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# Susceptibility of *Catalpa*, *Chilopsis*, and Hybrids to Powdery Mildew and *Catalpa* Sphinx Larvae

Richard T. Olsen<sup>1,4</sup> and Thomas G. Ranney<sup>2</sup>

Department of Horticultural Science, Mountain Horticultural Crops Research and Extension Center, North Carolina State University, Fletcher, NC 28732-9244

Charles S. Hodges<sup>3</sup>

Department of Plant Pathology, North Carolina State University, Raleigh, NC 27695-7616

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**Abstract.** A diverse collection of germplasm representing 24 taxa from *Catalpa* sect. *Catalpa* Paclt and sect. *Macrocatalpa* Grisebach, *Chilopsis* D. Don, and ×*Chitalpa* Elias & Wisura were screened for susceptibility to powdery mildew (PM) incited by *Erysiphe elevata* (Burr.) U. Braun & S. Takam and feeding by *catalpa* sphinx larvae (CSL), *Ceratonia catalpae* (Boisduval). PM screening was conducted on plants grown in a lathhouse (50% shade) in 2004 and a gravel pad (100% sun) in 2005. The PM causal organism was identified as *E. elevata* both years. Disease incidence and severity were recorded at 2-week intervals for 6 weeks and used to calculate area under the disease progress curves (AUDPC) for each year. North American *Catalpa* in sect. *Catalpa*, *Chilopsis*, and ×*Chitalpa* taxa were all moderately to highly susceptible to PM. Chinese *Catalpa* in sect. *Catalpa* and West Indian species in sect. *Macrocatalpa* were resistant to PM. Hybrids between North American and Chinese *Catalpa* in sect. *Catalpa* varied in susceptibility, indicating transmission of partial resistance to PM. No differences in survival or growth were found in a no-choice feeding study with CSL reared on taxa from *Chilopsis*, ×*Chitalpa*, or either section of *Catalpa*. Future breeding of ×*Chitalpa* can use sources of PM resistance identified in this study, but a source of resistance to CSL was not found.

The genus *Catalpa* Scop. (Bignoniaceae Juss.) is composed of 11 species in two well-defined sections, *Catalpa* and *Macrocatalpa*, differentiated by leaf morphology and seed characteristics as well as geographic distribution (Paclt, 1952). Section *Catalpa* contains six species of deciduous trees with a disjunct distribution between East Asia (four species) and eastern North America (two species). All species from this section are in cultivation except *C. tibetica* Forrest, but only the two North American species are commonly cultivated as ornamental trees. Southern catalpa, *C. bignonioides* Walt., is native to the southeastern United States

(Alabama to western Florida) and northern catalpa, *C. speciosa* (Ward. ex Barn.) Ward. ex Engelm., is native to the south-central United States. Both are cultivated as well as naturalized in many urban areas of the eastern United States (Rehder, 1940). Section *Macrocatalpa* is comprised of five species of semievergreen trees restricted to the West Indies. These species are poorly represented in cultivation, with the exception of *C. longissima* (Jacq.) Dum.-Cours. (Haitian yoke-wood), which is cultivated throughout the West Indies as an important landscape and timber species and in Florida and Hawaii for landscapes (Francis, 1990).

Desertwillow or desertcatalpa, *Chilopsis* D. Don., is a monotypic genus related to *Catalpa*. *Chilopsis linearis* (Cav.) Sweet is a small to medium-sized tree with willow-like leaves and attractive flowers in summer found in washes and arroyos in desert regions of the southwestern United States, from southern California to Texas, and south-central Mexico (Henrickson, 1985). The species and its cultivars are grown throughout its native range and adjacent regions and are valued for drought tolerance and attractive flowers (Dirr, 1998; Henrickson, 1985; Tipton, 1987).

*Catalpa* and *Chilopsis* are very similar but are differentiated by number of stamens, two in *Catalpa* vs. four in *Chilopsis*, and leaf morphology, large ovate to cordate leaves in *Catalpa* vs. linear to lanceolate leaves in *Chilopsis*. Traditional classifications have placed them in the large, pan-tropical tribe Tecomeae Endl. (Henrickson, 1985). However, this tribe was shown recently to be paraphyletic, suggesting that the tribe be divided with *Catalpa* (both sections) and *Chilopsis* forming a new tribe sister to the Oroxyloideae Gentry (Olmstead, unpublished data; Spangler and Olmstead, 1999). Intergeneric hybrids between *Chilopsis linearis* and *Catalpa bignonioides* bred by Rusanov (1964) were introduced into the United States in 1977 and formally described by Elias and Wisura (1991) as ×*Chitalpa tashkentensis*. ×*Chitalpa* has performed well in arid climates, but suffers in more humid climates from severe powdery mildew (PM) infections (Dirr, 1998) and in eastern North America from herbivory by *catalpa* sphinx moth larvae, *Ceratonia catalpae* (Lepidoptera: Sphingidae) (T.G. Ranney, personal observation).

Powdery mildews (PM) are obligate fungal parasites (Ascomycetes) characterized by epiphytic white mycelium that often cause distortions of new growth, chlorosis, necrosis, and premature leaf fall (Braun, 1987), limiting both growth and aesthetic qualities of infected plants. Seven different species of PM have been identified on *Catalpa* spp. with two host-specific to *Catalpa*: *Erysiphe catalpae* Simonyan and *E. elevata* (syn. *Microsphaera elevata* Burr.) (Ale-Agha et al., 2004; Braun, 1987; Braun et al., 2002; Farr et al., 1989). Of the two *Catalpa*-specific PMs, only *E. elevata* has been reported in North America, with *E. catalpae* currently restricted to Europe and Asia (Braun, 1987; Sinclair et al., 1987).

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<sup>1</sup>Current address: Floral and Nursery Plants Research Unit, USDA-ARS, US National Arboretum, 3501 New York Ave. NE, Washington, DC.

<sup>2</sup>Professor.

<sup>3</sup>Professor emeritus.

<sup>4</sup>To whom reprint requests should be addressed; e-mail OlsenR@usna.ars.usda.gov.

*Catalpa sphinx* moth is distributed throughout the eastern United States from New York to Florida west to Texas and Iowa overlapping with the native and naturalized range of natural host plant species *C. bignonioides* and *C. speciosa* (Baerg, 1935). Previous studies confirmed the suitability of Chinese *Catalpa* species as a food source for *Catalpa sphinx* larvae (CSL) (Baerg, 1935; Bowers, 2003). Host plant species significantly affected larval growth (fresh weight), but survival was unaffected for larvae reared on *C. bignonioides*, *C. bungei* C.A. Mey, *C. fargesii* Bureau, *C. ovata* G. Don, and *C. speciosa* (Bowers, 2003). *Ceratomia catalpae* larvae sequester catalpol, converted from catalposide and other iridoid glycosides ingested from *Catalpa* (Bowers, 2003), which serves as a defense against generalist predators (Bowers and Puttick, 1986).

Both *Catalpa* and  $\times$ *Chitalpa* are underused as ornamentals in north temperate zones, owing to a lack of diversity of available germplasm and susceptibility of the common species (*C. bignonioides* and *C. speciosa*) to pathogens and insects, particularly PM and CSL. The susceptibility of *Chilopsis* and *Catalpa* spp. in section *Macro-catalpa* to PM and CSL has not previously been reported. To establish a breeding program targeting improvement of *Catalpa* and  $\times$ *Chitalpa* hybrids, sources of resistance to both pest species are needed. Our objective was to assemble and screen a diverse collection of *Catalpa*, *Chilopsis*, and  $\times$ *Chitalpa* for 1) PM susceptibility and 2) host plant suitability for CSL.

## Materials and Methods

**Plant material.** Germplasm screened was from various botanical institutions and nurseries and accessioned at the Mountain Horticultural Crops Research and Extension Center (MHCREC), Fletcher, N.C., between 2002 and 2004, including several breeding lines from the  $\times$ *Chitalpa* breeding program at the MHCREC (Table 1). Germplasm was received as unrooted softwood or hardwood cuttings, seed, or young plants. Plants were propagated and grown under standard nursery conditions until needed for PM and CSL studies.

**Powdery mildew studies.** Two separate screening studies were conducted over successive years, 2004 and 2005. In July 2004, available taxa were potted into 11.2-L containers with a 3 pine bark:1 peat (by volume) substrate amended with 2.8 kg·m<sup>-3</sup> dolomitic limestone and 0.5 kg·m<sup>-3</sup> micronutrients (Micromax; The Scotts Co., Marysville, Ohio) and top-dressed with 35 g per container of 15N-3.9P-10.0K controlled-release fertilizer (15-9-12 Osmocote® Plus 3-4 mo. at 70 °C; The Scotts Co.). Plants were placed in a lathhouse providing 50% shade in 11 rows of  $\approx$ 20 plants on 0.75 m centers and watered as needed using drip irrigation. The experimental design was completely randomized with 19 treatments (taxa). For most taxa,  $n \geq 8$ , except *C. ovata* 'Flavescens' ( $n = 4$ ),

*Catalpa* sp. #2 ( $n = 3$ ), and *C. bungei* var. *heterophylla* ( $n = 2$ ).

*Catalpa bignonioides* stock plants were grown separately in the lathhouse and allowed to develop PM infections naturally. Beginning on 4 Aug. 2004, infected stock plants were placed in and around study plants and shaken over the study plants to release conidia every other day for 1 week (total 4 $\times$ ) to supplement natural inoculation. Powdery mildew incidence (I) and severity (S) were recorded for each replicate once every 2 weeks for a total of four observation dates. Incidence (I) represented the percentage of leaves infected per plant and severity (S) the mean percent leaf area covered with mycelium per infected leaf. After 6 weeks, when severely infected plants began abscising leaves, the study was ended.

Selected taxa from the 2004 study and several additional taxa were screened in 2005 for PM. On 23 May, plants were potted into 26.6-L containers using the substrate used in 2004 and fertilized with the same controlled-release fertilizer at 64 g per container. As a result of their size, plants were removed from the lathhouse and grown on a gravel pad in full sun and watered as needed using drip irrigation. The experimental design was completely randomized with 17 treatments (taxa). For most taxa,  $n \geq 6$ , except *C. punctata* ( $n = 5$ ), *C. ovata* 'Flavescens' ( $n = 4$ ), and *Catalpa* sp. #2 and *C. bungei* var. *heterophylla* ( $n = 2$ ). Plants were allowed to develop infections from natural inocula; no supplemental inoculation was provided. Measurements of I and S were made after the first signs of PM were noted on *C. bignonioides* plants (25 July) and thereafter every 2 weeks for 6 weeks ending on 5 Sept. for a total of four observation dates.

Cleistothecia (ascomata) were collected in 2004 and 2005 from infected senescent leaves in late fall after temperatures decreased and mildew ratings were concluded. Cleistothecia were mounted in 0.01% cotton blue-lactophenol (v/v) on glass slides and viewed under a compound light microscope (Nikon Eclipse E400; Nikon Instruments, Melville, NY) at  $\times$ 400 magnification. Pathogen identification was based on size of cleistothecia, length and branching characteristics of cleistothecial appendages, number of asci per cleistothecium, size and shape of ascospores, and number of ascospores per ascus. Voucher specimens were made and placed in the mycological herbarium, Department of Plant Pathology, NCSU.

Area under the disease progress curves (AUDPC) were constructed for each year using the formula of Shaner and Finney (1977) with modification:

$$\text{AUDPC} = \sum_{i=1}^n [(Y_{i+1} + Y_i)/2][X_{i+1} - X_i]$$

where  $Y_i = I \times S$  at the  $i$ th observation,  $X_i =$  time (d) at the  $i$ th observation, and  $n =$  total number of observations. Multiplying I by S results in a relative disease intensity rating for

a given plant at a given observation date (Seem, 1984). Then, AUDPC represents the cumulative disease intensity for a given plant over the length of the study (Jeger and Viljanen-Rollinson, 2001). Data for each year were analyzed separately. Differences between taxa were compared using analysis of variance (PROC GLM; SAS version 8.02; SAS Institute, Cary, N.C.) and means separated using Fisher protected least significant difference (LSD) at  $\alpha = 0.05$ .

***Catalpa sphinx* moth larvae screening.** A no-choice feeding study, with the addition of *C. linearis* 'Regal', was conducted in Summer 2005. On 22 June, fourth and fifth instars were collected from infested trees at the University of Georgia Horticulture Farm, Athens, Ga. Larvae were transported to the greenhouses at MHCREC and allowed to pupate in plastic boxes filled with sand and covered with perforated plastic. On 21 July, the first adult moth emerged, at which time the containers were transferred along with two stock plants of *C. bignonioides* to a mesh cage (2  $\times$  2  $\times$  2 m) located in a lathhouse (50% shade). Adults emerged daily with the first egg masses laid on 23 July. Eggs were collected from the walls of the flight cage and leaves and placed in Petri dishes (15 cm) and then incubated in an insect-rearing room. Conditions within the rearing room were maintained at 16 hours/d (15  $\mu$ mol·s<sup>-1</sup>·m<sup>-2</sup> PAR, fluorescent lights), 25 °C, and 60% relative humidity. Waxed paper cups (0.9 L) covered with cheesecloth served as individual rearing chambers with one cup per single plant replicate. Cups were located randomly on shelves within the chamber. Recently expanded leaves or small shoots from each taxon were placed in water picks and inserted into cups. Leaves and water were exchanged daily or as needed to maintain adequate leaf turgor and plant material for larvae.

The study began on 28 July when five first instar larvae (1-d-old) were placed in each cup. The study ended at 15 d when surviving larvae reached the fifth instar and feeding was negligible. Percent survival data on each taxon was recorded. For surviving larvae, final mass and headcapsule width (in millimeters) were recorded. Growth of the headcapsule was used to estimate instar stage (Baerg, 1935). Percentage survival data were arcsin-transformed before statistical analysis. The experiment was a completely randomized design with nine taxa (treatments) and eight replicates (except *C. punctata* and *C. longissima* in which  $n = 6$  and 5, respectively) and five subsamples (larvae) per replicate. Data were analyzed using the general linear model procedure of SAS (PROC GLM; SAS version 8.02; SAS Institute).

## Results and Discussion

Severe PM developed in the lathhouse in 2004 with moderate but similar pattern of infections developing in 2005 (Table 2). Infections generally began on recently expanded leaves rather than immature growth. Levels of natural inoculum in the

Table 1. Germplasm within the tribe Tecomeae Endl. (Bignoniaceae Juss.) screened for susceptibility to powdery mildew and catalpa sphinx larvae.

Taxa <sup>z</sup>	Source of plant material	Accession no. <sup>y</sup>	Comments <sup>x</sup>
<i>Catalpa</i> Section <i>Catalpa</i> Paclt <i>Catalpa bignonioides</i> Walt.	MHCREC, Fletcher, NC	NA	Southern catalpa; cuttings of a naturalized plant along the French Broad River, Asheville, N.C.; native to SE U.S. from Ala. to W. Fla.
<i>bignonioides</i> 'Aurea'	JCR Arboretum, Raleigh, N.C.	960617	Yellow new growth, maturing to green, introduced before 1871
<i>bignonioides</i> 'Koehnei'	Sir Harold Hillier Gard., Hampshire, UK	1976.9778	New growth broadly margined with yellow, c.1903. Syn. 'Aureo-marginata'
<i>bignonioides</i> 'Nana'	Sir Harold Hillier Gard.	1976.9602	Umbrella catalpa; densely branched, dwarf cultivar of French
<i>C. bungei</i> var. <i>heterophylla</i> C.A. Mey.	Brooklyn Bot. Gard., Brooklyn, N.Y.	340008	Lobed Manchurian catalpa; unknown provenance; form grows with type species in the wild, c. 1907. N. China
<i>C. xerubescens</i> Carr. 'J.C. Teas'	Cornell Plantations, Ithaca, N.Y.	97-072	Teas' hybrid catalpa ( <i>C. ovata</i> × <i>bignonioides</i> ); spontaneous hybrid occurring before 1869 in France and 1874 in the US
<i>xerubescens</i> 'Purpurea'	MHCREC	1996-139	Purple-leaf catalpa; new growth dark purple, fades to green, discovered in cultivation c. 1886 in US
<i>C. fargesii</i> f. <i>duclouxii</i> (Dode) Gilm.	Scott Arboretum, Swarthmore, Pa.	93-661-A	Ducloux's catalpa; smooth-leaf form with deeper pink flowers than type species, c.1908. W. China
<i>C. xgalleana</i> Dode	Arnold Arboretum, Jamaica Plain, Mass.	925-42B	Galle's hybrid catalpa ( <i>C. ovata</i> × <i>speciosa</i> ); spontaneous cross in France c. 1907; this clone is from artificial crosses made at the Arnold Arboretum in 1940 by Karl Sax
<i>C. ovata</i> G. Don	Arnold Arboretum	516-87B	Chinese catalpa; received as wild collected seed from Yunnan Inst. Trop. Bot., China as <i>C. fargesii</i> f. <i>duclouxii</i>
<i>ovata</i> 'Flavescens'	Sir Harold Hillier Gard.	1992-1036	Pale yellow Chinese catalpa; smaller, more yellow flowers than the species, c.1863 in Europe
<i>C. speciosa</i> (Ward. ex Barn.) Ward. ex Engelm.	Arnold Arboretum	1245-79-B	Northern catalpa; cuttings of a wild tree from Mo., U.S. Native to south-central US
<i>C. sp. #1</i>	Morton Arboretum, Lisle, Ill.	498-80 03-79	Cuttings of a plant raised from seed received from the Bot. Gard. at Uzbek Acad. of Sciences, Tashkent, Uzbekistan as <i>C. bungei</i> C.A. Mey but appears to be of hybrid origin
<i>sp. #2</i>	Morton Arboretum	498-80 38-39	Cuttings from sister seedling to <i>C. sp. #1</i> ; also appears to be of hybrid origin
<i>sp. #3</i>	Heritage Seedlings, Salem, Ore.	NA	Seedlings, originally from Lawyer Nursery, Plains, Mont.; labeled as <i>C. bungei</i> , but appears to be <i>C. ovata</i>
<i>Catalpa</i> Section <i>Macrocatalpa</i> Grisebach <i>Catalpa longissima</i> (Jacq.) Dum.-Cours.	Fairchild Tropical Bot. Gard., Coral Gables, Fla.	X.1-21B	Haitian yokewood; seedlings of a wild tree; native to Hispaniola, but cultivated in Caribbean, S. Fla., and Hawaii
<i>C. punctata</i> Griseb.	Fairchild Tropical Bot Gard.	66396C	Cuban catalpa; seedlings of a tree in the Bahamas; native to Cuba, rare in cultivation
<i>Chilopsis</i> D. Don <i>Chilopsis linearis</i> (Cav.) Sweet 'Bubba'	SFA Mast Arboretum, Nacogdoches, Texas	NA	Bubba desertwillow; popular cultivar with deep purple flowers, introduced by Paul Cox of San Antonio Bot. Gard., Texas
<i>C. linearis</i> 'Regal'	Native Texas Nursery, Austin, Texas	NA	Regal desertwillow; lavender flower with burgundy lower lip; introduced by Los Lunas Plant Material Center, N.M. in 1989
× <i>Chitalpa</i> ( <i>Chilopsis linearis</i> × <i>Catalpa bignonioides</i> ) × <i>Chitalpa tashkentensis</i> Elias & Wis. 'Morning Cloud'	Forestfarm Nursery, Williams, Ore.	2005-311	Morning Cloud chitalpa; white-flowered cultivar named in 1991; one of two clones introduced from Uzbekistan in 1977
× <i>C. tashkentensis</i> 'Pink Dawn' 2x	MHCREC	2005-312	Diploid Pink Dawn chitalpa; pink-flowered cultivar named in 1991; one of two clones introduced from Uzbekistan in 1977
× <i>C. tashkentensis</i> 'Pink Dawn' 4x	MHCREC	NA	Oryzalin-induced tetraploid form of 'Pink Dawn' chitalpa
× <i>C. tashkentensis</i> F <sub>2</sub> 4x seedlings	MHCREC	NA	Seedlings from selfed tetraploid 'Pink Dawn' chitalpa
× <i>C. tashkentensis</i> MHCREC#1	MHCREC	H2004-003	Diploid seedling from <i>Chilopsis</i> 'Bubba' × 24-2-1 'Pink Dawn' (2x + 4x) cytochimera

<sup>z</sup>Author of scientific name follows the first listing of each taxon above the rank of cultivar unless the taxon is solely represented by a cultivar(s).<sup>y</sup>Accession number from the original source, if available; NA, no accession number.<sup>x</sup>Accession information, including taxa description, origin, and date of introduction or discovery.

Table 2. Mean area under the disease progress curve for powdery mildew infection among a diverse collection of taxa within the tribe Tecomeae Endl. (Bignoniaceae Juss.) grown in containers under nursery conditions during 2004 and 2005.

Taxa		AUDPC <sup>z</sup>	
		2004 <sup>y</sup>	2005 <sup>x</sup>
× <i>Chitalpa tashkentensis</i>	MHREC#1	2416 a <sup>w</sup>	— <sup>v</sup>
	Pink Dawn 4x	2300 a	1167 c
	Pink Dawn 2x	2290 a	2154 a
	F <sub>2</sub> 4x seedlings	2268 a	—
	Morning Cloud	1300 b	1655 b
<i>Catalpa bignonioides</i>	Nana	1270 b	—
<i>C. speciosa</i>		1134 b	—
<i>C. xerubescens</i>	J.C. Teas	914 c	1261 c
<i>C. bignonioides</i>		694 d	172 d
<i>C. bignonioides</i>	Koehnei	637 d	—
<i>C. sp.</i>	#2	622 d	90 d
<i>C. bignonioides</i>	Aurea	273 e	—
<i>Chilopsis linearis</i>	Bubba	—	48 d
<i>C. xerubescens</i>	Purpurea	24 f	33 d
<i>C. sp.</i>	#1	15 f	0
<i>C. xgalleana</i>		4 f	1 d
<i>C. sp.</i>	#3	—	0
<i>C. bungei</i>	var. <i>heterophylla</i>	0	0
<i>C. fargesii</i>	var. <i>duclouxii</i>	—	0
<i>C. ovata</i>		0	0
<i>C. ovata</i>	Flavescens	0	0
<i>C. longissima</i>		0	0
<i>C. punctata</i>		—	0

<sup>z</sup>Area under the disease progress curve (AUDPC) calculated as the product of disease incidence (% leaves affected) and severity (% leaf area affected).

<sup>y</sup>Plants grown under 50% shade with drip irrigation. n ≥ 8 except *C. ovata* 'Flavescens' (n = 4), *C. sp.* #2 (n = 3), and *C. bungei* var. *heterophylla* (n = 2).

<sup>x</sup>Plants grown in full sun with drip irrigation. n ≥ 6 except *C. punctata* (n = 5), *C. ovata* 'Flavescens' (n = 4), *C. sp.* #2 (n = 3), and *C. bungei* var. *heterophylla* (n = 2).

<sup>w</sup>Means within a year followed by the same letter are not significantly different based on Fisher's LSD<sub>0.05</sub>.

<sup>v</sup>Dropped from study in 2005 or not available in 2004.

proximity of MHCREC were assumed to be high with epiphytic events observed in the years before 2004 on ×*Chitalpa tashkentensis* 'Pink Dawn' growing at MHCREC (personal observation). White superficial mycelium on the leaf surface was well developed and heavy cleistothecial development in the fall of 2004 facilitated identification of the causal organism. Length and branching of cleistothecial appendages are key taxonomic characters for distinguishing *Erysiphe* spp. (Ale-Agha et al., 2004; Braun, 1987). Cleistothecial appendages were hyaline, 4 to 7× longer than the width of the cleistothecial body and dichotomously branched at the terminus, characteristic of *Erysiphe elevata*. *Erysiphe catalpae* has nonbranched appendages, and *E. penicillata* [syn. *Microsphaera penicillata* (Wallr.:Fr.) Lév.], a broadly adapted PM in North America, has branched appendages 1 to 1.5× as long as the width of the cleistothecial body (Braun, 1987). In North America, *E. elevata* (including synonyms *Microsphaera vaccinii* auct. p. p. and *M. alnii* var. *vaccinii* auct. p. p.) is the most commonly reported PM on *Catalpa* spp. (Braun, 1987; Sinclair et al., 1987), but our collection and positive identification was the first for North Carolina. In Europe, *E. catalpae* is the common *Catalpa*-specific PM (Ale-Agha et al., 2004; Braun, 1987). However, *E. elevata* was recently reported in Hungary (Vajna et al., 2004) and is currently spreading in Europe (Ale-Agha et al., 2004; Cook et al., 2004).

There were significant differences among taxa in susceptibility to PM as measured by AUDPC values in 2004 (F value = 183.4, *P* < 0.0001) and 2005 (F value = 51.6, *P* < 0.0001). Taxa with no PM infection (0 AUDPC) were not used in determining differences among means using Fisher protected LSD. The natural host species for *E. elevata*, N. American *C. bignonioides* and *C. speciosa*, had intermediate levels of PM infection in 2004. All three cultivars of *C. bignonioides* ('Aurea', 'Koehnei', and 'Nana') likewise were susceptible, although 'Nana' was more susceptible than the other cultivars and type species (Table 2). All of these were dropped from the 2005 study, except *C. bignonioides*, that served as a susceptible control both years.

The Chinese species *C. bungei* var. *heterophylla*, *C. ovata*, and *C. ovata* 'Flavescens' were resistant to *E. elevata* in both study years. *Catalpa fargesii* var. *duclouxii* was not available in 2004 but was resistant during 2005. These taxa appear to be useful in breeding for PM resistance. The behavior of *C. sp.* #1, #2, and #3, received as *C. bungei*, is of special note. *Catalpa bungei* is confused in the nursery trade and herbaria with *C. bignonioides* 'Nana' and *C. ovata* (Bean, 1936; Dirr, 1998; Paclt, 1952). *Catalpa sp.* #1 and #2 were received from Morton Arboretum, Lisle, Ill., as unrooted cuttings from plants grown from seed received as *C. bungei* from the Uzbek Academy of Sciences Botanical Garden, Tashkent, Uzbekistan (Table 1).

These plants do not fit the description of *C. bungei* by Paclt (1952) nor Bean (1936), in that leaves are not glabrous, inflorescences are not corymb-like, and flowers are not rose-colored. *Catalpa* and *Chilopsis* are self-incompatible (Petersen et al., 1982; Stephenson and Thomas, 1977); therefore, trueness-to-type may be questioned in seed of cultivated origin. These plants appear to be hybrids with *C. bignonioides*, although this cross has not been reported previously. In terms of PM susceptibility, they responded similarly to cultivars of *C. xerubescens* (*C. ovata* × *C. bignonioides*) with moderate to low levels of susceptibility in both 2004 and 2005 (Table 2). *Catalpa sp.* #3 represented nursery collected seed and was identical to *C. ovata* in foliage and flower. It was available only for 2005, and in that year was resistant to *E. elevata*, as were the other taxa of *C. ovata* (Table 2). In our study, *C. bungei* var. *heterophylla* from the Brooklyn Botanic Garden was the only *C. bungei* taxon that matched its taxonomic description: leaves were dark green and glabrous and differed from the type species only in its more deeply lobed leaves (Paclt, 1952). Although we only had two plants, this taxon remained free of PM infection both years.

Hybrids between Chinese *C. ovata* and N. American *C. bignonioides* (*C. xerubescens*) and *C. speciosa* (×*galleana*) exhibited a broad range of susceptibility to *E. elevata*. Of the hybrids, *C. xerubescens* 'J.C. Teas' was most susceptible in both 2004 and 2005 (AUDPC of 914 and 1261, respectively) followed by *C. xerubescens* 'Purpurea' (24 and 33, respectively) and *C. xgalleana* (4 and 1, respectively). Our clone of *C. xerubescens* 'J.C. Teas' resembles the *C. bignonioides* parent, whereas *C. xerubescens* 'Purpurea' resembles the *C. ovata* parent. In the United States, *C. xerubescens* was first documented by Sargent (1889) who reported the existence of hybrid seedlings sent to the Arnold Arboretum by a Mr. J. C. Teas of Carthage, Ind. The origin of the cultivar 'J.C. Teas' is unknown but may represent one of the original F<sub>1</sub> hybrids sent to the Arnold Arboretum or an F<sub>2</sub> segregate derived from the original hybrids. Segregates were known to exist (Jones and Filley, 1920; Paclt, 1952; Sargent, 1889) and the greater susceptibility of 'J.C. Teas' to PM infection may reflect segregation toward susceptibility of *C. bignonioides* to *E. elevata*, and for *C. xerubescens* 'Purpurea' segregation toward resistance in *C. ovata* (Table 2). *Catalpa xgalleana* had extremely low levels of PM infection in both years with only a few spots noted on the new growth and no secondary infection or spread (Table 2). Our clone of Galle's hybrid *catalpa* is one of the original F<sub>1</sub> hybrid seedlings bred by Karl Sax at the Arnold Arboretum in 1940 (Table 1). Morphologically, the hybrid is intermediate between *C. ovata* and *C. speciosa* but has the largest leaves of the genus (personal observation). The lack of complete resistance in *C. xgalleana*, a known F<sub>1</sub>, and the range of susceptibilities in *C. xerubescens* clones

suggests inheritance of PM resistance in *Catalpa* is polygenic or quantitative in nature.

Evergreen species of sect. *Macrocatappa*, *C. longissima*, and *C. punctata* were resistant to PM infection by *E. elevata*. Section *Macrocatappa* is restricted to the New World with five poorly understood species occurring throughout the West Indies (Paclt, 1952). Little cultural information existed for these taxa with the exception of *C. longissima*, an important agro-forest tree species in Haiti. In seedling nurseries, leaf spots and anthracnose have been reported (Francis, 1990), but reports of PM infections on this species or other West Indian species was lacking in the literature.

Although *Chilopsis* taxa were not available for the 2004 study, in 2005, PM infections developed late on *C. linearis* 'Bubba' grown in full sun. Thus, the low AUDPC values recorded for this taxon (Table 2). Our limited data suggest that some *Chilopsis* taxa are not resistant to PM infection by *E. elevata*, but the degree of susceptibility needs further investigation.

*×Chitalpa* cultivars were among the most susceptible taxa in both 2004 and 2005. Infection and spread of mycelia were rapid as noted by the high AUDPC values for *×Chitalpa*'s in both years (Table 2). Powdery mildew infections on *×Chitalpa* have been observed previously in Georgia (Dirr, 1998), Arkansas (J. Lindstrom, personal communication), and North Carolina (T. Ranney, personal observation), but the causal organism was not identified. In both years, *×Chitalpa* 'Pink Dawn' was more susceptible than 'Morning Cloud' (Table 2). The induced allotetraploid 'Pink Dawn' was as susceptible to PM infection as the diploid 'Pink Dawn' in 2004, but in 2005 had significantly less PM. Also, progeny derived from allotetraploid 'Pink Dawn' (MHREC #1 and F<sub>2</sub> 4x seedlings) were highly susceptible to PM (Table 2). The progeny were uniform in appearance and susceptibility, which suggests that these allopolyploids have fixed heterozygosity (strong disomic pairing) resulting in little intergenomic recombination and segregation.

There were no significant differences for CSL survival (F value = 1.74, *P* = 0.113), final weight (F value = 2.09, *P* = 0.173), or

head carapace width (F value = 0.65, *P* = 0.723) in the no-choice feeding study (Table 3). In a no-choice feeding study using deciduous members of sect. *Catalpa*, Bowers (2003) found a significant effect of host plant on larval growth, but no differences in larval survival, although survivorship ranged from 47% for *C. ovata* to 70% for *C. bignonioides*. Bowers (2003) concluded that all deciduous species of *Catalpa* are suitable host plant species for *Ceratonia catalpae* larvae. We included deciduous representatives of sect. *Catalpa* and evergreens from sect. *Macrocatappa*, *Chilopsis*, and *×Chitalpa* in our no-choice feeding study. Survival of larvae reared on various taxa ranged from 27.3% for *×Chitalpa* 'Pink Dawn' to 84.1% for *C. longissima* (Table 3). Final weight and headcapsule width varied less among taxa than survival (Table 3). Headcapsule width of mature larvae ranged from 3.4 to 4.1 mm. Baerg (1935) reported that *C. catalpae* headcapsule width for fourth and fifth instars typically average 2.20 mm and 4.35 mm, respectively. Although head carapace width of surviving larvae in our study was slightly less than that reported for fifth instars by Baerg (1935), the majority of larvae pupated on completion of the study (data not shown), which suggests that they were indeed fifth instar larvae. North American *C. bignonioides* and *C. speciosa*, host plants that have coevolved with *Ceratonia catalpae*, were expected to be suitable hosts, as was Chinese *Catalpa* species in sect. *Catalpa* (Baerg, 1935; Bowers, 2003). This is the first report on suitability of taxa from *Catalpa* sect. *Macrocatappa*, *Chilopsis*, and *×Chitalpa* to act as host plants for CSL. The coriaceous leaves of *Catalpa* spp. in sect. *Macrocatappa* are known to contain calcium oxalate crystals (Elias and Newcombe, 1979) but were not detrimental to larval survival and growth. Other sources of resistance to CSL may lie in manipulation of iridoid glycoside content in *Catalpa* spp., particularly catalposide, which is thought to act as a larval feeding-stimulant (Nayar and Fraenkel, 1963) and may play a role in acceptance as a host for oviposition.

In conclusion, North American *Catalpa*-specific *E. elevata* was identified as the

causal organism of PM on study plants of *Catalpa* sect. *Catalpa* and *×Chitalpa*. Cultivars and hybrids derived from *×Chitalpa tashkentensis* were especially susceptible. Taxa of Chinese *Catalpa* in sect. *Catalpa* and West Indian evergreen species in sect. *Macrocatappa* were resistant. Existing hybrids between susceptible and resistant species (*C. ×erubescens* and *C. ×galleana*) demonstrated transmission of partial resistance to PM. *Catalpa* species from sect. *Macrocatappa* will be an alternative source of resistance for introgression of PM resistance into novel hybrids of *Catalpa* and *×Chitalpa*. Also, *C. linearis* was susceptible to PM infection by *E. elevata*; thus, its value to breeding programs will lie in introducing novel flower color, drought tolerance, refined foliage, and reduced height to new *×Chitalpa* cultivars. Unfortunately, no immediate source of resistance to CSL was found in existing germplasm, indicating that whereas *Ceratonia catalpae* is monophagous on *Catalpa* in the eastern United States, its sister genus *Chilopsis* in southwestern United States is also a suitable host.

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Table 3. Survival and final growth measurements for *Ceratonia catalpae* larvae on a known host (*Catalpa bignonioides*) and nonhost members of the Tecomeae tribe (Bignoniaceae) in a 15-d no-choice feeding study.

Taxa <sup>a</sup>	Larvae		
	Survival (%) <sup>b</sup>	Final wt (g) <sup>c</sup>	Head width (mm) <sup>d</sup>
<i>C. bignonioides</i>	59.5	1.4	3.7
<i>C. longissima</i>	84.1	2.0	4.1
<i>C. ovata</i>	47.5	2.2	4.0
<i>C. punctata</i>	70.7	1.5	3.9
<i>Chilopsis linearis</i> Bubba	70.7	1.6	3.6
<i>Chilopsis linearis</i> Regal	78.1	1.1	3.8
<i>×Chitalpa tashkentensis</i> Morning Cloud	45.6	1.7	3.9
	Pink Dawn 2x	27.3	1.3
	Pink Dawn 4x	44.0	2.5

<sup>a</sup>n = 8 except *C. punctata* (n = 6) and *C. longissima* (n = 5).

<sup>b</sup>Began with five larvae per replicate. Arcsin transformed for data analysis, untransformed data presented. Not significant (F = 1.74, *P* = 0.113).

<sup>c</sup>Final weight measured on d 15 before pupation. Not significant (F = 2.09, *P* = 0.173).

<sup>d</sup>Width measured across head capsule at day 15 (fifth instars ≈4.0 mm). Not significant (F = 0.65, *P* = 0.723).

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