DEVELOPMENTAL CHANGES IN RESISTANCE TO HERBIVORY: IMPLICATIONS FOR INDIVIDUALS AND POPULATIONS[1]

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Abstract. The hypothesis that individual plants undergo predictable changes in their resistance to herbivory as they mature was experimentally tested. The performance of two species of insects transferred onto different-aged trees of the same naturally occurring clones of narrowleaf cottonwood, *Populus angustifolia,* showed opposing and significant changes in host resistance as a function of tree age. The gall-forming aphid *Pemphigus betae* was 70 times as common on mature trees as on juvenile trees. Transfer experiments demonstrated that this pattern is adaptive; survivorship on mature trees was 50% higher than on juvenile trees. The leaf-feeding beetle *Chrysomela confluens* exhibited opposite distribution on hosts, with densities 400 times as high on juvenile as on mature trees. This is also adaptive; larvae transferred to mature hosts had 50% lower survival and took 25% longer to reach adulthood than those transferred to juvenile trees. These survivorship and performance data and our inability to support the hypotheses of other mechanisms that would produce the observed distributions suggest that the distributions result from the insects' preferences for different-aged hosts.

Several basic implications emerge. (1) Developmental changes in resistance and susceptibility of hosts are important components in determining the distribution of herbivores. (2) A single plant can change rapidly in its resistance traits with age such that a 10-fold change in resistance can occur over a 2-yr period. (3) As trees mature, increased and decreased resistances to different herbivores can produce nonoverlapping herbivore distributions that could be misinterpreted as being the result of competition (e.g., in this study, beetle abundance was strongly, negatively correlated with aphid abundance). (4) While host maturation processes have large effects on within- and between-tree variation in resistance to herbivores, the implications for herbivore population dynamics and community structuring have not been generally appreciated.

Key words: Chrysomela confluens; *clonal variation; developmental resistance; gall; herbivory; host resistance; interspecific competition;* Pemphigus betae; *plant–herbivore interactions;* Populus angustifolia.

INTRODUCTION

Between-plant variation in character states based on developmental stage of the plants has been documented in the horticultural and forest management literature for nearly two centuries (Brink 1962). Maturation (meristem-based changes in gene expression; Wareing 1959) can alter leaf size and shape, rooting capacity, stem thorniness, and growth form as plants grow (Furr et al. 1947, Ashby 1948, O'Rourke 1949, Schaffalitzky de Muckadell 1954, Robbins 1957*a, b,* 1961, Wareing 1959, Brink 1962). Reduction in plant vigor can affect shoot growth, resin flow, bud production, and wood-fiber characteristics (Zobel 1961, Kozlowski 1971).

Despite the variety of demonstrated effects of host maturity, ecologists have largely ignored their importance (except for studies of seasonality) or have encountered confounding factors while studying them. While studies such as those by Blais (1958), Niemelä

et al. (1980) and others (references in Furniss and Carolin 1977) have shown effects on herbivores at the whole-site level, they have not been able to examine the effects of host development independent of host genotype and microsite differences in herbivore density, soils, and moisture regimes. Studies that have been able to overcome these problems (Soegaard 1956, Zagory and Libby 1985, Craig et al. 1986) have concentrated on a single plant pest.

In this paper we define "developmental resistance" as the effect of predictable changes in host character states with host age on herbivores' behavior, developmental rates, survivorship, or fecundity. Resistance can either increase or decrease with age, depending on the herbivore. With the data presented here, we cannot argue whether or not developmental resistance is an evolved trait or simply a passive by-product of the developmental process. Craig et al. (1988) argue that developmental changes in growth patterns of *Salix lasiolepis* that produce an age-related increase in resistance to sawfly attack is a plant response to habitat instability (frequent flooding). They further argue that

the overriding importance of annual floods has prevented adaptation by *S. lasiolepis* to attack by *Euura lasiolepis.* However, Whitham and Slobodchikoff (1981), Whitham (1984), and Whitham et al. (1984) have argued that within- and between-plant variation in quality may be adaptive because it adds complexity to the host selection process and concentrates herbivores where they are more susceptible to predators, intraspecific competition, and induced plant defenses.

Here we document the contrasting effects of host development on two different insects attacking narrowleaf cottonwood, *Populus angustifolia.* By working within clones and with developmental classes of trees, we were able to examine age-related changes in resistance to herbivory while avoiding confounding factors of genotypic, site, and microclimatic differences. Specifically we were interested in the following questions.

1) What characters change in a predictable manner as a host develops? Plant traits affecting defenses (thorn production, leaf abscission, resin flow, leaf size and shape) and insect nutrition (shoot growth, phloem thickness, wood fiber characteristics) are known to change as plants age (Furr et al. 1947, Ashby 1948, O'Rourke 1949, Schaffalitzky de Muckadell 1954, Wareing 1959, Zobel 1961, Brink 1962, Kozlowski 1971, Amman 1972).

2) Do developmental changes affect the distributions of herbivores and the extent of herbivory? Experimentally documented instances of within-genotype effects on plant enemies' distributions have been rare (Soegaard 1956, Zagory and Libby 1985, Craig et al. 1986). Here we transferred herbivores onto different-aged trees of the same clones to test for changes in host resistance with developmental state.

3) Do alternative hypotheses account for insect distribution more than developmental changes in host resistance? Other considerations, such as disturbance (Dayton 1973), interactions with the third trophic level (Paine 1974, Price et al. 1980, Pierce and Mead 1981), and complex interactions with other species (Paine 1966, 1980, Feener 1981, West 1985) may be more important in determining the ultimate distribution of herbivory than host traits. These alternatives are infrequently examined.

In addition, by observing the distribution and performance of two herbivores within naturally occurring clones, we were able to examine several more subtle aspects of developmental changes in resistance. Specifically:

4) How rapid is the change between resistant and susceptible states? When viewed at the whole-site level, age-related changes in resistance are generally thought to occur gradually (Blais 1958, Amman 1972, Cole 1973, Niemelä et al. 1980). Within this overall pattern however, individuals may undergo transformations on a much shorter time scale.

5) Are a host species' herbivores all affected similarly by developmental changes in the plant? Given that host development has been shown to have both positive (Blais 1958, Cole 1973, Niemelä et al. 1980) and negative (Soegaard 1956, Zagory and Libby 1985, Craig et al. 1986) effects on herbivores in different systems, within a host species, one age class may be resistant to all herbivores. However, if different herbivore species respond in opposite ways to host maturation, a negative correlation between densities of the two species could be misinterpreted as being the result of competition.

Host age, maturity, and senescence

As tree development proceeds from germination onward, two plant-based processes cause changes in plant character states: maturation and senescence. These terms are well defined and documented elsewhere (Brink 1962, Fortanier and Jonkers 1976), but some confusion may arise because they are both correlated with tree chronological age, and, despite their having very specific meanings in relation to plant development, in common usage they are often used interchangeably. Maturation is an irreversible, programmed change in gene expression in which genes are activated, amplified, or suppressed after the apical meristem has undergone a predetermined number of cell divisions (Fortanier and Jonkers 1976). Tissues laid down by the meristem after changes have taken place produce mature characteristics, and will not revert to a more juvenile state without artificial (chemical or UV) stimulation (Robbins 1957). For example, rooted cuttings from mature, thornless parts of honeylocust will not pass through a thorny, juvenile stage as seedlings do (O'Rourke 1949). Senescence comes from a plant's inability to support all its parts. Whether this results from imbalances among root, leaf, and supportive tissues or the complexity of vascular connections, the changes can be reversed by propagation of cuttings or buds (Fortanier and Jonkers 1976). Reduction in stem growth is a common effect of senescence that is reversed when older, slower growing stems are propagated by rooting or grafting onto fast-growing stocks (see Craig et al. 1986).

In this paper, we will not differentiate between maturation and senescence except where explicitly stated. We will use the terms "development," "aging," and "maturity" to denote processes and stages in the aging of plants. The terms "juvenile" and "mature" likewise will be used to cover stages of tree growth without reference to process.

Natural history

Narrowleaf cottonwood, *Populus angustifolia,* grows in streambanks and bottomlands at elevations between 1500 and 5000 m in the southwestern United States (Rogers 1922, Johnson 1970). In northern Utah, clones commonly spread by suckering from extensive shallow root systems, covering up to 20 m of stream bank and containing 20–40 trees with an interconnecting root

system. Through their ontogeny, naturally occurring clones produce many ramets (trees) of similar, if not identical, genotypes whose ages range from 1 to ≥ 60 yr. The trees are heterophyllous (Critchfield 1960), producing both early and late leaves. Early-leaf primordia are produced in the previous season, overwinter in the buds, and are usually fully flushed within 2 wk of bud burst. Late-leaf primordia are produced distal to the early leaves and flushed in the same season after the early flush is over. Often, late leaves continue to flush well into July and August. For the purposes of this paper, we use the terms "tree" and "individual" to denote a ramet produced by these clones and "shoot" to denote the current year's growth from a vegetative bud.

In this paper, we do not discuss genet age or the question of whether or not clones themselves age. We concentrate instead on the effects of the developmental changes in ramets produced by these clones on herbivores.

Pemphigus betae is a leaf-galling aphid with a complex life cycle. Its primary (spring) host is narrowleaf cottonwood (*Populus angustifolia*), and in northern Utah its secondary (summer) hosts include species of *Rumex* and *Chenopodium,* especially *R. crispus, R. patientia,* and *C. album.*

In early spring, fundatrices (stem mothers) emerge from overwintering eggs on cottonwood and initiate gall formation along the midvein of developing leaves. In the galls, successful stem mothers parthenogenetically produce a generation of alate viviparae (spring migrants), which fly to the secondary hosts in late June or July. If a stem mother fails to complete gall formation, she dies and her attempt leaves a characteristic scar at the site (Whitham 1978). Data from observational (Whitham 1978) and experimental (M. Kearsley and T. G. Whitham, *personal observation*) studies have shown that if both scars and galls are counted, >85% of the colonizing stem mothers can be accounted for. The sexuparae (fall migrants) return from the secondary hosts in October and deposit the sexuales in deep bark crevices or under loose bark on dead branches. The sexuales undergo four moults, mate, and leave one overwintering egg per female in these same oviposition sites.

Adult *Chrysomela confluens* overwinter as sexual immatures in the litter, emerge in mid-April to May, and feed. Within a week they begin mating, and females lay 3–10 clutches of 20–40 eggs each on leaves. The larvae hatch in ≈ 10 d and skeletonize developing leaves in sibling groups. By mid-July, larvae have pupated and within a month the adults have emerged, fed briefly, and dropped into the leaf litter to overwinter.

METHODS

All fieldwork was done in sites along the Weber River, near the mouth of Weber Canyon, ≈ 12 km southeast of Ogden, Weber County, Utah, USA.

Tree size and age

For two reasons, we used tree size and other morphological characters as measures of developmental status. First, several authors have shown that plant height (Schaffalitzky de Muckadell 1954, Fortanier and Jonkers 1976, Zagory and Libby 1985) or area at breast height (Kaufmann and Troendle 1981) are better predictors of maturational state than is chronological age. Second, this removed the need for the time-consuming and potentially damaging practice of coring trees.

For within-clone studies, we simply used trunk diameter at breast height (dbh) as a measure of developmental state. A regression of age on dbh for a subset of trees within a clone studied showed that the two measures are nearly identical ($n = 21$, $R^2 = 0.94$, $F = 363.9$, $P < .001$). We lost several trees each year to beavers and floods, and using dbh allowed us to include other trees within clones without aging them.

Site-wide samples were taken in five developmental classes based on dbh, height, bark characteristics, and reproductive status. Many trees did not satisfy all descriptors of any one category; these were excluded from our samples. In this way we examined host developmental effects and avoided the confounding effects of stress, disease, and vigorous epicormic growth.

Aphid studies

To quantify the distribution of aphids among developmental stages of trees, we censused aphid densities, measured as the number of galls per 1000 leaves within a clone that had been selected for its broad range of ramet ages. Both galls and the scars produced by unsuccessful stem mothers were counted. From older trees in a clone (>10 cm dbh), 75–125 shoots (450–750 leaves) from all areas of the canopy were collected. On the most juvenile (<5 cm dbh), 50 shoots (300 leaves) were examined.

For site-wide measures of density change with tree development, we haphazardly chose 50 trees in each class and collected five shoots per tree from the top of the middle third of the crown. Since the number of aphids on a shoot could not be considered independent of those on adjacent shoots, we pooled densities within branches before performing statistical analyses.

To assess host-quality changes with development, we measured leaf area (see Whitham 1978) within and across clones. Since leaf area is predictable from both dry mass ($y = 1.64 + 0.0819\,x$; $n = 58$, $r = 0.97$, $P < .001$) and leaf length × width ($y = 0.227 + 0.00647\,x$; $n = 58$, $r = 0.99$, $P < .001$), and the two attributes do not make different predictions ($n = 58$, $t = 0.00$, $P > .9$), both techniques were used to estimate average leaf areas.

We examined the vertical distribution of fall migrants in the air column by erecting three 7.5-m poles around the periphery of a clone, each with 15 cm wide sticky traps at each 0.5 m height interval. After five

consecutive days of the fall migration in 1985, the number of aphids on each trap was converted to a percent of each pole's total aphids and arcsine transformed. The numbers were then analyzed by regressing the three-pole average against height.

We tested for oviposition-site limitation for fall migrants by isolating three pairs of smooth-barked branches in the canopy of a mature tree from potential overwintering sites with a band of Tanglefoot at their bases (stem mothers will not cross these barriers). We left one branch bare to serve as a control and created artificial oviposition sites on the other with layers of Tree Wrap. Within the same clone, we treated adjacent pairs of juvenile trees in an identical manner.

In the following summer, we censused all leaves on these branches and trees for galls. Oviposition site branches and trees were compared with their paired controls by using a Mann-Whitney U test. A Wilcoxon T was then used to compare densities on oviposition-site mature tree branches with oviposition-site juvenile trees.

Aphid survivorship was examined as a function of tree developmental stage by recording natural performance in the field. Natural mortality on each developmental class was quantified as the percent of the colonizing population of stem mothers that failed to produce successful galls (scars/scars plus galls). This percent data was arcsine transformed and subjected to a one-way analysis of variance.

To test for within-genotype effects of host development, we transferred stem mothers to different-aged trees in the same clone. The clone was selected on the basis of its known root connections and large number of juvenile trees. After they had emerged from overwintering eggs, >400 newly settled first-instar fundatrices were collected from buds on one of the oldest members of a clone. Within 30 min, these stem mothers were transferred to mature and juvenile trees within the same clone. The phenology of buds on both the donor and recipient trees was held constant. We recorded the survival of these stem mothers in June. To reduce the variation caused by extremes of weather and changes in fundatrix condition during the transfer period, data were pooled within transfer dates before being arcsine transformed and subjected to a paired t test with date as the pairing factor.

Beetle studies

The distributions of adults, larvae, and larval damage of *Chrysomela confluens* were measured in the same sites where *Pemphigus betae* was studied. Censuses utilized the same five developmental classes of trees.

We determined the distribution of adults across developmental classes of hosts in the summer of 1985 in a series of timed censuses. We conducted a preliminary set of six 1-min censuses of each age class to assure that the number of shoots examined would not differ among classes and to derive an average number of

shoots examined per unit time. We then conducted at least three sets of censuses in areas 10–20 m in diameter each day for 10 d. Two minutes were spent on each age class in each area examined. The counts were converted to a per 1000 shoot quantity and subjected to a one-way analysis of variance with developmental class as the treatment factor.

Larval densities and damage were quantified by censusing 50 trees in each of the five developmental classes. In each tree, we censused three height levels within the canopy (0–1.5, 1.5–3, and 3–10 m) by examining three branches at each level. Each branch was scored for the numbers of shoots, larvae, and damaged shoots. With the exception of some lepidopterous larvae, whose damage was distinguishable by the presence of bound leaves and/or silk, no other insect was observed skeletonizing leaves of *P. angustifolia* during two summers' observations. Since *C. confluens* eggs were laid in large clutches and larvae feed gregariously, damage on a shoot was not independent of damage on nearby shoots. Data were therefore pooled within trees, converted to a per 1000 shoot quantity, and analyzed in a one-way analysis of variance with age class as the treatment factor.

We determined within-shoot patterns of beetle feeding by recording the location of larvae and larval damage on shoots sampled in the within-clone aphid censuses. In addition, the number of early and late leaves present on shoots examined in all aphid censuses in 1984 and 1985 was determined.

The mode of between-plant movement was examined by selecting 20 pairs of adjacent juvenile (<4 yr old) trees. Below the lowest branch of one member of each pair we placed a barrier of Tanglefoot on masking tape, which prevents beetle movement. We censused these trees nine times over a 3-d period at intervals ranging from 20 min to 24 h. The numbers of adult beetles on exclusion and control trees were compared in a $2 \times 2 \chi^2$ table.

We determined the level of mortality (predation, parasitism, desiccation, etc.) for eggs, from mating pairs of adult *C. confluens* that had been caged on juvenile, intermediate, and mature trees' shoots in six naturally occurring clones. For 3 wk we rotated pairs to a different-age host in the same clone every 2 d, counted eggs, left them exposed, and returned to count surviving eggs each day until no eggs remained or larvae hatched. The numbers of surviving (at least five larvae hatching) and nonsurviving clutches in the three age classes were analyzed in a 3×2 contingency table.

We tested for changes in host suitability with tree development in two sets of transfer experiments. To measure overall suitability, we collected copulating pairs of adults in May of 1984 and caged them on shoots. When eggs hatched, clutches were split into two groups of first-instar larvae and transferred to two clones that had been selected for their large numbers of juvenile trees. Within each clone, clutches were split again be-
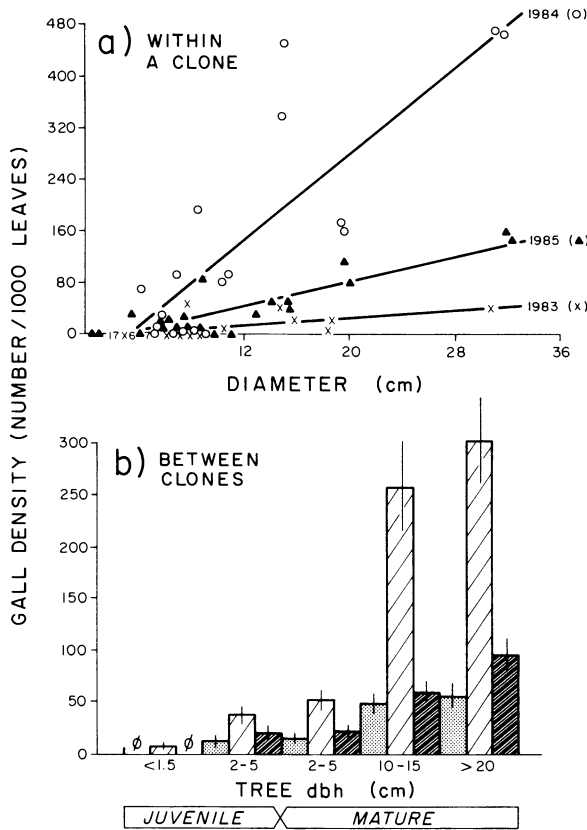
FIG. 1. The relationship between tree developmental stage and aphid gall density over a 3-yr period (a) within a naturally occurring clone of narrowleaf cottonwood (1983, $n = 29$, $r = 0.701$, $P < .001$; 1984, $n = 25$, $r = 0.864$, $P < .001$; 1985, $n = 29$, $r = 0.901$, $P < .001$), and (b) measured for 50 individuals in each of the five age classes. Stippled bars = 1983, $F_{4,245} = 10.47$, $P < .001$; hatched bars = 1984, $F_{4,245} = 24.91$, $P < .001$; doubly hatched bars = 1985, $F_{4,245} = 17.71$, $P < .001$. Narrow vertical bars represent ±1 SE.

tween young (<1.5 cm dbh) and old (>20 cm dbh) trees, and caged on a shoot. To prevent larvae from consuming all leaves in a cage and to avoid the effects of long-term caging on leaf chemistry (J. C. Schultz, *personal communication*), cages were moved to a new shoot every 3–5 d. The number and instar of live larvae present at each change were recorded, and adults were collected when they emerged.

In 1985, we conducted the second set of transfers. Clutches were collected in an identical way, but larvae from a clutch were transferred to a shoot of a juvenile tree in one of two other clones selected for the same reasons as in 1984. Within each shoot, clutches were split between young and old foliage. Old-foliage larvae were caged on the second or third leaf distal to the base of the shoot. Young-foliage larvae were caged on the most distal leaf on the same shoot that was at least 3 cm² in area. As in the previous experiment, cages were moved to new shoots at least once every 2 d.

We measured qualitative differences between young and old trees' leaves in two ways. The effects of shoot

position and tree developmental state on leaf water contents were examined in the 1984 caging-experiment clones by collecting first and last, early- and late-flush leaves from terminal shoots of juvenile and mature trees within the same clones. Percent data were arcsine transformed and subjected to a two-way analysis of variance with tree developmental stage and position as the factors.

We assessed the same factors' effects on leaf toughness within eight clones. In each clone three juvenile and three mature tree terminal shoots were chosen. Three toughness measures were taken in the field on the four terminal leaves using a handheld penetrometer (John Chatillon and Sons, Kew Gardens, New York). We used the lowest measure for each leaf (converted from grams per square centimeter to kilopascals) in an analysis of variance with leaf position and tree age class as treatment factors.

RESULTS

Aphid distribution on hosts

Within a clone, densities of *Pemphigus betae* were strongly correlated with the maturity of the host tree. During 3 yr of censusing, trees <4 cm dbh were, with one exception, aphid free, while larger trees in the same clone had progressively greater aphid loads (Fig. 1a). Comparisons among developmental classes in all clones show the same pattern (Fig. 1b).

Experimental examination of aphid distributions

These data suggest that cottonwood resistance characters change with age, and that aphids are showing an adaptive preference for the higher quality, mature trees. In this section, we examine the resistance characters of cottonwood trees in different developmental stages, and three alternatives to an hypothesis of aphid preference.

First, if plants are undergoing changes in resistance, morphological correlates of resistance should change with plant age. Whitham (1978) showed that stem mothers on larger leaves had higher survival and fecundity. Within natural clones, mean leaf area increased more than fivefold from the most juvenile to the most mature ramets (Fig. 2a). Comparisons made between developmental classes across clones showed the same pattern (Fig. 2b).

Second, and more important, aphid performance should be higher on more mature hosts than on juveniles. Our experimental and census data confirmed this prediction. Fundatrices transferred to a mature host had significantly higher survivorship (59 vs. 38%) than those transferred to a juvenile tree in the same clone (Fig. 3a). Similarly, naturally occurring stem mothers on mature trees had significantly higher survivorship (85 vs. 58%) than those on juvenile trees (Fig. 3b). These data, along with the leaf-area data, show that trees undergo predictable changes in resistance to aphids as they age.
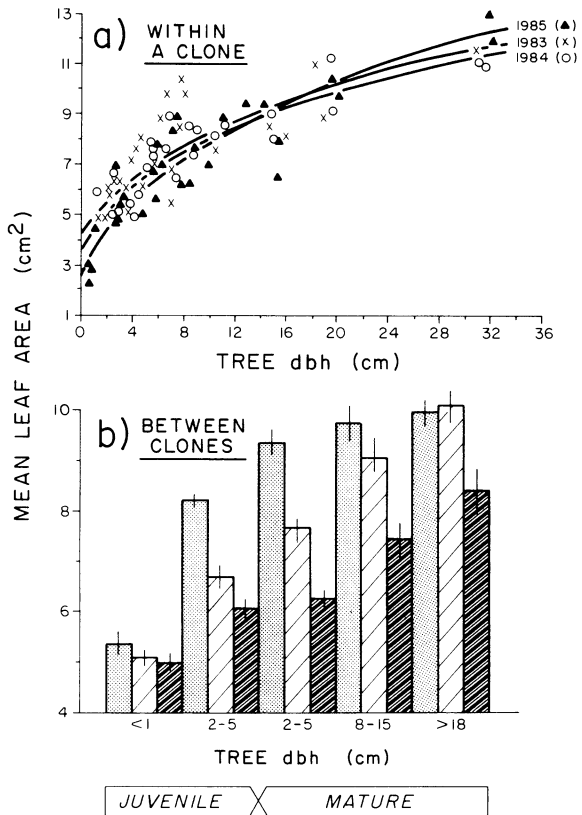
FIG. 2. The relationship between tree developmental stage and mean leaf area during 3 yr (a) in trees of a naturally occurring clone (1983, $n = 29$, $r = 0.701$, $P < .001$; 1984, $n = 25$, $r = 0.890$, $P < .001$; 1985, $n = 29$, $r = 0.918$, $P < .001$), and (b) for 50 trees in each of the five age classes. Stippled bars = 1983, $F_{4,245} = 67.08$, $P < .001$; hatched bars = 1984, $F_{4,245} = 52.85$, $P < .001$; doubly hatched bars = 1985, $F_{4,245} = 15.78$, $P < .001$. Narrow vertical bars represent ± 1 SE.

Within the mature classes of trees, aphid fall migrants are known to avoid those clones on which the survival of their granddaughters, the fundatrices, will be low (N. Moran and T. G. Whitham, *personal observation*). Therefore our next question was whether or not the aphids responded to changes in host quality by avoiding resistant, juvenile trees. Direct measures of host selection are difficult because the migrants are <1 mm long, fly only at dusk, and when caged for choice experiments, only fly against the cages. Rather than directly measuring preference, we examined three alternative mechanisms that would produce the observed distribution pattern without any host selection on the part of the aphids. We present these alternatives in the sequence of aphid life history phases, from fall migrants to fundatrices, that encounter the cottonwoods.

First, if colonizers fly above the tops of juvenile trees they will encounter only mature trees, producing the observed pattern without any active preference. Our sampling of fall migrants showed that aphid abundance

decreased with height in the air column (Fig. 4), with 33% of migrants trapped at or below 1.5 m. Thus, the trees that were colonized the least (juvenile trees) were those probably encountered most often in colonization.

Second, although aphids may be encountering all ages of hosts, their apparent preference could be due to a lack of overwintering sites on juvenile trees. Young trees have smooth bark and few dead branches with loose bark where eggs overwinter. If aphids are oviposition-site limited, densities should be higher on both adult tree branches and juvenile trees with oviposition sites. And, if juvenile trees escape attack simply through a lack of oviposition sites, we expected that juvenile trees with oviposition sites added would have aphid densities equivalent to mature tree branches treated in the same way.

Our data show that branches and trees with added oviposition sites had densities 20–500 galls/1000 leaves higher than their adjacent paired controls (Wilcoxon $T = 0$, $P < .025$; Table 1), indicating that aphids can be oviposition-site limited. Mature tree branches with added oviposition sites however, also had densities up to 550 galls/1000 leaves higher than juvenile trees with oviposition sites (Mann-Whitney $U = 8$, $P = .10$). Thus, the addition of oviposition sites resulted in an increase in aphid densities on both developmental host classes,
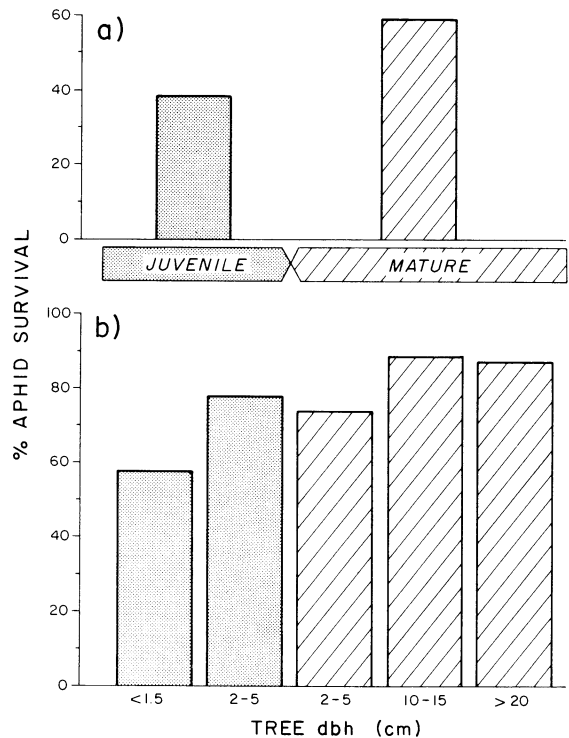

FIG. 3. The survivorship of stem mothers as a function of tree maturity. (a) Survival of 430 stem mothers transferred to juvenile and mature trees within the same naturally occurring clone; $n = 13$, $t = 3.183$, $P < .001$. (b) Data from 50 trees in each of the five developmental classes in 1984. $\chi^2_3 = 16.3$, $P < .005$.
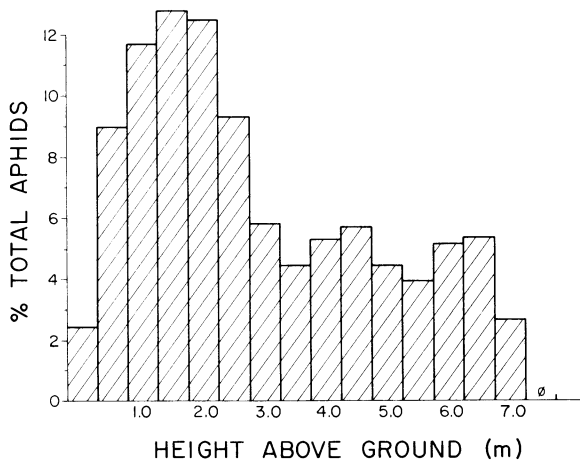
FIG. 4. The vertical distribution of aphids (sexuparae) in the air column over a period of five nights of the fall migration in 1985. Percent total aphids = 0.217−0.013 (height), $F_{1,13} = 54.4, P < .0005$.

TABLE 1. Effects of oviposition site addition before the fall migration on gall densities in the following spring. Numbers represent complete censuses of branches or trees.*

Tree or branch no.	Juvenile trees		Mature tree branches	
	Control	Oviposition sites added	Control	Oviposition sites added
	Gall densities (number per 1000 leaves)			
1	6	35	15	24
2	0	4	91	224
3	3	9	61	560

* Branches and trees with added oviposition sites had densities 20–500 galls/1000 leaves higher than their adjacent paired controls (Wilcoxon $T = 0, P < .025$). Mature tree branches with oviposition sites had densities up to 550 galls/1000 leaves higher than juvenile trees with oviposition sites (Mann-Whitney $U = 8, P = .10$).

most mature trees. Thus, because we censused both surviving and nonsurviving stem mothers we could eliminate the possibility that censuses based only on the number of survivors could suggest preference where none existed.
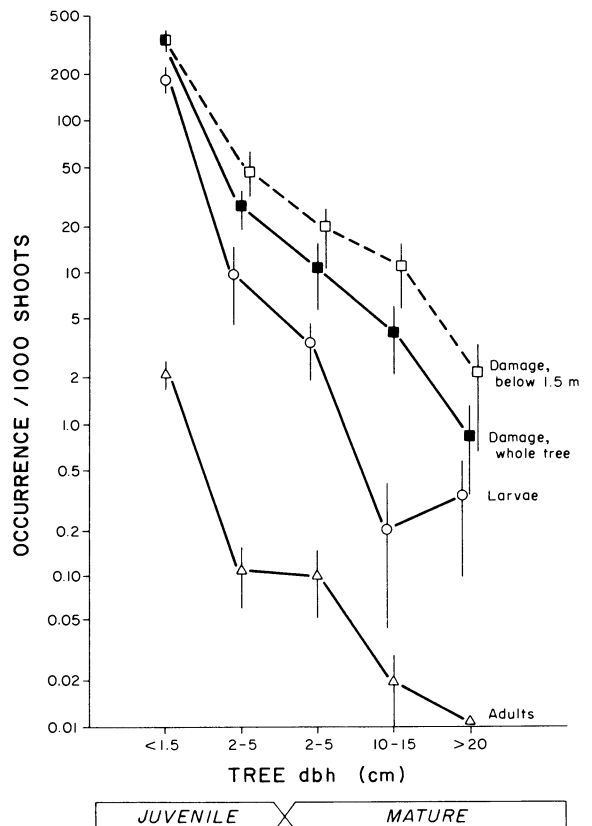
but the increase was far greater on mature trees than on juveniles.

Third, higher mortality of overwintering eggs on the more juvenile trees could produce a pattern of increasing densities of fundatrices with tree age. Although in 3 yr of experience in hatching stem mothers for transfer experiments we have seldom seen any failed eggs, we have begun experiments designed to test for differences in the overwintering mortality (freezing, desiccation, predation) of eggs in the branches of juvenile and mature trees. We expect that mortality will be either similar in the two situations or higher in the branches of mature trees for reasons relating to both abiotic and biotic factors. First, because Weber Canyon is a drainage for cold air from the High Uintas area and strong downcanyon winds usually blow for the first 4–5 h of each morning, freezing and desiccation would be a greater factor in the exposed branches of mature trees. Second, given the larger size and more heterogeneous nature of mature trees, we would expect to find a greater number and diversity of predatory invertebrates in mature trees. Those species we have observed in the past five springs (forficulids, phytoseiid mites, salticid spiders) generally do not appear until after leaf colonization is complete and gall formation has begun.

Finally, no host selection is required if fall colonizers randomly alight and then their granddaughters, the fundatrices, have higher mortality on juvenile trees in the following spring. Because gall-density measurement included both galls and the scars left by unsuccessful stem mothers, and because nearly all stem mothers left one or the other (see Introduction: Natural History) this alternative could be examined. In 1984, only seven fundatrices (three survived and four died leaving scars) were recorded from all 1491 juvenile tree leaves collected, and 492 fundatrices (426 survived and 66 left scars) were recorded from 1831 leaves from the

FIG. 5. Occurrence of Chrysomela confluens larval damage, larvae, and adults on trees in the five developmental classes. Damage (whole tree) $F_{4,245} = 47.73, P < .001$; Damage (<1.5 m from ground) $F_{4,245} = 41.27, P < .001$; Larvae $F_{4,245} = 24.99, P < .001$; Adults $F_{4,245} = 20.04, P < .001$. Vertical bars represent ±1 SE.
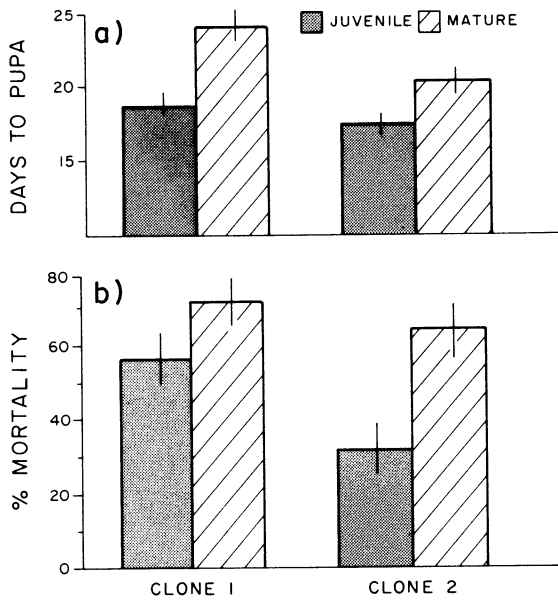
FIG. 6. The effect of host development on *Chrysomela confluens*. Increasing host age (a) decreases larval developmental rate ($n = 19$ clutches, $t = 5.12$, $P < .001$), and (b) increases larval mortality ($n = 20$ clutches, $t = 5.43$, $P < .001$). Vertical bars represent ± 1 SE.

While we did not eliminate the effects of overwintering mortality, the data in hand suggest that several interacting factors produce the observed distribution of aphids on hosts of different ages. Aphids selectively colonized mature trees where oviposition sites were more available, resources were most favorable, and survivorship was highest.

Beetle distribution on hosts

Within the same sites, densities of the leaf beetle *Chrysomela confluens* on different developmental classes of hosts were the opposite of those found for *P. betae* (Fig. 5). The proportion of shoots damaged by beetle larvae decreased over two orders of magnitude with increasing host development. Censuses of adults and larvae showed the same pattern (Fig. 5).

Experimental examination of beetle distribution

These data, like those for *P. betae*, suggested a change in the resistance of narrowleaf cottonwood and a response on the part of *C. confluens*. Again, because both of these phenomena would be important observations, we tested for changes in the resistance characters of the cottonwoods and alternatives to an hypothesis of preference.

Most important, the high densities of *C. confluens* on juvenile trees suggested that the distribution should be associated with higher performance on those trees. Our data on survival and developmental rates confirmed this. When larvae were transferred onto different-aged trees of the same naturally occurring clone, developmental rates averaged 22% faster on these ju-

venile trees (Fig. 6a). Likewise, survival was significantly higher on shoots of juvenile trees (Fig. 6b).

Since 98% of all beetle damage observed was on late leaves (as defined in Introduction: Natural History), beetle performance should be higher on these leaves. Data from the second set of transfer experiments showed larval development was 10–17% faster on immature leaves (clone 1, $n = 6$ clutches, $t = 2.671$, $P < .025$; clone 2, $n = 5$ clutches, $t = 4.097$, $P < .01$) and that mortality was 40–60% lower on these late leaves (clone 1, $n = 7$ clutches, $t = 2.788$, $P < .025$; clone 2, $n = 7$ clutches, $t = 4.430$, $P < .01$).

Furthermore, our measures of leaf quality were highest for leaves on juvenile trees (Fig. 7). Leaves of old trees were toughest, and this did not change appreciably with leaf position. By contrast, early (older) leaves on juvenile tree shoots were roughly 20% less tough than any mature tree leaves, and the most recently flushed leaf averaged 60% less tough than early leaves on the same shoot. Similarly, leaf water contents were low and insensitive to leaf position on mature trees. In comparison, leaf water contents were much higher in juvenile trees' leaves in the same clone, with a strong effect of leaf position (Fig. 8a, b).

The number of high-quality late leaves flushed decreases with tree maturity, consistent with our data on performance. Within clones, the number of late leaves on terminal shoots declined from ≈ 14 per shoot on juvenile trees to less than half that on mature trees (Fig. 9a). Between-clone comparisons show that late leaves represent $>40\%$ of leaves flushed on juvenile trees, but are $<15\%$ of those on mature trees (Fig. 9b).

Our next question was whether the beetles showed a preference for young trees where their survival and developmental rates were highest. Because detached leaves and shoots dried rapidly and experiments using them could not be considered good tests of preference, we instead examined three alternative mechanisms that did not involve host selection on the part of the beetles.
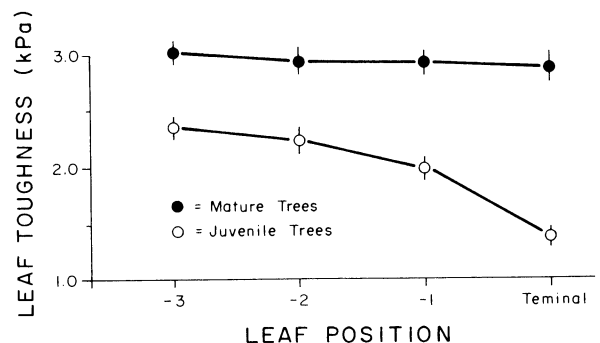

FIG. 7. Leaf toughness as a function of leaf position and tree maturity. Mature tree leaves are tough and toughness does not change with leaf position ($F_{3,92} = 0.21$, $P > .50$) while juvenile tree leaves are softer, and the most recently flushed leaves are 60% less tough than others on the shoot ($F_{3,92} = 21.57$, $P < .001$).
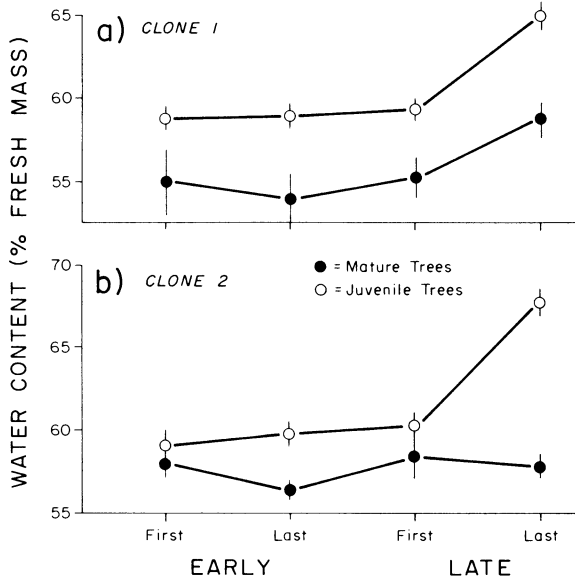
FIG. 8. Leaf water contents in two beetle-rearing clones are higher and more sensitive to position in juvenile trees. (a) Clone 1, position $F_{3,21} = 18.8$, $P < .001$, ramet age $F_{1,21} = 70.6$, $P < .001$; (b) clone 2, position $F_{3,21} = 8.1$, $P < .001$, ramet age $F_{1,21} = 31.7$, $P < .001$. Vertical bars represent ± 1 SE.

First, because adult *C. confluens* drop to the ground when disturbed, the predominance of beetles and damage on juvenile trees may have resulted from the fact that foliage on juvenile trees is closer to the ground and thus first encountered by crawling individuals. However, applying sticky barriers to the bases of juvenile trees to prevent crawling up the stem had no effect on the number of adults observed relative to adjacent control trees ($\chi^2_1 = 1.82$, $P > .25$), indicating that most beetles flew between hosts.

Second, by using whole-tree measures of density, we may have included parts of mature trees that beetles would never encounter if they flew only at or below the tops of juvenile trees. When we used data from only the lowest (<1.5 m) level on all trees, damage rates changed slightly, but damage rates still declined significantly across developmental classes (Fig. 5).

Finally, the distribution of larvae and larval damage on different developmental stages of host could have been the result of differential egg mortality on young and old trees rather than selective oviposition. According to this hypothesis egg mortality should have increased with host development. Our data showed no differences among developmental classes ($\chi^2_2 = 0.77$, $P > .50$).

DISCUSSION

Here we have documented changes in plant herbivore-resistance characters with host development. The effects on two herbivores were strong, resulting in changes of up to 50% in herbivore survival and reproduction. The effects of host development were positive

in the case of *Pamphigus betae* and negative on *Chrysomela confluens*, demonstrating that rather than a single vulnerable stage in the ontogeny of a plant, there can be many susceptible stages when many herbivores are considered.

Several lines of evidence also suggest an adaptive preference on the part of the herbivores. First, the distributions of the two herbivores track changes in the susceptibility of, and availability of resources on, their hosts. Second, the mode of, and vertical distribution during, between-plant movement by beetle adults and aphid fall migrants cannot explain the distribution of herbivory among host developmental classes. Third, although the lack of overwintering sites on juvenile trees does play a role in the distribution of *P. betae*, when juvenile trees were made equally "available" to fall colonizers with added oviposition sites, densities in the following spring were still as much as two orders of magnitude higher on branches in mature trees that had identical added oviposition sites. Fourth, while differential overwintering mortality could have pro-
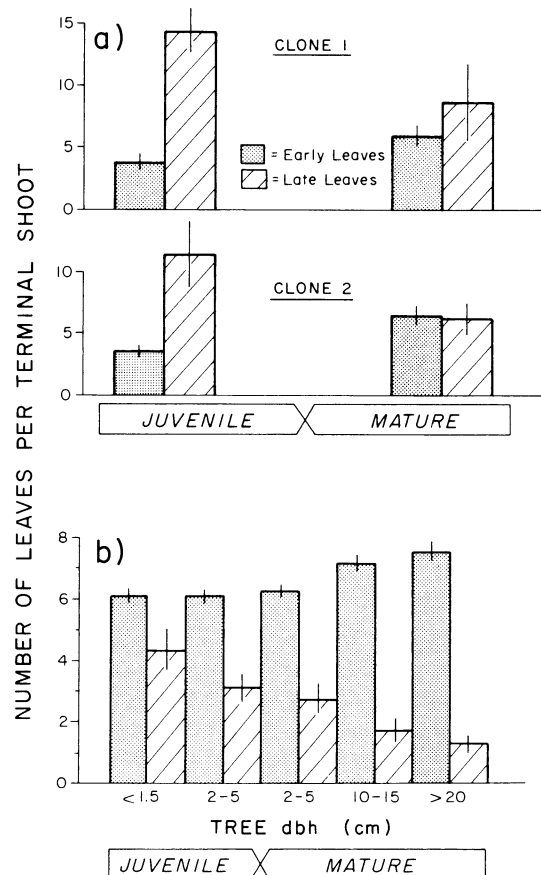

FIG. 9. Early and late leaf production on terminal shoots (a) by juvenile and mature members of two clones used in the beetle-rearing experiments (clone 1, $\chi^2_1 = 25.5$, $P < .01$; clone 2, $\chi^2_1 = 32.6$, $P < .01$), and (b) by 50 trees in each of the five age classes ($\chi^2_4 = 11.26$, $P < .025$). Vertical bars represent ± 1 SE.

duced this pattern, 3 yr of observations on hatching fundatrices for transfer experiments and an analysis of likely physical and biotic agents of egg mortality suggest that experiments currently under way will show this to be a minor factor. Fifth, fall trapping data by N. Moran and T. G. Whitham (*personal observation*) show that aphid fall migrants can discriminate among mature resistant and susceptible trees, and are significantly more likely to colonize susceptible clones. Finally, we cannot support the hypothesis that beetle egg mortality or aphid fundatrix mortality leads to the observed distributions of herbivory.

Horticulturalists distinguish between two types of age-related character changes. Those that result from maturation (ontogenetical aging) are meristem-based and stable to asexual propagation, while those arising from senescence (physiological aging) are size- or complexity-based and revertible by propagation (Wareing 1959, Fortanier and Jonkers 1976). Increased resistances with host age to western gall rust in radiata pine and leaf blight on *Thuja plicata* are stable to propagation (Soegaard 1956, Zagory and Libby 1985), and therefore the result of ontogenetical aging. In contrast, propagation of cuttings of *Salix lasiolepis* from older, more resistant parts of a plant causes reversion to vigorous juvenile growth that is susceptible to attack by galling sawflies, and therefore a result of physiological aging (Craig et al. 1986 and T. P. Craig, *personal communication*).

In this paper we have used tree size and other morphological characters as correlates of developmental state. These measures do not distinguish between these two mechanisms. Mature tree characters could come about either for reasons relating to a tree's large size and complex vascular connections (senescence) or from the effects of changes in the meristems during growth (maturation).

Although we have no direct evidence on the mechanisms operating in cottonwood, the loss of resistance to aphids may be an ontogenetical effect, while increased resistance to beetles is likely a senescence effect. When aphids were transferred to 4-yr-old stecklings (rooted cuttings) propagated from mature susceptible trees, their survival was nearly identical to those transferred to the parental trees (T. G. Whitham, *personal observation*), far higher than expected on 4-yr-old juvenile hosts. This suggests that increased tree susceptibility to aphids is stable to propagation, and hence in the class of maturation effects. *Chrysomela confluens* larvae survived and grew on these same stecklings, even though they were propagated from mature parent trees that would not support larval development. This reversion implies that increased resistance to beetles results from physiological aging. Thus, within individual host species, both ontogenetic and physiological

processes can produce patterns of age-related herbivory.

Rapidity of developmental change

Plant resistance changes with age are traditionally thought to result from the gradual process of plant senescence (Cole 1973, Safranyik et al. 1975, Raffa and Berryman 1982, Frankie and Morgan 1984) taking place over time periods of about a decade. In this system we have documented rapid, developmentally based changes in host suitability. Beetle damage deceased more than an order of magnitude between trees 1.5 cm dbh and trees 2–5 cm dbh, and aphid infestations increased fivefold between trees 2–5 cm dbh and 7–10 cm dbh (Figs. 1 and 5). These represented time scales of ≈2 and 5 yr, respectively. Only a few studies, including Washburn and Cornell (1981), Zagory and Libby (1985), and Craig et al. (1986) have reported such rapid developmental effects on herbivores.

When viewed at a sitewide level, this short time scale is equivalent to that reported for the effects on herbivore populations of changing stress levels (Davidson and Andrewartha 1948, White 1984, Price and Clancy 1986), and induced responses (Haukioja and Niemelä 1976a, b, Faeth et al. 1981, Baldwin and Schultz 1983). While induced responses could have accounted for the distribution of the beetles, we argue that the pattern resulted primarily from host aging effects, since reductions in the availability of late leaves across developmental classes were visible in clones and sites where aphids and beetles were rare or absent.

Competition vs. developmental changes in host resistance

Our documentation of both positive and negative effects of host development within the cottonwood system makes it clear that increased developmental resistance to one herbivore coincides with increased susceptibility to another. Previous studies documenting age-related herbivory have concentrated on host interactions with a single plant enemy. For example, juvenile ramets are attacked by sawflies on willows (Craig et al. 1986), cynipid wasps on oaks (Washburn and Cornell 1981, Frankie and Morgan 1984), leaf blight on *Thuja* (Soegaard 1956), and western gall rust on radiata pine (Zagory and Libby 1985). In contrast, older conifers are preferred by budworms (Blais 1958) and spruce beetles (Schmidt and Frye 1977, Hard 1985). Although these studies leave the impression of a single window of vulnerability within a host species (Washburn and Cornell 1981), our study suggests that when more of a host species' pests are considered, the number of windows increases as well.

Although nonoverlapping distributions of plants and animals, such as those shown in Figs. 1 and 5, are commonly associated with interspecific competition (Grant 1972, Connell 1980, 1985, West 1985), our
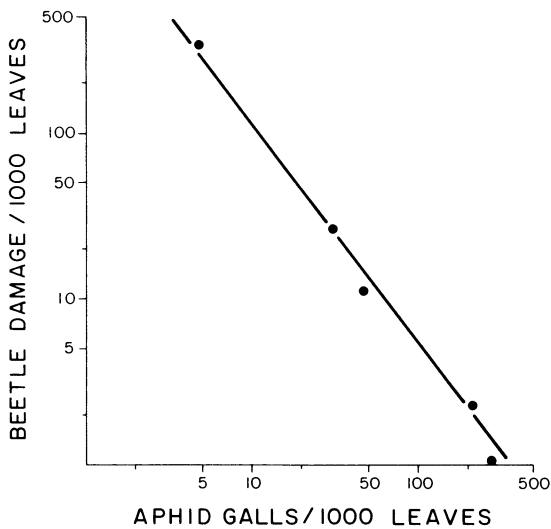
FIG. 10. Beetle damage and aphid gall density (1984 censuses of the five developmental classes plotted simultaneously; $n = 5$, $r = -0.956$, $P < .001$).

study presents a clear alternative. For example, when we plot beetle damage against aphid abundance data from the same year in the five developmental classes (Fig. 10), a strong, negative relationship is clearly visible between the two ($r = -0.956$, $n = 5$, $P < .001$). Such data could be interpreted as convincing evidence for the role of interspecific competition in determining herbivore distributions. Our experiments, however, demonstrate that developmental changes in host resistance represent a far more parsimonious explanation of these patterns.

If competitive interactions were the primary force behind these patterns, both species would do equally well when transferred to trees older or younger than those on which they typically occur. Our data show otherwise; each herbivore prefers and does best on a different developmental class of host. Also, the preference for juvenile hosts by *C. confluens* is seen in other closely related species (Brown 1956) which do not share hosts with *Pemphigus* aphids and vice versa.

While competitive interactions among different herbivore species can occur through their effects on the host plant (Karban et al. 1987), we do not see this in our system. K. C. Larson (*personal communication*) has shown that while *Pemphigus* aphids can affect the growth of adjacent shoots, the effect is measurable only at extremely high gall densities (>1200 galls/1000 leaves). Because the most susceptible clone we have encountered has averaged <380 galls/1000 leaves over the past 7 yr (range 33–841 galls/1000 leaves; T. G. Whitham, *personal observation*), it is doubtful that *Pemphigus* aphid feeding would have any effect on *C. confluens*.

Although age-related changes in trees and shrubs are well known (Ashby 1948, Schaffalitzky de Muckadell 1954, Njoku 1956, Brink 1962, Kozlowski 1971), few studies have experimentally examined the effects of plant development on herbivores. The importance of these effects where they have been studied (Soegaard 1956, Washburn and Cornell 1981, Zagory and Libby 1985, Craig et al. 1986) suggests that developmental resistance should be common and may frequently result in nonoverlapping herbivore distributions. Future studies of interspecific competition should be sensitive to the role of age-related resistances' effects on herbivore distributions.

Implications of developmental changes in resistance

Since the maturation process is a function of the number of cell divisions the apical meristem undergoes (Fortanier and Jonkers 1976), an individual tree's ontogeny may create a mosaic pattern of resistance through the presence of branches in different developmental stages. Passecker (1949 in Schaffalitzky de Muckadell 1954), and Robbins (1961) have shown within-plant heterogeneity in the developmental stage based on branch age and location. Zagory and Libby (1985), in a set of elegant experiments, showed that the location on a tree from which a cutting was taken determined the level of susceptibility to western gall rust in stecklings of radiata pine. Interestingly, within-tree data on aphids collected from trees studied by Whitham (1978) show that as branch diameter and height increase, so does leaf area, gall density, and aphid survivorship. Thus, in addition to other factors that can contribute to within-plant variation in resistance to pests (Whitham and Slobodchikoff 1981, Whitham et al. 1984), plants can become developmental mosaics of resistance.

Also, there may be a relationship between the clonal growth habit and the importance of developmental sources of resistance to enemies. According to the "variation principle" (Whitham et al. 1984), between-plant variability in resistance prevents rapidly evolving pests and pathogens from becoming virulent. Most documented cases of developmental resistance in woody plants come from species in which suckering or other asexual forms of reproduction are important (Bryant 1980, 1981, Washburn and Cornell 1981, Frankie and Morgan 1984, Lupo and Gerling 1984, Whitham et al. 1984, Craig et al. 1986; but see Soegaard 1956, Franich et al. 1977, Zagory and Libby 1985). Age-related variation in resistance may function in these species in the same way that genetically based variation resistance prevents the evolution virulence (Van der Plank 1963, 1984, Browning 1974, Segal et al. 1980, Gould 1984) in other species such as ponderosa pine, which grow exclusively from seed and in stands with even or stratified age distributions.

Developmental aspects of plant resistance may affect the structure of communities of herbivores and their enemies. Bannerjee (1981, 1983) has shown that the most important determinants of arthropod species

richness in tea plantations are the age of the plantation and the age of the plants. The latter component strongly determines the dominant arthropod type on the plant in the first 40 yr of its life, with an orderly progression from sap feeders in young, vigorously growing plants, through folivores and bark eaters, and finally to wood feeders in mature (≥ 36 yr old) plants. Similar patterns have also been recorded for deciduous forests (Smith 1976) and red pine plantations (Martin 1966). We have observed these patterns in stands of cottonwood with different age structures and suggest that these host-age-related herbivore distributions reflect underlying patterns of age-related resistances. More important, the role of the host plant population's age structure in determining the size and composition of herbivore communities should figure prominently in future studies of community dynamics.

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