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J. Mark Scriber
Michigan State University

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**DIFFERENTIAL SUITABILITY OF 12 GREAT LAKES
TREE SPECIES FOR *PAPILIO CANADENSIS*
(LEPIDOPTERA: PAPILIONIDAE)
LARVAL SURVIVAL AND GROWTH**

J. Mark Scriber¹

ABSTRACT

Differential nutritional suitabilities of 12 potential host plants of *Papilio canadensis* in the Great Lakes region of North America were determined with gravimetric techniques for penultimate and final larval instars. While leaf water content and leaf nitrogen content explain some of the variation, allelochemicals in different plants are likely to be involved in differential larval growth performances as well as mortality of neonate larvae on tuliptree and spicebush. Oviposition tests using 3-choice arenas with quaking aspen, paper birch, and balsam poplar showed no strong host preferences. Factors affecting patterns of *Papilio* host use in the Great Lakes region are discussed.

The eastern tiger swallowtail butterfly, *Papilio glaucus* L., has long been considered to be comprised of at least two interbreeding subspecies, *Papilio glaucus glaucus* L. and *P. g. canadensis* R&J (Luebke et al. 1988, Scriber 1990). The biological and genetic differences in various biochemical, physiological, behavioral and morphological traits are of sufficient number and magnitude that we recently have suggested species-level status of *Papilio canadensis* (Hagen et al. 1991).

Among the differences is the fact that *Papilio canadensis* are able to survive and grow successfully on quaking aspen, *Populus tremuloides* leaves, whereas neonate *Papilio glaucus* do very poorly and survival through the first larval instar is rarely greater than 15%. In fact, these survival differences are so dramatic that the zone of hybrid interaction in the Great Lakes region can almost be delineated by the step cline differences in survival on aspen among *P. canadensis* populations and *P. glaucus* populations (Fig. 1). A reciprocal pattern of survival is observed for these same populations on leaves of tuliptree, *Liriodendron tulipifera*, with a similar step cline pattern of geographic variation (Scriber 1988; Fig. 2). These traits are genetically based (Scriber 1986, Scriber et al. 1989) and are likely due to differential detoxification abilities (Lindroth et al. 1986, 1988).

It has been pointed out that *Papilio glaucus* is probably the most polyphagous of all 560+ species of swallowtail butterflies in the world (Scriber 1984). Similarly *P. canadensis* have been shown to have more than 10% neonate survival in laboratory no-choice studies on 40 different species of plants from 11 different plant families (Scriber 1988). While neonate survival is a critical prerequisite for further ecological success, the growth rates and total duration of surviving larvae on marginal host plants are of considerable significance, especially where predation or parasitism may be possible. Another important aspect of differential larval growth

¹Department of Entomology, Michigan State University, East Lansing, MI 48824.

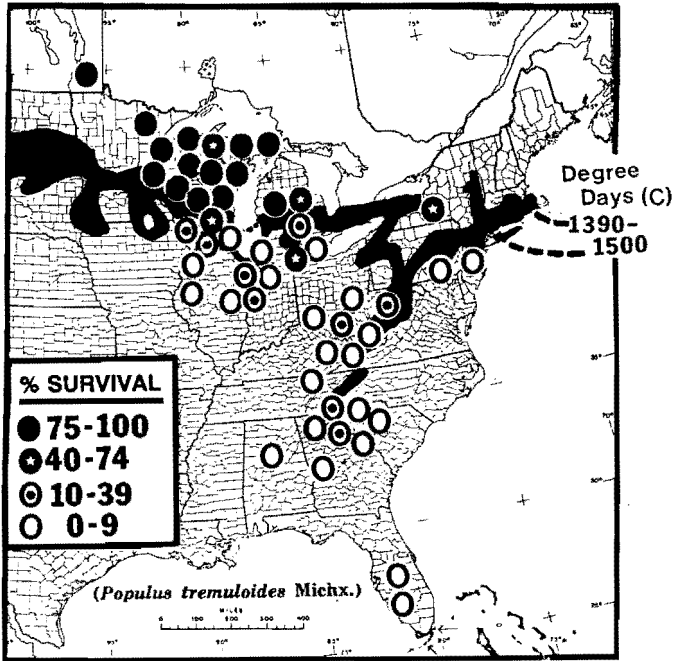


Figure 1. Geographic variation in neonate (1st instar) larval survival of *Papilio glaucus* and *P. canadensis* on quaking aspen, *Populus tremuloides*. (Data are from 1978–1987, and include 2803 larvae tested; Scriber et. al. 1988).

rates is whether or not an extra generation can be completed before adverse climatic conditions arrive at a given location. Differential larval growth rates on different host plants have been proposed as a basis for natural selection to favor specialists in areas where seasonal total thermal unit accumulations are marginal for completion of an extra generation as in central Michigan and Wisconsin (Scriber and Lederhouse 1992). Selection of the most favorable (nutritionally superior) hosts would aid in completing development, whereas selection of a poor host would be fatal for larvae since they would not be able to pupate before adverse conditions arrive. On the other hand, generalists might be favored in areas where thermal units are sufficient for the generation to be completed on most or all host plants, thus contributing to alternating latitudinal bands of specialization and generalization within a species (Scriber and Lederhouse 1992).

This study was conducted on *Papilio canadensis* larvae from northern Wisconsin which were fed leaves from 12 different Wisconsin tree species from 7 plant families. The goal of this study was to assess the differential suitability of various potential hostplants for *P. canadensis* larval survival and growth. Understanding the population variation in host use abilities and the differential nutritional suitability of various plants to *Papilio* populations is a prerequisite to subsequent evaluation of the voltinism/suitability hypothesis of Scriber and Lederhouse (1992).

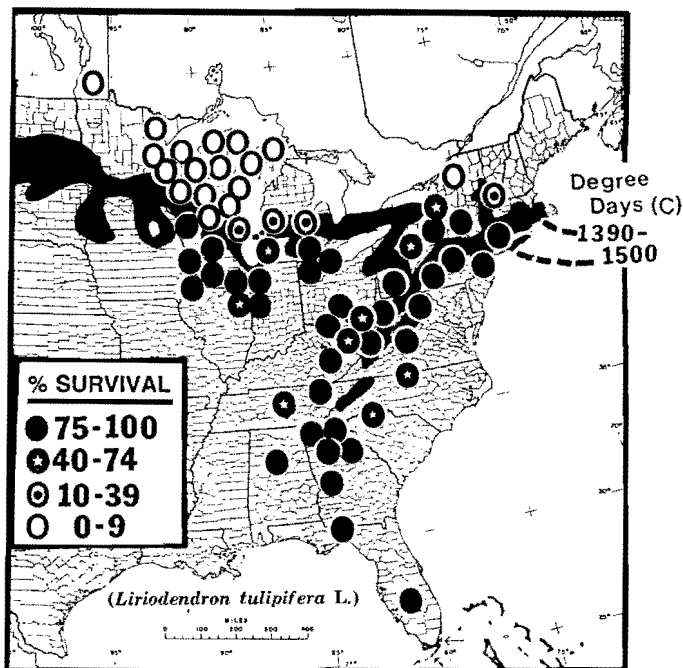


Figure 2. Geographic variation in neonate survival of *P. glaucus* and *P. canadensis* on tuliptree, *Liriodendron tulipifera* (Data are from 1978–1987, and include 3572 larvae tested; Scriber et. al. 1988).

MATERIALS AND METHODS

Adult female *Papilio canadensis* were collected from locations in northern Wisconsin (Burnett, Clark, Iron, Oneida, and Taylor counties) and immediately brought to the laboratory where they were set up in plastic boxes with sprigs of black cherry and aspen under illumination from incandescent lights (approximately 0.5 m distance away) to induce oviposition. Eggs obtained by these methods were identified for each source female. Resulting neonate larvae were carefully distributed with camel hair brushes to leaves of various plants and maintained in standard rearing conditions, 16:8 photo/scotophase and corresponding thermal periods of 23.5/19.5 C, to simulate summer conditions. Leaves (in water-filled rubber-capped plastic vials) were changed at intervals of 2–3 days and larval survival on each host was recorded at this time.

Fresh penultimate instar larvae were weighed and placed in individual plastic dishes with weighed leaf samples and returned to the growth chambers for standard gravimetric feeding experiments. Sample aliquots of leaves and larvae in each treatment were weighed, freeze-dried and weighed again, allowing estimation of dry weights. Standard indices of growth rates (RGR), consumption rates (RCR) and efficiencies (AD, ECD and ECI) were calculated for each treatment based on stadia durations, food ingested, fecal production, and larval weight gain for both penultimate and final instars (Scriber and Slansky 1981). Data are presented as a mean \pm

standard error. Tukey's test for unequal sample sizes was used for identifying significant differences between the means (Winer 1962, Snedecor and Cochran 1967).

Samples were analyzed for total nitrogen content using the micro-Kjeldahl method of McKenzie and Wallace (1954). The nitrogen content of each leaf sample was determined as a mean of 3 replicates. The overall mean nitrogen content was calculated for the larvae of each female independently for each host plant tested, and was based on the daily samples actually provided in the feeding experiments.

An additional group of wild females was used for 3-choice oviposition experiments (Chippewa and Taylor counties in Wisconsin, and Iron and Dickinson counties in the adjacent Upper Peninsula of Michigan, and a comparison sample from Fairbanks, Alaska). Each female was individually placed in a clear plastic box (10 cm x 20 cm x 27 cm) containing an array of similar size sprigs from 3 different tree species (P = paper birch, Q = quaking aspen, B = balsam poplar). These sprigs were positioned equal distances apart along one long side of the box such that the leaves carefully draped along the side. These boxes, with the leaves on the side nearest the light source, were placed 0.7 – 1.0 m from two vertical banks of four 100 watt incandescent bulbs which were on a 4 hr on/off cycle throughout the studies. The individual boxes were randomized daily.

Eggs were collected and counted at 24 hr intervals, and new leaves were substituted daily in a 3-day rotational schedule. Designed to minimize any potential "position effects," this rotation started on day 1 with either a P-Q-B or a B-Q-P sequence (i.e., with aspen separated by birch and balsam poplar). The 3-day sequence was then either P-Q-B, Q-B-P, B-P-Q or B-Q-P, Q-P-B, P-B-Q. Leaf moisture was maintained using water-filled, rubber-capped aquapics. Preferences were calculated and included in the analyses for all females which oviposited 5 or more eggs. The few stray eggs that were placed on the paper lining or plastic were generally immediately adjacent to a particular leaf, but nonetheless were excluded from the analyses. A similar 3-choice design using tuliptree, quaking aspen, and black cherry was also used for general comparison of female oviposition responses.

RESULTS

Survival through the third instar on tuliptree, *Liriodendron tulipifera* was non-existent for all populations tested, which is consistent with most of the neonate survival studies previously reported (Scriber 1983, 1988). Survival on spicebush was also zero (Table 1). The best larval survival was on black cherry (85%) followed by quaking aspen (71%), paper birch (67%), choke cherry (66%) and ash (57%). In addition, some plants found naturally only to the south of these *P. canadensis* populations resulted in relatively low survival for *P. canadensis*: cucumber magnolia (57%), sassafras (44%) and hoptree (34%). Survival through the third instar on balsam poplar and mountain ash (two plants whose ranges lie largely north of these *P. canadensis* populations) was also quite low (37% each; Table 1).

Larval growth rates (R.G.R.'s) were fastest on black cherry (.172 mg · g⁻¹ · d⁻¹) and slowest for ash (.129) and mountain ash (.129) during their penultimate instars. A basically similar pattern of ranking in larval growth rates is observed for the ten plant species in the final instar, with the exception of paper birch and balsam poplar, for which final instar growth is even slower (.067 and .081 mg · g⁻¹ · d⁻¹, respectively) than observed for ash and mountain ash (Table 2).

The total duration of larval development is shortest (32 days) for black cherry (where the 4th and 5th instar growth rates were also fastest) and longest (44 days) for white ash (where 4th instar growth was the slowest), however the total larval duration on the other eight plant species was variable between these extremes. The mean total larval duration of *P. canadensis* on a plant was correlated with both the penultimate and final instar growth rates (Fig. 3). However, it should be noted that

Table 1. — Larval survival and growth performance of *Papilio canadensis* on 12 Wisconsin plant species.

Host plant tested	Females (n)	Larvae (n)	Percent survival through:			Pupal weight	Total duration	All Family Relative Growth Rates ($\text{mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$)			
			1st instar	2nd instar	3rd instar			Penultimate (4th) instar mean (range)		Final (5th) instar mean (range)	
Black cherry (<i>Prunus serotina</i>)	15	73	88	85	85	219.1 ± 7.3 a	32.0 ± 0.7 a	.172	(.146–.219)	.135	(.117–.155)
Paper birch (<i>Betula papyrifera</i>)	12	61	85	72	67	187.2 ± 8.2 a	40.9 ± 1.2 a	.162	(.098–.194)	.067	(.052–.085)
Hop Tree (<i>Ptelea trifoliata</i>)	13	53	77	47	34	204.0 ± 12.5 a	36.6 ± 1.6 a b c	.158	(.128–.185)	.114	(.097–.140)
Balsam poplar (<i>Populus balsamifera</i>)	8	52	69	46	37	134.2 ± 14.5 b	34.3 ± 1.0 a b	.155	(.156–.160)	.081	(.064–.114)
Choke cherry (<i>Prunus virginiana</i>)	11	62	82	68	66	168.9 ± 6.6 a b	34.0 ± 0.7 a b c	.147	(.109–.180)	.111	(.092–.132)
Sassafras (<i>Sassafras albidum</i>)	10	55	62	51	44	199.8 ± 10.1 a	36.9 ± 1.0 a b c	.147	(.062–.197)	.109	(.082–.136)
Mountain magnolia (<i>Magnolia acuminata</i>)	11	54	70	63	57	167.6 ± 12.5 a b	34.6 ± 0.9 a b c	.136	(.091–.161)	.116	(.091–.146)
Quaking aspen (<i>Populus tremuloides</i>)	20	80	86	78	71	219.2 ± 7.2 a	38.7 ± 0.8 b c d	.133	(.101–.160)	.106	(.065–.116)
White ash (<i>Fraxinus americana</i>)	8	51	84	75	57	201.6 ± 10.6 a	44.1 ± 1.5 e	.129	(.096–.142)	.087	(.055–.113)
Mountain ash (<i>Sorbus americana</i>)	10	65	72	49	37	205.3 ± 119. a	40.2 ± 1.9 c d e	.129	(106–.168)	.084	(.073–.102)
Spicebush (<i>Lindera benzoin</i>)	19	69	1	1	0	—	—	—	—	—	—
Tuliptree (<i>Liriodendron tulipera</i>)	21	88	0	0	0	—	—	—	—	—	—

Table 2. — Larval growth performance of penultimate (4th instar) and final (5th) instar *Papilio canadensis* on ten plant species. Data are presented as a grand mean \pm s.e. (ie. with the average of all individual larvae for a particular mother as a single replicate).

Host Plant	Larval Instar	Leaf Water (% fresh)	Leaf Nitrogen (% dry)	Growth rate		Consumption rate		Efficiencies			Number of families (n)
				R.G.R. (mg·mg ⁻¹ ·d ⁻¹)	R,C,R ₁ (mg·mg ⁻¹ ·d ⁻¹)	AD (%)	ECD (%)	ECl (%)	Duration (days)		
Black cherry	(4th)	64.3 ± .8	3.18 ± .09	.172 ± .007	1.31 ± .07	47.6 ± 2.9	33.3 ± 4.3	13.8 ± 0.8	6.9 ± 0.3	(10)	
	(5th)	64.2 ± .3	3.09 ± .03	.135 ± .004	1.11 ± .04	42.5 ± 1.4	30.4 ± 1.9	12.4 ± 0.4	10.1 ± 0.3	(8)	
Paper birch	(4th)	67.3 ± 0.6	2.72 ± .01	.162 ± .008	1.20 ± .09	45.4 ± 1.7	31.3 ± 2.2	13.8 ± 0.5	7.7 ± 0.4	(8)	
	(5th)	64.1 ± 0.4	2.28 ± .05	.067 ± .003	1.11 ± .10	40.5 ± 1.7	15.4 ± 1.8	6.9 ± 0.4	17.0 ± 1.0	(8)	
Hop tree	(4th)	65.7 ± 1.0	3.08 ± .10	.158 ± .008	1.07 ± .07	53.6 ± 5.1	33.2 ± 6.6	15.3 ± 1.2	7.4 ± 0.3	(8)	
	(5th)	64.4 ± 1.5	2.76 ± .10	.114 ± .005	1.05 ± .06	49.2 ± 2.9	23.1 ± 2.1	11.1 ± 0.7	11.2 ± 0.5	(8)	
Balsam poplar	(4th)	76.8 ± 0.6	3.35 ± .15	.155 ± .001	1.10 ± .11	43.9 ± 3.5	34.5 ± 5.5	14.7 ± 1.3	7.5 ± 0.3	(3)	
	(5th)	74.1 ± 0.5	3.34 ± .03	.081 ± .016	.92 ± .08	43.5 ± 2.6	20.9 ± 4.0	8.8 ± 1.3	13.4 ± 2.0	(3)	
Choke cherry	(4th)	63.5 ± .23	2.85 ± .07	.147 ± .008	1.28 ± .07	45.7 ± 1.1	27.1 ± 2.4	12.0 ± 0.9	6.5 ± 0.4	(8)	
	(5th)	62.9 ± .67	2.47 ± .05	.111 ± .005	1.15 ± .03	43.2 ± 1.5	22.8 ± 0.9	9.8 ± 0.4	11.2 ± 0.3	(8)	
Sassafras	(4th)	66.1 ± .87	3.09 ± .10	.147 ± .013	1.25 ± .09	59.1 ± 1.5	21.9 ± 2.9	12.6 ± 1.5	8.8 ± 0.9	(9)	
	(5th)	65.8 ± 0.8	2.88 ± .04	.109 ± .006	1.08 ± .04	47.8 ± 1.4	21.4 ± 0.9	10.1 ± 0.3	11.1 ± 0.5	(8)	
Mountain magnolia	(4th)	76.7 ± 0.3	3.45 ± .03	.136 ± .011	.98 ± .07	41.9 ± 4.1	40.1 ± 9.5	14.3 ± 1.4	7.6 ± 0.5	(6)	
	(5th)	75.5 ± 0.4	3.32 ± .02	.116 ± .009	.99 ± .07	38.2 ± 4.3	38.9 ± 7.4	12.5 ± 1.6	9.9 ± 0.3	(6)	
Quaking aspen	(4th)	60.0 ± 0.6	2.32 ± .10	.133 ± .007	1.54 ± .11	48.9 ± 2.5	21.6 ± 2.7	9.2 ± 0.7	8.4 ± 0.3	(14)	
	(5th)	60.2 ± 0.4	2.31 ± .02	.106 ± .002	1.08 ± .05	38.7 ± 1.6	27.4 ± 2.4	10.1 ± 0.5	12.7 ± 0.4	(12)	
White ash	(4th)	60.0 ± 1.2	2.42 ± .07	.129 ± .007	1.21 ± .07	45.4 ± 5.0	25.6 ± 2.7	10.7 ± 0.2	8.8 ± 0.4	(6)	
	(5th)	57.5 ± 0.7	2.37 ± .03	.084 ± .008	1.11 ± .05	34.3 ± 2.3	25.3 ± 4.4	7.8 ± 0.9	14.1 ± 0.8	(6)	
Mountain ash	(4th)	65.4 ± 1.0	2.36 ± .14	.129 ± .009	1.05 ± .06	49.9 ± 2.5	27.0 ± 2.8	12.6 ± 0.8	10.0 ± 103	(8)	
	(5th)	63.6 ± 0.5	1.79 ± .05	.087 ± .005	1.06 ± .09	42.0 ± 1.8	20.2 ± 1.9	8.3 ± 0.4	14.9 ± 0.8	(5)	

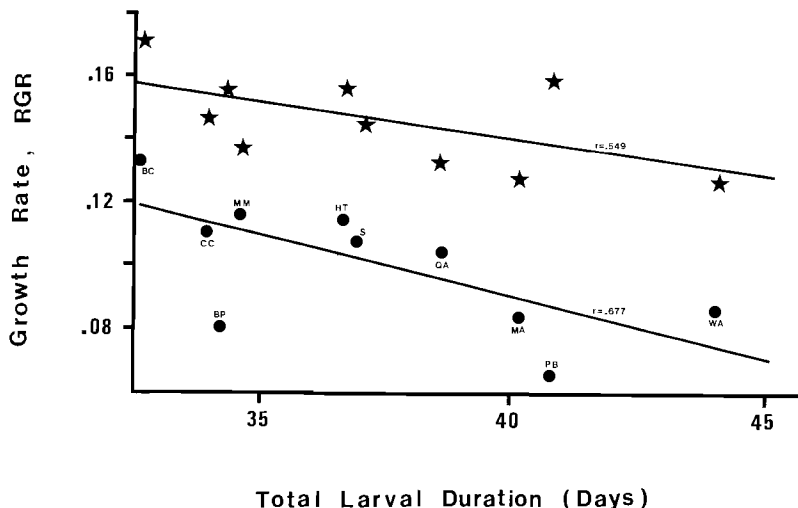


Figure 3. Relationship of total larval duration (neonate to pupa) with relative growth rate (R.G.R.s) of 4th (stars) and 5th (dots) instar *Papilio canadensis* larvae on 10 plant species (BC = black cherry, PB = paper birch, HT = hoptree, BP = balsam poplar, CC = choke cherry, S = sassafras, MM = mountain magnolia, QA = quaking aspen, WA = white ash, MA = mountain ash). Correlation coefficients are indicated for each instar.

there are specific exceptions where the rank-order is not parallel. These include, for example, the low relative growth rates of final instars on balsam poplar and paper birch.

Results of the 3-choice oviposition studies with northern Wisconsin and Upper Peninsula butterflies indicate considerable individual variation in responses (Table 3). A general overall preference is evident for balsam poplar (54% of the eggs) in these three-choice studies with smaller proportions placed on paper birch (25%) and quaking aspen (21%). This result is intriguing since balsam poplar is sparse and at the southern edge of its range in northern Wisconsin. However, Alaskan females of *P. canadensis* select balsam poplar no more frequently than quaking aspen or paper birch (Table 3) even though this may be their most common host. Sample sizes (numbers of females) and total eggs are low in number, however we can conclude that variable oviposition responses, with no strong favorites, were observed with this 3-choice study of northern hosts in spite of the fact that paper birch and quaking aspen were by far the most frequently found hosts for the Canadian populations of *P. canadensis* (McGugan 1958).

A similar 3-choice oviposition preference comparison using tuliptree, black cherry (which is an excellent host plant) and quaking aspen also shows considerable individual variation in preference (Scriber et. al., 1991). The most surprising thing is that tuliptree is selected as the favorite host (>50% of eggs) in these 3-choice situations by about half (14 of 29) of these *P. canadensis* females (Table 4), in spite of the fact that it is toxic to virtually all *P. canadensis*. Even those females not laying a majority of eggs on tuliptree nonetheless laid a substantial number of eggs on this unsuitable larval host plant species. This plant is not one that the *P. canadensis* females would normally encounter except at their southernmost distribution in

Table 3.—*Papilio canadensis* oviposition in a 3-choice area with *Populus balsamifera*, *P. tremuloides*, and *Betula papyrifera*. These trials followed the 3-day, 3-choice trials with aspen, tuliptree, and black cherry.

Identification number	Geographic Source	Percentage of egg distribution			Total eggs (n)
		Balsam poplar	Quaking aspen	Paper birch	
7038	Fairbanks, AK	7	79	14	(14)
7040	Fairbanks, AK	72	0	28	(18)
7043	Fairbanks, AK	42	42	16	(12)
7049	Fairbanks, AK	21	32	47	(19)
7052	Fairbanks, AK	13	37	50	(8)
7053	Fairbanks, AK	20	10	70	(10)
		29.2 ± 9.8	33.3 ± 11.3	37.5 ± 9.0	
7024	Chippewa Co., WI	71	29	0	(7)
7025	Chippewa Co., WI	0	100	0	(8)
7027	Taylor Co., WI	0	0	100	(10)
7028	Taylor Co., WI	100	0	0	(11)
7030	Taylor Co., WI	100	0	0	(8)
7033	Taylor Co., WI	18	32	50	(40)
7034	Taylor Co., WI	50	50	0	(16)
7035	Dickinson Co., MI	10	51	39	(41)
7081	Dickinson Co., MI	46	3	51	(33)
7082	Dickinson Co., MI	0	0	100	(6)
7083	Dickinson Co., MI	100	0	0	(5)
7084	Dickinson Co., MI	100	0	0	(9)
7055	Iron Co., MI	100	0	0	(19)
7061	Iron Co., MI	60	30	10	(20)
		53.9 ± 11.2	21.1 ± 8.0	25.0 ± 9.9	

Michigan and in central New York State (Scriber, 1975). Aspen was selected as a favorite (> 50% eggs) by only 5 of 29 females, and cherry by only 4 of 29 females.

DISCUSSION

Growth rate limitations vary with the nutritional quality of different plant species (Scriber and Feeny 1979, Scriber and Slansky 1981) and allow predictions of maximal larval growth performances on different plants that are correlated with plant water and nitrogen content. However, it is expected that various allelochemicals (eg., toxins, deterrents, growth suppressors) will alter the actual larval performance in some plants, reducing the rates or efficiencies of growth below that predicted by nutritional parameters alone (Scriber, 1984). Larval growth might also be enhanced or reduced from levels predicted by leaf nitrogen and water content in cases where physiological adaptation to specific hosts of the particular insect population is variable (Scriber 1983).

Papilio canadensis in these studies exhibits no significant correlation of larval growth rates with leaf water content for the penultimate and final instars ($r = .184$, $r = .077$, respectively) (Fig. 4), but growth rates are correlated with leaf nitrogen content (Fig. 5). In the penultimate instar, the greatest negative deviation of growth from the regression line (Fig. 5) appears to be for mountain magnolia, *Magnolia acuminata*. Since the related tuliptree is toxic and some phytochemical similarity of these two Magnoliaceae could be expected (see Scriber et. al 1991) it seems that the poor growth performance could be due to secondary phytochemicals with antibiotic

Table 4. — Individual female oviposition responses of *Papilio canadensis* in a 3-choice arena.

Mother #	Geographic Source	Tuliptree	Percent of eggs (3 day total) Black cherry	Quaking aspen	Total eggs (n)
7037	Fairbanks, AK	41.0	7.7	51.3	(39)
7038	Fairbanks, AK	58.7	19.6	21.7	(46)
7039	Fairbanks, AK	85.7	14.3	0.0	(28)
7040	Fairbanks, AK	80.5	2.4	17.1	(41)
7041	Fairbanks, AK	20.0	40.0	40.0	(10)
7043	Fairbanks, AK	32.0	16.0	52.0	(50)
7049	Fairbanks, AK	82.1	5.1	12.8	(39)
7053	Fairbanks, AK	92.3	7.0	0.0	(13)
7786	Fairbanks, AK	21.1	5.3	73.7	(19)
7788	Fairbanks, AK	53.8	23.1	23.1	(13)
7789	Fairbanks, AK	53.3	20.0	26.7	(30)
7790	Fairbanks, AK	31.6	52.6	15.8	(19)
7793	Fairbanks, AK	42.3	42.3	15.4	(26)
7795	Fairbanks, AK	34.8	45.7	19.6	(46)
7110	Nipissing, ONT	33.3	43.1	23.5	(51)
6938	Alger Co., MI	9.5	57.1	33.3	(21)
6985	Luce Co., MI	5.6	16.7	77.8	(54)
6997	Gogebic Co., MI	59.3	22.6	18.6	(113)
7046	Gogebic Co., MI	70.9	20.0	9.1	(55)
7048	Gogebic Co., MI	14.3	57.1	28.6	(14)
7781	Marquette Co., MI	52.2	21.7	26.1	(138)
7983	Bayfield Co., WI	47.1	5.8	47.1	(17)
7086	Roscommon Co., MI	54.1	0.0	45.9	(37)
7003	Chippewa Co., WI	15.9	41.3	42.9	(63)
7004	Chippewa Co., WI	15.3	4.2	80.6	(72)
7023	Chippewa Co., WI	42.5	20.0	37.5	(80)
7025	Chippewa Co., WI	100.0	0.0	0.0	(14)
7027	Taylor Co., WI	50.0	50.0	0.0	(14)
7029	Taylor Co., WI	55.1	42.9	2.0	(49)
Mean ± s.e. (n = 29)		46.7 ± 4.7	24.3 ± 3.4	29.0 ± 4.2	

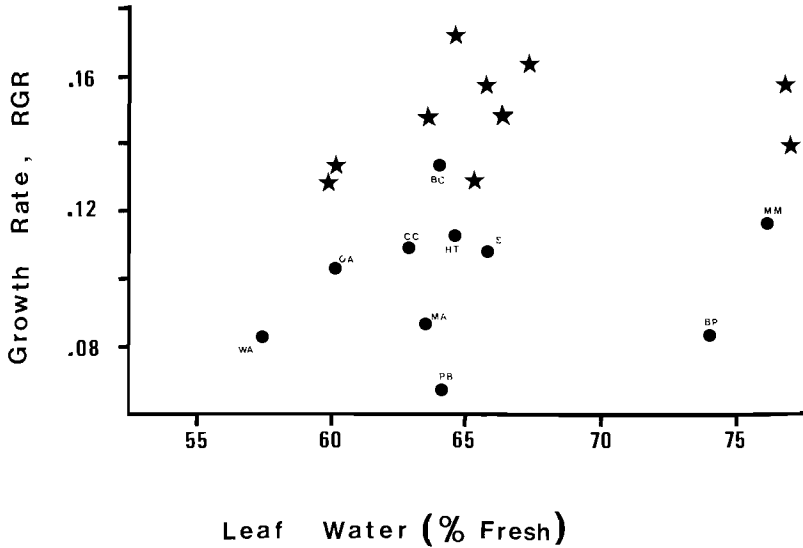


Figure 4. The relationship of leaf water content (% fresh weight) of 10 species of test plants with larval relative growth rates ($\text{mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$) of *P. canadensis* in the penultimate (4th) and final (5th) instar. Star symbols and dot symbols signify 4th and 5th instars, respectively.

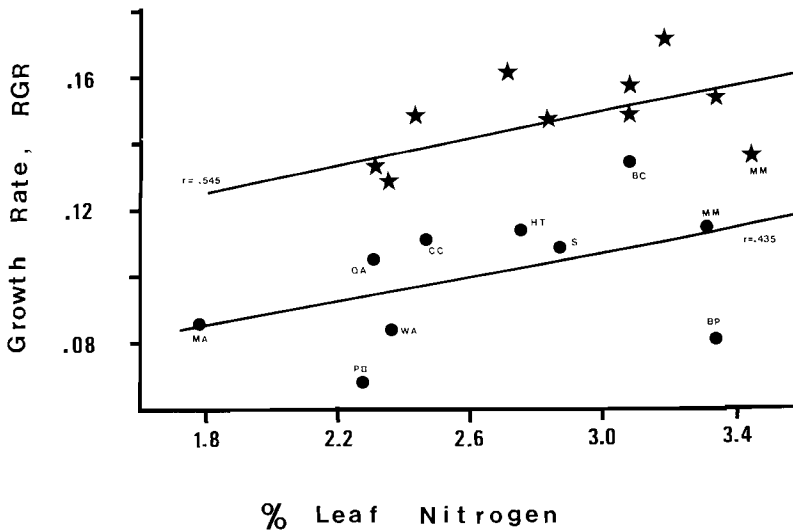


Figure 5. The relationship of total leaf nitrogen content (% dry weight) of 10 test plants with larval relative growth rates ($\text{mg}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$) of 4th and 5th instar *P. canadensis*.

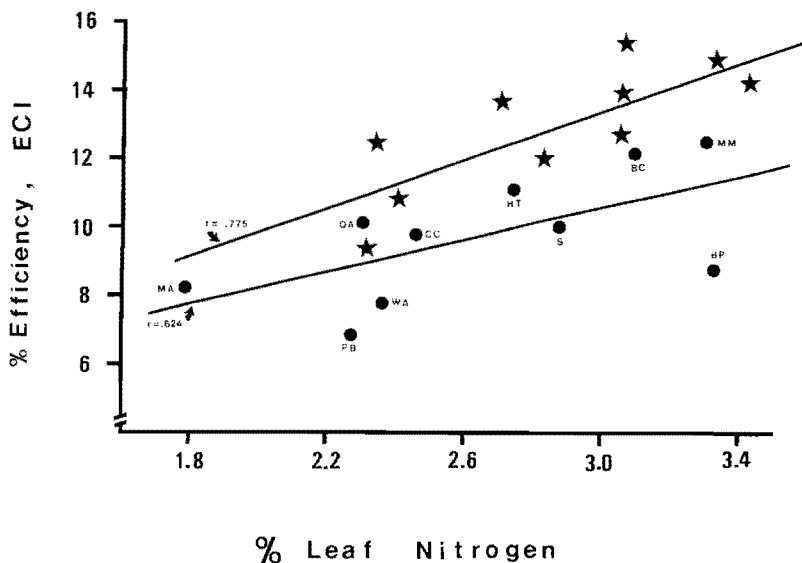


Figure 6. Efficiency of conversion of ingested plant biomass to larval tissue (ECI) on 10 hosts as a function of leaf nitrogen content for penultimate (star symbols) and final (dot symbols) instar *P. canadensis* larvae.

activity. In the final instar the greatest negative deviations from the regression based on nitrogen, are for paper birch and balsam poplar (Fig. 5). Since neither paper birch nor balsam poplar are low in leaf water content (Fig. 4, Table 2), it is likely that the deleterious effects could be caused by allelochemicals. Balsam poplar has a geographic range that is further north than quaking aspen. The populations of *P. canadensis* in this study (from Burnett, Clark, Oneida, and Sawyer counties, Wisconsin) would not have the opportunity to encounter balsam poplar except on rare occasions in very localized pockets south of its general range limits. It is speculated that such novelty may explain part of the slower growth of Wisconsin *P. canadensis* on balsam poplar in this study. The reasons for poorer than expected growth on paper birch are also unknown, but are likely to be allelochemical in nature.

To determine what might be the physiological/behavioral mechanisms that cause slower growth on mountain magnolia and balsam poplar than the empirical nutritional model (Scriber 1984) would predict, the consumption rates (RCR) and efficiencies (AD, ECD, ECI) were examined. It appears that the slow growth on mountain magnolia (*M. acuminata*) is due more to low consumption rates than to low efficiency in assimilation (AD) or conversion of plant biomass (ECD) for both penultimate and final instars (Table 2). A combination of reduced consumption rates and low efficiencies is responsible for slow growth of larvae on ash, whereas fast growth on black cherry is due to high consumption rates combined with high efficiencies (Table 2). As observed for other insects (Mattson 1980, Finke and Scriber 1988) there is a strong relationship between the efficiency of conversion of plant biomass (ECI) and the nitrogen content of the leaf tissues (Fig. 6). The lower than expected efficiencies on paper birch and balsam poplar support the hypothesis of allelochemical effects suggested in the previous paragraph.

Of the potential host plants in the Great Lakes region, *P. canadensis* larvae

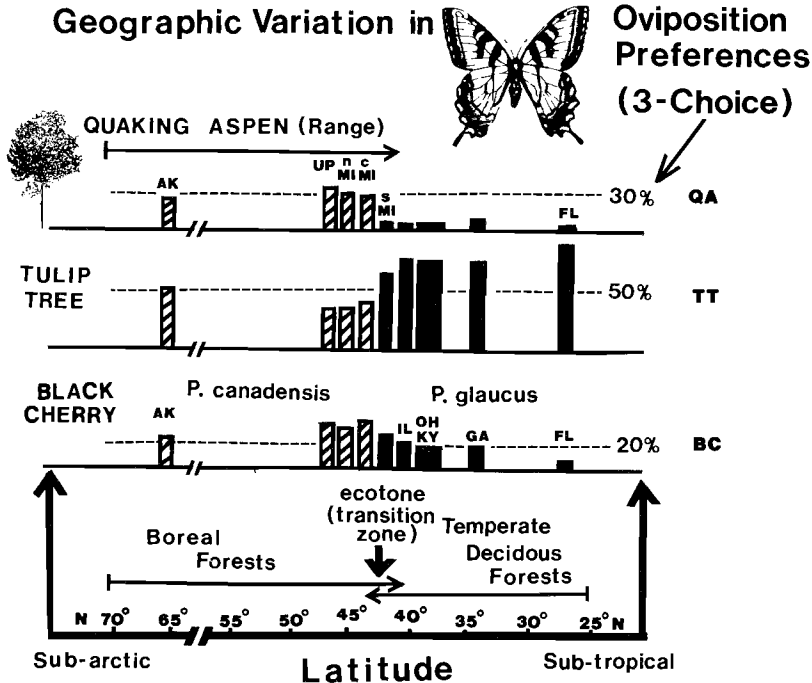


Figure 7. Relative oviposition preferences of *P. canadensis* and *P. glaucus* females from various latitudes in three-choice studies with quaking aspen (QA), tuliptree (TT) and black cherry (BC). Note the reciprocal change in relative preferences in the hybrid zone and plant ecotone between 42° and 45° N latitude (Data from Scriber et al. 1991).

obviously use each with differential success. Some are toxic but nonetheless elicit oviposition from females in lab studies (Scriber et al. 1991) and in the field (Scriber 1975). Ten of the 12 plants selected for these studies support growth to the pupal stage, however considerable differences in suitability for (and duration of) growth are observed. The phytochemical differences between host plant species included in these studies are doubtlessly significant in their effects on *P. canadensis* as has been shown with *P. glaucus* from the hybrid zone southward (Lindroth et al. 1986, 1988). At this time we remain uncertain about the allelochemical reasons for differences in larval growth performances observed.

While black cherry is the best host for rapid growth (for total duration as well as measured by R.G.R.s in the 4th and the 5th instar), it is still not the favored host for oviposition in 3-choice studies. The toxic tuliptree and the slow-growth supporting quaking aspen are equally preferred with black cherry by *P. canadensis* females in this Great Lakes ecotone (Fig. 7, and Scriber et al. 1991). A similar 3-choice study with balsam poplar, paper birch and quaking aspen reveals no strong oviposition preferences by *P. canadensis* females from northern Michigan and Wisconsin (Table 3).

These observations and the fact that at least 9 different host species have been documented for *P. canadensis* in Michigan and Wisconsin (Scriber and Ayres 1990)

suggest a "generalized" rather than "specialized" feeding classification. This may be in contrast to *P. canadensis* populations in Alaska where females appear to select host species where larval growth is fastest (Ayres and Scriber, in prep.; Scriber and Lederhouse 1992). This is in accord with the hypothesis that females in zones where total seasonal thermal units are barely sufficient to complete a generation (e.g. Alaska) will select the most nutritious plants for egg placement, whereas those in zones with sufficient thermal units to complete the generation (e.g. in the Great Lakes region) would not be under such selection. Since they would be able to complete a generation on any suitable plant, they could therefore generalize, using poor as well as good hosts (see Scriber and Lederhouse 1992 for discussion). This hypothesis is also currently being tested using *P. glaucus* at the threshold of bivoltine potential and further south, where sufficient thermal accumulations existing for 2 generations are possible on all suitable host plants.

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