Relationships Between Patterns of Defoliation by the Fruittree Leafroller (Lepidoptera: Tortricidae) and Foliage Morphology of Baldcypress in Forested Wetlands of Louisiana[1]

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ABSTRACT Baldcypress, *Taxodium distichum* (L.) Richard, has been threatened recently by a new insect herbivore, the fruittree leafroller, *Archips argyrospila* (Walker) (Lepidoptera: Tortricidae). Baldcypress foliage varies from long-leaved, open-faced branchlets with leaves arranged in two-ranked fashion to short-leaved, appressed, imbricate branchlets. Field surveys revealed that the tallest trees contained 72 – 85% appressed foliage, whereas intermediate and small-sized trees contained 55-92% open type foliage. Over a three-year period, open morphology trees repeatedly exhibited significantly higher levels of defoliation (percentage of crown loss) by the fruittree leafroller, compared with appressed morphology trees. There was no ovipositional preference (number of egg masses) associated with morphology type. Differences in defoliation levels, therefore, were attributed to morphologically related influences on foliage suitability for larval stages.

KEY WORDS Fruittree leafroller, baldcypress, host susceptibility.

The fruittree leafroller, *Archips agryrospila* (Walker), (Lepidoptera: Tortricidae) recently has become a serious pest on baldcypress, *Taxodium distichum* (L.) Richard, in southern Louisiana. The initial discovery occurred in 1983, when populations of fruittree leafroller reached epidemic proportions in Iberville Parish in south central Louisiana (Goyer and Lenhard 1988). Infestations caused severe defoliation of sapling and pole-sized baldcypress, a new host record, and have recurred annually since. Aerial detection surveys revealed that noticeable defoliation of baldcypress by the fruittree leafroller occurred on more than 100,000 ha in 1990 (Goyer and Feduccia 1990).

The fruittree leafroller is a native species occurring over most of the United States and southern Canada and is univoltine throughout its range (Chapman and Lienk 1971). Outside of Louisiana, the fruittree leafroller has been reported in damaging numbers on almost all types of orchard crops and has been known to locally defoliate a wide variety of angiosperm forest tree species (Gill 1913, Chapman and Lienk 1971). Isolated incidences of feeding on conifers have been reported but were considered to represent cases of secondary feeding (Powell 1964). Interestingly, the fruittree leafroller in Louisiana has exhibited a high degree of host specificity for baldcypress since detection. Overwintering eggs,

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deposited in masses on the undersides of terminal baldcypress branches, begin hatching between late February and early March, concurrent with foliage emergence. Larvae feed on emerging cypress foliage and undergo five larval instars before pupation and subsequent adult emergence (Braun et al. 1990). Severely defoliated trees commonly refoliate thereafter (Goyer et al. 1990).

Although the acreage of baldcypress infested has fluctuated annually, a marked increase in the geographic distribution of fruittree leafroller defoliation has occurred since 1983 (Goyer et al. 1990). Confined earlier to four parishes, serious defoliation has spread to a total of 11, with the fruittree leafroller being detected in additional parishes as far north as East Baton Rouge Parish. Furthermore, Goyer and Lenhard (1988) reported a continuous and significant reduction in the mean annual radial growth of infested trees. With 70% of Louisiana's baldcypress growing stock located within or near areas now infested with fruittree leafrollers, the persistence and continued spread of defoliation poses an additional threat to this dwindling and unique forest resource.

Within infested areas, defoliation often is highly variable among individual trees in a stand. Neighboring trees can show a full complement of foliage on one and complete defoliation on the other, indicating that baldcypress is of nonuniform suitability/susceptibility to the fruittree leafroller. Morphologically, baldcypress foliage also is highly variable (Fig. 1). Brown and Montz (1986) described the deciduous baldcypress branchlets as generally being flat and linear, with leaves arranged in two-ranked fashion and directionally extending away from the main axis of the branchlet. They noted that some trees will produce imbricate (scale-like) leaves in crowns exposed to direct sunlight. They also pointed out that secondary or tertiary growth may produce this appressed type foliage. The appressed foliage morphology may closely resemble that of pondcypress, *Taxodium ascendens* Brong., the natural range of which begins east of the current fruittree leafroller distribution and is a key component in forested wetlands in Florida. After making direct comparisons between baldcypress and pondcypress, Nuefeld (1983 and 1986) suggested that appressed foliage may function as a means of conserving water, and that cypress foliage morphology was controlled genetically and by environmental factors.

With these factors in mind, this study was designed to identify relationships between baldcypress foliage expression and fruittree leafroller defoliation, and to determine the abundance and distribution of the open and appressed foliage types in second-growth natural stands.

Methods and Materials

To identify potential trends or patterns in host utilization by the fruittree leafroller in Louisiana, two field sites within the current infestation were chosen to monitor individual tree defoliation levels and egg mass abundance. The Big Mallet site was located within the Atchafalaya Basin, ≈ 5 km south of Pigeon, LA, along Big Bayou Mallet. Baldcypress trees therein had exhibited high levels of annual defoliation since 1983. The Mardi Gras site was located ≈ 5 km southeast of Stephenville, LA, along Bayou Milhomme and was ≈ 26 km south of the Big Mallet site. Baldcypress trees growing at the Mardi Gras site were near the southern edge of their freshwater-limited range and had more recently (1988 or 1989) begun experiencing high levels of fruittree leafroller defoliation. Both sites were predominantly a mix of baldcypress and tupelo, growing under permanently flooded conditions. Although not specifically evaluated, both sites appeared to have a similar mix of open and appressed foliage types.

Four baldcypress "types" were identified for monitoring annual peak defoliation levels in May, and for assessing overwintering (diapausing) egg mass abundance. At the Big Mallet site, sample trees were selected and classified based on the two morphological extremes commonly exhibited: 1. open, where branchlets supported longer leaves, arranged in two-ranked fashion, extending more or less perpendicular to the axis of the branchlet, and 2. appressed, where branchlets supported short, scale-like foliage arranged concentrically about the branchlet and growing approximately parallel with it (Fig. 1). At the Mardi Gras site, sample trees were selected and classified as: (1) heavily defoliated or (2) undefoliated, based on 1988 defoliation levels, irrespective of foliage morphology. Our aim was to see if trees, once defoliated, continued to be defoliated in subsequent seasons. Foliage morphology of all sample trees was characterized by visual examination during fruittree leafroller egg hatch and, again, when field populations reached late instars.

In 1988, 10 sample trees each of open and appressed host types at Big Mallet, and 15 sample trees each of undefoliated and defoliated host types at Mardi Gras were selected, flagged, and tagged for subsequent sampling in 1989, 1990, and 1991. All sample trees were located on the sides of watercourses, where defoliation was readily apparent. All trees had high live crown ratios (live branches throughout the length of stem), and crowns were readily accessible.

The level of fruittree leafroller defoliation was recorded annually for each of the 50 sample trees soon after the period when adult moths could no longer be found in the field and when larval feeding had ceased. Defoliation was classified into one of five categories: 0 (little or no evidence of fruittree leafroller defoliation), 1 (5-25% of crown removed), 2 (26-50% of crown removed), 3 (51-75% of crown removed), and 4 (76-100% of crown removed). Defoliation data were categorical and thus ranked. Comparisons of ranked annual defoliation levels among host types were performed using Student's t as the test criterion, in the TTEST procedure of SAS (SAS Institute 1987). Means were considered significantly different at the $P = 0.05$ level.

Beginning in the fall/winter of 1988, branches were collected from each of the 50 tagged trees for evaluating potential fruittree leafroller ovipositional differences among the four host types. A sample from each tree consisted of three to six branches taken at approximately mid-crown height from all accessible aspects. All late-season terminal branch growth (non-hardened) was removed from the sample because it was not present during oviposition, and this new growth (which varied markedly) could bias comparisons of samples. Branch material greater than 6.5 mm in diameter also was removed from the sample because it is not used as an oviposition site by fruittree leafroller in Louisiana (Goyer, unpublished). From the remaining samples, 30, 0.5-m sections of branch material were measured and the number of fruittree leafroller egg masses counted. Similar samples were taken in 1989, 1990, and 1991. Comparisons of egg mass counts among hosts were conducted using Student's t test (SAS Institute 1987).

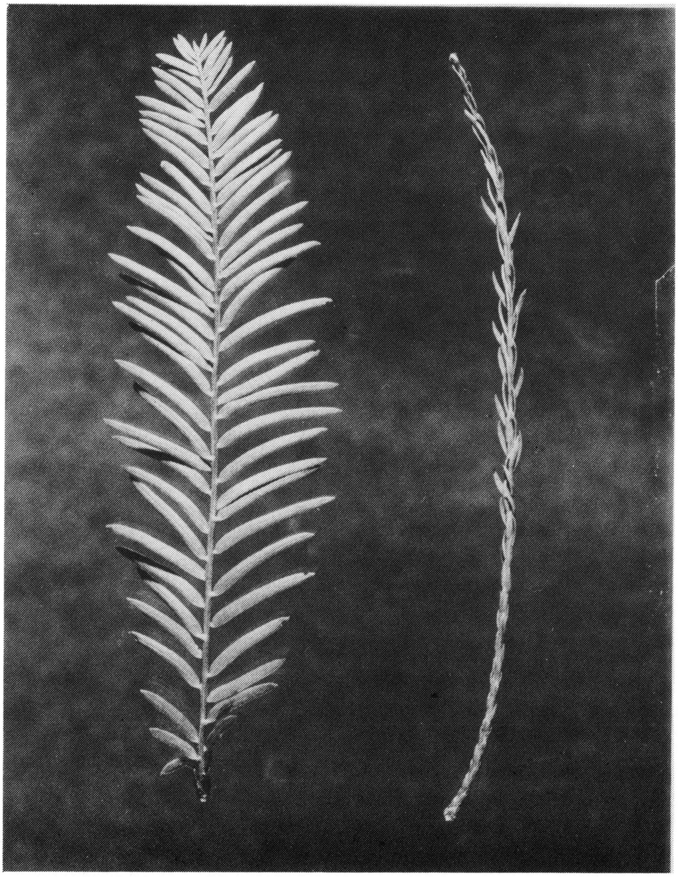

Fig. 1. Examples of baldcypress foliage exhibiting the two morphological extremes examined in this study, open morphology foliage (left) and appressed morphology foliage (right).

Morphology of baldcypress foliage was examined in relation to tree stature and foliage position in order to detect the frequency and patterns of occurrence of the open and appressed foliage types in unevenaged natural stands. Groups of individual baldcypress trees were inspected at three different geographical locales in the fall of 1991. One of these locales corresponded to an area in the immediate vicinity of the Big Mallet site and one to the Mardi Gras site both within the range of the current fruittree leafroller infestation. The third area was located east of the infestation, along the Petit Amite River in Ascension and Livingston Parishes, where fruittree leafrollers have not been detected. At each site, five groups of 20 consecutive baldcypress trees were examined. All trees in a group occurred along the edge of a waterway, for ease in evaluation by boat. Groups were located at least 300 m apart. Overall, 300 trees were evaluated by

JRM. Each tree was classified as either dominant, codominant, intermediate, or small. Also, trees were evaluated for the approximate percentage (in 10% increments) of their crown exhibiting the open, appressed, and/or mixed type of foliage morphology. The mixed category represented foliage that expressed some degree of both. Where crowns exhibited more than one type of foliage expression, the position of each morphology was noted as top, middle, and/or bottom stratum of the tree crown.

The frequencies and abundance of each type of foliage morphology among height classes was recorded and the percentage crown expression of each type of foliage morphology was calculated.

Results

Host Defoliation and Egg Mass Surveys. Analyses revealed significant differences in percentage of crown loss (defoliation) over a three-year period among baldcypress types (Table 1). On the Mardi Gras site those trees originally classified as defoliated continued to exhibit heavy defoliation over the period. Those originally having little defoliation continued to sustain little defoliation over the same period. We observed consistently lower defoliation for appressed morphology compared with open.

Fruittree leafroller egg mass abundance over a four-year period taken from branch samples indicated that there were no significant differences between host types at either site for 1989, 1990, and 1991 (Table 2). The inability to detect significant differences between annual means in each year was indicative of the high variability in egg mass counts among individual trees of each host type. Egg mass counts from individual trees ranged from 0 to 156. In 1992, mean egg mass counts were significantly different between defoliated and undefoliated host types (Table 2). The number of egg masses, unexpectedly, were lower on the more heavily defoliated host. The overall lack of significant differences between host types at either site suggested that there were no distinct ovipositional differences that could explain the differential levels of defoliation observed.

Leaf Morphology Surveys. In viewing the field survey data, one can see that baldcypress foliage type was associated with tree height, age, and exposure. All classes (dominant, codominant, intermediate, and small) and all foliage morphologies (open, appressed, and mixed) were represented at each of the three sites surveyed. Patterns of foliar morphology in relation to tree height were similar across sites, so all data were combined by height class. Of the 300 trees surveyed, 13% were classed as dominant, 24% as codominant, 36% as intermediate, and 27% as small (Table 3). Regardless of tree height, crowns exhibiting more than one type of foliage morphology invariably had the appressed foliage located above either the mixed or open type, and/or the mixed type above the open. Tops of crowns tended to be appressed and bottoms tended to be open.

The mean tree values of the percent crown coverage by a particular foliage morphology clearly indicated that the appressed morphology became more abundant, and the open morphology decreased with increased tree height (Table 3). A similar inverse relationship among height classes was exhibited for the expression

Table 1. Comparisons of annual fruittree leafroller defoliation levels between: 1. baldcypress trees of different foliage morphology (open vs. appressed), and 2. baldcypress trees of different defoliation history (heavily defoliated in 1988 vs. undefoliated in 1988).

				Mean Annual Fruittree Leafroller Defoliation					
				1989		1990		1991	
Class Variable	Host Type†	Site	Number of Trees per Year (1989, 90, 91)	Class Level‡	Ranked Score§	Class Level	Ranked Score	Class Level	Ranked Score
Foliage Morphology	Open	Big Mallet	10, 10, 10	3.9	50.1£	3.3	42.4	3.2	42.5
					*		*		*
	Appr.	Big Mallet	10, 10, 10	0.9	20.2	0.4	15.3	0.2	12.4
Defoliation History	Defol.	Mardi Gras	15, 15, 14	2.5	49.7	3.6	67.1	3.7	67.8
					*		*		*
	Undef.	Mardi Gras	15, 14, 14	0.2	15.1	1.5	34.6	1.1	29.7

† Appr. = appressed morphology, Defol. = heavily defoliated baldcypress in 1988, Undef. = undefoliated baldcypress in 1988.
‡ Individual whole-tree defoliation classed as: 0 = less than 10% crown loss, 1 = 10 to 25% crown loss, 2 = 26 to 50% crown loss, 3 = 51 to 71% crown loss and, 4 = greater than 75% crown loss.
§Class defoliation data were ranked and means compared using t-tests.
£ Standard deviations and/or standard errors of the mean available upon request.
* Means significantly different at the $P = 0.05$ level.

Table 2. Comparisons of the number of fruittree leafroller egg masses per crown sample between: 1. baldcypress trees of different foliage morphology (open vs. appressed), and 2. baldcypress trees of different defoliation history (heavily defoliated in 1988 vs. undefoliated in 1988).

Class Variable	Host Type†	Site	Number of Trees per Year (1989, 90, 91, 92)	Mean No. of Egg Masses/Sample‡ (± SEM) 1989	1990	1991	1992
Foliage Morphology	Open	Big Mallet	10, 10, 8, 10	25 (± 5.6)	17 (± 5.2)	9 (± 1.6)	11 (± 2.2)
	Appr.	Big Mallet	10, 10, 8, 10	22 (± 5.6)	29 (± 7.0)	17 (± 3.9)	13 * (± 2.8)
Defoliation History	Defol.	Mardi Gras	14, 14, 9, 14	34 (± 10.3)	23 (± 4.5)	50 (± 8.7)	14 (± 2.6)
	Undef.	Mardi Gras	14, 13, 9, 10	30 (± 6.0)	27 (± 7.6)	45 (± 7.2)	28 * (± 5.4)

† Appr. = appressed morphology, Defol. = heavily defoliated baldcypress in 1988, Undef. = undefoliated baldcypress in 1988.
‡ The number of egg masses per crown sample were derived from samples of 30, 0.5 meter branch sections.
* Means significantly different at the $P = 0.05$ level. All other means were not significantly different.

Table 3. Percentage crown expression of different baldcypress foliage morphologies in four height classes of trees.

			Percent Crown Expression Foliage Morphology		
Height Class	(N)	%	Open	Mixed	Appressed
Dominant	(39)	13	9	6	85
Codominant	(71)	24	15	13	72
Intermediate	(109)	36	55	24	21
Small	(81)	27	92	4	4
	(Total = 300)				

of open type foliage. For small trees, an average of 92% of the crown exhibited open foliage, compared with only 9% in the dominant class (Table 3).

Discussion

Consistent differences over three years in levels of fruittree leafroller defoliation among host types showed that baldcypress was of variable susceptibility/suitability to fruittree leafroller damage. Morphologically related, the opened and undefoliated trees were similarly heavily defoliated. By comparison, appressed and previously undefoliated trees together experienced low levels of defoliation. Susceptibility was associated with foliage morphology and was maintained from year to year over the course of this study. As such, open morphology (and defoliated) baldcypress trees were repeatedly more susceptible than appressed morphology trees (and undefoliated). Within a given area (such as either of the two sites examined), the climatic factors and site factors were similar. Therefore, the marked differences in defoliation found between host types in each of the two areas indicated that the relative susceptibility of each was directly attributable to morphologically-linked differences in host suitability.

Levels of fruittree leafroller defoliation changed in opposite directions at the two sites between 1989 and 1991. We believe these changes reflect local fruittree leafroller population fluctuations. Increased defoliation at the more recently infested Mardi Grass site indicated a rising population, as the fruittree leafroller expanded and occupied its range (Chapman and Lienk 1971). At the Big Mallet site, defoliation historically had been at high levels since 1983 but exhibited a decrease between 1989 and 1991. Declining populations at the Big Mallet site were possibly the result of induced host quality declines and/or increased predation, parasitism, and/or incidence of disease. Of related interest was the discovery of diseased larvae causing heavy fruittree leafroller mortality at the Big Mallet site in 1991. Larvae collected from this site were dissected and examined under phase/contrast microscopy and diagnosed as possessing signs and symptoms of granulosis virus and nuclear polyhedrosis virus infection. These diseases were first recognized in the fruittree leafroller population collected from a nearby infested area in 1990 (Goyer, unpublished). Together these two instances represented the only records of fruittree leafroller diseases in our studies. The disease outbreak at the Big Mallet site in 1991 may have stemmed from reduced fruittree leafroller vigor as a result of either high populations, and/or induced reductions in host suitability, and/or was possibly due to abnormally frequent and intense rainfalls during larval stages aiding disease transmission.

The significantly greater number of egg masses per tree on host types at the Mardi Gras site versus those at Big Mallet in 1991, as well as the contrasting trends in egg mass samples over time, lend evidence to the suspected shifts in fruittree leafroller population levels at each site.

Although egg mass counts were variable from tree to tree and from year to year, the overall lack of significant differences between host types at either site confirmed that there were no clearcut ovipositional differences that could explain the differential levels of defoliation observed. Defoliation differences were, therefore, believed to be a result of differences in the relative suitability of host foliage, as either a food source and/or shelter. Those trees heavily defoliated in one year continued to be affected in subsequent years. Those trees lightly affected in one year remained less defoliated in subsequent years than their counterparts.

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