A Novel Source of Resistance to *Pepper yellow leaf curl Thailand virus* (PepYLCThV) (*Begomovirus*) in Chile Pepper

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Abstract. Chile pepper (*Capsicum annuum* L.) is an increasingly important vegetable and spice crop. Among the most devastating chile pepper-infecting viruses, especially in tropical and subtropical regions, are members of the whitefly transmitted *Begomovirus*, which cause pepper yellow leaf curl (PYLC). An effective PYLC management strategy is the development of resistant cultivars. However, genetic recombination, acquisition of extra DNA components, and synergistic interactions among different begomoviruses have resulted in the rapid emergence of new viruses that can infect new hosts, cause new disease symptoms, and overcome host resistance. In this project, 98 *Capsicum* entries comprising breeding lines, open pollinated varieties, genebank accessions, and wild species were screened for resistance to strains of *Pepper yellow leaf curl Thailand virus* (PepYLCThV). We used a randomized complete block design with three replications and 10 plants per replication in field net-houses at two locations (Khon Kaen and Kamphaeng Saen, Thailand) using augmented inoculation by viruliferous whiteflies. Scoring was done at ≈60, 90, and 120 days after inoculation using a standardized 6-point scale (1 = no symptoms to 6 = very severe symptoms), and the average of the scores of 10 plants within each replication was used for analysis. Although no entry was immune to the disease, the breeding line 9852-123 was highly resistant. Several accessions and lines were moderately resistant at both locations, although a high level of variability within these entries was observed. Overall, the disease severity at the Khon Kaen location was greater compared with Kamphaeng Saen, highlighting the importance of multilocation testing for disease resistance. The resistant entry identified here can be used to study gene action and to move resistance genes into well-adapted germplasm.

Chile pepper (*Capsicum annuum* L.) is widely used as a vegetable and spice and a source of colorants and pharmaceuticals (Wall and Bosland, 1998). Consumer demand for chile pepper has substantially increased over the past 30 years, especially for hot pepper. It has been estimated that chile peppers are consumed daily by approximately a quarter of the world's population (Halikowski-Smith, 2015). Global production of chile pepper was 56.2 million tonnes on an area of 4.5 million hectares in 2016 and ≈65% of chile pepper was produced in Asia (Food and Agriculture Organization of the United Nations, 2016). Being a high value crop (DeWitt and Bosland, 1993), chile pepper can have economic benefits for small-

holder farmers, significantly increasing family income and socioeconomic mobility (Kahane et al., 2013; Weinberger and Lumpkin, 2007).

The primary limitations to increased chile pepper productivity and quality are biotic and abiotic stresses. In addition to consumer demand for chile pepper, the past 3 decades have seen the number of virus species identified as infecting chile pepper as well as virus disease incidence increase considerably (Kenyon et al., 2014b). Likely, the most devastating chile pepper-infecting viruses, especially in tropical and subtropical regions of Asia, are members of the whitefly (*Bemisia tabaci*)-transmitted genus *Begomovirus* (Geminiviridae), including PepYLCThV. Unlike in tomato (*Solanum lycopersicum*), the

emergence of begomoviruses as major chile pepper pathogens has been relatively recent. Pemezný et al. (2003) reported five begomoviruses causing disease in chile pepper in the Americas and only one in Asia. Since then, the number of chile pepper-infecting begomoviruses detected in Asia has greatly increased, with at least 29 species and a large diversity of strains reported (Kenyon et al., 2018). Although *Pepper yellow leaf curl virus* (PepYLCV) was first identified in Thailand in 1995 (Samretwanich et al., 2000), PepYLCThV was not identified in Thailand until 2012 (Chiemsoombat et al., 2018), and the sequences of both DNA-A and DNA-B components were submitted to National Center for Biotechnology Information in 2016. Across Thailand, PYLC is caused by at least three bipartite *Begomovirus* species, with a common PepYLCThV DNA-B component, and sometimes as mixed infections (Chiemsoombat et al., 2018). In some of the hotspots for the disease, losses of 95% have been reported, and farmers have been forced to grow alternative crops.

Management of begomoviruses has been based primarily on insecticides against the whitefly vector. However, the use of insecticides has been found to be only partially effective, costly for producers, and represents a hazard to farmers, consumers, and the environment (Borah and Dasgupta, 2012), while limiting export potential through presence of pesticide residue. Farmers often apply the insecticides after seeing early disease symptoms, by which time the whiteflies have already transmitted the virus to other plants (Kenyon et al., 2014a). An effective alternative to harmful insecticide applications for management of *Begomovirus* is the development of resistant cultivars (Shankarappa et al., 2008).

Sources of resistance to *Begomovirus* in chile pepper have been reported, including the *C. chinense* line BG-3821 in Mexico (Anaya-Lopez et al., 2003) and 'Bhut Jolokia' in India (Adluri et al., 2017). The *C. annuum* lines DLS-Sel-10, WBC-Sel-5, WorldVeg Pepper Breeding Collection (PBC) 142, PBC 145, PBC 345 (Srivastava et al., 2015, 2017), PBC 143, PBC 144, PBC 149, PBC 495, VI012005 (Kenyon et al., 2014a), GKC-29, BS-35, EC-497636 (Kumar et al., 2006), and 'Kalyanpur Chanchal' (Singh et al., 2016) have been reported to be resistant. However, many of these screenings were done several years ago, and the pathogen population most likely has changed since then (Singh et al., 2016) from largely monopartite to bipartite species; therefore, confirmation of resistance with recently developed virus species is required.

Materials and Methods

The experiment was conducted at two locations, Khon Kaen (lat. 16.469°N, long. 102.813°E; elevation 162 m) and Kamphaeng Saen (lat. 14.029°N, long. 99.964°E; elevation 9 m), Thailand. Site selection was based on the ability to conduct an effective bioassay, rather than on nearby

production or viral prevalence. *Capsicum* entries (98) comprising breeding lines, open pollinated varieties, genebank accessions, and wild species were screened for resistance to PepYLCThV. Among the 98 entries tested, two (PI 574547 and PI 674459) were members of the wild progenitor *C. annuum* var. *glabrusculum*, four (VI012478, VI102479, VI012528, and VI014924) were *C. baccatum*, 14 (PBC 206, PBC 506, PI 152225, PI 164561, PI 159234, PI 159236, PI 175622, VI012270, VI012271, VI012596, VI012642, VI012665, VI012668, and VI029244) were *C. chinense*, one (PI 566812) was *C. chacoense*, one (PBC 687) was *C. frutescens*, and the rest (76) were *C. annuum*. Selection of entries for screening was based on resistance reported in publications (Adluri et al., 2017; Kenyon et al., 2014a; Srivastava et al., 2015, 2017), historical breeding notes, and personal communications with private and public sector plant breeders working with the disease.

Seeds of the entries were sown into a commercial coconut coir and peatmoss seedling media in 96-cell plastic trays at a rate of three seeds per cell per entry. Seeds were sown into 32 cells. The growing media was monitored for moisture twice daily and hand irrigated as needed. Seeds were germinated and seedlings grown in an insect-proof net house where virus vectors (whiteflies, aphids, thrips) were excluded. Seedlings were fertilized as needed, usually once a week after the first 2 weeks. Throughout the first 3 weeks, germination was closely monitored, and entries with slow germination or poor growth were resown as needed. Plants were thinned to one seedling per cell, and some were transplanted into empty cells to ensure a minimum of 30 plants per entry.

Augmented inoculation by viruliferous whitefly was used. Whitefly were reared and multiplied on broccoli (*Brassica oleracea* var. *italica* Plenck) plants, a nonhost. To prepare the virus source plants for the experiments, clean, healthy whiteflies were given a 48-h acquisition access period (AAP) on initial source plants infected with PepYLCThV

Kanchanaburi isolate (provided by East West Seed for the Kamphaeng Saen location) and with PepYLCThV KON-KG5 isolate (for the Khon Kaen location). The two isolates of PepYLCThV used in this experiment were phylogenetically similar to one another, and both resulted in typical leaf yellowing and curling (Chiemsoombat et al., 2018; Sangsotkaew et al., 2019). Presence of the single isolates in the source plants was confirmed by collecting and drying leaf tissue, isolating DNA from the leaf tissue using Dellaporta extraction method. The universal begomovirus primer pair PAL1v1978B/PAR1c715H and the primers DNABLC1, DNABLC2, and DNABLV2 were used to test for the presence of DNA-A and DNA-B, respectively (Tsai et al., 2011). The amplicons were sequenced and aligned, and the viral DNA was classified based on sequence similarity to previously reported species. After the AAP, the viruliferous whiteflies were released on 5-week-old susceptible chile pepper ('Jindadang'; 20 whiteflies per plant) for an inoculation access period (IAP) of 48h inside cotton bags. The PepYLCThV-inoculated plants were maintained in insect-proof cages until typical symptoms of leaf vein yellowing and curling developed. When the seedlings of the test lines and entries reached the four to six leaf stage (≈ 4 weeks), they were randomly placed in an insect-proof cage (90 mesh) at a rate of 12 trays per cage, and the PepYLCThV source plants and viruliferous whiteflies were introduced with one source plant for every two trays and 60 viruliferous whiteflies per source plant. Source plants were hand-agitated twice daily to encourage viruliferous whiteflies to move between source plants and test plants. After 10 d, source plants were removed from the cage, and plants were directly transplanted to the field net houses. To increase virus infection stress, 500 healthy whiteflies and 800 viruliferous whiteflies per net house were released after transplanting, at Kamphaeng Saen. After 2 weeks, biweekly scouting and insecticide applications were made to manage insect vectors (whitefly, thrips, and aphids) and limit contamination from other pathogens.

Scoring was done at ≈ 60 , 90, and 120 d postinoculation (dpi). A standardized 6-point scale modified from Sangsotkaew et al. (2019) (1 = no symptoms; 2 = very mild symptoms with slight yellowing only occurring near the petiole of young leaves; 3 = mild symptoms of slight yellowing of the entire area of young leaves; 4 = moderate symptoms of dark yellowing of young leaves and some old leaves; 5 = severe symptoms of dark yellowing of young and most of the old leaves; 6 = very severe symptoms of complete plant yellowing, stunting, and lack of flower set) was used for evaluation. The experimental design was a randomized complete block design with three replications and 10 plants of each entry in each replication. The average of the score of 10 plants within each replication was used for analysis. Data

were analyzed for independence using the Kruskal-Wallis test in R.

To determine the presence of nontarget viruses, five to 10 leaves from 12 randomly selected plants with typical and atypical PepYLCThV symptoms were collected and rapidly dried using self-indicating silica gel at ambient temperature 90 dpi. DNA was isolated from the leaf tissue using Dellaporta extraction method. The DNA was subjected to polymerase chain reaction (PCR) using universal *Begomovirus* primers as described earlier. To test for the presence of *Cucumber mosaic virus*, *Potato virus Y*, *Tomato mosaic virus*, *Chili vein mottle virus*, *Pepper vein mottle virus*, *Pepper mild mottle virus*, *Tomato spotted wilt virus*, *Watermelon silver mottle virus*, *Pepper mottle virus*, and non-specific *Potyvirus*, crude sample homogenate (1:10 w/v) was subjected to double- or triple-antibody-sandwich enzyme-linked immunosorbent assay (ELISA) with appropriate proprietary antisera. To detect the presence of unspecified *Tospovirus* and *Polerovirus*, total RNA was extracted and subjected to reverse transcriptase (RT)-PCR using universal primers of *Tospovirus* and *Polerovirus*, respectively.

After 120 dpi, leaf tissue from 10 symptomatic and asymptomatic plants of the highly resistant breeding line 9852-123 were collected and dried following the aforementioned procedure. The DNA was subjected to PCR using universal *Begomovirus* primers (Tsai et al., 2011), and amplicons were sequenced. The sequences were aligned, and the viral DNA was classified on the basis of sequence similarity to previously reported species.

Results and Discussion

One sample from a plant of PBC 351 tested positive for presence of *Tospovirus* RNA by RT-PCR, indicating infection by thrips transmission occurred during the experiment. However, symptoms typical of *Tospovirus* were minimal throughout the experimental plots; no other tested sample contained *Tospovirus* or any other tested viral RNA, and none tested positive by ELISA for other viruses. This suggests that the experiment was valid and the disease ratings for PepYLCThV were not confounded with symptoms of other viruses.

The Kruskal-Wallis test by ranks ($\alpha = 0.05$) indicated that average disease ratings at 120 dpi across the 98 entries and at the two locations tested were nonidentical (Table 1). The average disease rating increased throughout the growing

Table 1. Kruskal-Wallis test by ranks of the diseases ratings of 98 *Capsicum* entries at 120 d postinoculation with *Pepper yellow leaf curl Thailand virus* at two locations (Kamphaeng Saen and Khon Kaen, Thailand).

	Degrees of freedom	χ^2	<i>P</i> value
Location	1	6.2	0.0128
Replication	2	17.1	0.0002
Entry	97	193.9	1.921×10^8

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Fig. 1. Average disease rating of 98 *Capsicum* entries at 120 d postinoculation with *Pepper yellow leaf curl Thailand virus*. Scores were averaged across three replications each with 10 plants within a location. The white boxes are the lower and upper quartiles of the scores from Kamphaeng Saen, and the gray boxes are the lower and upper quartiles of the scores from Khon Kaen. The dark line within each box is the overall mean for the entry at each location, and the whiskers represent the overall maximum and minimum scores. A standardized six-point scale modified from Sangsotkaew et al. (2019) (1 = no symptoms; 2 = very mild symptoms with slight yellowing only occurring near the petiole of young leaves; 3 = mild symptoms of slight yellowing of the entire area of young leaves; 4 = moderate symptoms of dark yellowing of young leaves and some old leaves; 5 = severe symptoms of dark yellowing of young and most of the old leaves; 6 = very severe symptoms of complete plant yellowing, stunting, and lack of flower set) was used for evaluation.

season; however, we only present the results of the last rating. Differences in disease rating by location were also found (Table 1), with the overall disease ratings being higher at Khon Kaen compared with Kamphaeng Saen (Fig. 1). The differences in entry symptom severity between locations highlights the importance of multilocation testing for disease resistance.

While no entry was immune to the disease, we identified one highly resistant breeding line, 9853-123, with an average rating of 1.6 at Khon Kaen and 1.1 at Kamphaeng Saen at 120 dpi (Fig. 1). Several other entries were moderately resistant, although there was a high level of variability in their disease reactions (Fig. 1). The entries PBC 186, PBC 518, PBC 581, PBC 1565, and PI 171555 had high average disease ratings at 120 dpi; however, we also found a large range in their scores, with some individual plants scoring near 1, or resistant (Fig. 1). This is evidence that these lines might be segregating for resistance and selection followed by self-pollination could be imposed to increase the resistance level of these entries.

The previously published resistant lines PBC 142, PBC 143, PBC 145, PBC 148, PBC 149, PBC 495 (Kenyon et al., 2014a; Srivastava et al., 2015, 2017) were not resistant in our study (Table 2). The reasons for these differences could be attributable to the use of different species of *Begomovirus*, with *Tomato yellow leaf curl Thailand virus* was used in Taiwan (Kenyon et al., 2014a) and *Chili leaf curl virus* (ChLCV), *Tomato leaf curl Joydebpur virus* (ToLCJoV) (monopartite), and *Tomato leaf curl New Delhi virus* under open field conditions were used in India (Srivastava et al., 2015, 2017). The differences could also be due to inoculation techniques used (viruliferous whitefly or natural field inoculation) or because we scored at 120 dpi and not at the seedling stage. Genetic recombination, the acquisition of extra DNA components, and the synergistic interaction among different begomoviruses has resulted in the rapid emergence of new viruses that can infect new hosts, cause new disease symptoms, and overcome host resistance (Chakraborty et al., 2003; Singh et al., 2016; Varma and Malathi, 2003).

None of the entries belonging to the other domesticated or wild *Capsicum* species were resistant, and some of the most susceptible entries evaluated here included PI 159236, VI012642, and VI012271 (*C. chinense*), VI012528 (*C. baccatum*), and PI 574547 (*C. annuum* var. *glabriusculum*) (Fig. 1). Although a member of *C. chinense*, the accession VI012271, as well as the *C. annuum* accession VI012911, have the potential to be used as susceptible checks in future studies because they displayed a consistent and high disease rating at both locations (Fig. 1).

Jabłńska-Sabuka et al. (2015) found that intensive farming and breeding partially resistant cultivars were the major triggers for aggressive *Begomovirus* adaptability through mutation speed-up. Therefore, it would be

Table 2. Average disease rating of previously identified sources of *Begomovirus* resistance at two locations in Thailand scored at 120 d postinoculation with *Pepper yellow leaf curl Thailand virus*.

Entry	Khon Kaen	Kamphaeng Saen
PBC 142	4.1 ^a	3.9
PBC 143	6.0	3.7
PBC 145	3.7	4.6
PBC 148	3.2	3.6
PBC 149	3.7	3.3
PBC 495	4.0	4.4

^aA standardized six-point scale modified from Sangsotkaew et al. (2019) (1 = no symptoms; 2 = very mild symptoms with slight yellowing only occurring near the petiole of young leaves; 3 = mild symptoms of slight yellowing of the entire area of young leaves; 4 = moderate symptoms of dark yellowing of young leaves and some old leaves; 5 = severe symptoms of dark yellowing of young and most of the old leaves; 6 = very severe symptoms of complete plant yellowing, stunting, and lack of flower set) was used for evaluation.

beneficial to use an integrated pest management (IPM) approach that combines resistant cultivars (potentially multiline cultivars) with different whitefly and viral control measures. It has been estimated that farmers who adopt minimal, moderate, and highly integrated management strategies for *Begomovirus* could improve incomes by 17%, 26%, and 80%, respectively (Swaminathan et al., 2016). Using *Begomovirus*-specific primers, the DNA-A and DNA-B of PepYLCThV were amplified and sequenced from both asymptomatic and symptomatic plants of 9853-123 (99.3% identity for DNA-A and 98.1% identity for DNA-B). The ability of the virus to colonize the plant, but the overall lack of severe symptoms indicates a recognition mechanism exists in 9853-123, and the low disease rating was not the result of the plants being missed during inoculation. This provides a basis for future inheritance studies as well as quantitative trait locus analysis and downstream resistance gene identification.

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