Susceptibility of Pecan to Black Pecan Aphids

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Abstract. The host–parasite interaction between the black pecan aphid (BPA) [*Melanocallis caryaefoliae* (Davis)] and pecan [*Carya illinoensis* (Wangenh.) K. Koch] was investigated. Three years of field observations of the ability of BPA populations to induce chlorotic blotches, or visual damage, on 32 pecan cultivars revealed considerable variation in cultivar susceptibility to BPA damage. Among the most commonly grown cultivars, ‘Sioux’, ‘Cape Fear’, ‘Farley’, ‘Cowley’, ‘Grabohls’, and ‘Barton’ exhibited the least damage, whereas ‘Choctaw’, ‘Oconee’, and ‘Sumner’ exhibited the greatest, with ‘Sioux’ and ‘Choctaw’ exhibiting the greatest extremes in susceptibility. Subsequent evaluation indicated that the foliage of pecan genotypes can exhibit an antibiotic-like effect, resulting in the suppression of resident BPA populations. However, the relationship between the degree of this antibiotic effect and the degree of damage exhibited by trees, or field tolerance, was negligible ($r = -0.10$). For example, while ‘Choctaw’ foliage greatly suppressed BPA population growth, this population was able to inflict relatively severe damage to leaves. An evaluation of feeding preference indicated that BPA alate viviparae (winged females) preferentially feed upon host cultivars on which they have been previously feeding. This feeding preference was eliminated by rinsing leaves with distilled water; hence, a water soluble factor(s) appears to be involved in host preference.

The black pecan aphid (BPA) is largely monophagous, feeding nearly exclusively on pecan, and is often the most economically significant of the several aphid species attacking pecan (Teddars, 1978). BPA feeding damage occurs throughout the growing season, but is typically only of economic significance during late summer and early autumn. Feeding is largely on the smallest veins of the foliar vascular system and tends to be on the most mature leaflets of the shoot. Feeding induces formation of large chlorotic blotches that tend to coalesce into large regions of damaged foliage (Teddars, 1978). Feeding clogs the vascular system, reduces photosynthesis, and induces premature defoliation (Wood and Tedders, 1986; Wood et al., 1985). Economic losses are manifested via poorly developed nut meats in the current year’s crop and diminished return bloom, or fruit-set, the following year (Dutcher et al., 1984; Tedders and Wood, 1985). Despite the economic impact of BPA, little is known about pecan’s resistance to BPA (Carpenter et al., 1979) or the nature of the host–parasite interaction.

Subjective field observations indicate considerable variation in the susceptibility of pecan cultivars and seedlings to BPA (Moznette et al., 1940; Worley 1978). However, definitive conclusions about resistance have been elusive because of confounding biotic and abiotic variables associated with the tree (i.e.,

leaf age, tree vigor, and interactions with environment), the aphid (i.e., age, gender, previous diet, and biotype), and the environment (i.e., differences in light, temperature, soil fertility factors, and humidity) (Smith et al., 1994). An examination of seasonal population density of BPA on 10 cultivars in the field provided evidence of differential susceptibility and identified probing behavior as a component of the “pecan–BPA” interaction (Kaakeh and Dutcher, 1994). However, an understanding of the “pecan–BPA” interaction is probably essential in order to utilize resistance factors for reducing economic losses. We document in this study: a) the existence of differences in susceptibility among 32 commercial pecan cultivars in the orchard environment; b) the existence of tree-associated antibiotic-like factor(s) affecting aphid population growth; and c) a water-soluble factor(s) on foliage that influences feeding preference or nonpreference of BPA for specific genotypes.

Materials and Methods

Experiment 1. Evidence for field resistance. The relative field tolerance of major commercial pecan cultivars to BPA populations was evaluated by rating orchard trees. Experimental design consisted of a randomized block structure (three single-tree replicates) encompassing 32 cultivars evaluated over three growing seasons. Trees ≈ 15 years old were managed according to commercial standards (Ellis et al., 1994), except that pesticides were not used. Assessment of susceptibility was based on the degree of BPA-induced chlorosis/necrosis of foliage, i.e., percentage of black aphid damaged leaflets (ex-

hibiting chlorosis) on each of 30 compound leaves (about 330 leaflets per tree). Monitored leaves were from the basal half of terminal shoots from the lower interior of the tree—the region where BPA is usually first detected during aphid infestations and where they tend to prefer to feed. Leaves were evaluated for cumulative, or “season-long,” aphid injury in mid-October. Data were analyzed by analysis of variance (ANOVA) (SAS Institute, 1995) methods, with cultivar susceptibility classes being identified by Scott–Knott Cluster Analysis (Gates and Bilbro, 1978; Scott and Knott, 1974; Willavize et al., 1980).

Experiment 2. Evidence for antixenosis. A series of “feeding choice” tests evaluated evidence for antixenosis-like resistance. An array of eight paired tests determined: a) if aphids exhibit a feeding preference when presented with a choice between two highly susceptible cultivars; b) whether feeding preference is influenced by their previous feeding experience (i.e., genotype); c) whether the feeding preference is evident in both highly susceptible and relatively resistant cultivars; and d) if preference can be nullified by rinsing the leaf with water prior to introduction of aphids. The relatively susceptible cultivars were ‘Sumner’ vs. ‘Schley’, whereas the relatively resistant cultivars were ‘Curtis’ vs. ‘Farley’. Aphid sources were one of these four cultivars, depending upon the test being conducted.

Feeding preference was tested by presenting BPA alate viviparae collected from orchard trees of ‘Sumner’ and ‘Schley’, with a choice of feeding on either of these two cultivars. For example, “Sumner aphids” were given a choice between ‘Sumner’ or ‘Schley’. This was also repeated for “Schley aphids”. These two studies were repeated after the foliage of both cultivars had been washed for 5 min in distilled water and allowed to dry prior to the introduction of aphids. This same protocol was duplicated using “Curtis aphids” and “Farley aphids” on ‘Curtis’ vs. ‘Farley’ foliage (including “washed” and “unwashed” foliage). This yielded eight separate choice tests.

All choice tests utilized a single compound leaf from the basal one-third of the shoot, the preferred feeding sites of BPA (Teddars, 1978). Selected leaves had approximately equal leaf areas. A 2-cm basal section of the petiole of each compound leaf was re-cut under water to insure subsequent water uptake after being removed from the tree. One leaf of each cultivar pair was positioned on opposite sides of a flask containing distilled water, and the leaves and flasks were covered by a 4-L glass beaker to form a chamber large enough for flight. Leaves were oriented to face the north and south sides of the test chamber (the position assigned to a specific cultivar was random). Chambers were located on a table beneath a tree (≈ 85 years old) within the orchard.

Alate viviparae habituating the appropriate orchard trees were collected via suction into a test tube where they were held for 1 to 2 h before release into test chambers. Opened test tubes, containing 15 individuals, were placed midway between the two test leaves. Aphids soon emerged from the tubes, flew

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around in the chamber, eventually alighted onto foliage, and settled into probing and feeding on test leaves. Aphids typically had selected their preferred host and were feeding within ≈ 12 h. The number of aphids per cultivar was counted after 24 h and the percentage of the total population on each then calculated.

The experimental design for each of the eight studies consisted of two cultivars and seven replicates (chambers). Variables evaluated included washed vs. unwashed foliage, aphid source, and cultivar pairings. Data were analyzed as a randomized complete block design by SAS-ANOVA (SAS Institute, 1995). Studies were conducted in September when aphids are abundant within orchards.

Experiment 3. Evidence for antibiosis. Investigations on the adverse effects of pecan on BPA population development was evaluated in vitro. Bioassay chambers were constructed according to Reilly and Tedders (1990); confined aphids fed on the abaxial surface of detached leaflets appressed to the surface of a 1% water agar matrix in an enclosed petri dish (60×15 mm), which was suspended upside down to simulate "field" orientation. This system allowed leaf sections to remain healthy and capable of supporting reproducing aphid populations for up to 5 weeks. Leaflets were collected in August from each of three mature trees of 29 cultivars within a randomized block planting.

The apical leaflet of the third compound leaf from the base of terminals located within the shaded interior portion of the tree was used for all experiments. Semicircular sections were cut from these leaflets and immediately placed on the agar surface of petri dishes, thus totally covering the surface. Each dish therefore displayed similar leaf areas to the aphid population. A single fourth instar aphid, an apterous morph that quickly develops into an alate that reproduces parthenogenetically, was collected in the field and immediately placed in the petri dish chamber. The aphid source was the same as that of the cultivar being tested so as to insure that differences in resulting aphid populations were related to an antibiotic mechanism, rather than being confounded by a preference or nonpreference mechanism. Thus, 'Cheyenne' was evaluated with aphids collected from 'Cheyenne' trees, 'Desirable' with aphids collected from 'Desirable', etc. Leaf chambers and their aphid residents were placed under fluorescent light in a growth chamber, where the population was allowed to develop at 23°C in a $40 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ photosynthetically active radiation environment partitioned into 14 h of light and 10 h of dark.

The population resulting from the single ancestral fourth instar aphid was rated after 21 d for the total number of living aphids per petri dish chamber. This population reflected three or more generations from the original aphid. The experiment was therefore comprised of 29 pecan cultivars and 20 replicates arranged in a randomized block design. Data were analyzed by SAS-ANOVA (SAS Institute, 1995) and susceptibility classes delineated by Scott-Knott Cluster Analyses (Gates and Bilbro, 1978; Scott and Knott, 1974; Willavize et al., 1980).

Results

Experiment 1. Evidence for field resistance. Examination of 32 cultivars for 3 years revealed substantial cultivar-related differences in the degree of damage induced by BPA and a cultivar $\times$ year interaction (ANOVA not included). Because of this interaction, data were evaluated by cluster analyses for each of the three growing seasons. Scott-Knott analysis segregated the cultivar population into five susceptibility classes for each growing season (Table 1). These five classes range from "very low" to "very high" (including low, moderate, and high). In 1994 three cultivars ('Sumner', 'Oconee', and 'Moore') were "very highly susceptible" (70% of leaflets exhibiting chlorotic blotches), whereas 17 cultivars (53%) exhibited "very low susceptibility". 'Curtis', 'Sioux', 'Cape Fear', and 'Farley' were among the least susceptible, exhibiting 2% to 8% of leaflets with chlorotic blotches. In 1995, those exhibiting "very high susceptibility" were 'Oconee', 'Sumner', 'Caddo', and 'Choctaw' (74% to 78% of leaflets exhibiting damage), whereas 12 cultivars were in the "very low susceptibility" class. 'Grabohls', 'Sioux', 'Mahan', 'Barton', and 'Farley' were among the least damaged. In 1996, seven cultivars (22%) exhibited "very high susceptibility" (57 to 75% of leaflets with chlorotic blotches), whereas 10 cultivars (31%) exhibited "very low susceptibility", 'Sioux', 'Grabohls', 'Wichita', and 'Riverside' exhibiting less than 5% of leaflets with chlorotic blotches. While the

degree of damage exhibited by cultivars sometimes varied with the year of evaluation, there was general agreement as to which cultivars exhibited very low or very high levels of aphid damage. Cultivars that exhibited "very low susceptibility" over all 3 years were 'Sioux', 'Grabohls', 'Riverside', 'Curtis', 'Cape Fear', 'Barton', 'Cowley', 'Mahan', and 'Farley'. Within this grouping, the cultivar that consistently exhibited the lowest level of damage was 'Sioux' ($\leq 3\%$ of leaflets damaged each year), followed by 'Grabohls', 'Curtis', and 'Cape Fear'. In contrast, cultivars consistently exhibiting the greatest susceptibility to BPA damage were 'Choctaw', 'Oconee', and 'Sumner' ($\geq 62\%$ of leaflets damaged each year).

Experiment 2. Evidence of antixenosis. Upon release, aphids initially distributed themselves randomly on the leaves and the chamber wall. Aphids settled into feeding after 8 to 12 h in the test chamber. Given a choice between two pecan genotypes, winged adult aphids of all sources preferentially fed on foliage from the same cultivar on which they had been feeding prior to being forced to choose (Table 2). When aphids originating from the relatively susceptible cultivars of 'Schley' and 'Sumner' were forced to choose between leaves from these two cultivars, most selected the cultivars from which they had originated. This was also true for those originating from the relatively resistant 'Curtis' and 'Farley' cultivars. Rinsing of the foliage with distilled water prior to an experiment resulted in random feeding between the two

Table 1. Classification of the relative field susceptibilities in central Georgia of 32 pecan cultivars to black pecan aphids. Classification is based on Scott-Knott cluster analyses of the percentage of leaflets of compound leaves exhibiting chlorotic blotches in Sept. 1994, 1995, and 1996. Compound leaves are from the basal portion of interior foliage.

Cultivar	Percentage of damaged foliage per year			
	1994	1995	1996	Ave.
Apache	55 d ^a	46 c	40 e	47 e
Barton	10 a	6 a	8 a	8 a
Caddo	40 c	78 e	61 e	60 e
Candy	18 a	32 b	20 c	23 c
Cape Fear	5 a	7 a	7 a	6 a
Cherokee	33 b	32 b	25 c	30 c
Cheyenne	40 c	27 b	32 d	33 c
Chickasaw	40 c	44 c	18 c	34 c
Choctaw	63 d	78 e	75 e	72 e
Cowley	10 a	10 a	8 a	9 a
Curtis	2 a	8 a	6 a	5 a
Elliott	10 a	15 a	16 b	14 b
Farley	8 a	6 a	9 a	8 a
Grabohls	10 a	1 a	3 a	5 a
Houma	25 b	19 b	12 b	19 b
Kiowa	48 c	48 c	47 e	48 d
Mahan	10 a	6 a	8 a	8 a
Mohawk	18 a	14 a	22 c	18 b
Moneymaker	10 a	26 b	16 b	18 b
Moore	70 e	63 d	57 e	63 e
Oconee	70 e	74 e	64 e	69 e
Osage	18 a	19 b	13 b	17 b
Pawnee	33 b	51 c	24 c	36 c
Riverside	18 a	14 a	5 a	12 b
Shawnee	33 b	44 c	30 d	35 c
Shoshoni	18 a	29 b	14 b	20 b
Sioux	3 a	1 a	2 a	2 a
Stuart	40 c	39 c	29 d	36 c
Success	10 a	10 a	14 b	11 a
Sumner	70 e	77 e	62 e	70 e
Western	25 b	20 b	34 d	27 c
Wichita	18 a	44 c	5 a	22 c

^aScott-Knott groupings were based on five splits ($\alpha \leq 0.10$) where different letters within each column designate different groupings.

Table 2. Paired tests with leaves of two pecan cultivars illustrating feeding preferences exhibited by black pecan aphid alate viviparae, as affected by aphid origin, leaf origin, and washing of foliage with distilled water.

Test	Leaf source (cultivar)	Aphid source (cultivar)	Leaf surface	
			Unwashed (% of population located on each leaf) ²	Washed
1	Sumner	Sumner	74 b ²	59 a
	Schley	Sumner	26 a	41 a
2	Sumner	Schley	27 a	53 a
	Schley	Schley	73 b	47 a
3	Curtis	Curtis	77 b	52 a
	Farley	Curtis	23 a	48 a
4	Curtis	Farley	28 a	48 a
	Farley	Farley	72 b	52 a

²After 24 h in test chambers.

³Mean separation within columns and tests by ANOVA at $\alpha \leq 0.05$.

cultivar options (Table 2). Thus, washing nullified the feeding preference regardless of the host genotype or aphid source.

Experiment 3. Evidence for antibiosis. When a single fourth instar aphid was placed on foliage of the cultivar from which it had developed, and the resulting population was allowed to expand for three or more generations, there were distinct cultivar-related differences in population size (Table 3). Thus, substantial variability existed within this cultivar pool in suppression of BPA population growth. Cluster analyses separated this cultivar population into three distinct subgroups: i.e., low, medium, and high suppression of BPA populations. After 21 d, the cultivars exhibiting the least ability to suppress population growth were 'Desirable' and 'Success', whereas those with greatest ability were 'Choctaw', 'Alley', 'Moneymaker', and 'Mahan'. The differences in population numbers between these "most" and "least" suppressive cultivars were ≈ 3 - to 7-fold.

Discussion

The data indicate that the interaction of BPA with pecan is complex and that at least three distinct general mechanisms are involved in determining a cultivar's apparent field resistance. The first mechanism involves nonpreference, or antixenosis (Painter, 1951). Nonpreference by BPA for certain cultivars has been suggested for 'Moneymaker', 'Curtis', 'Moore' (Moznette, 1940), and 'Success' (Nakayama, 1964), whereas preference has been speculated for 'Peruque', 'Gloria Grande' (Worley, 1978), 'Schley', 'Alley', and 'Stuart' (Moznette et al., 1940). Preferences, or nonpreferences, by BPA were first documented by Kaakeh and Dutcher (1994), as indicated by probing characteristics and population size in October. These data support the general conclusions that BPA prefer certain cultivars.

When presented with a choice of two different cultivars, winged adult aphids (alate viviparae) exhibited clear preferences for the cultivar on which they had been feeding (and probably developed). This held true for cultivars recognized as exhibiting relatively high field susceptibility ('Schley' and 'Sumner'), as well as for those exhibiting relatively low susceptibility ('Curtis' and 'Farley'). Failure to exhibit a clear feeding preference after the foliage had been rinsed with distilled water indicates that water soluble substances on the

leaf surface probably play a major role in determining preference. We cannot determine from the present study whether these factors are plant-produced or are produced by aphids within the same biotype. These data are taken as evidence that winged adults in the orchard environment preferentially select a host on which they were feeding, rather than an alternative genotype. Thus, the suppression of BPA populations by rain (Kaakeh and Dutcher, 1993) may also be influenced by the temporary removal of foliage-related factors that encourage the preferential feeding behavior exhibited by adults.

These data may explain a common occurrence in orchards inasmuch that "seedling" (i.e., trees originating from the open-pollinated rootstock) trees often appear resistant to BPA because resident populations are typically very low in comparison with those on adjacent main cultivars, yet many of these seedling trees may exhibit BPA damage 2–4 weeks later. We postulate that because BPA alate viviparae exhibit a nonpreference for cultivars with which they are unfamiliar, the relatively unfamiliar seedling genotypes are contributing to antixenosis (Kogan and Ortman, 1978) because of a water-soluble chemical factor(s) that affects aphid behavior. Although beyond the scope of this study, our data also raise questions as to the influence of the antixenic aspect of resistance on the genetic composition of the aphid population within an orchard. The migratory behavior of alate male aphids during the period of genetic recombination in early to mid-autumn, when photoperiodic conditions induce the development of sexual forms, could have such an influence (Bergerand, 1972). In the absence of other factors influencing migration (such as wind or pheromones), gene exchange would tend to be restricted to individuals habituating the host genotype on which the males developed. This implies that seedling trees within orchards comprised of only a few genotypes would typically harbor few, if any, overwintering (diapausing) BPA eggs, thus contributing to the commonly observed dearth of BPA on seedling trees.

The no-choice study of the influence of specific host cultivars on subsequent aphid population growth indicates the existence of a leaf-associated antibiotic effect on BPA characteristics that influences one or more parameters associated with population growth. Kaakeh and Dutcher (1992) observed that, under field conditions, certain cultivars influ-

ence parameters more than do others. This antibiotic-like effect was influenced by the host genotype; several distinct groupings were identified statistically, including several antibiotic-based resistance classes. This antibiotic-like factor(s) held the population development of BPA on 'Choctaw' to $\approx 15\%$ of that on 'Desirable' over the same time period. The nature of this antibiotic defense is unknown (chemical or morphological), nor was the exact growth/developmental factor(s) contributing to the suppression of population growth objectively determined. Visual observations failed to detect many dead individuals or notable differences in sizes of individuals within the individual morphs. Thus, the effect does not appear to be a result of inhibition of growth or the death of early instars. Additionally, individuals appeared to feed without exhibiting abnormal restlessness. The collection of the ancestral fourth instar viviparae from a BPA population habituating the cultivar on which they were being tested in the no-choice test for antibiosis indicated that antixenosis mechanisms had little or nothing to do with subsequent population development. We therefore postulate that the antibiotic-like factor(s) probably acts by either delaying the development of the various immature stages or by reducing adult longevity or fecundity, or both. This merits further investigation.

Assessment of several pecan cultivars for field resistance to BPA damage indicated clear differences in apparent cultivar susceptibility.

Table 3. Relative influence of pecan cultivar on population growth of black pecan aphids. Means are the total number of aphids (adults plus juveniles) originating from a single fourth instar individual after 21 d and are grouped by Scott-Knott Cluster Analyses. Individual aphids were obtained from the cultivar on which they were tested (i.e., 'Choctaw' aphids were placed on 'Choctaw' foliage).

Cultivar	No. aphids
Choctaw	31 a ²
Alley	42 a
Moneymaker	51 a
Mahan	59 a
Pawnee	67 a
Moreland	70 a
Ideal	70 a
Caddo	71 a
Gloria Grande	71 a
Shoshoni	73 a
Kiowa	78 a
Tejas	80 a
Schley	82 a
Creek	82 a
Wichita	86 a
Cape Fear	102 b
Cheyenne	103 b
Curtis	105 b
Stuart	107 b
Sioux	108 b
Elliott	114 c
Mohawk	121 c
Sumner	124 c
Farley	128 c
Pereque	132 c
Western	152 c
Oconee	154 c
Success	178 d
Desirable	210 d

²Mean separation by Scott-Knott Cluster Analyses ($\alpha \leq 0.09$).

Three years of observations indicated that 'Sioux', 'Grabohls', 'Riverside', 'Curtis', 'Cape Fear', 'Farley', 'Barton', 'Mahan', and 'Cowley' would probably be damaged far less than would 'Caddo', 'Moore', 'Oconee', 'Sumner', and 'Choctaw'. Whether or not the relative levels of resistance observed in the present study are unique for the local BPA population or is general for all BPA is not known, but this study does provide a basis for further evaluation. No report or direct evidence exists for races or biotypes of BPA, but biotypes are often observed in certain aphid species not feeding on pecan (Eastop, 1987). Because of the wide natural and cultivated range of pecan, distinct BPA biotypes probably exist. Thus, cultivars exhibiting "very low susceptibility" in this study may exhibit greater susceptibility at other locations.

These data indicate that, at least for the local aphid population and environment, 'Sioux' (highest resistance) and 'Choctaw' (highest susceptibility) possess genes uniquely suited for breeding and genetic studies on BPA resistance. 'Pawnee' is a cultivar recognized as exhibiting an unusually high level of field resistance to yellow pecan aphids, blackmargined aphids, and BPAs (Kaakeh and Dutcher, 1994; Thompson et al., 1992). In this study, it exhibited "moderate susceptibility" (in terms of field damage) to BPAs, but was among the most effective of all cultivars in suppressing BPA population growth (i.e., relatively high level of antibiotic-like activity on BPA populations). This indicates the possible existence of BPA biotypes, and/or that 'Pawnee' is easily damaged by BPA although relatively few aphids are found on the tree. This response of 'Pawnee', and especially that of 'Choctaw' (exhibiting the greatest level of antibiosis but also the greatest number of leaflets with chlorotic blotches), raises the question as to the nature of the BPA/pecan interaction giving rise to such blotches. Do these blotches enhance the aphid's diet (and reproduction) or are blotches a tree defense mechanism that suppresses food availability to, and reproduction of, the aphids? In any event, these data indicate that BPA population levels on foliage and feeding behavioral characteristics are not necessarily a good indicator of the level of field resistance (as measured by the percentage of leaflets with chlorotic blotches). Thus, field resistance may best be determined by evaluating germplasm, under field conditions, for damage to the tree.

Note that there was no association between the levels of "field resistance" and "antibiosis" observed in this study ($r = -0.10$; $P = 0.71$). For example, 'Choctaw' exhibited the most antibiotic resistance, but the least field resistance, of all cultivars tested. Because field resistance was based on the percentage of leaflets exhibiting yellow or chlorotic blotches so typical of BPA feeding injury, physiological factors leading to the production of chlorotic blotches probably contribute to BPA resistance. We therefore postulate that cultivar resistance to BPA is partially attributable to differential host sensitivity to aphid factors eliciting chlorosis and subsequent loss of photosynthetic efficiency (Wood and Tedders, 1986) and defoliation.

Kaakeh and Dutcher (1994) observed that 'Oconee', 'Shoshoni', 'Cheyenne', and 'Gloria Grande' were highly preferred by BPA. This was based on recording the number of adults and nymphs in early October. Our observations confirm that 'Oconee' is highly susceptible in the field environment, although 'Shoshoni' and 'Cheyenne' exhibited only moderate susceptibilities based on feeding damage to field trees. Conversely, Kaakeh and Dutcher (1994) reported that the least preferred cultivars were 'Pawnee' and 'Cape Fear'. Our observations indicated that 'Cape Fear' exhibited very low susceptibility in the field to BPA-induced chlorotic blotches, whereas 'Pawnee' exhibited only moderate resistance. These differences may be attributed to the fact that resistance was based on population size at a particular time in one case and on cumulative, season-long damage as reflected by necrotic blotches in the other. Similarly, 'Pawnee' exhibited resistance when aphid population levels on orchard trees were used as the criteria for resistance (Thompson et al., 1992). Our observations indicated that while 'Pawnee' greatly suppressed aphid population growth on its foliage, there was only moderate field resistance to the development of chlorotic blotches from BPA feeding. Thus, observations indicate that conclusions about the resistance of pecan cultivars to BPAs may vary depending upon the factor being measured. Hence, if practical levels of field resistance are the objective, the frequency and magnitude of chlorotic blotches on foliage are probably better indicators than is the aphid population level at a particular time, or cumulative levels throughout the season (standing aphid days). This measure of field resistance takes into account the tolerance of a particular host genotype to aphid feeding. Ultimately, the degree of damage that a host genotype exhibits, rather than the size of the aphid population, is probably the best measure of practical field resistance. Our data indicate that these two are not always highly correlated.

In conclusion, our data indicate that the mechanisms controlling the susceptibility of pecan cultivars to BPA feeding are complex. The cultivar-related variability in this study is taken as evidence for the existence of considerable genetic variability in resistance to BPA, and that the breeding of field resistant cultivars is attainable. However, successful screening for field-tolerant genotypes probably will be done in a field environment; this should account for the antixenosis and antibiotic aspects of aphid resistance. The leaf factors imparting preference and antibiotic-like responses merit further study, but may not be as important as an understanding of factors that enable host genotypes to tolerate feeding while experiencing relatively little damage.

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