Host Range Determination of *Puccinia jaceae* from Yellow Starthistle

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ABSTRACT

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Six rust fungus acquisitions from yellow starthistle (YST) were evaluated for biological control of YST in North America. Each acquisition (= field isolate) was identified as *Puccinia jaceae* on the basis of urediniospore morphology and host plant. All isolates caused limited infection of 12 plant species in the genera *Carthamus*, *Centaurea*, *Cirsium*, and *Senecio* under containment greenhouse conditions. Safflower inoculated with *P. jaceae* had only 5% as many pustules per square centimeter of leaf tissue as plants inoculated with *P. carthami*, the cause of safflower rust. Amounts of disease were much less on the other nontarget suscepts than on YST controls, except *Centaurea cyanus*, which was very susceptible. *P. jaceae* from YST is considered a good candidate for biological control of YST because of the limited infection occurring on a few nontarget species under conditions very favorable for infection of the intended target species.

Additional keywords: biological weed control, natural enemies, plant pathogen, Uredinales

Yellow starthistle (YST), *Centaurea solstitialis* L., is an introduced winter annual displacing valuable grazing lands, particularly in the western United States. Presently, large infestations occur in California, Oregon, and Washington. It is estimated to infest 3,085,000 hectares in 52 of the 58 counties in California (9). Yellow starthistle seems to be spreading and has potential to occupy all the semiarid to subhumid rangeland in the western United States because of its ecological plasticity. There is speculation that it also may become a problem in the eastern United States (9).

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The plant is considered weedy because of its low forage value. It is allelopathic and poisonous to animals, factors that enhance its competitiveness in pastures and ranges (8). Chemical or cultural control is not practical because infestations cover large areas and monetary returns from range and pasture agriculture are low. For these reasons, host-specific pathogens and predators from the geographic origin of YST are being evaluated for use in classical biological control. Stress from several such host-specific natural enemies that become part of the ecosystem is expected to reduce competitiveness of the target species and result in lower weed density.

Protocols for evaluation of exotic (foreign) plant pathogens for biological control of weeds have been described (2). The main objectives in such evaluations are to quantify virulence and determine specificity of the pathogen. Pathogens for biological weed control must not threaten plants of economical or ecological importance in North America. This is determined by inoculating nontarget plant species under controlled greenhouse conditions. The centrifugal phylogenetic method described by Wapshere (18) is used as a guide to identify related plant species for the host range determination, and it provides a framework for interpretation of results. Species of economic or ecologic importance in North America not closely related to the target also are tested.

Fungi in the Uredinales have been regarded as good candidates for classical biocontrol of weeds because they are host-specific, aggressive, and very mobile under favorable conditions. *Puccinia chondrillina* Bubak & Syd. has been used successfully for biological control of rush skeletonweed (*Chondrilla juncea* L.) in Australia (3) and the United States (1,4,17).

Surveys for YST pathogens have been

made since 1978 in Eurasia, where the plant is native. Of the YST pathogens received at the Foreign Disease-Weed Science Research Unit (FDWSRU) through 1986, 86% were rust fungi. Selected individual acquisitions (= field isolates) of rust fungi from Greece, Italy, Turkey, the Union of Soviet Socialist Republics, and Yugoslavia were identified and evaluated. *P. centaureae* DC., *P. jaceae* Otth., and *P. ourmiahensis* Viennot-Bourgin occur on YST in

Table 1. Reaction of selected plant species to *Puccinia jaceae* isolated from *Centaurea solstitialis*[a]

Plants inoculated	Source of seed[b]	Infection[c] (+/−)	Notes[d]
Amaryllidaceae			
Allium cepa L., onion			
Yellow Bermuda	B (5266-2)	−	A
Chenopodiaceae			
Beta vulgaris L., beet			
Detroit Dark Red	B (6192-9)	−	A
Compositae			
Ageratum houstonianum Mill.			Tribe Eupatorieae
Blue Mink	B (4355)	−	O
Spindrift Hybrid	B (2067)	−	O
Calendula officinalis L., pot marigold	B (4055)	−	Tribe Calenduleae, O
Callistephus chinensis (L.) Nees, China aster			Tribe Astereae
American Beauty	B (4033)	−	O
Dwarf Border	B (3256)	−	O
Carduus thoermeri Weinm., musk thistle	FDWSR	−	Tribe Cardueae, I, W
Carthamus tinctorius L., safflower			Tribe Cardueae
CH 65	CS	+	A
CH 353	CS	+	A
C 44	CS	+	A
CARMEX	CS	+	A
S-400	ST	+	A
S-541	ST	+	A
CW 74	CWS	+	A
CW 4440	CWS	+	A
Pacific 1	BCWLD	+	Old cultivar, very susceptible to *P. carthami*
UC 41	BCWLD	+	Old cultivar, less susceptible to *P. carthami*
Centaurea species			Tribe Cardueae
C. americana Nutt., basket flower	DBS	+	N
C. calcitrapa L., purple starthistle	CDFA	+	I, W (2)
C. cyanus L., cornflower	B (4073), FDWSR	+	I, O/W (2)
C. diffusa Lam., diffuse knapweed	CDFA, UBC, UH, WSU	+	I, W (5)
C. jacea L., brown knapweed	WSU	−	I
C. macrocephala Puschk. ex Willd., lemon fluff	WSU	−	I
C. maculosa Lam., spotted knapweed	CDFA, UBC, UH, WSU	+	I, O/W (6)
C. melitensis L., Napa thistle	CDFA	−	I
C. moschata L. (=*Amberboa moschata*), sweet sultan	T & M	+	I, O
C. nigrescens Willd., short-fringed knapweed	WSU	−	I
C. paphlagonica (Bournm.) Wagenitz	MC	−	Balkin Peninsula
C. pratensis Thuill., meadow knapweed	WSU	−	I
C. repens L. (=*Acroptilon repens*), Russian knapweed	CDFA, UBC, UH, WSU	−	I, W (3)
C. rothrockii Greenm., basket flower	SwNS, UCB	−	N (2)
C. solstitialis L., yellow starthistle	CDFA, UI, UH, WSU	+	I (14)
C. virgata Lam. var. *squarrosa* (Willd.) Boiss.	CDFA	+	I
Chrysanthemum carinatum Schousb., tricolor chrysanthemum			Tribe Anthemideae
Korean	B (4613)	−	O
Rainbow	B (4349)	−	O

(*continued on next page*)

[a]Taxonomic organization from: Bailey, L. H., and Bailey, E. Z. 1976. Hortus 3rd. Macmillan Publ. Co., Inc., NY. 1290 pp.

[b]Numbers in parentheses represent catalog numbers. A&M = Texas A&M University, College Station (R. A. Frederiksen); ARA = Artichoke Research Association, Salinas, CA (N. DeVos); B = W. Atlee Burpee Co., Warminster, PA; BCWL = ARS-Biological Control Weeds Laboratory, Albany, CA (S. S. Rosenthal); BCWLD = Biological Control Weeds Laboratory, Davis, CA (J. M. Klisiewicz); BWCR = ARS-Biological Weed Control Research, Stoneville, MS (H. L. Walker); CWS = Cal West Seeds, Woodland, CA; CS = Cargill Seeds, Dixon, CA; CDFA = California Department of Food and Agriculture, Sacramento, CA (D. M. Supkoff); DBG = Desert Botanical Garden, Phoenix, AZ; FDWSR = ARS-Foreign Disease-Weed Science Research, Frederick, MD; HS = Harris Seeds, Rochester, NY; LHN = Lafayette Home Nursery, Lafayette, IN; MC = Macdonald College, Ste. Anne de Bellevue, Quebec, Canada (A. K. Watson); P = Park Seeds, Greenwood, SC; PRN = Prairie Ridge Nursery, Mt. Horeb, WI; ST = Seed Tech, Woodland, CA; SwNS = Southwestern Native Seeds, Tucson, AZ; T & M = Tompson and Morgen, Jackson, NJ; UBC = University of British Columbia, Vancouver, Canada (D. Nolan); UCB = University of California, Berkeley (E. I. Hecht); UH = University of Hawaii, Honolulu (E. E. Trujillo); UI = University of Idaho, Moscow (R. H. Callihan); UW = University of Waterloo, Ontario, Canada (J. K. Morton); WSU = Washington State University (C. Roche).

[c]+/− = Infected/not infected by *P. jaceae*.

[d]A = agronomically important, E = considered for listing as endangered or threatened, I = introduced species, N = native North American species, O = ornamentally important, W = weed species. Numerical values indicate the number of different seed acquisitions included in this study, if more than one.

Eurasia (6).

P. jaceae evaluated in Canada for biological control of two knapweeds (*Centaurea* spp.) caused limited infection of *Carthamus tinctorius* L. (safflower [11,19]), so particular attention was given to the susceptibility of safflower in the present study.

MATERIALS AND METHODS

Evaluation of the YST rusts included selection of 16 isolates from Greece, Italy, Turkey, the Union of Soviet

Table 1. (*continued from preceding page*)

Plants inoculated	Source of seed[b]	Infection[c] (+/−)	Notes[d]
C. × *superbum* Bergmans ex J. Ingram, shasta daisy			Tribe Anthemideae
Silver Princes	B (3030)	−	O
Cichorium endivia L., endive			Tribe Cichorieae
Green Curled	B (6038)	−	A
Cirsium species			Tribe Cardueae
C. cymosum (Greene) J. T. Howell	BCWL	−	N
C. hillii (Canby) Fern., Hill's thistle	LHN	−	N, E
C. occidentale (Nutt.) Jeps., western thistle	BCWL	−	N, E
C. ochrocentrum Gray, yellowspine thistle	BCWL	−	N
C. pastoris J. T. Howell	BCWL	+	N
C. pitcheri (Torr.) Torr. & Gray	UW	−	N, E
C. proteanum J. T. Howell	BCWL	+	N
C. undulatum (Nutt.) Spreng, wavyleaf thistle	BCWL	−	N
C. vulgare (Savi) Ten., bull thistle	BCWL	−	I, W
Cosmos sulphureus Cav.			Tribe Heliantheae
Sensation	B (4083)	−	O
Cynara scolymus L., globe artichoke	ARA	−	Tribe Cardueae, A
Gaillardia × *grandiflora* Van Houte			Tribe Helenieae
Monarch strain	P (0848-6)	−	O
Gazania ringens (L.) Gaertn.			Tribe Arctoteae
Sunshine	B (3636-8)	−	O
Gerbera jamesonii H. Bolus ex Hook. f.			Tribe Mutisieae
Florist's strain, mixed	P (3271-6)	−	O
Helianthus annuus L., sunflower			Tribe Heliantheae
S37-388	FDWSR	−	A
TT9834	FDWSR	−	A
Helichrysum bracteatum (Venten.) Andr., strawflower	B (4103)	−	Tribe Inuleae, O
Senecio cineraria DC. (=*Centaurea maritima*), dusty miller			Tribe Senecioneae
Maritima	B (3698)	−	O
Silver Dust	B (3397)	+	O
Tagetes patula L., French marigold			Tribe Heliantheae
Brownie Scout	B (3094)	−	O
Orange Hawaii	B (3730)	−	O
Red Pygmie	B (3211)	−	O
Vernonia fasciculata Michx., common ironweed	PRN	−	Tribe Vernonieae, N
Zinnia elegans Jacq.			Tribe Heliantheae
Giant Flowered	B (4327)	−	O
Cruciferae			
Brassica oleracea L., Capitata Group, cabbage			
Flat Dutch	B (5002)	−	A
Cucurbitaceae			
Cucurbita moschata (Duchesne) Poir., squash			
Waltham Butternut	B (5339)	−	A
Gramineae			
Sorghum bicolor (L.) Moench, sorghum			
TX 430	A&M	−	A
Top Hand	A&M	−	A
Triticum aestivum L., wheat			
Max	FDWSR	−	A
Zea mays L., corn			
Indian Chief	A&M	−	A
3369 A	A&M	−	A
Leguminosae			
Glycine max (L.) Merr., soybean			
Wayne	FDWSR	−	A
Malvaceae			
Gossypium barbadense L., Sea Island cotton			
Pima S-5	BWCR	−	A
G. hirsutum L., Upland cotton			
DPL-61	BWCR	−	A
STU-213	BWCR	−	A
Solanaceae			
Lycopersicon lycopersicum (L.) Karst. ex Farw., tomato			
Roma	HS	−	A
Big Boy	B (6123)	−	A
Umbelliferae			
Daucus carota L., carrot			
Danvers	B (6016-0)	−	A

Socialist Republics, and Yugoslavia. Twelve of the 16 isolates were successfully established for preliminary evaluation in the containment greenhouse (11). Six of these isolates, from Greece-1, Italy-1, Turkey-2, and Yugoslavia-2 (location-number of acquisitions), were selected for further study on safflower. The remainder of the host range determination was made with an isolate from Ankara, Turkey, that was very aggressive on YST.

Isolates received as uredinia on dried leaves were stored in a liquid-nitrogen freezer upon receipt. All isolates were increased on YST in separate cubicles inside the containment facility. Urediniospores for inoculation of plants were refrigerated (2–4 C) and used within 1 mo of harvest, or they were stored over liquid nitrogen.

A complete list of plant species inoculated in the present study is given in Table 1, and reason for inclusion of each species is noted. All plants were grown from seed planted in a standard steamed greenhouse soil mix (2:1:1, v/v, soil, sand, and peat) in 10-cm clay pots, except safflower plants, which were grown in 20-cm clay pots. Seedlings were thinned to one plant per pot, and plants were inoculated once 4–5 wk after seeding, except where noted. Inoculation involved either a simulated spore shower using a turntable settling tower (10) or "painting" individual leaves with a suspension of urediniospores in water containing 0.125% (v/v) oxysorbic 20 polyoxyethylene sorbitan monooleate. Plants were inoculated with 0.3–1.2 mg of urediniospores each in settling tower inoculations or 0.1–1.0 mg of urediniospores per milliliter of suspension in the "painting" procedure. Inoculum applied in each experiment was more than enough to ensure infection of the YST controls. Inoculation of plants in each replicate within an experiment used the same procedure and concentration of inoculum. Yellow starthistle controls and germination of urediniospores from each inoculation on water agar were included in each experiment, except the inoculation of *Cirsium* spp., to verify that conditions for infection were suitable.

Table 2. Susceptibility of 16 *Centaurea* and one *Senecio* species to *Puccinia jaceae* from Turkey

Species	No. of plants infected/ inoculated	Rating[a]	
		IA	IT
C. americana	1/9	0.2	0.2
C. calcitrapa	13/18	0.8	1.1
C. cyanus	21/23	3.5	2.7
C. diffusa	12/50	0.4	0.5
C. jacea	0/4	0.0	0.0
C. macrocephala	0/20	0.0	0.0
C. maculosa	3/58	0.2	0.1
C. moschata	1/12	0.1	0.2
C. melitensis	0/10	0.0	0.0
C. nigrescens	0/8	0.0	0.0
C. paphlagonica	0/9	0.0	0.0
C. pratensis	0/11	0.0	0.0
C. repens	0/19	0.0	0.0
C. rothrockii	0/9	0.0	0.0
C. solstitialis	128/135	3.0	2.8
C. squarrosa	2/9	0.6	0.7
S. cineraria	3/30	0.1	0.3

[a] IA = infection amount, a visual rating from 0 = no infection to 4 = more than 40 pustules total on leaves designated for rating. IT = infection type, a visual rating from 0 = no macroscopic symptoms (resistant) to 4 = large, expanding pustules (very susceptible).

Table 3. Disease ratings of *Cirsium* spp. inoculated with *Puccinia jaceae*

Species	No. of plants infected/ inoculated	Rating[a]			
		IA		IT	
		1	2	1	2
C. cymosum	0/3	0	0	0	0
C. hillii	0/3	0	0	0	0
C. occidentale	0/4	0	0	0	0
C. ochrocentrum	0/3	0	0	0	0
C. pastoris	7/7	1.7	0	2.3	0
C. pitcheri	0/3	0	0	0	0
C. proteanum	1/6	0.2	0	0.2	0
C. undulatum	0/13	0	0	0	0
C. vulgaris	0/6	0	0	0	0

[a] IA = infection amount, a visual rating from 0 = no infection to 4 = more than 40 pustules on the three most infected leaves. IT = infection type, a visual rating from 0 = no macroscopic symptoms (resistant) to 4 = large, coalescing, or spreading pustules (very susceptible). Each plant was inoculated twice, 1 = 4 wk after planting and 2 = 6 wk after planting.

A field isolate of *P. carthami* Cda., from safflower with rust disease in California, was used as one treatment in an experiment designed to quantify susceptibility of safflower to *P. jaceae*. Additional data on the potential for infection of safflower by *P. jaceae* in North America resulted from this study. Procedures for production, storage, and inoculation of *P. carthami* were the same as those described for *P. jaceae*.

The level of disease in each experiment was quantified either by counting pustules per unit area of leaf tissue or by use of two visual rating schemes. For most determinations, quantification involved the two visual rating schemes. These provided more information regarding susceptibility of a large number of nontarget species than a simple "+" and "−" system. Details for ratings of infection type (IT) have been published (13), and values range from 0 = no macroscopic symptoms (resistant reaction) to 4 = large, often coalescing pustules (very susceptible reaction). Values for infection amount (IA) and their descriptions are as follows: 0 = no pustules on designated leaves, 1 = 1–5 pustules total on designated leaves, 2 = 6–15 pustules total on designated leaves, 3 = 16–40 pustules total on designated leaves, and 4 = more than 40 pustules total on designated leaves.

In the case of safflower, where a more critical evaluation was deemed important, quantification involved counting the number of pustules per unit area of leaf tissue. Pustules occurring inside 1-cm^2 disks placed on the leaf in a predetermined pattern were counted, and three counts were made per leaf. Counts and ratings were made on the three most infected leaves of each inoculated plant.

Means of IA, IT, or pustule counts were calculated for each species. The pustule count data were subjected to analysis of variance, and means were separated using the Waller-Duncan *k*-ratio test. Statistical analysis was performed using SAS Institute procedures (14). For comparisons that used the visual rating schemes, interpretation of results was based upon values relative to ratings for the YST controls. Statistical analysis was not performed on these data because sample size was not consistent, and differences between species were large enough for clear understanding of plant susceptibility.

RESULTS

Urediniospores of all 16 isolates in the original selection were spherical to obovate in shape with two germ pores supraequatorial in location. All were identified as *P. jaceae* on the basis of morphology and host plant (15).

Of the 56 species of plants inoculated in this study, only 12 species had individuals infected by *P. jaceae* from YST. All but one are members of the

Tribe Cardueae in the Compositae and included species of *Centaurea*, *Carthamus*, *Cirsium*, and *Senecio* (Table 1). Artichoke (*Cynara scolymus* L.), which has tribal affiliation to YST, was not infected under conditions of the study.

Results from inoculation of *Centaurea* spp. and *Senecio cineraria* DC. (=*Centaurea maritima*) are detailed in Table 2. Yellow starthistle and cornflower (*Centaurea cyanus* L.) were much more susceptible to *P. jaceae* than the other species. Usually, only one or a few individuals of each susceptible species was infected by *P. jaceae*, but at least one pustule occurred on 13 of 18 plants of *Centaurea calcitrapa* L., 12 of 50 plants of *Centaurea diffusa* Lam., and 21 of 23 plants of *Centaurea cyanus*.

Limited infection by *P. jaceae* also occurred on *Cirsium pastoris* J. T. Howell and *Cirsium proteanum* J. T. Howell, but six other native and one introduced species of *Cirsium* were not infected (Table 3). Values for IA and IT were higher on *C. pastoris* than were observed on other nontarget species after one inoculation, but neither *C. pastoris* nor *C. proteanum* sustained new infections after reinoculation 2 wk later.

Results from inoculation of safflower are given in Tables 4 and 5. Six isolates of *P. jaceae* caused 20 times more pustules per square centimeter of leaf tissue on YST than on the safflower cultivars (Table 4). Safflower also was much less susceptible to *P. jaceae* than to *P. carthami* in side-by-side comparisons of the two pathogens under the same conditions, and reciprocal inoculation of YST with *P. carthami* resulted in no infections (Table 5). Some contamination by *P. carthami*, which is very aggressive on safflower, occurred on plants inoculated with *P. jaceae* and in the uninoculated controls. This was determined by microscopic examination of urediniospores from each treatment. Urediniospores of these two species are easily distinguished on the basis of morphology (15).

DISCUSSION

Klisiewicz (7) reported that YST is generally free from disease in North America, although several fungal and viral pathogens were identified in his survey. He regarded these to be of little potential as classical biocontrol agents because they lacked host specificity and would probably require considerable manipulation in order to be effective.

All 16 acquisitions studied to date at FDWSRU were identified as *P. jaceae*, an autoecious, demicyclic rust (15) reported on 45 species of *Centaurea* throughout Europe, Turkey, and parts of Asia Minor (6). Evidence for races of *P. jaceae*, distinguished by susceptibility of *Centaurea* spp. in standard inoculation tests, includes the differential reaction of the *Centaurea* spp. by *P. jaceae* from YST in this study. Nearly all hosts of *P. jaceae* in Guyot's list (6) (*C. calcitrapa*, *C. diffusa*, *C. jacea* L., *C. maculosa* Lam., *C. nigrescens* Willd., and *C. virgata* Lam.) were of limited susceptibility in this study; this is further evidence for specificity of *P. jaceae* within the genus *Centaurea*. Similar host range data were summarized by Gaumann (5) from experiments conducted by Jacky and Hasler. Contrary to results from this study, *C. solstitialis* was not susceptible to infection, and *C. cyanus* was only weakly infected. Morphological evidence that distinct forms of *P. jaceae* exist is presented by Savile (15), who distinguishes *P. jaceae* var. *solstitialis* from two other varieties on the basis of urediniospore morphology. Specialization of a pathogen by host species is one indication that it will not damage other species in that host genus, much less plants in other genera.

Infections were found on certain nontarget species in this study. However, these species were always much less susceptible than YST, except in the case of *Centaurea cyanus* and possibly *Cirsium pastoris*. *Centaurea cyanus* is considered an introduced weed despite its ornamental appeal, and it is attacked in North America by *P. cyani* Pass. (16). *Cirsium pastoris* is not considered threatened because no new pustules developed on plants after reinoculation by *P. jaceae*, and it, too, is host to another rust fungus in North America, *P. californica* Diet. and Holw. (16). Also, similar reactions occurred on *Cirsium* spp. during evaluation of *P. carduorum* Jacky for biological control of *Carduus thoermeri* Weinm. (13). Both *Cirsium pastoris* and *Cirsium proteanum* were very susceptible to infection of *P. carduorum* 4–5 wk after planting, but did not sustain any new infection upon reinoculation 2 wk later.

Infection of safflower by *P. jaceae* was much less than infection on YST inoculated with *P. jaceae* or on safflower inoculated with *P. carthami*. Similar results were reported by both Watson and Alkhoury (19) and M ortensen (12) in their evaluations of *P. jaceae* from *Centaurea diffusa* and *Centaurea maculosa*, respectively. Safflower was found susceptible to each *Centaurea* rust fungus when inoculated by the two-true-leaf stage, but plants inoculated near the time of flowering were not susceptible.

One of two cultivars of *Senecio cineraria* in the Tribe Senecioneae also developed pustules in this study, but only three of the 30 individuals inoculated became infected and ratings were very low for the number and size of pustules. Infection occurred only on the cotyled-

Table 4. Number of pustules per square centimeter of leaf tissue on three cultivars of safflower and on yellow starthistle (YST) inoculated with five isolates of *Puccinia jaceae*

	Isolate[a]					Average[b]	
Host, cultivar	PJ 1-79	84-9	84-94	85-186	85-191	Plants (no.)	Pustules
YST	2.3	3.3	2.2	1.0	1.6	138	2.1 x
Safflower							
Gila	0.1	0.3	0.0	+	+	210	0.1 y
Pacific 1	0.0	0.0	0.0	0.1	0.4	210	0.1 y
UC 41	+	+	0.0	0.0	0.0	210	+ y

[a] + = Mean values; less than 0.06 pustules/cm^2 of leaf tissue.
[b] Combined data for five isolates. Values are number of plants inoculated and mean number of pustules. Means followed by the same letter are not significantly different according to the Waller-Duncan *k*-ratio test ($P = 0.05$).

Table 5. Number of pustules per square centimeter of leaf tissue resulting from inoculations with *Puccinia carthami* and *P. jaceae* on 10 cultivars of safflower and on yellow starthistle (YST) inoculated with each pathogen

	Plants inoculated	Pathogen[a]	
Host, cultivar	(no.)	*P. carthami*	*P. jaceae*
Safflower			
Pacific 1	12	9.8 v	0.7 w
CH 65	12	6.6 w	0.2 xyz
CH 353	12	6.3 w	0.3 xy
C 44	12	6.3 w	0.2 xyz
CARMEX	12	5.9 w	0.4 x
S 400	12	5.0 yz	0.4 x
CW 4440	12	5.8 w	0.1 yz
S541	12	5.7 w	0.1 yz
CW 74	12	4.7 xy	+ yz
UC 41	12	4.6 y	+ yz[b]
YST	12	0.0 z	2.9 v

[a] Mean values for each combination of host and pathogen. Means followed by *t* letter in each column are not significantly different according to the Waller-Duncan *k*-ratio test ($P = 0.05$).
[b] + = Mean values less than 0.1 pustules/cm^2 of leaf area.

onary leaves and no new infections developed upon reinoculation of individuals infected after one inoculation.

Despite limited nontarget infections by *P. jaceae* under greenhouse conditions, the pathogen is very aggressive on only YST and *Centaurea cyanus*. These results suggest that *P. jaceae* would be safe to use for biological control of YST in North America. The potential of this organism will be more fully understood if the fungus can be evaluated under field conditions.

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