

Cottonwood hybrid zones as centres of abundance for gall aphids in western North America: importance of relative habitat size

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Summary

1. In western North America, populations of the leaf-galling aphid *Pemphigus betae* are concentrated in natural zones of overlap and hybridization between species of cottonwoods (*Populus*). Averaged over seven drainages in four American states and one Canadian province, *P. betae* galls were 28-fold more abundant in hybrid zones than in adjacent pure zones of the narrowleaf host species.

2. The strength of this pattern is impressive in that it occurred in all of the river drainages surveyed and spanned a north–south gradient of 1600 km (15° latitude). Furthermore, this pattern was not restricted to one species-pair of cottonwoods, but occurred in zones of narrowleaf × Fremont, narrowleaf × Eastern, and narrowleaf × balsam × Eastern cottonwood.

3. The concentration of galls in the hybrid zone was not influenced by the absolute size of the hybrid zone. However, there was a significant inverse relationship ($P = 0.02$) between relative gall density and the relative size of the hybrid zone. All else being equal, small hybrid zones supported higher concentrations of aphids than large hybrid zones. Three hypotheses, ‘hybrid zones as aphid sinks’, ‘hybrid zones as aphid sources’ and an ‘introgression’ hypothesis, are proposed which may explain this regional pattern.

4. Riparian cottonwood forests shelter a rich diversity of animal and plant species that is threatened by habitat loss through anthropogenic activities. If the concentration of *P. betae* in cottonwood hybrid zones is a pattern common to other hybridizing plants and their dependent species, preserving these relatively small areas could have a disproportionately positive role in preserving biodiversity.

Key-words: bioconservation, hybrid zones, *Pemphigus betae*, *Populus*, riparian forests.

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Introduction

Natural zones of overlap and hybridization between plant species have increasingly been shown to be centres of abundance for phytophagous arthropods and pathogens. In the USA, a cottonwood (*Populus*) hybrid zone represents <3% of the host population, but contains >85% of the populations of a leaf-galling aphid (Whitham 1989) and a free-feeding beetle (Floate, Kearsley & Whitham 1993). Other examples include concentrations of organisms in zones of

hybrid sedge (*Carex*; Ericson, Burdon & Wennström 1993), eucalypt (*Eucalyptus*; Whitham, Morrow & Potts 1994), pine (*Pinus*; Christensen, Whitham & Keim 1995) and sage (*Artemisia*; Graham, Freeman & McArthur 1995). Although these concentrations may reflect the greater susceptibility of hybrid genotypes, hybrids may also be less, equal or intermediate in susceptibility relative to the parent species (reviewed by Strauss 1994; Hanhimäki, Senn & Haukioja 1994). Because the patterns of hybridization (i.e. F₁ sterility, unidirectional and bidirectional introgression; Keim *et al.* 1989; Floate & Whitham 1993), the interactions of genes associated with plant defence (e.g. additive, dominance, recessive, heterosis; Fritz, Nichols-Orians & Brunsfeld 1994; Christensen *et al.* 1995) and

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environmental interactions (e.g. Paige & Capman 1993; Christensen *et al.* 1995) are likely to produce diverse phenotypes in hybrids, a variety of herbivore responses to hybridizing plants should be expected.

The above confounding factors may prevent a herbivore species from exhibiting a general response to the hybridization of its host species. Only one study to date has examined this question over a large geographical area. In Sweden, Ericson *et al.* (1993) found the smut *Anthracoidea fischeri* (Karst.) Kukk. at each of 13 localities where its host sedges (*Carex canescens* L. and *C. mackenziei* V. Krecz.) hybridized. The incidence and severity of infection at these sites were much higher on hybrid hosts than on adjacent parental plants. In contrast, the pathogen was absent at each of 10 localities where sympatric host species did not hybridize. Hybridization in sedge appears to generate just one response in smut populations; the severity of floral smut is 30–80-fold greater on hybrid sedges than on sympatric parent genotypes. Thus, although the strength of the interactions appears to vary geographically, hybrids are more susceptible to smut attack than the parental species. The authors of this study concluded that selection against hybrids acts to maintain separate sedge species and that local populations of smut may be totally reliant upon hybrid sedge for survival. Their study emphasizes the importance of a geographical perspective and suggests that hybridization has broad implications for the ecology, evolution and conservation of both the plants and their dependent species (reviewed by Strauss 1994; Rieseberg 1995; Whitham & Maschinski 1996).

Having demonstrated that the leaf-galling aphid *Pemphigus betae* Doane is concentrated in a natural hybrid zone of one river drainage, we examined the potential generality of this observation by surveying aphid distributions in other river drainages through the Rocky Mountains of the USA and southern Canada. A general pattern might be expected if the herbivore is responding to hybridization *per se*. However, the herbivore may also be responding to factors that change for each hybrid zone, e.g. its age, size, long-term stability and elevation (Boecklen & Spellenberg 1990; Paige & Capman 1993). In the latter event, hybrid zones as centres of abundance for *P. betae* may be circumstance dependent, which would preclude general predictions.

In addition, because our study included hybrid zones of different sizes, we examined how aphid abundance was influenced by the abundance of hybrid and parental hosts. For example, although Ericson *et al.* (1993) observed that the severity and incidence of smut was greater on hybrid sedges than on the parent species, the strength of this pattern varied geographically. In the present study we reasoned that hybrid zone size, or its size relative to that of the pure host zone, could result in different patterns in different river drainages. Such differences are expected based upon island biogeography theory (MacArthur & Wil-

son 1967) and the recent synthesis of co-evolving species (Thompson 1994).

Methods

STUDY SYSTEM

Native species of cottonwood of sect. *Tacamahaca* Spach (*Populus angustifolia* James, *P. balsamifera* L., *P. trichocarpa* Torr. & A. Gray) hybridize with native species of sect. *Aigeiros* Duby (*P. fremontii* S. Wats., *P. deltoides* Marsh). Hybrids are found wherever species in the two sections are sympatric (Eckenwalder 1984b), which includes virtually all rivers originating in the Rocky Mountains of western North America. Narrowleaf cottonwoods (*P. angustifolia*) grow at higher elevations in drainages of the Rocky Mountains from southern Alberta to northern Mexico. Fremont (*P. fremontii*) and Eastern (*P. deltoides*) cottonwoods grow at lower elevations on flood-plains extending out from the western and eastern fronts of these mountains, respectively. Hybridization occurs at intermediate elevations where these species come into contact.

Genetic analyses show that in the field F_1 hybrids backcross only to narrowleaf. This pattern of unidirectional introgression forms a gradient of genetic and morphological intermediates between narrowleaf and F_1 s, but leaves a distinct gap between the morphologies of F_1 s and Fremont (Keim *et al.* 1989; Paige & Capman 1993). Allozyme analyses (J. Mitton, personal communication) and our own observations indicate that the pattern of hybridization is similar between narrowleaf and Eastern cottonwood, i.e. F_1 s backcross to narrowleaf, leaving a distinct gap between the morphologies of F_1 s and Eastern cottonwood.

The aphid *P. betae*, forms galls on cottonwoods of sect. *Tacamahaca* (Palmer 1952; Harper 1959). Galls are initiated in early spring beside the midribs of attacked leaves, and develop into pouch-shaped structures opening onto the upper leaf surface. Complex backcross hybrids can be highly susceptible, but F_1 and BC_1 (the progeny of F_1 and narrowleaf trees) hybrids are almost totally resistant (Paige *et al.* 1990; Floate & Whitham 1995). Because they are easily distinguished from the galls of other *Pemphigus* species (Maxson & Knowlton 1929; Palmer 1952; Harper 1959) and remain on trees until late summer, *P. betae* galls can be quickly and accurately surveyed from May to August.

RIVER DRAINAGES

River drainages were identified where upper elevations supported stands of narrowleaf cottonwood and lower elevations supported stands of either Fremont or Eastern cottonwood. Cottonwood species overlapped and hybridized at intermediate elevations

in each drainage. The hybrid zone was defined as the riparian sites supporting the two parent species and their hybrid intermediates. These categories were distinguished by differences in petiole length, and the length and width of the leaf blade. Although many morphological traits and genetic analyses are needed to distinguish between closely related classes of hybrids (e.g. between backcross 2 and backcross 5 hybrids, or between complex backcrosses and pure narrowleaf hosts; Floate, Whitham & Keim 1994), at a much broader level these three leaf characters clearly distinguish cottonwoods of sect. *Tacamahaca* from cottonwoods of sect. *Aigeiros*. For example, Fig. 1 shows the typical leaf morphologies in pure stands of narrowleaf cottonwood, broadleaf cottonwood (Eastern or Fremont cottonwood), and in an intervening zone of overlap and hybridization. There is no overlap of leaf morphologies in pure stands of the parental species, but the hybrid zone contains trees with the morphologies of both parental species and trees of inter-

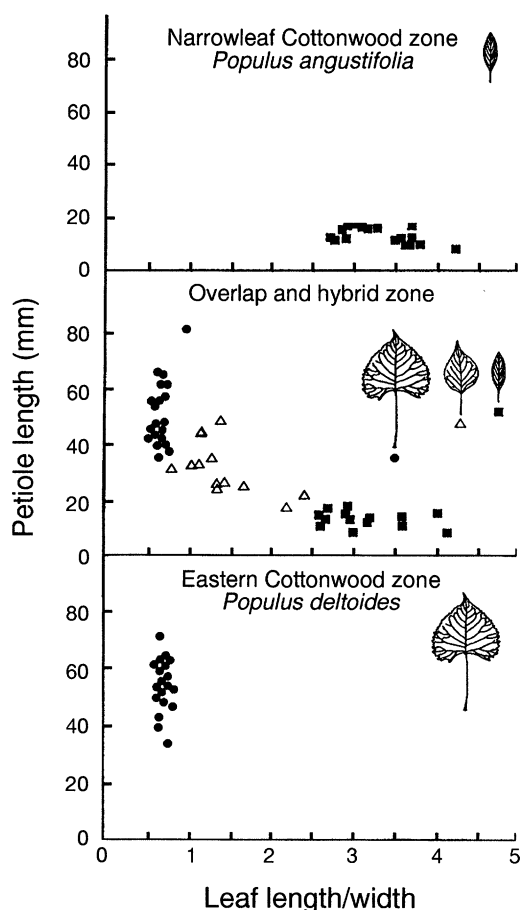


Fig. 1. Data for the Rio Nambe, New Mexico, illustrate how leaf morphologies were used to segregate zones of narrowleaf cottonwood, broadleaf cottonwood and an intervening zone of overlap and hybridization. There was no overlap of leaf morphologies between trees growing in stands of narrowleaf cottonwood (*Populus angustifolia*) and Eastern cottonwood (*P. deltoides*). However, trees in the intervening zone displayed a continuum of leaf morphologies indicative of the two parent species and hybrid intermediates. Leaf icons characteristic of each zone are shown.

mediate leaf morphology. Because little within-tree variation was found among leaves standardized for node position, we measured only one leaf per tree at a 4–5th acropetal node. Leaves at this position are produced from leaf primordia formed the previous summer and are termed ‘early flush’ leaves to distinguish them from ‘late flush’ leaves which are produced from leaf primordia formed in the current year.

Genetic data (Keim *et al.* 1989; G.D. Martinsen *et al.* unpublished data) on 600+ cottonwood trees distributed throughout the drainage of the Weber River (Fig. 2) show this morphological-based definition of a hybrid zone to be appropriate. At sites where Fremont and narrowleaf cottonwoods co-occur and obvious hybrids are uncommon, subsequent restriction fragment length polymorphism (RFLP) analyses have identified most of the ‘narrowleaf’ trees as complex backcross hybrids. Until further molecular analyses are available over a broad geographic region, we believe our definition of a cottonwood hybrid zone provides an objective approach and probably underestimates the true size of the hybrid zone.

APHID DISTRIBUTIONS

To test whether hybrid zones were centres of abundance for *P. betae*, gall densities in each drainage were compared between trees in hybrid and narrowleaf zones. Comparisons did not include Fremont and Eastern cottonwoods, as these species are not hosts for *P. betae* (Palmer 1952; Harper 1959; Paige *et al.* 1990; authors’ personal observation). Gall densities were initially measured as the number of galls per 1000 leaves per tree. This method proved unnecessary, so density was subsequently measured as the number of galls per tree counted during a 2-min census. Galls were censused at several sites in the narrowleaf and hybrid zones of each drainage to reduce potential site differences. Tree heights were standardized by sampling the lowest 3 m of foliage on all sides of a tree (trees grew 5–30 m in height). Only reproductively mature trees were surveyed because *P. betae* is concentrated on mature trees, where their survival and fecundity are greatest (Kearsley & Whitham 1989). The number of trees sampled in a drainage varied with the size and accessibility of narrowleaf and hybrid zones. Gall densities were normalized by $\log(x + 1)$ transformation and then average gall densities per tree between hybrid and narrowleaf zones were compared using *t*-tests ($P = 0.05$).

To examine whether the size of a hybrid zone affected its ability to concentrate aphids within a drainage, we calculated a ‘relative gall density’ for each river drainage and then regressed this measure against both the absolute and relative size of the hybrid zone. Relative gall density was calculated as the average number of galls per tree in the hybrid zone divided by the average number of galls per tree in the narrowleaf zone. For example, if gall densities were threefold

Cottonwood Rivers with Hybrid Swarms and *Pemphigus betae*

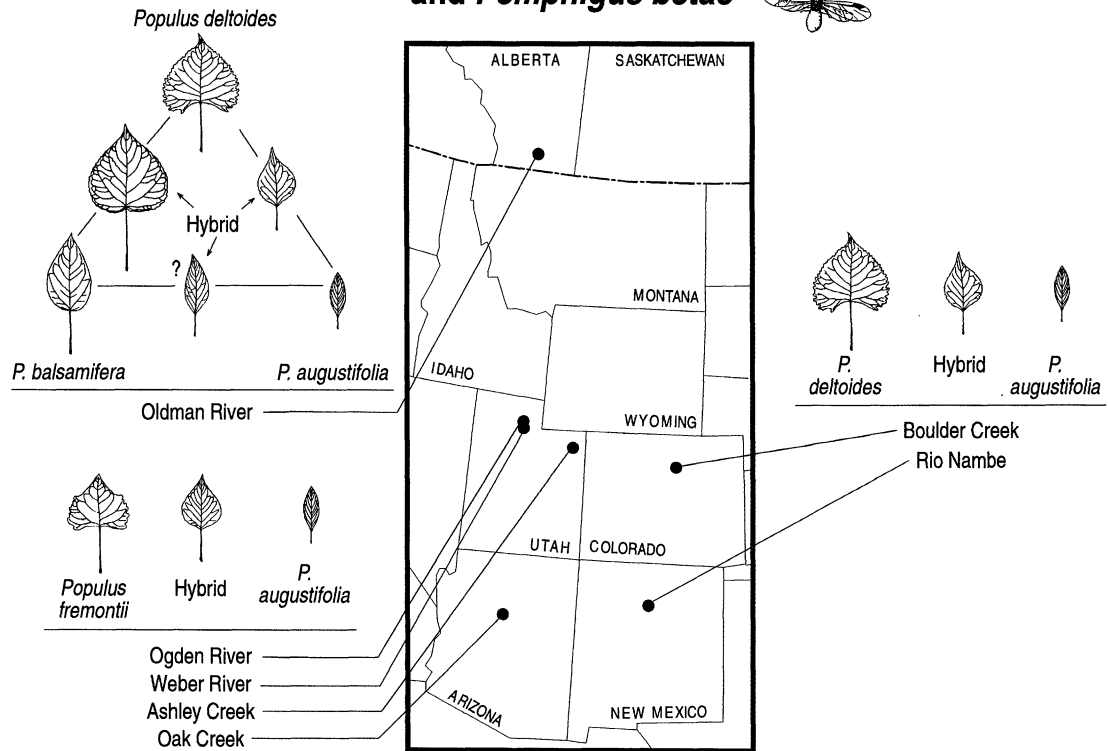


Fig. 2. Drainages surveyed for the distribution of the leaf-galling aphid *Pemphigus betae*. In each drainage, there was a high elevation zone of the host species (narrowleaf cottonwood *Populus angustifolia*), a low elevation zone of a non-host species (Fremont *P. fremontii* or Eastern cottonwood *P. deltoides*) and an intermediate elevation zone of overlap and hybridization. Leaf icons depict the morphologies of early flush leaves (additional examples in Eckenwalder 1984b).

higher in the hybrid zone than in the adjacent narrowleaf zone, the relative gall density would be '3'. Hence the greater the concentration of aphids in the hybrid zone, the higher the relative gall density.

The absolute size of the hybrid zone was quantified as the linear kms of riparian habitat composed of overlapping species and their hybrids. The relative size of the hybrid zone measured the availability of susceptible hybrids (kms of hybrid zone) divided by the total host population (kms of hybrid and narrowleaf zones combined). Note that neither Fremont nor Eastern cottonwood are hosts, so the size of their zones is not relevant. The size of the narrowleaf zone was quantified as the linear kms of riparian habitat on the main river channel composed solely of narrowleaf cottonwood. The length of tributaries could not be calculated accurately due to their inaccessibility and were not included. Although this omission underestimated the size of the narrowleaf population, the main channel measurement should represent a good index of the overall size of the narrowleaf zone. Absolute sizes were $\log(x + 1)$ transformed prior to analysis. Values of relative size appeared to be distributed normally and were not transformed prior to analyses. SYSTAT (Wilkinson 1992) was used for all statistical analyses.

We did not regress absolute gall density against

hybrid zone size because variation in abiotic factors among river drainages confounds interpretation of the regression. For example, a 6-year study in Weber Canyon, Utah, found *P. betae* populations to be significantly affected by rainfall during the previous summer ($r^2 = 0.69$, $P < 0.03$; Moran & Whitham 1988b). Hence, the influence of precipitation would need to be considered in assessing the effect of hybrid zone size on absolute gall density. Our measure of relative gall density allowed us to standardize data across drainages. The ecological interpretations of these standardized data sets are developed in the following section.

Results and discussion

HYBRIDIZATION THROUGHOUT THE ROCKY MOUNTAINS

Seven drainages were identified that contained zones of overlap and hybridization between stands of narrowleaf and Fremont or Eastern cottonwood (Fig. 2). Narrowleaf and Fremont cottonwood hybridize in the drainages of the Ogden River, the Weber River, Ashley Creek and Oak Creek, which flow through the cities of Ogden, South Weber and Vernal, Utah, and Sedona, Arizona, respectively.

Narrowleaf and Eastern cottonwood hybridize in the drainages of Boulder Creek and the Rio Nambe, which flow through the communities of Boulder, Colorado, and Espanola, New Mexico, respectively. In the Oldman River drainage, narrowleaf, balsam (*P. balsamifera*) and Eastern cottonwood interbreed to form a trispecific hybrid swarm centred in the city of Lethbridge, Alberta, Canada (Brayshaw 1965; Rood, Campbell & Despins 1986; Greenaway *et al.* 1991).

Zones of overlap and hybridization were distinguished from adjacent pure zones by variation in leaf morphology. The pattern of this variation is specifically illustrated for the Rio Nambe (Fig. 1), but was common to each of the drainages surveyed (Fig. 3). Leaf morphology did not overlap between trees in narrowleaf zones and trees in zones of Fre-

mont or Eastern cottonwood. Trees in narrowleaf zones had leaf petioles generally <25 mm in length and leaf blades 2–5 times longer than wide. Trees in zones of Fremont or Eastern cottonwood had leaf petioles 30–100 mm in length and leaf blades typically of greater width than length. Trees in hybrid zones exhibited both of these leaf morphologies and intermediate forms associated with F_1 and backcross hybrids (Eckenwalder 1984a,b; Floate & Whitham 1995). The only apparent exception to this pattern was in the drainage of the Oldman River, where trees with wide leaf blades and long petioles were found in the narrowleaf zone. These trees were balsam cottonwood, which are easily distinguished from Eastern and Fremont cottonwood by other characters (Brayshaw 1965; Eckenwalder 1984b; Rood *et al.* 1986).

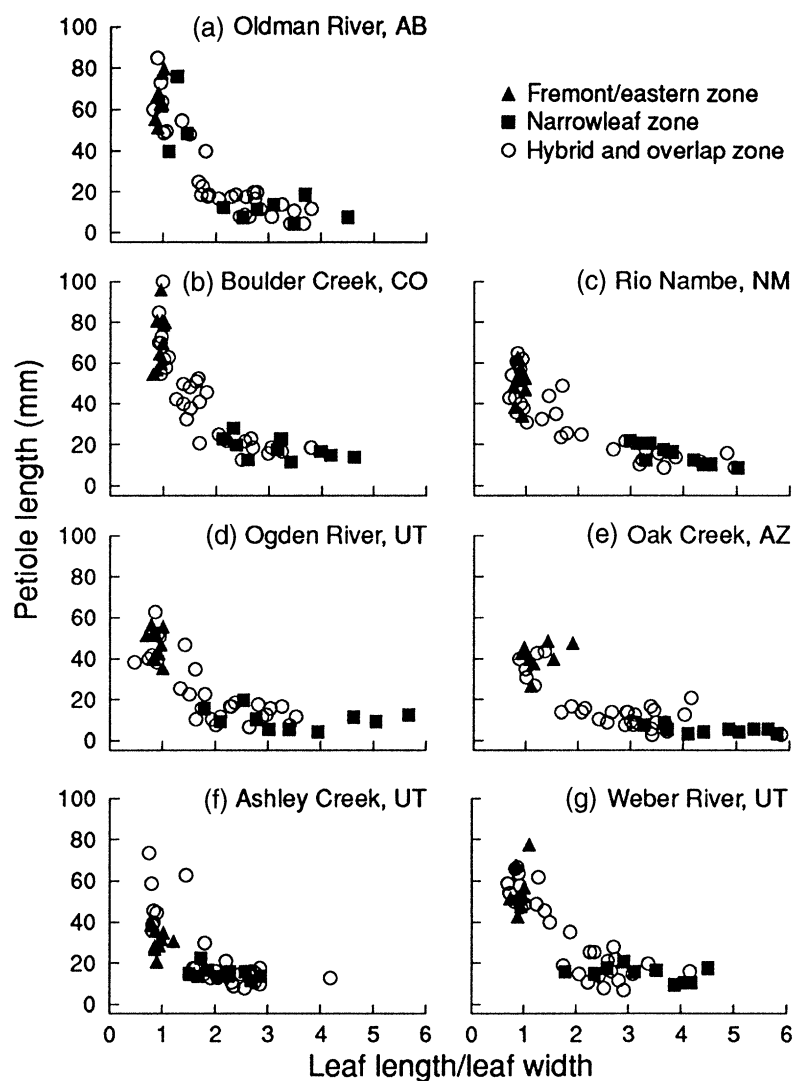


Fig. 3. Variation in leaf morphology identified the morphological boundaries of the hybrid/overlap zone. Leaf morphology did not overlap between pure zones of the parent cottonwood species, but the hybrid/overlap zone exhibited a full-range of leaf morphologies including intermediate forms associated with F_1 and BC_1 hybrids. (a) Eastern \times balsam \times narrowleaf cottonwood; (b,c) Eastern \times narrowleaf cottonwood; (d–g) Fremont \times narrowleaf cottonwood. Trees in the narrowleaf zone of the Oldman River drainage (a) with a morphology that apparently overlapped with Eastern cottonwood were balsam cottonwoods (*P. balsamifera*), which are readily distinguished from Eastern cottonwoods by other characters (see text). The trees plotted for each drainage were a subset of the total trees sampled and were selected to show the maximum amount of leaf variation encountered in each zone.

GEOGRAPHICAL CONCENTRATION OF APHIDS
IN HYBRID ZONES

Aphid populations were concentrated in the hybrid zone of each of the seven drainages surveyed (Fig. 4). This pattern was significant ($P \leq 0.001$) in six drainages, where average gall densities were 8–119-fold greater on trees in the hybrid zone than on trees in the narrowleaf zone. In the seventh drainage (the Rio Nambre), gall densities were 1.8-fold greater on trees in the hybrid zone than on trees in the narrowleaf zone, but this difference was not significant ($P = 0.279$). Averaged over these seven drainages on western and eastern fronts of the Rocky Mountains, *P. betae* galls were 28-fold more abundant in hybrid zones than in adjacent narrowleaf zones. No galls were found in pure zones of Fremont or Eastern cottonwood, which are not host species for *P. betae*.

We conclude that the concentration of *P. betae* in a cottonwood hybrid zone, as reported by Whitham (1989), is not merely a local event, but a general phenomenon that may occur in hundreds of drainages where cottonwoods hybridize. The strength of this pattern is impressive in that: (i) cottonwood hybrid zones were centres of abundance for *P. betae* in each of seven drainages examined; (ii) these drainages spanned 15 degrees of latitude or about 1600 km of the Rocky Mountains in the USA and southern Canada; (iii) we have not surveyed any drainages in which this pattern did not occur; and (4) this pattern was not restricted to one species-pair of cottonwoods, but occurred in zones of narrowleaf \times Fremont, narrowleaf \times Eastern and narrowleaf \times balsam \times Eastern cottonwood.

In agreement with these findings, Eckenwalder (1984a) noted that natural hybrids of Fremont and black cottonwood (*Populus trichocarpa*) are more heavily attacked by arthropods and fungal pathogens than either parent species. In eight river drainages in California and western Nevada where cottonwood pathology was great, weak or non-existent, he re-

corded a total of 17 great or weak pathologies on hybrids, but only four such pathologies on each parent species. Although no statistical analyses were applied to these data in the original study, our analyses indicate that these differences are significant and that hybrids exhibit a much higher incidence of pathologies than either parent species ($\chi^2 = 13.52$, d.f. = 2, $P < 0.005$). Pathologies included eriophyid mite bud galls, eriophyid mite leaf galls, *Pemphigus* aphid leaf-petiole gall, ascomycete perithecia on leaves, terminal bud abortion, stem cankers and leaf curl.

Similarly, hybrids propagated artificially for shelterbelts or urban forests can be particularly susceptible to attack by organisms that occur at low levels on native species of cottonwoods, e.g. the fungal species *Septoria musiva* Pk. and *Dothichiza populea* Sacc. & Briard., the hymenopteran species *Messa populifoliella* (Townsend) and *Janus abbreviatus* (Say), the coleopteran species *Cryptorhynchus lapathi* (Linnaeus) and *Chrysomela scripta* Fabricius, the lepidopteran species *Gypsonoma haimbachiana* (Kearfott) and *Aegeria tibialis* Harris, and the mite species *Aceria parapopuli* (Keifer) (Davidson & Prentice 1968; Rose & Lindquist 1982; Ives & Wong 1988).

CAUSES FOR THE OBSERVED PATTERNS

Several hypotheses may account for the concentration of *P. betae* in cottonwood hybrid zones. Tree genetics is strongly implicated by several lines of experiments and observations. First, although F_1 hybrids are highly resistant to aphid attack, complex backcrosses can be extremely susceptible (Paige *et al.* 1990; Paige & Capman 1993). This pattern suggests that complex backcrosses may suffer from hybrid breakdown, i.e. co-adapted gene complexes contributing to plant defence have become genetically scrambled during hybridization. Secondly, individual clones vary greatly in their suitability as hosts for aphids. Aphid survival on some clones is 0%, whereas survival on other

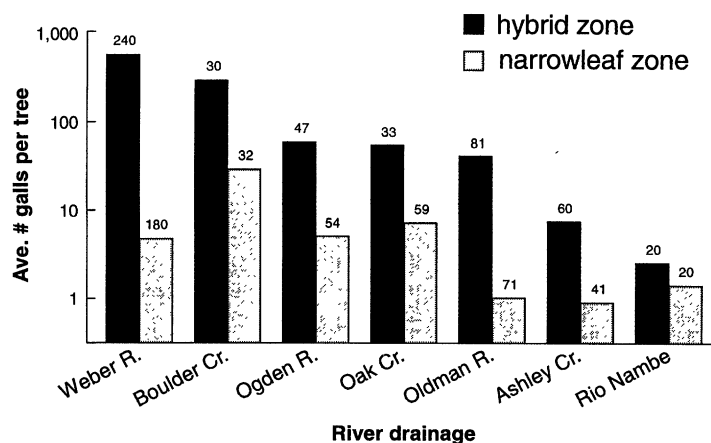


Fig. 4. In each of seven drainages surveyed, *Pemphigus betae* galls were more abundant on trees in the hybrid/overlap zone than in the adjacent narrowleaf zone. This difference was significant ($P < 0.001$) for all drainages with the exception of the Rio Nambre, New Mexico ($P = 0.28$). Numbers above bars indicate the number of trees sampled.

clones may be as high as 75%. Thirdly, associated with large differences in aphid survival on different clones, aphid transfer experiments demonstrate that the resistance traits of trees are maintained when these trees are cloned and grown in common gardens ($r^2 = 0.81$, $P < 0.001$, $n = 16$ tree clones). Fourthly, the survival of aphids transferred onto trees in the hybrid zone was significantly greater than the survival of aphids transferred onto trees in the narrowleaf zone (61% vs. 39% survival, respectively). Fifthly, the survival of aphids naturally colonizing trees in hybrid and narrowleaf zones nearly mirrors the results of our experimental aphid transfers (points 2–5 in Whitham 1989). Lastly, disease resistance of hybrid cottonwoods grown commercially shows high heritabilities. For example, the susceptibility of hybrid cottonwoods to an isolate of the rust *Melampsora medusae* is governed by the presence of a single dominant gene (Newcombe *et al.* 1996).

Alternatively, trees growing at the boundary of their distribution may suffer greater environmental stress and be more susceptible to insect attack than trees growing at the centre of their distribution (Whitham 1989; Paige & Capman 1993; Whitham *et al.* 1994; Christensen *et al.* 1995). However, when cloned trees were grown both in a hybrid zone and in the adjacent narrowleaf zone, site had no effect on aphid performance, whereas tree clone had a major effect (T.G. Whitham *et al.*, unpublished data). Other factors may contribute to a tree's susceptibility and resistance traits, but the genetic effects of hybridization on resistance appear to be important to *P. betae*.

EFFECT OF RELATIVE HOST DISTRIBUTION ON APHID CONCENTRATION

Our initial prediction that larger hybrid zones would support greater concentrations of aphids per tree was not met. There was no significant relationship between the relative density of aphid galls in the hybrid zone (gall density in the hybrid zone divided by gall density in the narrowleaf zone) and the absolute size of the hybrid zone (Fig. 5a; $r^2 = 0.35$, $P = 0.16$, $y = 0.76x + 0.31$, $n = 7$ drainages). This was surprising since it is known that the size of the host patch can affect insect densities (Strong, Lawton & Southwood 1984).

Although the relative density of aphids in the hybrid zone was not affected by the absolute size of the hybrid zone, it was inversely affected by the relative size of the hybrid zone (Fig. 5b; $r^2 = 0.67$, $P = 0.02$, $y = -8.97x + 2.36$, $n = 7$ drainages). Rivers with hybrid zones comprising a small portion of the total available host habitat had far greater concentrations of aphids in the hybrid zones than rivers in which the hybrid zones comprised a large portion of the available host habitat. For example, the relative density of aphid galls in the hybrid zone of the Weber River was 119, although this zone only represents about 13% of the

total host population (<3% when cottonwoods on tributaries are included). In contrast, relative gall density in the hybrid zone of the Rio Nambe was only 1.8 and there the hybrid zone represents about 50% of the total host habitat. All else being equal, *P. betae* populations were most concentrated in hybrid zones of the smallest relative size.

What does this pattern mean in an ecological and evolutionary sense? We offer three hypotheses. First, hybrid zones may represent ecological sinks for aphids such that there is an overall movement of aphids from the narrowleaf zone onto susceptible hosts in the hybrid zone (i.e. the 'hybrid zones as aphid sinks' hypothesis). Presumably, the concentration of aphids on trees in the hybrid zone would increase as the size of the hybrid zone decreased, relative to that of the narrowleaf zone (Fig. 5b). If true, then the hybrid zone is a sink and the narrowleaf zone is a source in an ecological sense. Whitham (1989) proposed that the susceptible plants in hybrid zones could act as sinks, much the same as 'trap crops' have been shown to concentrate pests in agricultural settings. The surprising aspect of this hypothesis is not so much that herbivores have higher densities on susceptible plants, but that they could be attracted to susceptible plants over a whole river drainage system.

A second hypothesis (the 'hybrid zones as aphid sources' hypothesis) is that the movement of winged aphid migrants from the hybrid zone into the narrowleaf zone serves to equalize gall densities between them. Because this 'spill-over' effect should decline as a function of distance from the hybrid zone, differences in gall densities between hybrid and narrowleaf zones should remain greater in drainages with large narrowleaf zones, all else being equal. In this case, the hybrid zone would be a source of colonizing aphids.

Alternatively, this negative relationship may reflect the introgression of the hybrid genome into the narrowleaf zone, modified by the size of the narrowleaf zone (i.e. the 'introgression' hypothesis). Because trees in the narrowleaf zone are more resistant to aphid attack than trees in the hybrid zone (39% vs. 61% aphid survival, respectively; Whitham 1989), the introgression of susceptibility traits into the narrowleaf zone would tend to equalize susceptibilities across zones and reduce differences in gall densities. All else being equal, the overall level of susceptibility would decline in narrowleaf zones of increasing size because the degree of introgression is presumably reduced as one moves further into the narrowleaf zone and away from the hybrid zone. In this scenario, the hybrid zone could be considered as a source of susceptible host genotypes.

Although our second and third hypotheses both envisage the hybrid zone as a source rather than a sink (as per our first hypothesis), they are fundamentally different. The 'hybrids as aphid sources' hypothesis explains higher aphid densities in the narrowleaf zone by an increase in the number of aphids colonizing

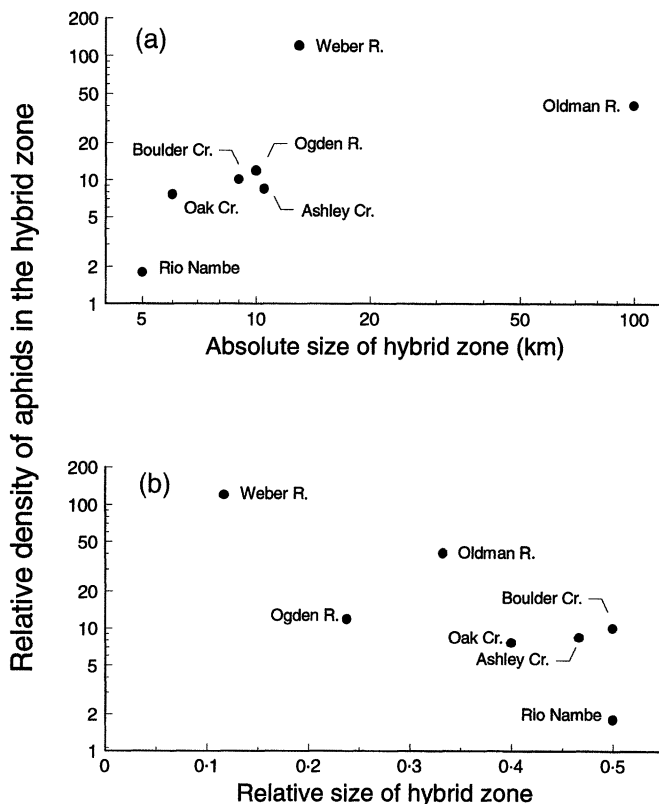


Fig. 5. (a) Relative aphid density was not affected by the absolute size of the hybrid zone ($r^2 = 0.35$, $P = 0.16$, $y = 0.76x + 0.31$, $n = 7$ drainages). Relative aphid density measures the concentration of *P. betae* galls in the hybrid zone compared to the narrowleaf zone (see text for details). (b) Relative aphid density was inversely affected by the relative size of the hybrid zone such that aphids were most concentrated in hybrid zones of the smallest relative size ($r^2 = 0.67$, $P = 0.02$, $y = -8.97x + 2.363$, $n = 7$ drainages). The relative size of the hybrid zone is its length divided by the length of hybrid and narrowleaf zones combined.

these trees, whose susceptibilities remain unchanged. The 'introgression' hypothesis explains increased aphid densities on trees in the narrowleaf zone as a response to an actual increase in host susceptibility.

Much broader testing is needed to address these hypotheses, but they each suggest that a relatively small number of susceptible plants can influence herbivores at both local and geographic levels. This conclusion not only has obvious implications for pest management, but also for conservation.

IMPLICATIONS FOR CONSERVATION

The degradation of riparian habitat in many river drainages precluded their incorporation in the present study. Noss, LaRoe & Scott (1995) estimate that 70–84% of the riparian habitat throughout the USA has been destroyed, converted to other land uses, or has been significantly degraded since European settlement. In our surveys, degradation was particularly prevalent at lower elevations where stands of cottonwoods had been eliminated or were in decline due to dams, canals diverting water, river channelization, farming up to the edge of the river, cattle grazing, sand and gravel mining, and urban development (Rood & Mahoney 1993). The loss of these forests is par-

ticularly disturbing because they shelter a rich diversity of fauna (Finch & Ruggiero 1993) and are frequently the only wooded habitat on the northern Great Plains and foothills of the Rocky Mountains. The level of degradation we observed is representative of the overall situation in the south-western USA, where the decline in riparian cottonwood forests has been estimated at 70–95% (Johnson & Haight 1984).

As centres of abundance, hybrid zones may merit special consideration as sites for conservation (Whitham, Morrow & Potts 1991). If the concentration of *P. betae* in cottonwood hybrid zones is a pattern common to other riparian species, preserving these relatively small areas could conserve a disproportionately large amount of riparian biodiversity. In support of this conclusion, the hybrid zone on the Weber River is also the centre of abundance for a leaf-feeding beetle *Chrysomela confluens* Rog. (Floate *et al.* 1993) and contains a density of bird nests that is almost threefold higher than densities in adjacent zones of Fremont and narrowleaf cottonwood (Martinsen & Whitham 1994). Similarly, in an examination of 40 insect and fungal species on endemic Tasmanian eucalypts, Whitham *et al.* (1994) found that 73% were significantly more abundant in the hybrid zone than in the adjacent pure zones and five

species were largely restricted to the hybrid zone. Potentially, the loss of the hybrid zone could result in the local extinction of these latter species.

Because hybrid zones are centres of plant speciation, their preservation also protects future lineages that may survive best in a changing environment. *Tragopogon mirus* Ownbey and *T. miscellus* Ownbey are species of goat's beard (family Compositae) that arose this century in Washington and Idaho in the USA. Originally sterile F₁ hybrids between species of diploid *Tragopogon* introduced from Europe, they became fertile following chromosome doubling events (Ownbey 1950). These new species have since increased their distributions and may be regionally more common than their parent species (Novak, Soltis & Soltis 1991). Further examples are presented in Grant (1981) and Stace (1987).

The conservation of natural plant hybrid zones may also protect sites of accelerated evolution for species associated with these zones. Race formation in *P. betae* may be a consequence of hybridization between Fremont and narrowleaf cottonwood. In the hybrid zone of the Weber River, susceptible hosts are common, and this aphid annually alternates between cottonwoods and herbaceous plants. In the adjacent narrowleaf zone, trees are more resistant and *P. betae* remains primarily on herbaceous plants (Whitham 1989; but see Paige & Capman 1993 and rebuttal by Floate *et al.* 1994). Laboratory and field experiments indicate that these differences in aphid life cycles are genetically based (Moran & Whitham 1988a; Moran 1991). Hybrid zones may also accelerate insect speciation by facilitating host shifts between the parent species (Floate & Whitham 1993). Such shifts may lead to reproductive isolation between ancestral and colonizing populations and subsequent speciation (Bush 1969).

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