp for assistance in the field. Stewart Rood, Andrea Kalischuck, and Kevin Floate provided manuscripts and shared their personal knowledge of *Aceria parapopuli*. The Ogden Nature Center provided a long-term protected site for our common garden. NSF grants DEB-9726648 and DEB-0078280 and USDA grant 95-37302-1801 to T. Whitham, and a Sigma Xi grant-in-aid to P. McIntyre provided financial support.

LITERATURE CITED

- Agresti, A. 1996. An introduction to categorical data analysis. John Wiley and Sons, New York, New York, USA.
- Anderson, R. M., and R. M. May. 1991. Infectious diseases of humans: dynamics and control. Oxford University Press, New York, New York, USA.
- Ayres, R. D., D. Garcia-Rossi, G. H. Davis, and D. R. Strong. 1999. Extent and degree of hybridization between exotic (*Spartina alterniflora*) and native (*S. foliosa*) cordgrass (Poaceae) in California, USA determined by random amplified polymorphic DNA (RAPDs). *Molecular Ecology* **8**:1179–1186.
- Boecklen, W. J., and K. C. Larson. 1994. Gall forming wasps (Hymenoptera: Cynipidae) in an oak hybrid zone: testing hypothesis about hybrid susceptibility to herbivores. Pages 110–120 in P. W. Price, W. J. Mattson, and Y. N. Baranchikov, editors. Ecology and evolution of gall-forming insects. North Central Forest Experiment Station, USDA Forest Service, Saint Paul, Minnesota, USA.
- Bronner, R., E. Westphal, and F. Dreger. 1991. Pathogenesis-related proteins in *Solanum dulcamara* L. resistant to the gall mite *Aceria cladophthirus* (Nalpea) (syn *Eriophyes cladophthirus* Nal.). *Physiological and Molecular Plant Pathology* **38**:93–104.
- Brown, C. E. 1964. Habits and control of the poplar bud-gall mite. Canada Department of Forestry, Information Report, Forest Entomology and Pathology Laboratory, Calgary, Alberta, Canada.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58**:445–449.
- Campbell, L. M., R. J. Bilodeau, and R. F. Deboo. 1969. Research on the poplar gall mite in the prairie provinces. Internal Report MS-96, Forest Research Laboratory, Winnipeg, Manitoba, Canada.
- Cappuccino, N. 1992. The nature of population stability in *Eurosta solidaginis*, a nonoutbreeding herbivore of goldenrod. *Ecology* **73**:1792–1801.
- Caresche, L. A., and A. J. Wapshere. 1974. Biology and host specificity of the *Chondrilla* gall mite, *Aceria chondrillae* (G. Can.) (Acarina, Eriophyidae). *Bulletin of Entomological Research* **64**:183–192.
- Conover, W. J. 1999. Practical nonparametric statistics. Third edition. John Wiley and Sons, New York, New York, USA.
- Crawford, D. J. 1974. A morphological and chemical study of *Populus acuminata* Rydberg. *Brittonia* **26**:74–89.
- Cullen, J. M., and A. D. Moore. 1983. The influence of three populations of *Aceria chondrillae* on three forms of *Chondrilla juncea*. *Journal of Applied Ecology* **20**:235–243.
- Dangl, J. L., R. A. Dietrich, and M. H. Richberg. 1996. Death don't have no mercy: cell death programs in plant–microbe interactions. *Plant Cell* **8**:1793–1807.

- De Wit, P. G. J. M. 1997. Pathogen avirulence and plant resistance: a key role for recognition. *Trends in Plant Science* **12**:452–458.
- Drouin, J. A., and D. W. Langor. 1992. Poplar bud gall mite. Forestry Leaflet 15, Forestry Canada, Northwestern Region, Northern Forest Centre, Edmonton, Alberta, Canada.
- Dungey, H. S., B. M. Potts, T. G. Whitham, and H. F. Li. 2000. Plant genetics affects arthropod community richness and composition: evidence from a synthetic eucalypt hybrid population. *Evolution* **54**:1938–1946.
- Eckenwalder, J. E. 1984. Natural intersectional hybridization between North American species of *Populus* (Salicaceae) in sections *Ageiros* and *Tacamahaca*. I. Population studies of *P. parryi*. *Canadian Journal of Botany* **62**:317–324.
- Floate, K. D., G. D. Martinsen, and T. G. Whitham. 1997. Cottonwood hybrid zones as centers of abundance for gall aphids in western North America: importance of relative habitat size. *Journal of Animal Ecology* **66**:179–188.
- Floate, K. D., and T. G. Whitham. 1993. The “hybrid-bridge” hypothesis: host shifting via plant hybrid swarms. *American Naturalist* **141**:651–662.
- Floate, K. D., and T. G. Whitham. 1995. Insects as traits in plant systematics: their use in discriminating between hybrid cottonwoods. *Canadian Journal of Botany* **73**:1–13.
- Fritz, R. S. 1999. Resistance of hybrid plants to herbivores: genes, environment, or both? *Ecology* **80**:382–391.
- Fritz, R. S., C. Moulia, and G. Newcombe. 1999. Resistance of hybrid plants and animals to herbivores, pathogens and parasites. *Annual Review of Ecology and Systematics* **30**:565–591.
- Fritz, R. S., C. M. Nichols-Oriens, and S. J. Brunsfeld. 1994. Interspecific hybridization of plants and resistance to herbivores: hypotheses, genetics, and variable responses in a diverse herbivore community. *Oecologia* **97**:106–117.
- Fritz, R. S., B. M. Roche, and S. J. Brunsfeld. 1998. Genetic variation in resistance of hybrid willows to herbivores. *Oikos* **83**:117–128.
- Fritz, R. S., B. M. Roche, S. J. Brunsfeld, and C. M. Oriens. 1996. Interspecific and temporal variation in herbivore responses to hybrid willows. *Oecologia* **108**:121–129.
- Graham, J. H., D. C. Freeman, and E. D. MacArthur. 1995. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). II. Selection gradients and hybrid fitness. *American Journal of Botany* **82**:709–716.
- Graham, J. H., E. D. MacArthur, and D. C. Freeman. 2001. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). XII. Galls on sagebrush in a reciprocal transplant garden. *Oecologia* **126**:239–246.
- Grant, B. R., and P. R. Grant. 1996. High survival of Darwin’s Finch hybrids: effects of beak morphology and diets. *Ecology* **77**:500–509.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73**:724–732.
- Kalischuck, A. R., L. A. Gom, K. D. Floate, and S. B. Rood. 1997. Intersectional cottonwood hybrids are particularly susceptible to the poplar bud gall mite. *Canadian Journal of Botany* **75**:1349–1355.
- Kane, T. C., D. C. Culver, and R. T. Jones. 1992. Genetic structure of morphologically differentiated populations of the amphipod *Gammarus minus*. *Evolution* **46**:272–278.
- Karban, R. 1989. Fine-scale adaptation of herbivorous thrips to individual host plants. *Nature* **340**:60–61.
- 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.
- Kermack, W. O., and A. G. McKendrick. 1927. A contribution to the mathematical theory of epidemics. *Proceedings of the Royal Society of London, Series A* **115**:700–721.
- Kiefer, H. H. 1940. Eriophyid studies VIII. *Bulletin of the California Department of Agriculture* **29**:21–46.
- Lande, R. 1988. Extinction thresholds in demographic models of territorial populations. *American Naturalist* **130**:624–635.
- Larsson, S., B. Ekbom, and C. Bjorkman. 2000. Influence of plant quality on pine sawfly population dynamics. *Oikos* **89**:440–450.
- Levin, D. A., J. Francisco-Ortega, and R. K. Jansen. 1995. Hybridization and the extinction of rare plant species. *Conservation Biology* **10**:10–16.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America* **15**:237–240.
- Lindquist, E. E., and G. N. Oldfield. 1996. Evolution of eriophyid mites in relation to their host plants. Pages 277–300 in E. E. Lindquist, M. W. Sabelis, and J. Bruin, editors. *Eriophyid mites: their biology, natural enemies, and control*. Elsevier Science, Amsterdam, The Netherlands.
- Losos, J. B., T. R. Jackman, A. Larson, K. de Queiroz, and L. Rodriguez-Schettino. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* **279**:2115–2118.
- Maddox, G. D., and N. Cappuccino. 1986. Genetic determination of plant susceptibility to an insect depends on environmental context. *Evolution* **40**:863–866.
- Martinsen, G. D., T. G. Whitham, R. J. Turek, and P. Keim. 2001. Hybrid populations selectively filter gene introgression between species. *Evolution* **55**:1325–1335.
- Messina, F. J., J. H. Richards, and E. D. MacArthur. 1996. Variable responses of insects to hybrid vs. parental sagebrush in common gardens. *Oecologia* **107**:513–521.
- Mittler, R., and E. Lam. 1996. Sacrifice in the face of foes: pathogen-induced programmed cell death in plants. *Trends in Microbiology* **4**:10–15.
- Mopper, S., P. Stiling, K. Landau, D. Simberloff, and P. van Zandt. 2000. Spatiotemporal variation in leafminer population structure and adaptation to individual oak trees. *Ecology* **81**:1577–1587.
- 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.
- Paige, K. N., and W. C. Capman. 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 RFLP’s. *Evolution* **47**:36–45.
- Philip, H., and E. Mengersen. 1989. *Insect pests of the prairies*. University of Alberta, Edmonton, Alberta, Canada.
- Price, P. W., T. P. Craig, and H. Roininen. 1995. Working toward theory on galling sawfly population dynamics. Pages 321–338 in N. Cappuccino and P. W. Price, editors. *Population dynamics: new approaches and synthesis*. Academic Press, New York, New York, USA.
- Pulliam, H. R. 1988. Sources, sinks and population regulation. *American Naturalist* **132**:652–661.
- Renshaw, E. 1991. *Modeling biological populations in space and time*. Cambridge University Press, Cambridge, UK.
- Rieseberg, L. H., and N. C. Ellstrand. 1993. What can morphological and molecular markers tell us about plant hybridization? *Critical Reviews in the Plant Sciences* **12**:213–241.
- Robinson, B. W., and D. Schluter. 2000. Natural selection and evolution of adaptive genetic variation in northern

- freshwater fishes. Pages 65–94 in T. A. Mousseau, B. Sinervo, and J. Endler, editors. Adaptive genetic variation in the wild. Oxford University Press, New York, New York, USA.
- Rossiter, M. C. 1992. The impact of resource variation on population quality in herbivorous insects: a critical aspect of population dynamics. Pages 13–42 in M. D. Hunter, T. Ohgushi, and P. W. Price, editors. Effects of resource distribution on animal plant interactions. Academic Press, San Diego, California, USA.
- Sabelis, M. W., and J. Bruin. 1996. Evolutionary ecology: life history patterns, food plant choice and dispersal. Pages 329–366 in E. E. Lindquist, M. W. Sabelis, and J. Bruin, editors. Eriophyid mites: their biology, natural enemies, and control. Elsevier Science, Amsterdam, The Netherlands.
- Schotzko, D. J., and N. A. Bosque-Perez. 2000. Seasonal dynamics of cereal aphids on Russian wheat aphid (Homoptera: Aphididae) susceptible and resistant wheats. Journal of Economic Entomology **93**:975–981.
- Scribner, T. C. 1993. Hybrid zone dynamics are influenced by genotype-specific variation in life-history traits: experimental evidence from hybridizing *Gambusia* species. Evolution **47**:632–646.
- Sokal, R. R., and F. J. Rohlf. 1995. Biometry. Third edition. Freeman, New York, New York, USA.
- SPSS. 1999. SPSS, version 10.0.7. SPSS, Chicago, Illinois, USA.
- Stiling, P., and A. M. Rossi. 1996. Complex effects of genotype and environment on insect herbivores and their enemies. Ecology **77**:2212–2218.
- Strauss, S. Y. 1994. Levels of herbivory and parasitism in host hybrid zones. Trends in Ecology and Evolution **9**:209–214.
- Thompson, J. N. 1994. The coevolutionary process. University of Chicago Press, Chicago, Illinois, USA.
- Underwood, N., and M. D. Rausher. 2000. The effects of host-plant genotype on herbivore population dynamics. Ecology **81**:1565–1576.
- Wang, H., E. D. McArthur, S. C. Sanderson, J. H. Graham, and D. C. Freeman. 1997. Narrow hybrid zone between two subspecies of big sagebrush (*Artemesia tridentata*: Asteraceae). IV. Reciprocal transplant experiments. Evolution **51**:95–102.
- Westphal, E. 1992. Cecidogenesis and resistance phenomena in mite-induced galls. Pages 141–156 in J. D. Shorthouse and O. Rohfritsch, editors. Biology of insect induced galls. Oxford University Press, New York, New York, USA.
- Westphal, E., F. Dreger, and R. Bronner. 1990. The gall mite *Aceria cladophthirus*. I. Life-cycle, survival outside the gall and symptoms' expression on susceptible or resistant *Solanum dulcamara* plants. Experimental and Applied Acarology **9**:183–200.
- Whitham, T. G. 1989. Plant hybrid zones as sinks for pests. Science **244**:1490–1493.
- Whitham, T. G., G. D. Martinsen, K. D. Floate, H. S. Dungey, B. M. Potts, and P. Keim. 1999. Plant hybrid zones affect biodiversity: tools for a genetic-based understanding of community structure. Ecology **80**:416–428.
- Whitham, T. G., P. A. Morrow, and B. M. Potts. 1991. Conservation of hybrid plants. Science **254**:779–780.
- Ylloja, T., H. Roininen, M. P. Ayres, M. Rousi, and P. W. Price. 1999. Host driven population dynamics in an herbivorous insect. Proceedings of the National Academy of Sciences (USA) **96**:10735–10740.