Survivorship, Development, and Fecundity of Buck Moth (Lepidoptera: Saturniidae) on Common Tree Species in the Gulf Coast Urban Forest[1]

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ABSTRACT   *Hemileuca maia maia* (Drury), the buck moth, is abundant in urban areas of the Gulf Coast region where it defoliates oaks. However, the extent to which the buck moth can survive on other tree species common in the southern urban forest has not been reported. In the laboratory, we studied the suitability and acceptability to larvae of 14 common tree species in New Orleans and determined the extent to which larvae were able to switch to species other than oak midway in their development. Larvae had greater survival, pupal weight, and fecundity, as well as reduced development time, on live oak, water oak, black oak and black cherry than on green ash, sugarberry, sweetgum, red maple, a deciduous ornamental magnolia, American holly, tallow tree, crapemyrtle, mulberry, and black willow. Larvae showed some ability to switch from oak to some non-oak species, but fecundity, pupal weights, and development time were affected as assessed from the time of switch. The implications of these findings are discussed in terms of outbreak dynamics of the moth in urban forests.

Key Words   *Hemileuca maia*, larval stage, host plants, host suitability, southern trees, urban forest

The buck moth, *Hemileuca maia maia* (Drury) (as defined by Tuskes et al. 1996) (Saturniidae: Hemileucinae), is a locally abundant urban forest defoliator. High caterpillar populations can threaten the health of urban trees which may already be under stress from a variety of causes (Houston 1985, Talarchek 1987). In addition, larvae possess scoli which cause painful "stings" so that the species is of concern to human health as well. The outbreak dynamics of the buck moth are poorly known; however, the Gulf Coast region of southern Louisiana and Mississippi experienced a widespread regional outbreak that lasted from 1980 to 1993, with locally heavy infestations shifting in an unpredictable manner from year to year. Documentation of earlier outbreaks is poor, but the buck moth seems to have the potential of reaching outbreak numbers in the northeastern United States as well as in southern states (Anonymous 1921, 1932, 1936, 1938, 1941, Anonymous 1990, 1992). Throughout most of its range, *H. maia maia* is associated with a variety of habitats dominated by oaks, including oak-pine sand barrens in the Northeast, and oak forests in the Southeast and Midwest (Tuskes et al. 1996).

Hemileuca maia is univoltine throughout its range. In southern Louisiana, eggs eclose in late February to early March and are roughly synchronized with host tree bud break. Siblings initially feed gregariously on the host tree. They exhibit processionary behavior in their foraging, i.e., they follow one another in tandem to new feeding sites. Later-instar larvae are more solitary in their foraging behavior and frequently leave the initial host tree. In high density populations, older larvae can be observed almost anywhere, often far removed from a food source. Anecdotal evidence suggests they may be diurnal in their feeding. During the daytime, large clumps of larvae can be found at the base of the trunk of host trees. Pupation occurs in the litter most commonly near the host tree in mid- to late-May. Pupae enter summer diapause (Foil et al. 1991), and adults emerge in late-November to early-December in southern Louisiana. Males are active daytime fliers. Females, although rarely observed flying, must be able to at least fly up to the crown of a tree to oviposit where eggs are laid in masses of 300 or more around the twigs of host trees. The mechanism of oviposition site selection by females is unknown.

Hemileuca maia maia host plant relations are mostly anecdotal. Ferguson (1971) list species of *Populus, Prunus, Quercus,* and *Salix* as hosts. Tietz (1972) adds *Artemesia filifolia* Torr., *Aster* sp., *Corylus, Prosopis glandulosa* Torr., *Rubus allegheniensis* Porter, *Spiraea salicifolia* Linn., and *Vaccinium macrocarpon* Ait. However, Ferguson (1971), Smith (1974), and Stamp and Bowers (1986) suggest that some host records may be in error because of moth misidentification. Tuskes et al. (1996), for example, lists *Prunus, Quercus, Salix, Spiraea,* and *Vaccinium* as host plants of *H. lucina,* a closely related species. The only experimental studies of *H. maia maia* host plant relations are those of Stamp and Bowers (1986) on *Quercus* and *Spiraea* and Foil et al. (1991) on *Quercus.*

The objectives of our study were to concentrate on *H. maia maia* as a defoliator of urban trees, and to determine the extent to which the larvae can survive and develop on the most common deciduous tree species in New Orleans. *Hemileuca maia maia* is known principally as a defoliator of oaks; however, in high-density populations late-instar larvae can be observed on almost any type of foliage. It is unknown whether these larvae are able to complete development on non-oak species, or whether they constitute a loss to the population. We hypothesized that later-instar larvae have a broader diet than early instars, and that diet switching occurs.

Materials and Methods

Laboratory studies were conducted during the spring of 1992, 1993, and 1995 in New Orleans. Selection of host plant species was based on Talarchek (1987) who identified the most abundant deciduous trees on city property in New Orleans. From his list we selected: live oak, *Quercus virginiana* Mill.; water oak, *Q. nigra* L.; crapemyrtle, *Lagerstroemia indica* L.; sugarberry, *Celtis*

laevigata Willd.; red maple, *Acer rubrum* L., and sweetgum, *Liquidambar styraciflua* L. Additional tree species selected on the basis of their abundance as ornamentals or along fencerows and in abandoned areas were: saucer magnolia, *Magnolia soulangiana* (Buchoz) Dandy; American holly, *Ilex opaca* Ait.; green ash, *Fraxinus pennsylvanica* Marsh.; red mulberry, *Morus rubra* L.; black willow, *Salix nigra* Marsh.; tallow tree, *Sapium sebiferum* (L.) Roxb.; black cherry, *Prunus serotina* Ehrh.; and black oak, Q. *velutina* Lam. Three trees of each species were used in the studies as food sources for laboratory colonies of larvae.

We collected pupae from litter under live and water oak trees in the summer and held them until adult emergence in the fall. Mating and oviposition took place inside cages. Eggs were kept in cold storage until needed in the spring for experiments. We broke up egg masses into clusters of approximately 10 eggs each. Clusters were then assigned randomly to experimental treatments. In order to insure that all neonates were fed foliage of approximately the same age regardless of tree species, the setup of experimental groups was synchronized with tree species bud break. Approximately 1 wk following bud break of the tree species to which a group of eggs had been assigned, we removed the eggs from cold storage and surface sterilized them with a 20-min wash in 20% formalin, followed by a 20-min rinse in cold tap water. Eggs were then placed *in* an incubator at 25° C until eclosion, 4 to 8 days later. Upon eclosion, larvae were used in laboratory studies described below.

Neonate choice tests. On the assumption that neonates will demonstrate host plant preference by the relative amount of feeding, naive neonates 24 to 48-h-old were offered a choice between two different species of tree foliage. Disks of foliage (12 mm diam, 113.1 mm²) were cut with a cork borer. Two discs from both tree species were placed in an alternating pattern around the center of a 60-mm diam Petri dish. A moistened filter paper served as the substrate to prevent leaf desiccation. One neonate was introduced into each dish and allowed to feed freely for 24 h. At the end of the test, uneaten portions of all leaf discs were photocopied. The photocopies were then enlarged, and relative amounts of feeding were measured using a map reader's dot grid. The results were analyzed as percent feeding of the total in each dish on each of the two choices. Testing all possible combinations of 14 tree species was beyond the scope of the study. Therefore, water oak was selected as a standard, and all trees were tested with water oak (13 tests). Each choice test was replicated 10 times.

Neonate frass production and feeding initiation. Naive neonate feeding intensity was measured indirectly by counting the number of frass pellets produced over a 24-h period. Leaf discs were prepared and set up in a manner similar to that described in the previous experiment. Four leaf discs of a single species were placed in each dish. One naive neonate was introduced into each dish, and the number of frass pellets produced by each insect was counted every 24 h for 10 days, or until death. There were 10 replications for each tree species.

Fitness of single host tree species diets. Within 48 h of eclosion, we placed neonates individually in 227.3 cm³ (8-oz) Styrofoam containers and maintained them at 25" C and constant light on foliage from the tree to which

they had been assigned. Twenty larvae were assigned to each tree in the study. Foliage was collected twice per week from each tree, washed in 5% bleach solution for 10 min, thoroughly rinsed and bagged, and placed in cold storage. With every collection of new foliage, the unused older foliage was discarded. Foliage was changed and cups cleaned or changed every day until caterpillar death or pupation. Dependent variables recorded for each larva were survivorship, development time from setup to pupation, pupal weight, and number of eggs produced by females. Variation between trees within tree species (n = 3, df = 2) was used as an error term in testing for tree species differences in the dependent variables.

Fitness on switch host tree species diets. The procedure was the same as described in the previous experiment except that larvae were fed foliage from a single water oak tree from first through fourth instars, then switched to the foliage of a non-oak or a different oak tree species for the remaining two instars. The trees were the same ones used in the experiments described above. Larvae reared on water oak throughout served as a control. Twenty fifth-instar larvae were assigned randomly to each switch tree. Survivorship (from switch date to death), development time (from switch date to death), pupal weight, and number of eggs per egg mass were the dependent variables recorded for each larva. As with the previous experiment, variation between trees within tree species was used as an error term in testing for tree species differences.

Field study. This study was conducted to provide information on larval behavior on trees in a natural setting. Five small trees, 10 to 15 cm diameter breast height, on the campus of Xavier University were infested with 20 fifth-instar larvae, and their behavior was observed over a 24 h period. The trees chosen were two live oaks, one crapemyrtle, one green ash, and one red maple. Larvae were released on the trunk of the tree 1 m from the ground, and subsequent observations were made within 1 h, then every 4 h afterwards throughout the first 2 days (nighttime excluded). Positions of larvae, the number of feeding, and the number remaining on each tree were noted at each observation.

Results and Discussion

Survival of neonates was poor on all species except black cherry and the oaks (Table 1, Fig. 1). No neonate feeding (as evidenced by total absence of frass) was observed on American holly, red mulberry, saucer magnolia, or tallow tree. These larvae moved about the dish in a processionary manner for up to 6 days, then died, presumably of starvation. Among the other tree species, the mean time of feeding initiation varied from 1.4 days for sweetgum and oaks to 4.8 days for ash (Fig. 2). Minimal neonate feeding was observed on crapemyrtle and sugarberry, and larvae did not survive long enough to fully evaluate the extent of feeding initiation. In neonate feeding choice tests involving water oak and an alternate, only black oak was more preferred than water oak (of the total amount of feeding, 68% occurred on the black oak disks, and 32% on the water oak disks). Among the other species paired with water oak, the relative amounts of feeding were: water oak/sweetgum, 66%/33%; water oak/black willow, 86%/14%; water oak/live oak, 87%/13%; water oak/black cherry,

Table 1. Survivorship and average number of days to death of buck moth larvae reared from neonate to death or pupation on ten non-oak tree species.

Tree Species	% Survival	Number of Larvae	Days from Setup to Death''' $\overline{X} \pm SEM^{**}$
Sweetgum	5	57	33.3 ± 3.0 At
Black Willow	2	59	31.7 ± 1.7 A
Crapemyrtle	0	60	29.3 ± 0.1 A
Green Ash	0	60	19.7 ± 0.13 B
Red Maple	0	60	8.9 ± 0.20 C
Sugarberry	0	60	7.2 ± 0.14 C
Tallow Tree	0	60	6.6 ± 0.13 c
Saucer Magnolia	0	60	6.6 ± 1.63 C
Red Mulberry	0	60	6.5 ± 0.02 C
American Holly	0	60	4.9 ± 0.06 C

*Data given and statistical tests performed only for those treatments in which survival was 0 to 5%.
**SEM is that of tree replications within tree species, (n=3).
†Means accompanied by the same letter are not significantly different ($P < 0.05$; Student-Newman-Keuls multiple range test, Sokal and Rohlf, 1981). Overall tree species effect MS was highly significant ($P < 0.001$) using tree replications within tree species as the error term (SAS Institute. PROC ANOVA).

91%/9%; water oak/red maple, 96%/4%. As with the previous experiment, there was no evidence of feeding by neonates in the choice tests on crapemyrtle, green ash, sugarberry, tallow tree, saucer magnolia, red mulberry, or American holly.

Due to poor survival on most tree species, larval development time and fitness was evaluated only for black cherry and the oaks. Among these tree species, there were no significant differences in development time, pupal weights, or fecundity (Table 2), and values obtained were similar to those obtained by Foil et al, (1991).

Larvae reared to the fifth instar then switched to an alternate species also varied in their response, as assessed from the date of switch. As with neonates, no frass production was observed for fifth-instar larvae placed on American holly, red mulberry, saucer magnolia, or tallow tree, and most died within a week. Larvae switched to tallow tree died within 3 days, suggesting the presence of a toxic allelochemical in the foliage. Frass production and feeding was noted from larvae placed on green ash, sugarberry, and red maple; many survived the molt to sixth instar, but none survived to pupation (Fig. 3). Average survival time ranged from 8.3 days for red maple to 26.3 days for green ash (Table 3).
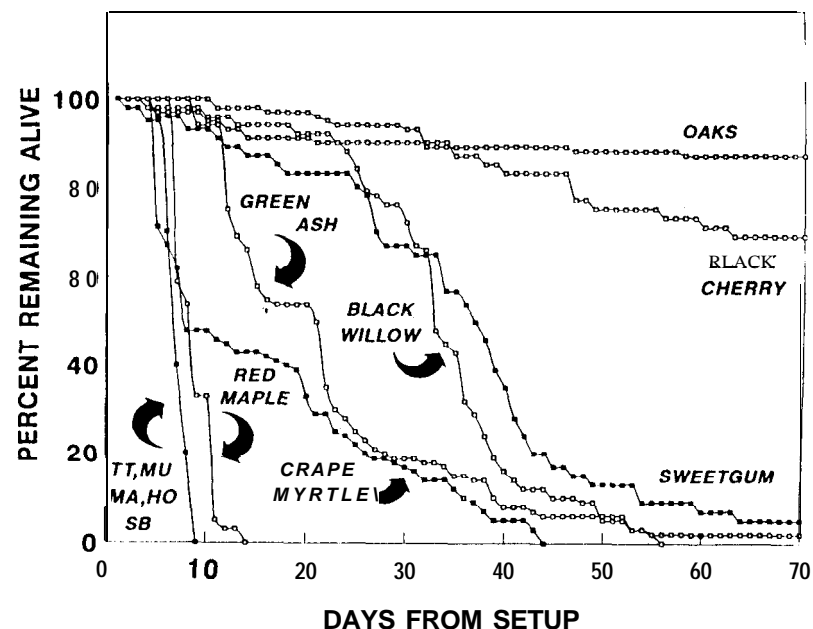
Fig. 1 Survivorship curves of buck moth neonates given foliage of 14 species of trees. Data producing nearly identical curves were pooled, i.e. tallow tree (TT), red mulberry (MU), saucer magnolia (MA), American holly (HO), and water oak, black oak, live oak (OAKS).

Survival was at least 50% for larvae switched to the remaining tree species However, significant differences were observed in female development times. pupal weights and fecundity, when non-oak alternate tree species were compared with the pooled values for the oaks (Table 4). Fifth instars switched to crapemyrtle, although most survived, took the longest to complete development, and produced females with low pupal weights and poor fecundity With at least two species (black cherry and black willow), development time was reduced by the switch, compared with larvae switched to another oak. The more rapid development did not translate to a difference in pupal weight or fecundity, however. The trends in development time and pupal weight among males were consistent with those of the females, but differences were not statistically significant (Table 4).

With respect to the field study, larvae placed on the two oaks initiated feeding almost immediately upon moving out to twigs. Twenty-four hours later. most of the larvae were still in the trees and could be observed actively feeding
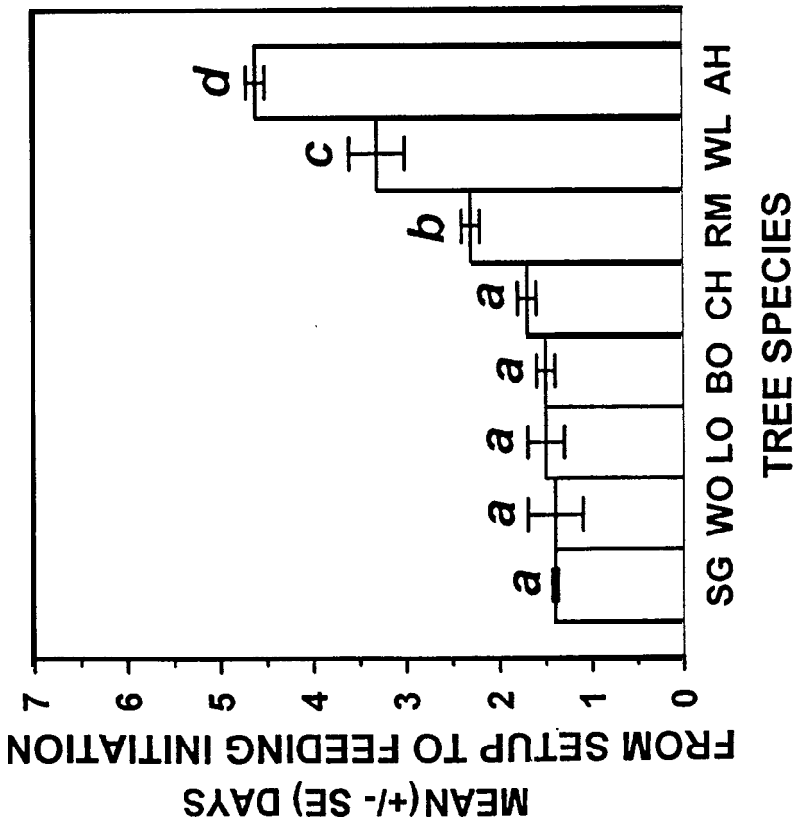
Table 2. Survivorship, development, and fitness of buck moth larvae reared on four species of suitable hosts.

Tree Species	% Survival	Days from Setup to Pupation*				Pupa Weight (grams)*				Egg Mass Size*	
		Females		Males		Females		Males			
		N	$\overline{X}$ ± SEM**	N	$\overline{X}$ ± SEM**	N	$\overline{X}$ ± SEM**	N	$\overline{X}$ ± SEM**	N	$\overline{X}$ ± SEM**
Black Cherry	77	26	52.5 ± 2.83 NS†	20	49.0 ± 2.32 NS†	26	1.93 ± 0.12 NS‡	20	1.34 ± 0.03 NS‡	26	416 ± 20 NS§
Live Oak	80	24	49.6 ± 0.77	24	44.9 ± 0.46	24	2.27 ± 0.05	24	1.33 ± 0.09	24	334 ± 58
Water Oak	88	29	47.3 ± 0.55	24	43.6 ± 1.41	29	2.12 ± 0.02	24	1.42 ± 0.06	29	396 ± 10
Black Oak	92	26	51.4 ± 1.06	29	46.4 ± 1.06	26	2.34 ± 0.27	29	1.53 ± 0.09	25	419 ± 27

*Data given and statistical tests performed only for those tree species on which survival was 50% or greater.

**SEM is that of tree replications within tree species (n = 3).

†Overall tree species effect on larval development time was NOT significant (P > 0.05) using tree replications within tree species as the error term (SAS Institute, PROC ANOVA).

‡Overall tree species effect on pupal weight was NOT significant (P > 0.05) using tree replications within tree species as the error term (SAS Institute, PROC ANOVA).

§Overall tree species effect on egg mass size was NOT significant (P > 0.05) using tree replications within tree species as the error term (SAS Institute, PROC ANOVA).

Fig. 2. Buck moth neonate feeding initiation on 8 species of southern trees: sweetgum (SG), water oak (WO), live oak (LO), black oak (BO), cherry (CH), red maple (RM), black willow (WL), green ash (AH). Means (± SEM) accompanied by the same letter are not significantly different (P < 0.05, Student-Newman-Keuls mean separation test, Sokal and Rohlf 1981) using trees within species as the error term (n = 3) (SAS Institute, PROC ANOVA).
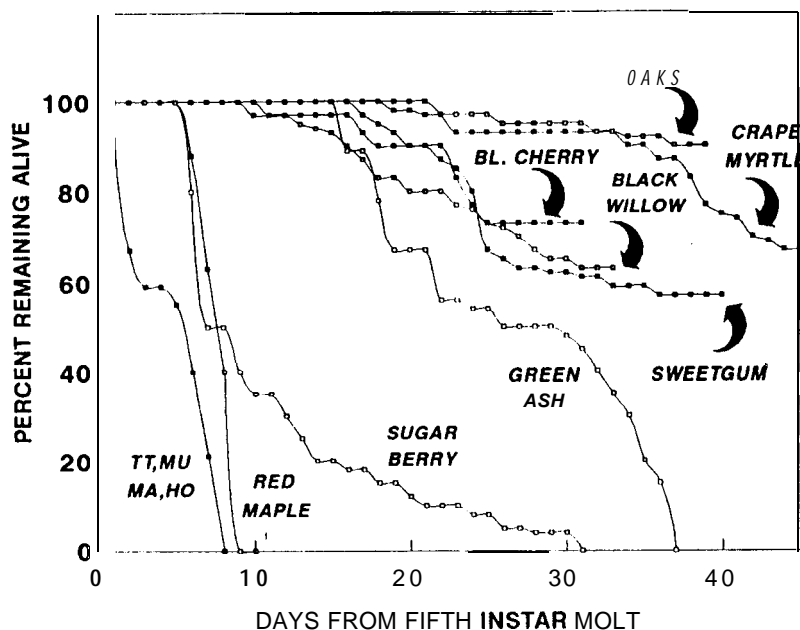
Fig. 3. Survivorship curves of fifth- and sixth-instar buck moth larvae following a diet switch from water oak to an alternate tree species. Data producing nearly identical curves were pooled, i.e., tallow tree (TT), red mulberry (MU), saucer magnolia (MA), American holly (HO), and water oak, black oak, and live oak (OAKS).

However, larvae placed on the non-oak species disappeared rapidly from the trees. Within 1 h, for example, five of the larvae placed on the ash could be observed on the ground around the base of the tree, and five others were on the trunk moving down. The others could be found on the twigs and branches of the tree, but all were actively moving. Four hours later only 3 larvae, one of which was feeding, remained in the tree. Similar observations were made with the larvae on crapemyrtle and **red maple trees.**

Our study identities only one-non-oak species on which buck moth fitness on a single host-plant diet is comparable to that of oaks, i.e., black cherry. Larvae reared from neonates on the other non-oak species exhibited poor survival. Buck moth larvae also exhibited only a limited ability to switch to an alternate species midway through development and successfully complete development. Our study identifies only three: black cherry, black willow, and sweetgum. However, even with these, survival was not as good as on the oaks. Larvae

Table 3. Survivorship **data of buck moth larvae reared on water oak until molt to fifth instar, then switched to an alternate tree species on whose foliage they failed to complete development.**

Switch Tree Species	% Survival	Number of Larvae	Days from Switch Date to Death'" $\overline{X} \pm SEM$**
Green Ash	0	60	26.3 ± 0.70 A[†]
Sugarberry	0	60	11.5 ± 0.20 B
Red Maple	0	60	8.3 ± 0.20 c
American Holly	0	60	7.9 ± 0.66 C
Saucer Magnolia	0	60	7.3 ± 0.43 c
Red Mulberry	0	60	5.7 ± 0.07 D
Tallow Tree	0	60	3.1 ± 0.12 E

*Data given and statistical tests performed only for those treatments in which survival was 0%.
* SEM is that of tree replications within tree species, (n = 3).
[†]Means accompanied by the same letter are not significantly different ($P <$ **0.05;** Student-Newman-Keuls multiple range test. Sokal and Rohlf 1981). Overall tree species effect MS was highly significant ($P < 0.001$) using tree replications within tree species as the error term (SAS Institute, PKOC ANOVA).

switched to the other host tree species experienced either greatly reduced survival, prolonged development, or reduced size and/or fecundity. Therefore, we conclude that in natural populations of buck moth larvae, individuals that leave their original host tree either by accident or in response to overcrowding, may represent a substantial source of mortality if nearby trees are non-oak species. Late instars, at least, seem capable of extensive foraging and may actually leave a tree in search of another, if the foliage is not suitable. However, it is unknown how long a foraging larva's energy reserves last before it must accept foliage or starve. The local composition of the urban forest may have important ramifications for the outbreak dynamics of the buck moth. City streets lined with a single oak species will most likely serve as an epicenter for population buildup. Other areas of the city where the urban forest is more diverse (such as parks), should sustain only much smaller buck moth populations even during widespread regional outbreaks. Therefore, planting a variety of tree species along city streets, in parks, and around homes and businesses may well provide a deterrent to buck moth population expansion.

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Table 4. Survivorship, development, and fecundity of buck moth larvae reared on water oak until molt to fifth instar, then switched to an alternate tree species on whose foliage survival was at least 50%.

Switch Tree Species	Survival %	Days from Switch Date to Pupation*				Pupa Weight (grams)*				Egg Mass Size*	
		Females		Males		Females		Males			
		N	$\bar{X} \pm SEM$**	N	$\bar{X} \pm SEM$**	N	$\bar{X} \pm SEM$**	N	$\bar{X} \pm SEM$**	N	$\bar{X} \pm SEM$**
Crapemyrtle	67	18	$45.7 \pm 0.15\ p = 0.001$†	22	35.6 ± 2.97‡	18	$1.31 \pm 0.14\ p < 0.001$†	22	0.86 ± 0.05‡	18	$243 \pm 19\ p = 0.020$†
Sweetgum	57	14	38.2 ± 6.75 (NS)	20	29.6 ± 2.40	14	$1.56 \pm 0.12\ p = 0.014$†	20	1.11 ± 0.04	14	265 ± 27 (NS)
Black Cherry	73	30	$29.5 \pm 1.32\ p = 0.007$†	14	23.7 ± 1.96	30	1.82 ± 0.14 (NS)	14	0.15 ± 0.15	30	360 ± 41 (NS)
Black Willow	63	21	$28.0 \pm 1.26\ p = 0.013$†	26	23.1 ± 2.48	12	1.69 ± 0.27 (NS)	26	1.20 ± 0.04	23	316 ± 26 (NS)
Live Oak	87	32	34.0 ± 1.90	20	27.8 ± 1.13	32	1.88 ± 0.10	20	1.17 ± 0.11	30	317 ± 26
Water Oak	83	24	37.2 ± 2.28	36	26.1 ± 5.49	24	2.07 ± 0.10	26	1.16 ± 0.01	23	389 ± 16
Black Oak	100	28	36.2 ± 0.75	32	24.4 ± 0.70	28	2.17 ± 0.09	32	1.16 ± 0.05	27	319 ± 22

*Data given and statistical tests performed only for those treatments in which survival was 50% or greater.

**SEM is that of tree replications within tree species (n = 3).

†Probabilities are of F values given in apriori orthogonal comparisons with the pooled oak species (Sokal and Rohlf 1981). Overall tree species effect on female development time and pupal weight were highly significant ($P < 0.001$, $P < 0.01$, respectively) using tree replications within tree species as the error term. Tree species effect on egg mass size was not quite significant ($P = 0.06$) (SAS Institute, PROC ANOVA).

‡Overall tree species effect on male development time or pupa weight was NOT significant ($P > 0.05$) using tree replications within tree species (SAS Institute, PROC ANOVA).